

1 **Running title:** Seed dispersability in an OCBIL grassland

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4 **Limited seed dispersability in a megadiverse OCBIL**
5 **grassland**

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31 Abstract

32 Some tropical grasslands can be referred as OCBILs (old climatically-buffered, infertile
33 landscapes). OCBIL theory predicts that species should exhibit reduced dispersability, linked
34 with long-term stable environmental conditions. Seed rain, i.e. the number of seeds reaching a
35 given area, is poorly known in OCBIL grasslands despite its role in modulating resilience. We
36 aim to test the prediction of limited dispersability as one cause of slow recovery capacity in
37 *campo rupestre*, a megadiverse OCBIL grassland, southeastern Brazil. We ran a field
38 experiment to compare annual seed rain dynamics between preserved sites and sites disturbed
39 by gravel exploitation. We chose three paired preserved and disturbed plots, placing six
40 sampling blocks in each plot. We installed one sticky and one funnel trap per block. We
41 collected the samples monthly for 12 months to estimate seed density and richness. We provide
42 the first community-level study on seed rain in *campo rupestre* which suggests widespread
43 seed limitation in both preserved and disturbed areas, expressed by the low seed density in traps
44 (average of 2.6 seeds/m²/day) and a remarkable low seed density found for 90% of the taxa.
45 Although seed density was much lower in relation to other seed rain studies in grasslands,
46 species richness (92 seed morphospecies) is the highest reported in the literature. Funnel traps
47 were the most efficient trap type in catching seeds. We found a significant increase in the
48 number of seeds and species richness captured in funnel traps during the rainy season.
49 Disturbance seems to reduce seed arrival dynamics in sticky traps and increase seed arrival
50 dynamics in funnel traps. Approximately 32% of morphospecies were registered exclusively
51 in disturbed plots and 25% exclusively in preserved plots. The limited seed dispersability found
52 is of high relevance for a better understanding of seed ecology and resilience in *campo rupestre*
53 and may partially explain the poor recovery of these disturbed areas after soil removal.

54

55 **Keywords:** seed rain, seed trap, tropical grassland, resilience, seed limitation

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57 **Introduction**

58 Some tropical grasslands can be referred as OCBILs (old climatically-buffered, infertile
59 landscapes). OCBILs host disproportionately high levels of terrestrial global biodiversity
60 hotspots, where edaphic conditions play a key role in structuring plant communities and
61 shaping plant populations (Hopper, 2009; Hopper et al., 2016). OCBIL theory predicts that
62 species should exhibit reduced dispersability, linked with long-term stable environmental
63 conditions (Hopper, 2009). Indeed, dispersal away from maternal plants is associated with high
64 costs of dispersal (Bonte et al., 2012), and high mortality risks as it increases the likelihood of
65 seed arrival on a different soil type therefore creating a competitive disadvantage (Hopper,
66 2009; Rajakaruna, 2018; Corlett & Tomlinson, 2020). Indirect evidence of reduced
67 dispersability includes: i) the absence of obvious means of seed dispersal and ii) high local
68 endemism across many phylogenetically-distant lineages. This phenomenon has been well
69 demonstrated for the Southwest Australian Floristic Region, where many native plant species
70 do not display dispersal structures, and some display phylogenetic clustering (Hopper et al.,
71 2016). Such landscapes are also highly vulnerable to many kinds of soil disturbances (e.g.
72 cultivation or plantation after ploughing, topsoil removal, quarrying, etc.) (Hopper et al., 2016;
73 Buisson et al., 2019), and the precise mechanism driving poor recovery is still a matter of
74 controversy (Standish & Hobbs, 2010; Dayrell et al., 2016; Arruda et al. 2020), and warrants
75 further investigation.

76 The megadiverse and nutrient-poor Brazilian *campo rupestre* vegetation is an OCBIL
77 presenting extremely high levels of plant endemism (Echternacht et al., 2011; Colli-Silva et al.,
78 2019). The lack of dispersal mechanism has been reported for several dominant families in this
79 ecosystem such as Poaceae, Cyperaceae, Xyridaceae, Eriocaulaceae and Velloziaceae (e.g.
80 Silveira et al., 2016; Morellato & Silveira, 2018). While local endemism and unassisted

81 dispersal constitute evidence of reduced seed dispersability, there is still no direct, empirical
82 evidence that seed rain is limited. The lack of knowledge on dispersal limitation prevents us
83 assessing how endemic species and plant communities respond to changing climate conditions
84 and land uses (Corlett & Tomlinson, 2020).

85 Generally speaking for grasslands, major anthropogenic soil disturbances have widespread
86 and long-lasting effects on ecosystem resilience (*sensu* Hodgson et al., 2015). Natural recovery,
87 and thus plant community assembly, after drastic soil disturbances is mainly based on seed
88 dispersal from surrounding sites, and not on the internal species pool (i.e. remaining vegetation,
89 seed bank or bud bank) which is often reduced or sometimes absent (Bakker et al., 1996;
90 Poschlod et al., 1998; Campbell et al., 2003; Shu et al., 2005; Buisson et al., 2006; Le Stradic
91 et al., 2018b; Torök et al., 2018). Anthropogenic soil disturbances are common in *campo*
92 *rupestre* as they are highly threatened by iron ore mining, sandstone and gravel quarrying,
93 which have intensified over the past decades (Silveira et al., 2016; Fernandes et al., 2018).
94 Plant communities from *campo rupestre*, although highly resilient to natural endogenous
95 disturbances, such as fires (Le Stradic et al., 2018a), seem extremely vulnerable to human-
96 caused exogenous soil disturbances (Le Stradic et al., 2018b). The latter study has shown that
97 disturbed plant communities in *campo rupestre* remained very different from reference sites
98 even eight years after disturbance, with almost no recovery of the natural vegetation (Fig. 1).

99 Seed dispersal is the first and a critical step in the hierarchical filter model proposed to
100 summarize processes shaping plant community composition and assembly (Lortie et al., 2004;
101 Poschlod et al., 2013; Török et al., 2018). It is a complex, multi-step ecological phenomenon
102 (Schupp et al., 2010). Seed rain, the quantity and diversity of seeds reaching a given area
103 (Baskin & Baskin, 2014), is a crucial part of the seed dispersal process. Studying seed rain can
104 provide key information on regeneration and vegetation dynamics (e.g. which species, how
105 many seeds, where and when seeds are arriving at a given location), thereby it is a useful tool

106 to assess recovery (*sensu* Hodgson et al., 2015) potential in disturbed areas (Turnbull et al.,
107 2000). Unfortunately, only less than 10% of the seed rain studies in grasslands were carried out
108 in the tropics (Arruda et al., 2018), therefore preventing us from understanding recovery
109 potential in some of the world's most biodiverse and impacted areas (Parr et al., 2014).

110 Seed rain is usually quantified and qualified by placing traps in the plant community to catch
111 seeds that are then counted and identified (Arruda et al., 2018), and the use of different seed
112 trap types has been shown to contribute to a more reliable estimate of the seed rain (Chabrierie
113 & Alard, 2005). The time of year at which seeds integrate the seed bank has a bearing on the
114 establishment of vegetation after disturbance (Roberts, 1986; Torök et al. 2018). Additionally,
115 seasonality can influence abiotic-related secondary dispersal processes, such as water runoff
116 during the rainy season (de Rouw et al., 2018). *Campo rupestre* is characterized by distinct
117 seasonal climatic patterns and for the total annual fruit production in plant communities in
118 sandy soils, with significantly more fruits being produced during the dry season (Le Stradic,
119 2018c).

120 Here, we aim to test the prediction of OCBIL theory (Hopper, 2009) of limited
121 dispersability of species in *campo rupestre* vegetation as one cause of this slow recovery. The
122 underlying assumption is that vegetation and soil patchiness on OCBIL create non-linear
123 relationships between distance from the parental plants and suitable conditions for seedling
124 establishment. In most cases, the optimum conditions for establishment occur near the
125 surroundings of the parental plant. Our specific goals were: (1) to characterize the annual seed
126 rain dynamics in preserved areas and disturbed areas in *campo rupestre*; (2) to compare seed
127 rain in disturbed areas and preserved areas to examine whether seed limitation is linked to low
128 recovery and whether it is intrinsic to the ecosystem. We predict that a pronounced dispersal
129 limitation is intrinsic to the *campo rupestre* vegetation, in both disturbed and preserved
130 habitats. Nevertheless, we expect to find important differences in seed rain composition

131 between preserved and disturbed areas, due to the predominance of short distance dispersal on
132 OCBIL species. Additionally, considering that *campo rupestre* is characterized by distinct
133 seasonal patterns for the total annual fruit production in the plant community in its sandy soils,
134 we expect to find higher densities of seed rain during the dry season.

135

136 **Material and methods**

137

138 *Study region*

139 We conducted this study at the vicinity of the Serra do Cipó National Park, in the southern
140 portion of the Espinhaço Range, south-eastern Brazil (43° 35'W, 19° 17'S). The annual
141 precipitation averages around 1,400 mm and climate is markedly seasonal with dry months
142 from April to middle September, especially during the winter, and rainy months from October
143 to March, with most rainfall occurring in the hot summers (Silveira et al., 2019). We considered
144 the dry season from April to September and the rainy season from October to March (Silveira
145 et al., 2019). Altitude at the study site ranges between 1,150 and 1,300 m a.s.l.. The main
146 vegetation comprises the *campo rupestre*, a megadiverse, fire-prone montane grassland
147 establishing on quartzite-derived rocks, with shallow and severely nutrient-impooverished sandy
148 soils (Silveira et al., 2016).

149 The landscape encompasses a mosaic formed by patches of rocky outcrops and boulders
150 where sclerophyllous small trees grow and patches of grasslands, dominated by monocots and
151 sparsely distributed shrubs and forbs (Le Stradic et al., 2015). Small quarries were exploited
152 for soil extraction during the paving of the MG-010 road in 2002. As a result of this exogenous
153 disturbance, the aboveground vegetation and upper soil horizons were totally destroyed (Le
154 Stradic et al., 2018b). We chose these small quarries as the target disturbed plots for the present
155 study as they have slow recovery and very little vegetation cover (Appendix S1).

156

157 *Sampling design*

158 We performed a factorial experiment involving the assessment of seed rain on three paired
159 disturbed and preserved plots of 100 m² each (20 m × 5 m). In all sites, the paired disturbed
160 and preserved plots were adjacent at approximately 30 meters away from each other (i.e. thus
161 away from site margins) (Fig. 2). Each pair is composed by a preserved area of *campo rupestre*
162 with white sandy soils where no soil disturbances occurred, and an area disturbed by soil
163 removal for gravel extraction which resulted in drastic or even complete removal of both bud
164 and seed banks (Appendix S1). The three disturbed plots were placed inside small scale
165 disturbed areas (<500m²) surrounded by a vast matrix of preserved areas of *campo rupestre*.
166 Sites were distant at least 2 km from each other to ensure spatial independence. In April 2016,
167 we placed six sample blocks in each plot (Fig. 2).

168 We used sticky and funnel traps (Fig. 2; Appendix S2), which allow capturing
169 complementary information on seed rain (Chabrierie & Alard, 2005), and are the most common
170 traps used to estimate seed rain in grasslands (Arruda et al., 2018). Sticky traps allow seed
171 catch from primary seed dispersal by wind, and funnel traps allow seed catch from seeds
172 dispersed by wind and secondary dispersal by wind on the ground and by water run-off. To
173 assess seed rain, we used a total of 72 seed traps (36 sticky traps and 36 funnel traps) placed in
174 pairs inside each block on the six plots (three disturbed and three preserved) (Fig. 2).

175 Funnel traps presented a total area of 0.0176 m² / trap and were buried in the soil so their
176 opening was levelled with the soil surface. The sticky traps presented a total area of 0.0225 m²
177 / trap and were situated 25 cm above ground and at a 45° sloping angle, to feature the optimum
178 design to capture seed rain (Appendix S2). We also chose this experimental setting to make
179 our data comparable to previous seed rain studies in grasslands (Chabrierie & Alard, 2005). We
180 placed all the sticky traps facing the main wind direction registered for the year 2014 in the

181 closest meteorological station, which it is located approximately 30 km from the study area
182 (INMET Instituto Nacional de Meteorologia, 2015).

183 We collected the samples on all seed traps monthly over one year (from April 2016 to
184 March 2017), and immediately prepared them for a subsequent period of sampling. For the
185 sticky trap samples, we examined the material retained under a magnifying glass to count and
186 identify seeds. For the funnel trap samples, we washed the material retained inside the bags in
187 a 250- μm sieve to reduce the amount of fine soil particles before examining them under a
188 stereoscope. Species could be either identified to the genus or family level. In most cases, they
189 could not clearly be assigned to a genus or family. Therefore, we morphotyped the seeds. For
190 our questions, morphotyping is acceptable (see also Jara-Guerrero et al., 2020), since we were
191 interested in seed rain quantity, density and seed species richness.

192 We reported our data as seeds/m²/day in order to make our data comparable with other seed
193 rain studies (Arruda et al., 2018). To evaluate if our sampling area was adequate to sample the
194 communities, we built rarefaction curves for each trap type and plot type based on the methods
195 developed by Chao et al. (2014), using an R package for rarefaction and extrapolation of
196 species diversity (iNEXT package) on presence/absence data of each species (Appendix S3).
197 First, the data from each trap was summed over the year. Then, we calculated seed density
198 using cross-multiplication to transform seed density/trap/year to seed density/m²/year. Finally,
199 we divided values by 365 days to obtain seed density/m²/day. Considering that using the same
200 protocol for seed species richness would have led to overestimation, we 1) used the function
201 *estimateD()* to compute species richness estimates for a 1 m² level of sample size (44 sticky
202 traps and 57 funnel traps in order to reach 1 m²) using the extrapolated data generated by
203 rarefaction curves (Hsieh et al., 2016), and then 2) re-sampled species richness from the
204 confidence intervals supplied by *estimateD()* in order to estimate species richness in m²/day.

205 Finally, we conducted a floristic survey (species presence/absence) to determine species
206 richness and composition for the standing vegetation (Jara-Guerrero et al., 2020) for each plot
207 in both preserved and disturbed sites during the rainy season (plot size = 20 m × 5 m = 100
208 m²). The total area covered by vegetation in all degraded plots was less than 5% and in
209 preserved ones higher than 70%. We identified the plant species by consulting herbarium
210 collections, literature and taxonomists. The nomenclature of the floristic checklist follows APG
211 IV (2016). For taxa at the seedling stage, species-level identification was not possible, but it
212 was not essential as our interest was mature plants potentially producing seeds found in the
213 seed rain. All permits to visit and collect biological data were authorized by ICMBio of the
214 Brazilian Ministry of Environment. Data collection in sites located on private lands was
215 authorized by the owners and ICMBio.

216

217 *Statistical analyses*

218 We performed all analyses assuming a Gamma error distribution of the two response
219 variables (seed density and species richness) as there were count data transformed to m²/day,
220 thus continuous variables. We employed generalized linear mixed effects models (GLMM,
221 glmer, in lme4 package in R) with fixed and random effects (Crawley, 2013). In order to show
222 the effects of plot types on response variables, each of the four models (one for each trap type
223 and response variable) included “plot type” as the fixed effect and “plots” nested in “sites” as
224 a random effect (Bates et al., 2014).

225 In order to show the effects of temporal patterns on seed rain, each of the four models (one
226 for each trap type and response variable) included “seasons” × “plot type” as the fixed effects
227 and “plots” nested in “sites” as a random effect. We also performed post-hoc Tukey
228 comparisons among treatments (Crawley, 2013). For all analyses, we established α values of
229 0.05.

230 Differences between plant community composition in the standing vegetation and in the
231 seed rain at each site were analyzed using two Correspondence Analyses, designed to explore
232 categorical variables, such as the presence / absence data (Garson, 2012; with *ade4* package in
233 R). We compared the similarity for seed rain data for sticky and funnel traps between plot types
234 using the Sørensen index, based on presence/absence of the species (Kent & Coker 1992;
235 Sørensen, 1948). We present the results for Sørensen index as values from zero to one in a
236 similarity index, where a value of 1 means that the two subsets compared share all their species,
237 while a value of 0 means they share none. We used the floristic survey data, as well as with the
238 seed rain data (in funnel traps and sticky traps separately and in both traps together), from
239 species or morphospecies lists compiled for each plot type.

240

241 **Results**

242

243 *Seed rain richness and abundance*

244 For the overall data for all seed traps over one year, we found 92 seed morphospecies.
245 From the 92 seed morphospecies, we were able to identify 29% at family-level and 14% at
246 genus-level. From the 10 more common morphospecies, we identified 70% at family-level and
247 40% at genus-level (Appendix S4). We found a total of 1,378 seeds over one year in a total
248 area of 1.45 m² covered by all seed traps, representing an average of 2.6 seeds/m²/day. We also
249 found less than 20 seeds in the annual accumulated seed rain for 90% of the morphospecies
250 and that 75% of the seeds belonged to only 10 morphospecies, with only four morphospecies
251 presenting more than 100 seeds in the annual accumulated seed rain (Fig. 3). *Lychnophora* sp1
252 (Asteraceae) was the most common species retrieved with 331 seeds, followed by Poaceae sp2
253 with 300 seeds, *Rhynchospora* sp3 (Cyperaceae) sp. with 108 seeds, and Morphospecies 1 with
254 102 seeds (Fig. 3).

255

256 *Seed rain between plot types and seed trap types*

257 We found a significant difference in seed density and species richness/m²/day between plot
258 types. We found that 33% of the morphospecies were exclusively registered in preserved plots
259 and 26% exclusively in disturbed plots considering the data for both trap types. From all seeds
260 (i.e. 1,378 seeds) in the seed rain, 77% were exclusively registered in funnel traps, 10% only
261 in sticky traps and 13% in both trap types. When we consider only the data for sticky traps,
262 52% of the morphospecies occurred exclusively in disturbed plots and 26% exclusively in
263 preserved plots. For funnel trap data, we found that 24% of the morphospecies were exclusively
264 registered in disturbed plots and 34% exclusively in preserved plots. Overall, the Sørensen
265 similarity indices for the presence-absence of species in the seed rain between plot types was
266 low for sticky (0.32) and high for funnel (0.6) traps (Table 1). Sørensen similarity indices
267 between trap types on similar plots were low (disturbed = 0.17; preserved = 0.16; Table 1).

268 Disturbed plots had a lower average seed density in sticky traps ($0.4 \pm \text{SE } 0.1$ seeds/m²/day)
269 than preserved plots ($1.9 \pm \text{SE } 0.4$ seeds/m²/day) but higher average in funnel traps ($5.4 \pm \text{SE } 0.9$
270 seeds/m²/day) than in preserved plots ($3.5 \pm \text{SE } 0.5$ seeds/m²/day; Fig. 4). We found the
271 same patterns for species richness. Funnel traps allowed catching the highest species richness,
272 first in disturbed and then in preserved plots although these were not significantly different
273 (respectively $0.24 \pm \text{SE } 0.02$ and $0.011 \pm \text{SE } 0.01$ species/m²/day; $\chi^2=1.60$, $p=0.206$; Fig. 4).
274 Sticky traps on disturbed plots caught fewer species, and significantly the fewest on disturbed
275 plots ($0.14 \pm \text{SE } 0.001$ species/m²/day; $\chi^2=22.32$, $p<0.001$; Fig. 4).

276

277 *Temporal patterns of seed rain*

278 We found significant differences in the seed density and species richness in both plot types
279 between the dry and rainy seasons (Fig. 5). The significantly higher seed density during the

280 rainy season collected in funnel traps ($\chi^2=6.69$, $p=0.010$; Fig. 5), was driven by a larger arrival
281 of seeds from the three most common morphospecies [*Lychnophora* sp1 (Asteraceae); Poaceae
282 sp2; *Rhynchospora* sp3 (Cyperaceae)] in December and January. This higher seed density was
283 coupled with a higher species richness, although this was only marginally significant ($\chi^2=3.30$,
284 $p=0.069$; Fig. 5). In sticky traps, we found a higher species richness during the dry season
285 ($\chi^2=16.30$, $p<0.001$) and a higher species richness on preserved areas ($\chi^2=4.88$, $p=0.027$; Fig.
286 4).

287

288 *Seed rain and floristic similarity between plot types*

289 The Correspondence Analysis on the seed rain showed strong dissimilarities in species
290 composition between disturbed plots (Fig. 6). One disturbed plot had 22 species in common
291 with its preserved plot (e.g. *Rhynchospora* sp., while only 10 and five species in common for
292 other sites; Fig. 6). While preserved sites had some species in common on the seed rain, such
293 as Poaceae sp1, *Perama* sp1 (Rubiaceae), *Xyris* sp1 (Xyridaceae), Asteraceae sp4, they also
294 had species characteristic of each one of them, such as Asteraceae sp3, Poaceae sp4 and
295 Poaceae sp6, and *Rhynchospora* sp1 (Cyperaceae) and *Rhynchospora* sp4 (Cyperaceae). The
296 only species common to all three sites was *Lychnophora* sp1 (Asteraceae).

297 The total species richness in the standing vegetation was 74 species, distributed in 48 genera
298 and 26 families (Appendix S5). Poaceae, Cyperaceae and Asteraceae were the most
299 representative families in both plot types. We found 39 species occurring exclusively in
300 preserved plots, 18 exclusively in disturbed plots and 17 in both plot types. Preserved plots
301 shared 15 species, like *Bulbostylis paradoxa*, *Homolepis longispicula* (Cyperaceae),
302 *Lychnophora ericoides* (Asteraceae), *Gomphrena* sp. (Amaranthaceae), *Vellozia albiflora* and
303 *Vellozia variabilis* (Velloziaceae), which were exclusive from preserved plots. Axis 1 of the
304 Correspondence Analysis run on vegetation data separated the three preserved plots from the

305 three disturbed plots (Fig. 6). All disturbed plots were characterized by the presence of
306 *Rhynchospora riedeliana* (Cyperaceae) and *Mesosetum loliiforme* (Poaceae), but these species
307 were also found on most preserved plots (Appendix S6). Axis 2 separated two disturbed plots
308 characterized with *Andropogon* sp., *Croton* sp. and *Rhynchospora brasiliensis* from the other
309 disturbed plots characterized by *Polygala paniculata* and *Schwenckia americana*.

310

311 Discussion

312

313 Campo rupestre has limited seed dispersability

314 The significant differences in seed arrival across time and space found here provide valuable
315 information about seed rain dynamics and show an intrinsic seed dispersal limitation within
316 preserved disturbed areas of *campo rupestre*. Our data suggests widespread seed rain
317 limitation, expressed by the low seed density in traps, supporting the prediction of OCIBLs
318 theory of limited dispersability (Hopper, 2009), and suggest that seed limitation may strongly
319 influence plant community re-assembly and limits plant recovery after soil disturbance.

320 The overall averages of seed density per day registered here are much lower than those
321 reported in other grasslands, despite the fact that the species richness found here is among the
322 highest already reported in the literature (Jackel & Poschlod, 1994; Urbanska et al., 1998;
323 Lyaruu, 1999; Chabrierie & Alard, 2005; Jakobsson et al., 2006; Shang et al., 2013; Fibich et
324 al., 2013; Marteinsdottir, 2014). For example, Jackel & Poschlod (1994) found 11786
325 seeds/m²/year and 9634 seeds/m²/year respectively in two calcareous grasslands; and Chabrierie
326 & Alard (2005) found 22.13 seeds/m²/day (8,079 seeds/m²/year) in funnel traps and 4.84
327 seeds/m²/day (1,766 seeds/m²/year) in sticky traps in a chalk temperate grassland. These values
328 are almost ten times higher those found here. As another example, Buisson et al., (2006) found
329 153.2 seeds/m²/day in sticky traps in a study over six months in a degraded grassland composed

330 mostly by annuals species. The low density in the seed rain found here also support the idea of
331 dispersal limitation in *campo rupestre*.

332 The remarkable low seed density found for 90% of the morphospecies corroborates the
333 predictions of OCBIL theory of accentuated dispersal limitation on this ancient ecosystem
334 (Hopper et al., 2016; Silveira et al., 2016). In young, often disturbed, fertile landscapes
335 (YODFELs), large-scale disturbances create vast areas free of vegetation, which offer
336 opportunities for recolonization and succession. As a result, plant species with strategies for
337 long distance dispersal are successful in YODFELs (Hopper, 2009). In contrast, the
338 combination of higher climatic stability with lower soil fertility in OCBILs results in conditions
339 that select for short distance seed dispersal, probably because the benefits of staying close to
340 the parental plant has been higher than the benefits of dispersing seeds away from the parental
341 plants for millions of years (Hopper, 2009; Bonte et al., 2012). Unassisted seed dispersal is
342 common in many lineages of dominant species in *campo rupestre* (Morellato & Silveira, 2018),
343 suggesting that community dynamics and resilience may be hampered by dispersal limitation,
344 as in other OCBIL grasslands. Additionally, factors related to low seed set, such as the
345 predominance of small and isolated populations (Morgan, 1999), may be related to the
346 important seed dispersal limitation registered in our study and deserve further investigations in
347 *campo rupestre*.

348

349 *Seed rain is different in preserved and disturbed plots*

350 The ability of plant communities to recover from exogenous disturbances from both internal
351 and external species pool is a key driver of vegetation dynamics and resilience. The intense
352 disturbances linked to soil removal by gravel exploitation in *campo rupestre* result in a drastic
353 or even complete removal of both bud and seed banks (Le Stradic et al., 2018; Buisson et al.,
354 2019; Arruda et al., 2020). Thus the natural recovery success in these disturbed areas relies on

355 the arrival of new diaspores. Our data is in accordance with studies that place seed limitation
356 as an important driver of low resilience in disturbed grasslands (Urbanska & Fattorini, 2000;
357 Lehouck et al., 2009). The limited seed arrival in both preserved and disturbed plots,
358 particularly in sticky traps, can be explained by a widespread lack of obvious seed dispersal
359 mechanisms in the majority of species in *campo rupestre* (Morellato & Silveira, 2018). The
360 higher average seed density in sticky traps in preserved plots shows the importance of short
361 distance dispersal events from plants inside the plots (Chabrerie & Alard, 2005). Some seeds
362 retrieved in sticky traps did not represent any classical adaptation for wind dispersal, such as
363 wings or plumes, and may not accurately describe all components of the dispersal processes
364 for many species (Howe & Smallwood 1982). For example, some light seeds may disperse
365 from tall mother plants by wind over several meters and may be caught in sticky traps
366 (Chabrerie & Alard, 2005). This may partially explain why disturbance seems to affect seed
367 arrival dynamics in sticky traps, due to the absence of parental plants or to the small height of
368 the mother plants on these plots.

369 Only 17 species from the floristic survey occur in both plot types, indicating a strong
370 dissimilarity between preserved and disturbed areas even 15 years after the disturbance. The
371 strong dissimilarity within disturbed plots and the fact that 57% from all plant genera from the
372 floristic survey were only recorded in preserved plots sustain the poor and unpredictable
373 recovery trajectory in these plots (Leps et al., 2000; 2007), which is likely caused by a high
374 spatial species turnover and dispersal and/or establishment limitation. Poaceae and Cyperaceae
375 were the most representative families in the standing vegetation in both plot types and presented
376 together with Asteraceae the high abundance in the seed rain in both plot types, suggesting that
377 these plant families could be prioritized in restoration projects in *campo rupestre*. On the other
378 hand, *Vellozia* (Velloziaceae), one of the richest genera in the standing vegetation in preserved

379 plots, was absent in disturbed plots both in the standing vegetation and in the seed rain, which
380 place them as challenging key plant groups for assisted reintroduction in disturbed areas.

381

382 *Seed rain varies with trap types*

383 Funnel traps were the most efficient trap type in catching seeds, supporting the idea that this
384 trap type is the most effectiveness in estimating seed rain in grasslands (Page et al., 2002;
385 Chabrierie & Alard, 2005). Although we retrieved only a small portion of the annual
386 accumulated seed rain in sticky traps, 10% of the morphospecies were exclusively found in this
387 trap type, including two out of the ten more common ones. These findings indicate that the
388 combination of different seed trap types increases the accuracy and sampling of seed rain
389 studies (Chabrierie & Alard, 2005). The higher average of seeds/m²/day found for funnel traps
390 in disturbed plots can be related to a reduced activity of ground-dwelling animals in these areas
391 (Brandão et al., 2011), relaxing the strength of seed predation, and thus increasing the chances
392 of seed arrival in funnel traps *via* secondary wind dispersal or runoff water (Chambers &
393 MacMahon, 1994; de Rouw et al., 2018).

394 The total species richness in the seed rain was higher than that in the floristic survey,
395 implying a species influx from seeds coming from outside the plots. However, this influx may
396 be more related to plant megadiversity and high spatial species turnover in *campo rupestre* than
397 to high dispersal potential by the plant community (Silveira et al., 2016). Approximately 32%
398 of morphospecies were registered exclusively in disturbed plots and 25% exclusively in
399 preserved plots, suggesting differences in the seed rain composition between disturbed and
400 preserved areas. The Correspondence Analysis for the morphospecies occurrence indicates a
401 certain similarity of seed rain patterns among preserved plots and a marked difference in seed
402 rain composition between disturbed plots, which together with seed rain limitation may
403 partially explain the poor recovery of these disturbed areas after soil removal.

404

405 *Seed rain varies with seasons*

406 *Campo rupestre* is characterized by distinct seasonal patterns for the total annual fruit
407 production in the plant community in its sandy soils, with significantly more fruits being
408 produced in the dry season (Le Stradic, 2018c), which may partially explain the significant
409 increase in the number of barochoric seeds (e.g. Poaceae) captured in sticky traps during the
410 dry season. On the other hand, the significant increase in the number of seeds and species
411 richness captured in funnel traps during the rainy season, may indicate a strong influence of
412 seasonal abiotic-related secondary dispersal processes, such as water runoff during the rainy
413 season (e.g. Cyperaceae seeds, de Rouw et al., 2018) and may explain the relative lower seed
414 density in funnel traps during the dry season. The ability of rainfall to disperse seeds depends
415 on local surface cover (de Rouw et al., 2018). Bare or sparsely covered soils in disturbed plots
416 can favor seed dispersal by runoff water and wind along the ground, whereas dense ground
417 cover in preserved plots represents barriers to secondary dispersal by these abiotic factors
418 (Schurr et al., 2005). Cyperaceae are characterized by a high proportion of species with
419 buoyant, water-dispersed seeds (Leck & Schütz, 2005), which may partially explain the
420 equivalent seed arrival rates between disturbed and preserved plots for species in this family.

421

422 **Conclusion**

423 This study brings the first community-level information about seed dispersal in *campo*
424 *rupestre* and represents a novel contribution for seed rain studies on tropical grasslands. Our
425 data suggest widespread seed limitation in both preserved and disturbed areas and a remarkable
426 low seed density found for 90% of the taxa captured on the seed traps. As a consequence, the
427 recovery success in these disturbed areas of *campo rupestre* cannot only rely on the natural
428 arrival of new diaspores. Active restoration techniques, such as direct seeding, should be

429 considered in future restoration practices in *campo rupestre*. Approximately 1/3 of seeds of
430 morphospecies were registered exclusively in disturbed plots and 1/4 exclusively in preserved
431 plots, proving that the collection of data on both degraded and preserved areas is crucial for a
432 better understanding of the seed rain in a restoration context. Despite the fact that funnel traps
433 were the most efficient trap type in catching seeds, the use of more than one type of seed trap
434 proved to be crucial for a more reliable and complete measurement of the seed rain and its
435 ecological aspects. The significant difference in the number of seeds and species richness
436 captured within trap types between seasons, shows the importance of seasonal comparisons in
437 tropical environments when studying seed rain.

438

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449

450 **Authors' contributions**

451 A.J.A, F.A.O.S., P.P. and E.B conceived the ideas and designed methodology; A.J.A., P.A.J.,
452 H.T.S.R., F.Y and E.B. collected the data; A.J.A. and E.B. analyzed the data; A.J.A. led the

453 writing of the manuscript with inputs from F.A.O.S, P.P. and E.B. All authors contributed
454 critically to the drafts and gave final approval for publication.

455

456 **Supporting Information**

457 **Appendix S1:** Picture of the disturbed site

458 **Appendix S2:** Seed trap types design

459 **Appendix S3:** Rarefaction curves

460 **Appendix S4:** Seed image bank

461 **Appendix S5:** Plant species occurrence according to plot type considering all sites.

462 **Appendix S6:** Multidimensional representation of the composition of plant species

463

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