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Dispersal syndrome influences the match between seed rain and soil seed bank of woody species in a Neotropical dry forest.

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1 **Dispersal syndrome influences the match between seed rain and soil seed bank of woody**
2 **species in a Neotropical dry forest**

3 Seed compartments and vegetation similarity

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23

24 **ABSTRACT**

25 Aim

26 Long-distance seed dispersal and the ability to form soil seed banks are alternative strategies
27 to plant regeneration. These strategies are known to be mediated by adaptations of seed
28 dispersal and reproductive phenology, which if analyzed together can provide valuable
29 information about the regeneration strategies of species. We explored whether dispersal
30 syndrome and/or seed dispersal phenology control the similarity between standing vegetation,
31 seed rain and soil seed bank in a seasonally dry tropical forest (SDTF) in Southern Ecuador.

32 Location

33 Arenillas Ecological Reserve, Southwestern Ecuador, the biogeographic region of Pacific
34 Coastal Ecuador.

35 Methods

36 We recorded standing vegetation of woody species in a 9 ha permanent plot and sampled soil
37 seed bank from 265 cores of 0.06 m². Additionally, we sampled seed rain along 1 yr from 265
38 seed traps of 0.64 m². We evaluated similarity in species composition, species richness, and
39 abundance between the three compartments for all species and for each dispersal syndrome.

40 Results

41 Our studied community showed a high similarity in species composition between
42 compartments. The similarity was influenced by dispersal syndrome and the seed dispersal
43 phenology. Seed rain – standing vegetation similarity was high in species that dispersed in the

44 rainy season, such as zoochorous species, while seed bank – standing vegetation was higher
45 for autochorous species compared with the other dispersal syndromes.

46 Conclusions

47 In our SDTF, dispersal phenology seemed to influence whether seeds had direct germination
48 or entered the soil seed bank and influenced the match between seed rain and soil seed bank,
49 suggesting different regeneration strategies related to dispersal ability.

50 Key words

51 Regeneration strategies, seed dispersal, seed dispersal phenology, seed rain density, seed bank
52 density, seasonally dry tropical forest, similarity, species composition.

For Review Only

54 **Introduction**

55 Seed dispersal is critical for the recruitment of new individuals (Schupp & Fuentes, 1995;
56 Nathan & Muller-Landau, 2000) and a key process for the regeneration of plant populations
57 and communities (Howe & Smallwood, 1982). Recruitment may occur immediately upon the
58 arrival of seeds to the ground after seed release from the mother plant (*i.e.* seed rain), or be
59 delayed through the formation of transient or permanent soil seed banks (Uhl et al., 1981;
60 Álvarez-Buylla & Martínez-Ramos, 1990; Moles & Drake, 1999; Silva et al., 2016; Vandvik
61 et al., 2016). The relative importance of these two primary regeneration sources conform a
62 remarkable evolutionary dilemma with variations among habitats (Thompson, 2000; Vandvik
63 et al., 2016), and its clarification is a crucial step to understand the community structure and
64 composition and to apply appropriate management measures.

65 Several studies have focused on the understanding of the structure and composition of plant
66 communities based only in the standing vegetation (Bakker et al., 1996; Dungan et al., 2001;
67 Savadogo et al., 2017). However, as seed availability is a first ecological filter for plant
68 regeneration, the understanding the local structure and composition of plant communities
69 requires a joint consideration of the standing vegetation, the spatial extent achieved by
70 dispersal (seed rain) and the temporal exploration obtained through the existence of soil seed
71 banks (Bakker et al., 1996; Nathan and Muller-Landau, 2000; Thompson, 2000;
72 Hopfensperger, 2007; Pärtel, 2014; Vandvik et al., 2016; Savadogo et al., 2017).

73 The match among these three community compartments –standing vegetation, seed rain and
74 soil seed bank– will depend on the filters exerted by the local environment on the regional
75 floristic pool along the history of the plant community (Caballero et al., 2008). Tight matches
76 among standing vegetation and soil seed banks have been documented in some pioneer

77 communities such as those of ephemerals in some drylands (Caballero et al., 2008).
78 Nevertheless, in mature communities, the match can be low due to inputs of seeds coming
79 from surrounding sites and communities, or due to the long-standing permanence in the soil
80 seed bank of species from previous successional stages (Beatty, 1991; Thompson, 2000;
81 Laskurain et al., 2004; Martins & Engel, 2007, Gomes et al., 2019), even if they are not
82 currently present in the standing vegetation (Pärtel, 2014). Mismatches can also emerge from
83 the differential ability of plant species to establish soil seed banks. This implies that if most of
84 the species in the community rely on dispersal for their regeneration, the similarity between
85 standing vegetation and seed rain will be high, but the similarity between standing vegetation
86 and seed soil bank will be low.

87 The ability to establish soil banks has been studied in relation to a few plant functional traits,
88 e.g., regeneration guild (Vázquez-Yanes & Orozco Segovia, 1984, 1993; Garwood, 1989;
89 Chandrashekara & Ramakrishnan, 1993; Rees, 1997), life form (Garwood, 1989; Rees, 1997;
90 Thompson, 2000; Silva et al., 2016), seed chemistry (Thompson, 2000), seed size and
91 dispersal capacity (Bakker et al., 1996; Thompson, 2000; Valenta et al., 2015; Douh et al.,
92 2018; Ssali et al., 2018), and phenology (Heydel & Tackenberg, 2017). For instance,
93 observational studies suggested that large seed size and long dispersal distance should be
94 negatively related to persistence in soil (Klinkhamer et al., 1987; Bakker et al., 1996;
95 Thompson, 2000). In this sense, species from mature stages typically have bigger and heavier
96 seeds than pioneer species, which germinate immediately after dispersal without entering the
97 soil bank, thereby avoiding seed eaters (Swaine & Hall, 1983; Teketay, 2005). However,
98 information is scarce for those more complex interactions between plant functional traits and
99 the establishment of soil seed banks. In particular, a relationship between dispersal syndrome
100 and persistence in the soil can be mediated by the tight evolutionary connection of dispersal

101 syndrome with dispersal phenology (Heydel & Tackenberg, 2017; Douh et al., 2018).
102 Namely, by confining dispersal to periods with relatively low air humidity and windy
103 weather, anemochorous species seem to benefit by increased flying distances. In autochorous
104 species, the formation of soil seed banks would be unnecessary when optimal conditions for
105 dispersal match those required for germination (Bakker et al., 1996).

106 It has been hypothesized that in seasonally dry tropical forest (SDTF) soil seed banks are
107 more important than in tropical rain forests due to the need of released seeds to survive the
108 dry and unfavourable season (Vázquez-Yanes & Orozco Segovia, 1984). However, the few
109 studies available have shown that soil seed banks of woody species are also variable among
110 SDTFs. While some studies have revealed a high presence of standing woody species in the
111 soil bank (Garwood, 1989), other studies found a low similarity between the seed bank and
112 standing vegetation (Rico-Gray & García-Franco, 1992; Uasuf et al., 2009; Savadogo et al.,
113 2017; Gomes et al., 2019). Among other factors, these discrepancies could be related to
114 differences in the seed banking ability of the different dispersal syndromes (Valenta et al.,
115 2015). Unfortunately, the few works exploring the relationship between dispersal syndrome
116 and soil permanence of seeds in SDTF have not provided a clear explanation for these
117 discrepancies (Antunes et al., 1998; Barbosa, 2003; Rodrigues da Luz & Ferreira-Nunes,
118 2014; Valenta et al., 2015). In our opinion, such contradictory results are the consequence of
119 ignoring the connection between dispersal syndrome and dispersal phenology. If the need to
120 establish a soil seed bank depends on the lag between seed dispersal and the optimal
121 conditions for germination, species dispersing during the dry months should dominate seed
122 banks. In this sense, anemochorous trees are good candidates to be part of soil banks since
123 they tend to disperse into periods with relatively low humidity and windy weather (Heydel &
124 Tackenberg, 2017), which in SDTFs coincides with the dry season. In SDTFs the dry season

125 has optimal conditions for dispersal of anemochorous species but poor germination conditions
126 that induce the entrance of these seeds in the soil seed bank. Contrarily, the formation of soil
127 seed banks would be unnecessary for zoochorous species, in which seed dispersal occurs in
128 the rainy season, precisely during the activity peak for most animal populations. Thus, a
129 complex interaction between dispersal syndrome, dispersal phenology, and soil seed bank
130 formation could be operating in tropical dry forests. Such information is critically needed in
131 SDTF of the Neotropics, where forest remnants reach only a 10% of original distribution
132 (Banda et al., 2016), and where the common practice of direct seedling sowing is ineffective
133 due to high desiccation (Vieira et al., 2008). The knowledge of seed bank and seed rain
134 structure and its role in natural regeneration can be useful to implementation of alternative
135 restoration strategies (Vieira et al., 2008).

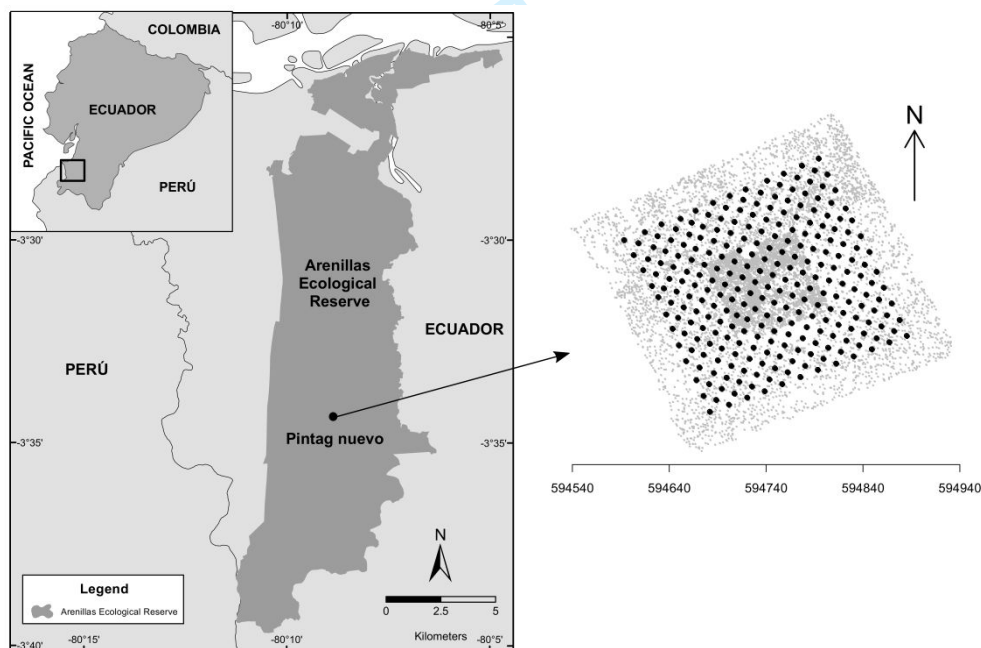
136 In this study, we quantified standing vegetation, seed rain, and soil seed bank in a 9 ha forest
137 plot of SDTF with the aim to examine to what extent these two primary seed sources –seed
138 rain and seed bank– are contributing to the community assemblage, and how the dispersal
139 phenology and dispersal syndrome can explain those contributions. We developed this study
140 in a small-protected area of SDTF in Southwestern Ecuador. This area represents one of the
141 last SDTF remnants below 100 m a.s.l. along the South America Pacific coast. We considered
142 this area might be useful as reference site of “pristine forest” to guide restoration actions.

143 **Materials and Methods**

144 **Study site**

145 The study was conducted in the Arenillas Ecological Reserve (REA for its acronym in
146 Spanish), which is located in the southwestern most tip of Ecuador (03° 34' 15.44''S; 80° 08'
147 46.15''E, 30 m a.s.l.) (Fig. 1). Mean annual rainfall is 667 mm, with a dry season extending

148 from June to December (with less than 40 mm during this 7-month period). Annual mean
 149 temperature is 25°C (Huaquillas weather station, n = 45 years). REA holds one of the last
 150 remnants of SDTF in the Ecuadorian coast, as well as lowland dry scrub communities and
 151 mangroves in the lowest areas (Sierra, 1999). It was included within the Ecuadorian
 152 Patrimony of the State Natural Areas in 2001 (BirdLife International, 2013) and has been
 153 protected from extractive activities and man-driven perturbations for about 60 years. In the
 154 center of REA, in one of the best-conserved sectors, we established a 9 ha permanent plot
 155 (300 x 300 m) consisting of transitional vegetation between dry deciduous forest and lowland
 156 scrub (Fig. 1).



157

158 **Fig. 1** Left map: location of the Arenillas Ecological Reserve (square) in Ecuador. Central
 159 map: location of the permanent plot in "Pintag Nuevo" (black dot). The draft on the right
 160 shows the permanent plot with the spatial location of each individual (light gray dots) in the
 161 300 x 300 m plot and shrubs (dark gray dots) in the central 100 x 100 m plot. The black dots
 162 show the location of sampling points for seed rain and soil bank.

163 **Sampling of the standing vegetation**

164 In the 9 ha of the permanent plot, all tree individuals with a diameter at breast height (DBH) \geq
165 5 cm were recorded in 2009 (Fig. 1). Additionally, in the central 1 ha plot, we recorded all
166 shrub and subshrub individuals with DBH \geq 1 cm.

167 **Sampling of the seed rain**

168 Seed traps were used to sample the seed rain. Traps were made of a mesh fabric with holes $<$
169 0.5 mm to allow water runoff while preventing seed loss. The fabric was placed on a square
170 metal frame 80 cm long (0.64 m²) located 80 cm above the ground (Stevenson & Vargas
171 2008). A heavy object was placed in the center of each trap to prevent seed loss by wind.

172 We placed 265 traps in a regular grid in an area of 220 x 220 m of forest (4.8 ha), in the
173 central part of the 9 ha plot (Fig. 1). Traps were located in each corner and the center of each
174 20 x 20 m cells of the grid. The total sampled area for seed rain was 169.6 m². Seed rain was
175 collected monthly between August 2011 and July 2012 for 12 surveying times. All seeds
176 falling into the traps were identified (see below) and counted. When the dispersal units were
177 whole fruits or their parts, the number of seeds contained in them was counted.

178 **Sampling of the soil seed bank**

179 Soil seed bank was sampled once between November and December 2011, at the end of the
180 dry season, when most seeds had been dispersed and before germination started in the rainy
181 season. This sampling date corresponds with the moment in which the soil seed samples reach
182 their maximum diversity and density, i.e., it includes both the transient and the persistent soil
183 seed bank (Caballero et al., 2005; Espinosa et al., 2013). As in the case of the seed rain, 265

184 soil samples were collected in 0.25 x 0.25 x 0.03 m squares located adjacent to the seed traps
185 (Fig. 1), adding up to a total sampled area of 16.56 m².

186 Seed bank composition was assessed using the germination method, which allows estimating
187 viable seeds in the soil (Bigwood & Inouye, 1988; Holzapfel et al., 1993; Caballero et al.,
188 2008). Soil samples were placed in trays with a basal layer of pumice to control the moisture.
189 Trays were kept under controlled watering for six months, and emerging seedlings were
190 identified, counted and removed at 3-4 day intervals (Caballero et al., 2008). After six
191 months, the remaining material of each sample was watered with a gibberellic acid (GA3)
192 solution (1000 ppm) to stimulate germination in seeds with secondary dormancy (Caballero et
193 al., 2008). From here on, soil samples were kept under watering for two additional months.
194 Unidentified seedlings were transplanted for subsequent identification.

195 **Statistical analyses**

196 From the mapping of the standing vegetation, we obtained the number of species present in
197 the permanent plot, and the density (individuals per hectare) and basal area by species. Both
198 density and basal area were estimated from the 9 ha plot for tree species and from the central
199 1 ha plot for shrub species. We also assembled two data sets for the seed density, one in the
200 seed rain and another one in the soil bank. The density of each species in the three
201 compartments –standing vegetation, seed rain and soil bank– was transformed by dividing
202 each density value by that of the most abundant species in each compartment.

203 According to fruit and seed features, and direct observation in the field, species were
204 classified into three dispersal syndromes: zoochory, anemochory and autochory (Jara-
205 Guerrero et al., 2015). To assess the contribution of seed rain and soil bank to woody
206 community assemblage we considered the similarity in species composition between the three

207 compartments. We used the Sørensen similarity index (Oksanen et al., 2012) with presence-
208 absence. To evaluate similarities based in abundance, we calculated Bray-Curtis similarity
209 using the transformed density of the three compartments, and also, comparing the basal area
210 of standing vegetation and transformed density of seed rain and seed bank. Both similarity
211 indices range from 0 to 1, where 1 indicates identical composition. The similarity was
212 analyzed both for all species together and for each dispersal syndrome separately.

213 We used an extension of the Fisher exact test for large contingency tables to test differences
214 in the frequency of species among dispersal syndromes in the three compartments.

215 Significance was obtained from 2000 Monte Carlo simulations (R Core Team, 2016).

216 To analyze the temporal pattern in species composition of the seed rain we used time-
217 constrained agglomerative clustering analysis (Legendre & Legendre, 1998), following
218 Ward's (1963) method. First, we computed a Euclidean distance matrix by using a species-
219 by-month matrix, with the total number of seeds for each species recorded in each matrix cell.
220 Second, to find the best cluster solution for the annual seed rain data, we tested clustering
221 results with 2 to 6 groups using cross-validation with 100 iterations for each set of groups.
222 The clustering with the lowest cross-validation residual error was retained. This analysis was
223 performed with the 'const.clust' package (Legendre, 2011). Third, we assessed whether any
224 species was significantly associated with the temporal clusters revealed previously, using the
225 "signassoc" function, from the 'indicspecies' package (De Cáceres and Legendre, 2009). The
226 null hypothesis tested was that the average abundance of a species was not higher in the target
227 month group than in other groups. All statistical analyses were carried out with the R
228 environment, version 3.2.4 (R Core Team, 2016).

229

230 **Results**

231 **Species richness and abundance in the standing vegetation, seed rain and seed bank**

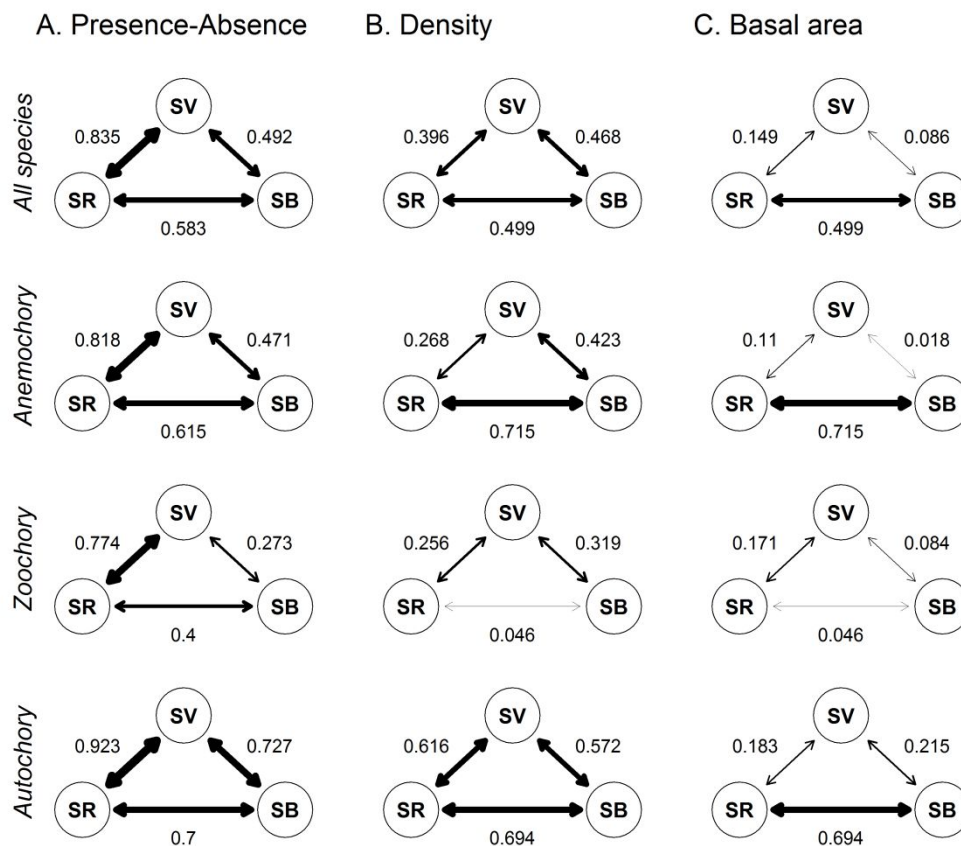
232 A total of 47 species were recorded pooling the three compartments studied, from which 23
233 were trees and 24 were shrubs (Appendix S1). All of them were present in the standing
234 vegetation, with 8211 individuals. *Handroanthus billbergii* and *Croton rivinifolius* were the
235 most abundant tree and shrub with 57 and 721 individuals per hectare, respectively (Appendix
236 S1). In the seed rain, we collected 15083 seeds (88.9 seeds m⁻²) from 33 woody species, with
237 a mean density (\pm standard deviation) per species of 2.69 (\pm 4.95) seeds m⁻² (Appendix S1).
238 The main contribution to the seed rain came from *Alternanthera* sp., *Croton* spp. and
239 *Erythroxylum glaucum* (Appendix S1). In the seed bank, we recorded 613 emerged seeds
240 (37.01 seeds m⁻²) from 15 woody species, with a mean density (\pm standard deviation) of 2.47
241 \pm 3.9 seeds m⁻² (Appendix S1). The main contribution to the seed bank came from
242 *Alternanthera* sp. and *Croton* spp. (Appendix S1). The only taxon that was abundant in the
243 three compartments was *Croton* spp.

244 **Similarity among standing vegetation, seed rain and soil seed bank**

245 All species recorded both in seed rain and in soil bank occurred in the standing vegetation; 33
246 were present in the seed rain and 15 in the soil bank. Seeds of 19 species from the standing
247 vegetation were recorded only in the seed rain, and seeds of one species (*Piptadenia flava*)
248 were recorded only in the soil bank. Fourteen species of the standing vegetation were absent
249 in both the seed rain and the seed bank, including three dominant trees (the two *Handroanthus*
250 species and *Cynophalla mollis*).

251 In general, Sørensen similarity index based on presence-absence data showed a relatively high
252 similarity among compartments and decreased from standing vegetation–seed rain through

253 seed rain–seed bank to standing vegetation–seed bank (Fig. 2A). For transformed density and
 254 basal area data, the seed rain and soil seed bank were the components with the highest
 255 similarity (Fig. 2B, C).



256

257 **Fig. 2** Similarity in species composition among standing vegetation (SV), seed rain (SR) and
 258 seed bank (SB) considering all species or each dispersal syndrome separately. Results are
 259 based on presence-absence (A), density of the three compartments (B) and basal area of
 260 species in standing vegetation (C). Width arrows is proportional to similarity.

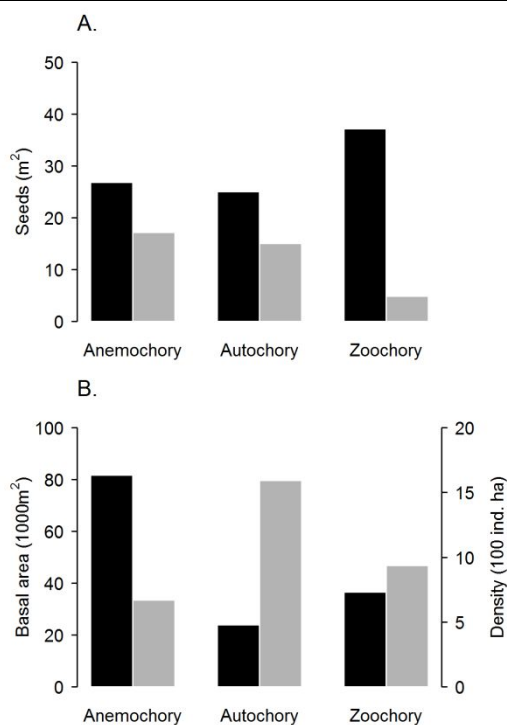
261 Dispersal syndromes and similarity among compartments

262 The number of species of each dispersal syndrome did not vary significantly among
 263 compartments (Table 1, Fisher's exact test, $p = 0.55$). Zoochory was the dispersal syndrome
 264 with most seeds in the seed rain, while the anemochory showed a highest density in the soil

265 bank (Fig. 3A). Autochory was the dispersal syndrome with the highest density in the
 266 standing vegetation, while anemochory was the syndrome with the highest accumulated basal
 267 area (Fig. 3B, Appendix S1).

268 **Table 1.** Number of species (percentage) of each dispersal syndrome in each compartment
 269 studied: standing vegetation, seed rain and seed bank.

<i>Number of species</i>			
<i>Syndrome</i>	<i>Standing vegetation</i>	<i>Seed rain</i>	<i>Seed bank</i>
Anemochory	13 (28)	9 (28)	4 (27)
Autochory	14 (30)	12 (36)	8 (53)
Zoochory	20 (42)	12 (36)	3 (20)



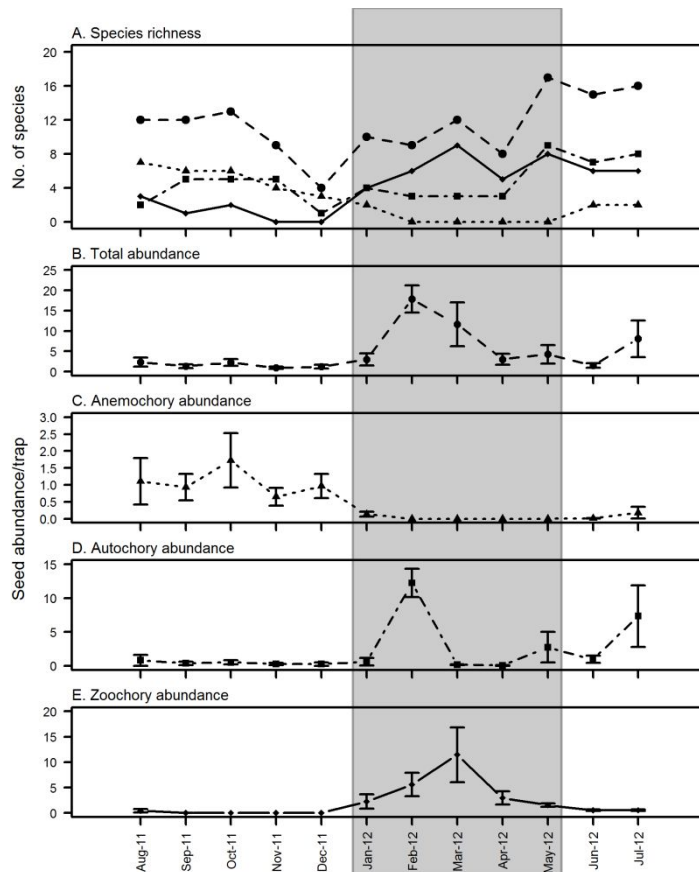
270

271 **Fig. 3** Abundance of the three dispersal syndromes in (A) the seed rain (black bars) and the
 272 soil seed bank (grey bars) and (B) in the standing vegetation estimated as basal area (black
 273 bars) or density (grey bars).

274 For anemochory and zoochory, Sørensen similarity index based on presence-absence data
275 showed a relatively high similarity among compartments and decreased from standing
276 vegetation–seed rain through seed rain–soil bank to standing vegetation–soil bank (Fig. 2A).
277 From the three dispersal syndromes, autochorous species showed the highest similarities, with
278 standing vegetation and seed rain relationship showing the highest similarity. When we
279 considered the transformed density and basal area data, similarity among compartments was
280 dependent on dispersal syndrome (Fig. 2B, C). Autochorous species showed the highest
281 similarity between compartments, followed by anemochorous species (Fig. 2bB, C).
282 Zoochorous species showed the lowest similarities among compartments (Fig. 2B, C). The
283 match between standing vegetation and seed compartments was stronger with density than
284 with basal area.

285 **Temporal variation in the seed rain**

286 Seed rain fluctuated monthly in species richness (4–17 species: Fig. 4A) and seed abundance
287 (1.3–27.9 seeds m⁻²: Fig. 4B). The highest species richness was recorded at the transition from
288 the rainy to the dry season (between May to June), and the lowest in December, just before
289 the beginning of the rains (Fig. 4A). Seed abundance collected in traps showed a bimodal
290 pattern, reaching a maximum in February (rainy season) and another in July (dry season),
291 while the minimum was observed in December (transition between dry and rainy season)
292 (Fig. 4B).

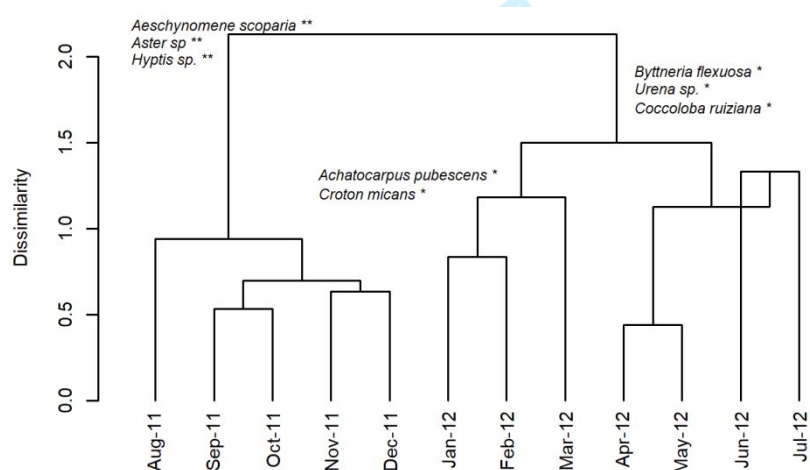


293

294 **Fig. 4** Temporal variation in woody species number (A) and abundance (B-E) in the seed rain.
 295 Circles represent total richness, triangles represent anemochorous, quadrates represent
 296 autochorous and diamonds represent zoochorous species. The gray area indicates the rainy
 297 season. Wiskers indicate ± 1 standard error.

298 Chronological constrained clustering analysis separated three well-defined groups of months
 299 regarding seed rain composition (cross-validation residual error = 0.773). The first group
 300 corresponded to the months of the dry season, from August to December. The second group
 301 corresponded to the beginning of rainy season, from January to March; while months of the
 302 third group, April to July, corresponded to the transition from the rainy to dry season (Fig. 5).
 303 Thirteen species showed a significantly positive association to one of the three compositional
 304 groups (Fig. 5, Appendix S2). Among them, the anemochorous species were associated to the

305 first group (dry months), while zoochorous and autochorous species were associated to the
 306 second (rainy months) or third group (transition from the rainy to dry season). Along the first
 307 months of the dry season we recorded a very low seed density of zoochorous species, most of
 308 them corresponded to species that started the dispersal process during the rainy months. We
 309 did not record seeds of zoochorous species at the end of the dry season (November and
 310 December) (Fig. 4). By contrast, anemochorous species were recorded during the dry months,
 311 and only two species continued their dispersal once the rains started. Only autochorous
 312 species were present in the seed rain throughout the year, with a peak in richness at the
 313 transition from the rainy to dry season (Fig. 4).



314

315 **Fig. 5** Dendrogram presenting the results of the seed rain partitioning between months.

316 Species significantly associated are shown for each group. *: $p < 0.05$, **: $p < 0.01$; ***: $p <$
 317 0.001.

318 DISCUSSION

319 As expected, the seed rain of woody species in this STDF showed a seasonal variation in
 320 species number and seed abundance. As observed in other studies (Swaine & Hall, 1983;
 321 Douh et al., 2018; Escobar et al., 2018), in our SDF the timing of seed dispersal seems to be

322 an important factor defining the input of seeds to the soil bank. Seed release was staggered
323 along the year, with a dominance of anemochorous species in the dry season and zoochorous
324 species in the wet season. In relation to this staggering, abundance in the soil seed bank was
325 maximal for anemochorous woody species and minimal for zoochorous ones. Overall, these
326 findings suggest that dispersal syndromes are a major factor explaining mismatches between
327 abundance in the seed rain and in the soil bank in tropical dry forests.

328 The timing of seed release differed among dispersal syndromes, with most of zoochorous
329 species dispersing during the rainy season while anemochorous species dispersed in the dry
330 season. This temporal segregation of dispersal syndromes has been found in temperate
331 ecosystems (Heydel & Tackenberg, 2017) and, to different extents, in other SDTFs (Frankie
332 et al., 1974; Gottsberger & Silberbauer-Gottsberger, 1983; Griz & Machado, 2001; Carvalho
333 & Sartori, 2015; see, however, Escobar et al., 2018 and Cortes-Flores et al., 2019 for an
334 availability of fleshy fruits throughout the year in other seasonally dry ecosystems of
335 Neotropic). This phenological separation of dispersal syndromes fits long-held expectations
336 for reproductive events in SDTFs, that have traditionally been considered to occur at
337 opportune times from a performance perspective (Janzen, 1967). The rainy season coincides
338 with the maximal activity of seed dispersers for zoochorous species, while the dry season
339 provides leafless canopies and windy conditions suitable for long-distance dispersal in
340 anemochorous species (Frankie et al., 1974; Gottsberger & Silberbauer-Gottsberger, 1983; Du
341 et al., 2009).

342 Nevertheless, it is difficult to adjust all phases of a reproductive event, from flowering to seed
343 germination, to match the most suitable conditions for each phase. For example, flowering
344 phenology can constrain fruiting phenology (Primack, 1985; Bolmgren & Cowan, 2008;
345 Bolmgren & Eriksson, 2015). In our SDTF, dispersal timing seemed to influence subsequent

346 events, namely direct germination vs. entrance in the soil seed bank, and influenced the match
347 between seed rain and soil seed bank. In SDTFs, a distinction has been suggested between
348 rapid-rainy and intermediate-dry syndromes as a function of the delay between seed release
349 and germination (Garwood, 1983). By dispersing and germinating during the rainy season,
350 zoochorous species were apparently following a rapid-rainy syndrome, adjusted to the
351 maximum size of animal populations. In addition, synchrony between dispersal and rain
352 maximizes the chances of seedling establishment and recruitment (Howe & Smallwood, 1982;
353 Garwood, 1983; Bullock, 1995; Fornara & Dalling, 2005; Jara-Guerrero et al., 2011; Espinosa
354 et al., 2012). This result concurs with the extended idea that zoochorous species depend
355 mainly on seed rain for regeneration (Bakker et al., 1996; Thompson, 2000). In our study, the
356 only three zoochorous species found in the soil bank were *Lantana* sp., which released seeds
357 during the dry season and *Bursera graveolens* and *Cordia macrocephalla*, which dispersed at
358 the end of the rainy season. Nevertheless, the abundance of the latter two species in the soil
359 bank was very low. All of them have a hard seed coat, a morphological trait that is considered
360 as a typical strategy to survive the dry season (Garwood, 1983; Baskin & Baskin, 1998), and
361 thus to facilitate the incorporation of seeds into soil banks.

362 Anemochorous species showed two strategies of dispersal timing. The most common strategy
363 was to disperse during the dry season when conditions are very poor to germination but very
364 favorable for efficient dispersal as the canopy is mostly open. These dry conditions lead to an
365 entrance of anemochorous seeds in the soil seed bank, at least in a transient way until the next
366 rainy season, i.e., an intermediate-dry syndrome (Garwood, 1983). The other strategy of this
367 guild was to disperse just immediately before or at the beginning of the rainy season. Species
368 with the latter strategy were characterized by large seeds (> 0.5 cm), i.e., *Handroanthus*
369 *chrysantha*, *H. billbergii*, *Ceiba trischistandra* and *Eriotheca ruizii* (Romero-Saritama, 2016).

370 In this case, seeds find conditions for rapid germination and a relatively large period for
371 guaranteeing seedlings with large sizes enough for surviving the first dry season. Survival to
372 this critical period is usually size dependent since large seedlings normally have a higher
373 chance of survival (Escudero et al., 1999, 2000).

374 In the case of autochorous species, which were dominant in the three studied compartments,
375 no clear seasonal pattern was found in the seed rain, suggesting a high variation in
376 germination requirements and regeneration strategies (Escobar et al., 2018). It is widely
377 accepted that interspecific competition promotes strong selection for differentiation in
378 resource use (Grant, 1972; Pfennig & Pfennig, 2009). This character displacement (Brown &
379 Wilson, 1956) can promote evolutionary divergence in phenology of seed dispersal between
380 species with the same dispersal syndrome (see Snow, 1965, for similar reasoning concerning
381 zoochorous species). Thus, the formation of soil seed banks is advantageous in autochorous
382 species because it decreases competition caused by their limited dispersal capacity and keeps
383 the seed viability during unfavorable periods for germination and seedling development
384 (Venable & Brown, 1988; Bakker et al., 1996). This strategy is particularly important in
385 highly stochastic environments such as SDTF, where the bet-hedging strategy typical of
386 species with soil banks dictates a sacrifice in the mean fitness to reduce fitness variance
387 (Evans et al., 2007).

388 The similarity between seed rain, soil seed bank and standing vegetation in our SDTF was
389 higher than values reported for forest ecosystems (45% vs. an average of $31\% \pm 3.7$:
390 Hopfensperger, 2007), and among the highest for tropical forests (Hardesty & Parker, 2002;
391 Hopfensperger, 2007; Gomes et al., 2019). This remarkably high similarity can be related to
392 two not mutually exclusive factors. First, the input of seeds came mainly from local standing
393 vegetation, and there are no hidden species in the soil seed bank (Pärtel, 2014). In this SDTF,

394 dispersal was not very efficient in any species independently of the dispersal syndrome (Jara-
395 Guerrero et al., 2015). Second, this high similarity could be at least partially associated with a
396 small degree of disturbance (Hopfensperger, 2007) in this well-preserved forest. In this sense,
397 high similarity could prevent the presence of pioneer species in the soil seed bank. Although
398 scarce, available information about the similarity between standing vegetation and soil seed
399 banks in SDTF is contradictory, with some studies showing high similarity (Garwood 1989)
400 and others finding a low similarity (Rico-Gray & García-Franco, 1992; Uasuf et al., 2009;
401 Savadogo et al., 2017, Gomes et al., 2019). This apparent discrepancy could be explained, at
402 least partially, if the effects of dispersal syndrome and dispersal phenology are explicitly
403 considered.

404 Although comparisons between these community compartments sometimes are based on
405 presence-absence data sets (*e.g.* Hall & Swaine, 1980; Dungan et al., 2001; Grombone-
406 Guaratini et al., 2004; Reubens et al., 2007, Uasuf et al., 2009, Greulich et al. 2019), the
407 explicit consideration of the area basal and density as complementary estimates of
408 interspecies differences in performance provided new insights. First, these estimates
409 introduced important differences with the presence-absence comparisons. Second, these
410 functional estimates weakened the strong match found in all the cases between the standing
411 vegetation and seed rain, which suggests that variations in the reproductive performance
412 between species reduce the similarity. In general, the density of standing vegetation was
413 better matched with the abundance in the seed bank than the total basal area. This suggests
414 that the number of individuals per species, rather than the basal area, is a better descriptor of
415 the total number of seeds released.

416 In conclusion, the dispersal syndrome was a critical determinant of the timing of events
417 related to seed dispersal, seed banking and germination in the studied SDTF. The

418 phenological staggering of seed release by different dispersal syndromes led to different
419 window opportunities for direct germination or delayed emergence and, thus, for the presence
420 of species in the soil seed bank. Apparently, conditions for effective seed dispersal set the
421 stage in which subsequent phases of the reproductive event develop in these highly seasonal
422 environments. Earlier events can indirectly shape seed traits related to persistence in soil.
423 More studies about seed bank persistence are needed to determine the adaptive potential in
424 population terms of this separation between seed maturation, release, and emergence. In any
425 case, it seems evident that the correct interpretation of soil seed banks in SDTFs on the longer
426 demographic terms need to be evaluated considering the differences in dispersal ability of co-
427 occurring species.

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432 **AUTHOR CONTRIBUTIONS**

433 AJG, MC, MM, and CE conceived and designed research; AJG, and CE performed research;
434 AJG, MC, MM, CE, and AE analyzed data; AJG, MC, MM, CE, and AE wrote the paper.

435 **SUPPORTING INFORMATION**

436 Please see Appendix S1 for data from woody species present in the standing vegetation, seed
437 rain and soil seed bank, and Appendix S2 for a summary of the association analysis of species
438 in the compositional groups of seed rain.

439

440 **REFERENCES**

- 441 Álvarez-Buylla, E.R. & Martínez-Ramos, M. (1990). Seed bank vs seed rain in the
442 regeneration of a tropical pioneer tree. *Oecologia*, 84, 314-325.
- 443 Antunes, N.B., Ribeiro, J.F. & Salomão, A.N. (1998). Caracterização de frutos e sementes
444 de seis espécies vegetais em matas de galeria do distrito federal. *Revista Brasileira de*
445 *Sementes*, 20, 112–119.
- 446 Bakker, J.P., Poschod, P., Strykstra, R.J., Bekker, R. & Thompson, K. (1996). Seed banks
447 and seed dispersal: important topics in restoration ecology. *Acta Botanica*
448 *Neerlandica*, 45, 461–490.
- 449 Banda, K., Delgado-Salinas, A., Dexter, K.G., Linares-Palomino, R., Oliveira-Filho, A.,
450 Prado, D., et al. (2016). Plant diversity patterns in neotropical dry forests and their
451 conservation implications. *Science*, 353, 1383–1387.
- 452 Barbosa, D.C.A. (2003). Estratégias de germinação e crescimento de espécies lenhosas da
453 caatinga com germinação rápida. In: I.R. Leal, M. Tabarelli, J.M.C. Silva (Eds).
454 *Ecologia e conservação da caatinga* (pp. 625–656). Editora Universitaria da UFPE,
455 Recife.
- 456 Baskin, C.C., & Baskin, J.M. (1998). *Seeds: Ecology, biogeography and evolution of*
457 *dormancy and germination*. Academic Press, San Diego, California.
- 458 Beatty, S.W. (1991). Colonization dynamics in a mosaic landscape: the buried seed pool.
459 *Journal of Biogeography*, 18, 553–563.
- 460 Bigwood, D.W. & Inouye, D.W. (1988). Spatial pattern analysis of seed banks: an improved
461 method and optimized sampling. *Ecology*, 69, 497–507.
- 462 Birdlife International. (2013). *Important Bird Areas factsheet: Reserva Ecológica Arenillas*.
463 Downloaded from <http://www.birdlife.org> on 12/03/2013.

- 464 Bolmgren, K., & Cowan, P.D. (2008). Time-size tradeoffs: a phylogenetic comparative study
465 of flowering time, plant height and seed mass in a north-temperate flora. *Oikos*, 117,
466 424–429.
- 467 Bolmgren, K. & Eriksson, O. (2015). Are mismatches the norm? Timing of flowering,
468 fruiting, dispersal and germination and their fitness effects in *Frangula alnus*
469 (Rhamnaceae). *Oikos*, 124, 639–648.
- 470 Brown, W.L. & Wilson, E.O. (1956). Character displacement. *Systematic Zoology*, 5, 49–64.
- 471 Bullock, S.H. (1995). Plant reproduction in Neotropical dry forests. In S. Bullock, H.
472 Mooney, E. Medina (Eds.), *Seasonally dry tropical forests* (pp. 277–297). Cambridge
473 University Press, Cambridge, UK.
- 474 Caballero, I., Olano, J.M., Luzuriaga, A.L. & Escudero, A. (2005). Spatial coherence between
475 seasonal seed banks in a semi-arid gypsum community: density changes but structure
476 does not. *Seed Science Research*, 15, 153–160.
- 477 Caballero, I., Olano, J.M., Loidi, J. & Escudero, A. (2008). A model for small-scale seed bank
478 and standing vegetation connection along time. *Oikos*, 117, 1788–1795.
- 479 Carvalho, F.S. & Sartori, A.L.B. (2015). Reproductive phenology and seed dispersal
480 syndromes of woody species in the Brazilian Chaco. *Journal of Vegetation Science*,
481 26, 302–311.
- 482 Chandrashekara, U.M., & Ramakrishnan, P.S. (1993). Germinable soil seed bank dynamics
483 during the gap phase of a humid tropical forest in the Western Ghats of Kerala, India.
484 *Journal of Tropical Ecology*, 9, 455–467.
- 485 Cortés-Flores, J., Cornejo-Tenorio, G., Urrea-Galeano, L., Andresen, E., González-
486 Rodríguez, A., & Ibarra-Manríquez, G. (2019). Phylogeny, fruit traits, and ecological
487 correlates of fruiting phenology in a Neotropical dry forest. *Oecologia*, 189, 159–169.

- 488 De Caceres, M., & Legendre, P. (2009). Associations between species and groups of sites:
489 indices and statistical inference. *Ecology*, 90, 3566–3574.
- 490 Douh, C., Daïnou, K., Loumento, J.J., Moutsambote, J.M., Fayolle, A., Tosso, F., Forni, E.,
491 Gourlet-Fleury, S., & Doucet, J.L. (2018). Soil seed bank characteristics in two central
492 African forest types and implications for forest restoration. *Forest Ecology and*
493 *Management*, 409, 766–776.
- 494 Du, Y., Mi, X., Liu, X., Chen, L., Ma, K. (2009). Seed dispersal phenology and dispersal
495 syndromes in a subtropical broad-leaved forest of China. *Forest Ecology and*
496 *Management*, 258, 1147–1152.
- 497 Dungan, R.J., Norton, D.A., & Duncan, R.P. (2001). Seed rain in successional vegetation,
498 Port Hills Ecological District, New Zealand. *New Zealand Journal of Botany*, 39, 115–
499 124.
- 500 Escobar, D.F.E., Silveira, F.A.O., & Morellato, L.P.C. (2018). Timing of seed dispersal and
501 seed dormancy in Brazilian savanna: two solutions to face seasonality. *Annals of*
502 *Botany*, 121, 1197–1209.
- 503 Escudero, A., Somolinos, R., Olano, J.M., & Rubio, A. (1999). Factors controlling the
504 establishment of *Helianthemum squamatum* an endemic gypsophile of semi-arid
505 Spain. *Journal of Ecology*, 87, 290–302.
- 506 Escudero, A., Albert, M.J., Pita, J.M., & Pérez-García, F. (2000). Inhibitory effects of
507 *Artemisia herba-alba* on the germination of the gypsophyte *Helianthemum*
508 *squamatum*. *Plant Ecology*, 148, 71–80.
- 509 Espinosa, C.I., De La Cruz, M., Luzuriaga, A.L., & Escudero, A. (2012). Bosques tropicales
510 secos de la región Pacífico Ecuatorial: diversidad, estructura, funcionamiento e
511 implicaciones para la conservación. *Ecosistemas*, 21, 167–179.

- 512 Espinosa, C.I., Luzuriaga, A.L., De La Cruz, M., Montero, M., Escudero, A. (2013). Co-
513 occurring grazing and climate stressors have different effects on the total seed bank
514 when compared to the persistent seed bank. *Journal of Vegetation Science*, 24, 1098–
515 1107.
- 516 Evans, M.K., Régis, F., Kane, M.J. & Venable, D.L. (2007). Bet Hedging via Seed Banking
517 in Desert Evening Primroses (*Oenothera*, Onagraceae): Demographic Evidence from
518 Natural Populations. *The American Naturalist*, 169, 184–194.
- 519 Fornara, D.A. & Dalling, J.W. (2005). Seed bank dynamics in five Panamanian forests.
520 *Journal of Tropical Ecology*, 21, 223–226.
- 521 Frankie, G.W., Baker, H.G., & Opler, P.A. (1974). Comparative phenological studies of trees
522 in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, 62,
523 881–919.
- 524 Garwood, N. (1983). Seed germination in a seasonal tropical forest in Panama: a community
525 study. *Ecological Monographs*, 53, 159–181.
- 526 Garwood, N.C. (1989). Tropical soil seed banks: a review. In: M.A. Lek, V.T. Parker, R.L.
527 Simpson (Eds). *Ecology of soil seed banks* (pp. 149–209). Academic Press, San Diego,
528 CA.
- 529 Gomes, F.M., Oliveira, C.C., Rocha Miranda, R., Costa, R.C., & Loiola, M.I.B. (2019).
530 Relationships between soil seed bank composition and standing vegetation along
531 chronosequences in a tropical dry forest in north-eastern Brazil. *Journal of Tropical*
532 *Ecology*, 35, 173–184.
- 533 Gottsberger, G., & Silberbauer-Gottsberger, I. (1983). Dispersal and distribution in the
534 cerrado vegetation of Brazil. *Sonderbände des Naturwissenschaftlichen Vereins in*
535 *Hamburg*, 7, 315–352.

- 536 Grant, P.R. (1972). Convergent and divergent character displacement. *Biological Journal of*
537 *the Linnean Society*, 4, 39–68.
- 538 Greulich, S., Chevalier, R., & Villar, M. (2019). Soil seed banks in the floodplain of a large
539 river: a test of hypotheses on seed bank composition in relation to flooding and
540 established vegetation. *Journal of Vegetation Science*, 30, 732–745.
- 541 Griz, L.M.S., & Machado, I.C.S. (2001). Fruiting phenology and seed dispersal syndromes in
542 caatinga, a tropical dry forest in the northeast of Brazil. *Journal of Tropical Ecology*,
543 17, 303–321.
- 544 Grombone-Guaratini, M.T., De Freitas Leitão Filho, H., & Kageyama, P. (2004). The seed
545 bank of a gallery forest in southeastern Brazil. *Brazilian Archives of Biology and*
546 *Technology*, 47, 793–797.
- 547 Hall, J.B., & Swaine, M.D. (1980). Seed stocks in Ghanaian forest soils. *Biotropica*, 12, 256–
548 263.
- 549 Hardesty, B., & Parker, V. (2002). Community seed rain patterns and a comparison to adult
550 community structure in a West African tropical forest. *Plant Ecology*, 164, 49–64.
- 551 Heydel, F., & Tackenberg, O. (2017). How are the phenologies of ripening and seed release
552 affected by species' ecology and evolution? *Oikos*, 126, 738–747.
- 553 Holzapfel, C., Schmidt, W., & Shmida, A. (1993). The role of seed bank and seed rain in the
554 recolonization of disturbed sites along an aridity gradient. *Phytocoenologia*, 23: 561–
555 580.
- 556 Hopfensperger, K.N. (2007). A review of similarity between seed bank and standing
557 vegetation across ecosystems. *Oikos*, 116, 1438–1448.
- 558 Howe, H.F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology*
559 *and Systematics*, 13, 201–228.

- 560 Janzen D. H. (1967). Synchronization of sexual reproduction of trees within dry season in
561 Central America. *Evolution*, 21, 620–637.
- 562 Jara-Guerrero, A., De La Cruz, M., & Méndez, M. (2011). Seed dispersal spectrum of woody
563 species in South Ecuadorian dry forests: environmental correlates and the effect of
564 considering species abundance. *Biotropica*, 43, 722-730.
- 565 Jara-Guerrero, A., De La Cruz, M., Espinosa, C.I., Méndez, M. & Escudero, A. (2015). Does
566 spatial heterogeneity blur the signature of dispersal syndromes on spatial patterns of
567 woody species? A test in a tropical dry forest. *Oikos*, 124, 1360–1366.
- 568 Klinkhamer, P.G.L., De Jong, T. J., Metz, J.A.J., & Val, J. (1987). Life history tactics of
569 annual organisms: the joint effects of dispersal and delayed germination. *Theoretical*
570 *Population Biology*, 32, 127–156.
- 571 Laskurain, N.A., Escudero, A., Olano, J.M., & Loidi, J. (2004). Seedling dynamics of shrubs
572 in a fully closed temperate forest: greater than expected. *Ecography*, 27, 650–658.
- 573 Legendre, P., & Legendre, L. (1998). *Numerical ecology* (2nd ed.). Elsevier.
- 574 Legendre, P. (2011). const.clust: space- and time-constrained clustering package. Available at
575 <http://adn.biol.umontreal.ca/~numerica/ecology/Rcode/>
- 576 Martins, A.M., & Engel, V.L. (2007). Soil seed banks in tropical forest fragments with
577 different disturbance histories in southeastern Brazil. *Ecological engineering*, 31, 165–
578 174.
- 579 Moles, A.T., & Drake, D.R. (1999). Potential contributions of the seed rain and seed bank to
580 regeneration of native forest under plantation pine in New Zealand. *New Zealand*
581 *Journal of Botany*, 37, 83–93.
- 582 Nathan, R., & Muller-Landau, H. (2000). Spatial patterns of seed dispersal, their determinants
583 and consequences for recruitment. *Trends in Ecology and Evolution*, 15, 278–285.

- 584 Oksanen, J., F. Guillaume Blanchet, Kindt, R., Legendre, P., Minchin, P., O'hara, R. B.,
585 Simpson, G., Solymos, P., Stevens, M., & Wagner, H. (2012). Package "vegan".
586 Community Ecology Package. URL <http://vegan.r-forge.r-project.org/>
- 587 Pärtel, M. (2014). Community ecology of absent species: hidden and dark diversity. *Journal*
588 *of Vegetation Science*, 25, 1154–1159.
- 589 Pfennig, K.S., & Pfennig, D.W. (2009). Character displacement: ecological and reproductive
590 responses to a common evolutionary problem. *Quarterly Review of Biology*, 84, 253–
591 276.
- 592 Primack, R.B. (1985). Relationships among flowers, fruits and seeds. *Annual Review of*
593 *Ecology, Evolution, and Systematics*, 18, 409–430.
- 594 R Core Team. (2016). *R: A language and environment for statistical computing*. R
595 Foundation for Statistical Computing, Vienna, Austria.
- 596 Rees, M. (1997). Seed dormancy. In: Crawley, M.J. (Ed.). *Plant Ecology* (pp. 214–238).
597 Blackwell Science.
- 598 Reubens, B., Heyn, M., Gebrehiwot, K., Hermy, M., & Muys, B. (2007). Persistent soil seed
599 banks for natural rehabilitation of dry tropical forests in northern Ethiopia.
600 *Tropicultura*, 25, 204–214.
- 601 Rico-Gray, V., & García-Franco, J.G. (1992). Vegetation and soil seed bank of successional
602 stages in tropical lowland deciduous forest. *Journal of Vegetation Science*, 3, 617–
603 624.
- 604 Rodrigues Da Luz, G., & Ferreira-Nunes, Y. R. (2014). Seed germination of arboreal-shrub
605 species with different dispersal mechanisms in a Brazilian tropical dry forest. In: A.
606 Sánchez-Azofeifa, J. S. Powers, G. W. Fernandes, & M. Quesada (Eds.). *Tropical dry*

- 607 *forests in the Americas: ecology, conservation, and management* (pp. 281–299). CRC
608 Press, Boca Ratón, FL.
- 609 Romero-Saritama, J.M. (2016). Caracterización morfofisiológica de semillas de especies
610 leñosas distribuidas en dos zonas secas presentes en el Sur del Ecuador. *Ecosistemas*,
611 25, 93–100.
- 612 Savadogo, P., Sanou, L., Dayamba, D., Bognounou, F., & Thiombiano, A. (2017).
613 Relationships between soil seed banks and above-ground vegetation along a
614 disturbance gradient in the W National Park trans-boundary biosphere reserve, West
615 Africa. *Journal of Plant Ecology*, 10, 349–363.
- 616 Schupp, E., & Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of
617 plant population ecology. *Écoscience*, 2, 267–275.
- 618 Sierra, R. (Ed.). (1999). *Propuesta preliminar de un sistema de clasificación de vegetación*
619 *para el Ecuador Continental*. Proyecto INEFAN/GEF-BIRF y EcoCiencia. Quito,
620 Ecuador.
- 621 Silva, E.P., Figueiredo, F.G., Séfara, S., & Fernandes, L. (2016). Evaluation of the potential
622 of seed rain as an alternative for forest restoration in Permanent Preservation Areas.
623 *Revista Árvore*, 40, 21–28.
- 624 Snow, D.W. (1965). A possible selective factor in the evolution of fruiting seasons in tropical
625 forest. *Oikos*, 15, 274–281.
- 626 Ssali, F., Stein, R.M., & Sheil, D. (2018). Tree seed rain and seed removal, but not the seed
627 bank, impede forest recovery in bracken (*Pteridium aquilinum* (L.) Kuhn)-dominated
628 clearings in the African highlands. *Ecology and Evolution*, 8, 4224–4236.
- 629 Stevenson, P., & Vargas, I. (2008). Sample size and appropriate design of fruit and seed traps
630 in tropical forests. *Journal of Tropical Ecology*, 24, 95–105.

- 631 Swaine, M.D., & Hall, J.B. (1983). Early succession of cleared forest land in Ghana. *Journal*
632 *of Ecology*, 71, 601–627.
- 633 Teketay, D. (2005). Seed and regeneration ecology in dry Afromontane forests of Ethiopia: I.
634 Seed production - population structures. *Tropical Ecology*, 46, 29–44.
- 635 Thompson, K. (2000). The functional ecology of soil seed banks. In: M. Fenner (Ed.). *Seeds:*
636 *the ecology of regeneration in plant communities* (2nd ed., pp. 215–235). CAB
637 International. UK.
- 638 Uasuf, A., Tigabu, M. & Odén, P.C. (2009). Soil seed banks and regeneration of Neotropical
639 dry deciduous and gallery forests in Nicaragua. *Bois et Forêts des Tropiques*, 299, 49–
640 62.
- 641 Uhl, C., Clark, K., Clark, H., & Murphy, P. (1981). Early plant succession after cutting and
642 burning in the upper Rio Negro region in the Amazon Basin. *Journal of Ecology*, 69,
643 631–649.
- 644 Valenta, K., Steffens, T. S., Rafaliarison, R.R., Chapman, C.A., & Lehman, S.M. (2015).
645 Seed banks in savanna, forest fragments, and continuous forest edges differ in a
646 tropical dry forest in Madagascar. *Biotropica*, 47, 435–440.
- 647 Vandvik, V., Vandvik, V., Klanderud, K., Meineri, E., Måren, I.E., & Töpper, J. (2015). Seed
648 banks are biodiversity reservoirs, species-area relationships above versus below
649 ground. *Oikos*, 125, 218–228.
- 650 Vázquez-Yanes, C., & Orozco Segovia, A. (1984). Ecophysiology of seed germination in the
651 tropical humid forests of the world: a review. *Tasks for Vegetation Science*, 12, 37–50.
- 652 Vázquez-Yanes, C., & Orozco-Segovia, A. (1993). Patterns of seed longevity and
653 germination in the tropical rainforest. *Annual Review of Ecology and Systematics*, 24,
654 69–87.

- 655 Venable, D. L., & Brown, J.S. (1988). The selective interactions of dispersal, dormancy, and
656 seed size as adaptations for reducing risk in variable environments. *American*
657 *Naturalist*, 131, 360–384.
- 658 Vieira, D.L.M., de Lima, V.V., Sevilha, A.C., & Scariot, A. (2008). Consequences of dry-
659 season seed dispersal on seedling establishment of dry forest trees: Should we store
660 seeds until the rains? *Forest Ecology and Management*, 256, 471–481.
- 661 Ward, J. H., Jr. (1963). Hierarchical grouping to optimize an objective function. *Journal of*
662 *the American Statistical Association*, 58, 236–244.

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Supporting information to the paper

Jara-Guerrero et al. Dispersal syndrome influences the match between seed rain and soil seed bank of woody species in a Neotropical dry forest.

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Appendix S1. Woody species present in the 9-ha plot of standing vegetation, seed rain and/or soil seed bank. Number of individuals per hectare (No. Ind./ha), relative abundance as percentage of the total of individuals (RA), mean \pm standard error DBH (cm), total number of seeds, seed density seed /m² (s/m²), dispersal season (Season), growth form (GF.: T, tree; S, shrub; C, climber) and dispersal syndrome (Zo, zoochory; An, anemochory; Au, autochory). NP: not present.

Family	Species	Standing vegetation			Seed rain		Seed bank		GF	Dispersal syndrome
		No. Ind./ha	RA	DBH	No. seeds	s/m ²	No. seeds	s/m ²		
Achatocarpaceae	<i>Achatocarpus pubescens</i>	38	0.573	3.11 \pm 1.89	639	3.8	NP	NP	S	Zo
Amaranthaceae	<i>Alternanthera</i> sp.	94	1.417	1.48 \pm 0.46	2979	17.6	210	12.7	S	An
	<i>Iresine diffusa</i>	1	0.015	2.48 \pm NA	3	0.02	NP	NP	S	An
	<i>Verbesina</i> sp.	25	0.377	1.78 \pm 1.06	133	0.8	NP	NP	S	An
	<i>Viguiera</i> sp.	53	0.799	1.15 \pm 0.19	NP	NP	NP	NP	S	An
Asteraceae	Asteraceae unknown	4	0.060	1.67 \pm 0.84	10	0.1	NP	NP	S	An
Bignoniaceae	<i>Handroanthus billbergii</i>	515	7.765	28.01 \pm 12.62	NP	NP	NP	NP	T	An
	<i>Handroanthus chrysantha</i>	340	5.127	16.37 \pm 11.03	NP	NP	NP	NP	T	An
Bixaceae	<i>Cochlospermum vitifolium</i>	220	3.317	23.72 \pm 12.11	345	2.0	2	0.1	T	An

Boraginaceae	<i>Cordia lutea</i>	13	0.196	10.62 ± 5.02	NP	NP	NP	NP	T	Zo
	<i>Cordia macrocephala</i>	148	2.232	1.69 ± 0.81	50	0.3	15	0.9	S	Zo
	<i>Cordia rosei</i>	137	2.066	1.84 ± 1.05	885	5.2	NP	NP	S	Zo
Burseraceae	<i>Bursera graveolens</i>	110	1.659	21.21 ± 7.7	131	0.8	8	0.5	T	Zo
Cactaceae	<i>Armatocereus</i> sp.	391	5.896	6.42 ± 3.08	49	0.3	NP	NP	T	Zo
Capparaceae	<i>Colicodendron scabridum</i>	194	2.925	14.52 ± 7.44	NP	NP	NP	NP	T	Zo
	<i>Cynophalla mollis</i>	476	7.177	12.13 ± 5.28	NP	NP	NP	NP	T	Zo
Caricaceae	<i>Vasconcellea parviflora</i>	19	0.286	2.12 ± 1.36	NP	NP	NP	NP	S	Zo
Convolvulaceae	<i>Ipomoea carnea</i>	255	3.845	1.59 ± 0.55	19	0.1	63	3.8	S	An
	<i>Erythroxylum glaucum</i>	232	3.498	11.43 ± 5.93	2851	16.8	NP	NP	T	Zo
Euphorbiaceae	<i>Croton rivinifolius</i>	721	10.872	1.45 ± 0.45	2919	17.2	170	10.3	S	Au
	<i>Croton micans</i>	217	3.272	3.67 ± 2.12	27	0.2	10	0.6	S	Au
Fabaceae	<i>Aeschynomene scoparia</i>	43	0.648	1.4 ± 0.62	41	0.2	9	0.5	S	An
	<i>Chloroleucon mangense</i>	254	3.830	13.93 ± 5.9	259	1.5	8	0.5	T	Au
	<i>Erythrina velutina</i>	40	0.603	30.3 ± 16.14	19	0.1	3	0.2	T	Au
	<i>Geoffroea spinosa</i>	226	3.408	13.66 ± 6.78	NP	NP	NP	NP	T	Zo
	<i>Leucaena trichodes</i>	311	4.689	7.2 ± 2.32	56	0.3	52	3.1	T	Au
	<i>Mimosa acantholoba</i>	3	0.045	1.86 ± 1.15	1	0.0	NP	NP	S	Au
	<i>Piptadenia flava</i>	55	0.829	8.06 ± 2.39	NP	NP	1	0.1	T	Au

	<i>Pithecellobium excelsum</i>	21	0.317	3.43 ± 2.17	24	0.1	NP	NP	S	Zo
	<i>Caesalpinia glabrata</i>	188	2.835	15.09 ± 7.64	10	0.1	NP	NP	T	Au
	<i>Senna bicapsularis</i>	31	0.467	1.42 ± 0.47	NP	NP	NP	NP	S	Au
	<i>Senna mollissima</i>	14	0.211	8.68 ± 1.82	116	0.7	2	0.1	T	Au
Lamiaceae	<i>Hyptis</i> sp.	47	0.709	1.97 ± 0.83	852	5.0	NP	NP	S	An
Malpighiaceae	<i>Malpighia emarginata</i>	158	2.382	4.12 ± 2.17	140	0.8	NP	NP	S	Zo
Malvaceae	<i>Byttneria flexuosa</i>	442	6.665	1.58 ± 0.66	150	0.9	3	0.2	S	Au
	<i>Ceiba trichistandra</i>	4	0.060	0.99 ± 0.06	NP	NP	NP	NP	T	An
	<i>Eriotheca ruizii</i>	9	0.136	44.54 ± 21.01	165	1.0	NP	NP	T	An
	Malvaceae unknown sp1	30	0.452	1.14 ± 0.21	255	1.5	NP	NP	S	Au
	Malvaceae unknown sp2	265	3.996	20.05 ± 9.03	7	0.0	NP	NP	S	Au
	<i>Urena</i> sp.	1	0.015	$1.05 \pm \text{NA}$	420	2.5	NP	NP	S	Au
Moraceae	<i>Ficus</i> sp.	6	0.090	21.66 ± 8.54	1200	7.1	NP	NP	T	Zo
Nyctaginaceae	<i>Pisonia aculeata</i>	17	0.256	15.91 ± 6.95	NP	NP	NP	NP	T	Zo
Polygonaceae	<i>Coccoloba ruiziana</i>	42	0.633	10.26 ± 2.66	202	1.2	NP	NP	T	Zo
Primulaceae	<i>Bonellia sprucei</i>	36	0.543	11.62 ± 7.11	NP	NP	NP	NP	T	Zo
Rhamnaceae	<i>Ziziphus thyrsoiflora</i>	1	0.015	$7.51 \pm \text{NA}$	NP	NP	NP	NP	T	Zo
Rubiaceae	<i>Randia aurantiaca</i>	55	0.829	2.14 ± 1.47	118	0.7	NP	NP	S	Zo
Verbenaceae	<i>Lantana</i> sp.	130	1.960	1.28 ± 0.41	8	0.0	57	3.4	S	Zo

Supporting information to the paper

Jara-Guerrero et al. Dispersal syndrome influences the match between seed rain and soil seed bank of woody species in a Neotropical dry forest. *Journal of Vegetation Science*.

Appendix S2. Summary of the association analysis of species in the compositional groups of seed rain. P-value of association is shown for each species. The best group corresponds to the group with the lower p-value after Sidak's correction for multiple testing with 33 species.

Dispersal syndrome	Species	Best group	P-value			
			Best group	Group 1	Group 2	Group 3
Anemochory	<i>Aeschynomene scoparia</i>	1	0.006	0.002	1	1
Anemochory	<i>Alternanthera</i> sp.	3	0.140	0.79	0.77	0.049
Anemochory	Asteraceae unknown	1	0.006	0.002	1	1
Anemochory	<i>Cochlospermum vitifolium</i>	1	0.115	0.04	1	1
Anemochory	<i>Eriotheca ruizii</i>	1	0.167	0.059	0.659	1
Anemochory	<i>Hyptis</i> sp.	1	0.006	0.002	0.844	1
Anemochory	<i>Ipomoea carnea</i>	1	0.276	0.102	1	0.606
Anemochory	<i>Iresine</i> sp.	1	0.790	0.406	1	1
Anemochory	<i>Verbesina</i> sp.	1	0.542	0.229	1	0.256
Autochory	<i>Byttneria flexuosa</i>	3	0.059	1	1	0.02

Autochory	<i>Caesalpinia glabrata</i>	1	0.281	0.104	1	0.644
Autochory	<i>Chloroleucon mangense</i>	3	0.469	0.437	1	0.19
Autochory	<i>Croton micans</i>	2	0.096	1	0.033	1
Autochory	<i>Croton rivinifolius</i>	2	0.416	1	0.164	0.482
Autochory	<i>Erythrina velutina</i>	3	0.115	0.7	0.915	0.04
Autochory	<i>Leucaena trichodes</i>	3	0.377	0.478	1	0.146
Autochory	<i>Malvaceae</i> sp. 1	3	0.687	1	1	0.321
Autochory	<i>Malvaceae</i> sp. 4	2	0.573	1	0.247	0.556
Autochory	<i>Mimosa acantholoba</i>	1	0.801	0.416	1	1
Autochory	<i>Senna mollissima</i>	1	0.386	0.15	1	1
Autochory	<i>Urena</i> sp.	3	0.059	1	1	0.02
Zoochory	<i>Achatocarpus pubescens</i>	2	0.021	1	0.007	0.793
Zoochory	<i>Armatocereus</i> sp.	3	0.686	1	0.471	0.32
Zoochory	<i>Bursera graveolens</i>	3	0.501	0.969	0.308	0.207
Zoochory	<i>Coccoloba ruiziana</i>	3	0.059	1	1	0.02
Zoochory	<i>Cordia macrocephala</i>	3	0.259	1	1	0.095
Zoochory	<i>Cordia rosei</i>	2	0.554	1	0.236	0.463

Zoochory	<i>Erythroxylum glaucum</i>	2	0.660	1	0.302	0.326
Zoochory	<i>Ficus</i> sp.	3	0.686	1	1	0.32
Zoochory	<i>Lantana</i> sp.	1	0.758	0.377	0.479	0.589
Zoochory	<i>Malpighia emarginata</i>	2	0.559	1	0.239	0.578
Zoochory	<i>Pithecellobium excelsum</i>	3	0.261	1	1	0.096
Zoochory	<i>Randia aurantiaca</i>	1	0.188	0.067	1	0.569

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