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1 **Habitat diversity associated with island size and environmental filtering control the species**
2 **richness of rock-savanna plants in neotropical inselbergs**

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14

15 **Abstract**

16 Disentangling the multiple factors controlling species diversity is a major challenge in ecology. Island
17 biogeography and environmental filtering are two influential theories emphasizing respectively island
18 size and isolation, and the abiotic environment, as key drivers of species richness. However, few
19 attempts have been made to quantify their relative importance and investigate their mechanistic basis.
20 Here, we applied structural equation modelling, a powerful method allowing test of complex
21 hypotheses involving multiple and indirect effects, on an island-like system of 22 French Guianan
22 neotropical inselbergs covered with rock-savanna. We separated the effects of size (rock-savanna
23 area), isolation (density of surrounding inselbergs), environmental filtering (rainfall, altitude) and
24 dispersal filtering (forest-matrix openness) on the species richness of all plants and of various
25 ecological groups (terrestrial *versus* epiphytic, small-scale *versus* large-scale dispersal species). We
26 showed that the species richness of all plants and terrestrial species was mainly explained by the size

27 of rock-savanna vegetation patches, with increasing richness associated with higher rock-savanna area,
28 while inselberg isolation and forest-matrix openness had no measurable effect. This size effect was
29 mediated by an increase in terrestrial-habitat diversity, even after accounting for increased sampling
30 effort. The richness of epiphytic species was mainly explained by environmental filtering, with a
31 positive effect of rainfall and altitude, but also by a positive size effect mediated by enhanced woody-
32 plant species richness. Inselberg size and environmental filtering both explained the richness of small-
33 scale and large-scale dispersal species, but these ecological groups responded in opposite directions to
34 altitude and rainfall, that is positively for large-scale and negatively for small-scale dispersal species.
35 Our study revealed both habitat diversity associated with island size and environmental filtering as
36 major drivers of neotropical inselberg plant diversity and showed the importance of plant species
37 growth form and dispersal ability to explain the relative importance of each driver.

38 **Keywords:** Environmental filtering; Island biogeography; Island size; Isolation; Patchy habitats; Plant
39 diversity; Tropical inselbergs; Structural equation modelling

40

41 **Introduction**

42 Understanding the multiple determinants regulating species diversity has long been a major theme
43 in ecology, in particular within the fields of island biogeography and community ecology (MacArthur
44 and Wilson 1967, Leibold et al. 2004). Plant species richness of vegetation patches has been shown to
45 increase with patch area (Connor and McCoy 1979, Honnay et al. 1999, Van Noordwijk et al. 2015),
46 patch heterogeneity (Huston 1999, Dufour et al. 2006), habitat amount (Lindgren and Cousins 2017),
47 disturbance (Pickett 1980, Lavorel et al. 1994), mildness of the environment (Gray 1989, Fonty et al.
48 2009, Cheng et al. 2013), resource availability (Neri et al. 2017), size of regional species pools (Zobel
49 1997), and to decrease with patch isolation (Gadgil 1971, Hanski 1991, Martín-Queller et al. 2017).
50 Those drivers of species richness could potentially have interactive effects and tradeoffs can exist
51 among them (Allouche et al. 2012). Biotic interactions, internal to the plant community, may also
52 modulate these effects, either negatively for competition or positively for facilitation (Houle and

53 Phillips 1989). Disentangling the complex relationships between all these factors suffers from severe
54 technical limitations, resulting in often partial or even erroneous conclusions when multiple theories
55 are evaluated in isolation (Shmida and Wilson 1985, Laliberté et al. 2014). Among the methods that
56 allow assessment of the relative importance of various factors and disentanglement of direct and
57 indirect effects of these factors, structural equation modeling (SEM) is increasingly used as a powerful
58 statistical framework to address those issues (Grace and Pugesek 1997, Gazol et al. 2012, Laliberté et
59 al. 2014, Pepler-Lisbach et al. 2015).

60 Given their isolation within a landscape matrix and their distinctive abiotic environment supporting
61 particular vegetation communities (Porembski et al. 1996, Prance 1996), inselbergs are good
62 candidates for disentangling the various determinants of plant species richness in vegetation patches
63 (Parmentier and Hardy 2009). Inselbergs are widespread on old crystalline shields and occur
64 particularly in tropical and subtropical regions (Porembski and Barthlott 2000). Consisting of
65 Precambrian granites and gneisses, they are defined as remnants of erosion processes forming isolated
66 mountains which rise from the surrounding landscape (Bremer and Sander 2000). They can range in
67 elevation from a few to several hundred meters and their size ranges from a few square meters to
68 several square kilometers (Bremer and Sander 2000). They are characterized by harsh conditions
69 including a high degree of insolation combined with high evaporation rates and locally very restricted
70 soil occurrence, which in turn leads to rapid loss of rainwater by runoff (Porembski 2007, Szarzynski
71 2000). Due to these specific edaphic and microclimatic conditions, inselberg vegetation is clearly
72 distinct from that of their surroundings, forming an island-like ecosystem (Itescu 2018). In particular
73 trees, which form the bulk of the vegetation of the surrounding forest matrix, are replaced by low-
74 stature woody species highly tolerant of shallow soils, and shade-tolerant plant species are replaced by
75 light-demanding species (Porembski et al. 1997).

76 In French Guiana, inselbergs embedded in the rain forest are covered with discontinuous vegetation
77 forming a type of mosaic locally called rock-savanna. This vegetation is characterized by numerous
78 scattered herbaceous and shrubby patches separated by bare rock (de Granville 1978, Sarthou 1992,
79 Sarthou and Villiers 1998, Sarthou et al. 2003). Rock-savanna vegetation is kept in a dynamic state by

80 erosion and fire events (Kounda-Kiki et al. 2008, Sarthou et al. 2009). It undergoes extreme local
81 climate variation during day-night cycles: high and frequent variations in temperature (18–55°C) and
82 relative humidity (20–100%; Sarthou 1992). Soils are generally shallow and acid, with low water-
83 holding capacity (Sarthou and Grimaldi 1992). At the scale of the whole French Guianan territory, the
84 distribution of inselberg plant species and their traits is mostly driven by a spatially-structured gradient
85 embracing regional climate, forest matrix and inselberg features and the variation observed at coarse
86 scale is explained by biogeographic, environmental and past historical factors, such as savannization
87 (Sarthou et al. 2017). Despite numerous attempts to explain the floristic composition of neotropical
88 inselbergs by adaptive traits of rock-savanna plant species (Shure and Ragsdale 1977, de Granville
89 1982, Houle and Phillips 1989, Ibisch et al. 1995, Meirelles et al. 1999, Sarthou et al. 2003,
90 Parmentier and Hardy 2009, Sarthou et al. 2017), much still needs to be known about the determinants
91 of plant-species diversity in these ecosystems (Porembski et al. 2000b).

92 In this study, we aimed at investigating the multiple drivers of plant species diversity in French
93 Guianan inselberg rock-savanna ecosystems. The factors considered here include rock-savanna
94 vegetation area, isolation from surrounding inselbergs, the number of habitats this vegetation type
95 featured, rainfall, altitude, as well as openness of the surrounding forest matrix. We used a network of
96 22 inselbergs located throughout French Guiana and featuring contrasting environmental conditions
97 and inherent characteristics (Fig. 1, Table 1). We applied structural equation modeling as a tool to test
98 simultaneously multiple hypotheses about the drivers of plant species diversity as well as to
99 disentangle the direct and indirect mechanisms involved (Grace and Pugsek 1997). Based on *a priori*
100 knowledge of the studied ecosystem and ecological theories, four distinct hypotheses were tested (Fig.
101 2). The first hypothesis is related to island size (area of rock-savanna vegetation on inselbergs), the
102 second to island isolation (density of the surrounding inselbergs), the third to environmental filtering
103 (rainfall and altitude) and the fourth to dispersal filtering (openness of the surrounding forest matrix).
104 H₁: Inselbergs of larger rock-savanna vegetation area harbour higher plant diversity, either directly
105 (H_{1a}) by allowing the establishment of more individuals (Connor and McCoy 1979) and by reducing
106 stochastic extinction rate (Lindgren and Cousins 2017), and/or indirectly (H_{1b}) by promoting higher

107 habitat diversity and heterogeneity (Dufour et al. 2006). This observation may also be trivially related
108 to higher sampling effort (H_{1c}). H_2 : Higher density of surrounding inselbergs promotes higher plant
109 diversity of a given inselberg by enhancing immigration rate due to larger number of colonisation
110 sources (Moritz et al. 2013). H_{3a} : Higher rainfall increases the diversity of epiphytes by enhancing
111 moisture (Cardelús et al. 2006) and that of large-scale dispersal (zoochorous) species by promoting
112 higher abundance of dispersing animals (Correa et al. 2015), but it reduces the diversity of small-scale
113 dispersal (autochorous) species by increasing water flow intensity on inselberg slopes (Isichei et al.
114 1990). H_{3b} : Larger altitude at the top of inselberg increases the diversity of epiphytes by promoting
115 long fog periods, and of large-scale dispersal (anemochorous) species by enhancing downslope winds,
116 but it reduces the diversity of small-scale dispersal (autochorous) species due to steeper inselberg
117 slopes (Obregon et al. 2011). H_4 : Higher openness of the surrounding forest matrix increases the
118 diversity of inselberg plant species by increasing permeability to immigration from the surroundings
119 (Martín-Queller et al. 2017).

120

121 **Material and methods**

122 **Study sites**

123 We studied 22 inselbergs (of which 15 are grouped in 4 archipelagos) scattered over the territory of
124 French Guiana (Table 1, Fig. 1). As part of the Guiana Shield in northern Amazonia, French Guiana
125 ($4^{\circ}13'N$, $52^{\circ}59'W$) covers about 85,000 km² and has a mean altitude of about 140 m above sea level
126 with few mountainous peaks exceeding 800 m. Its basement, approximately 2.2–1.9 Gyr in age,
127 corresponds to the oldest and most homogeneous part of the Guiana Shield (Delor et al. 2003). Its
128 climate is equatorial and is characterized by 3000 mm mean annual rainfall, distributed along a
129 Northeast to Southwest gradient decreasing from about 4000 to 2000 mm (Sarhou et al. 2017).
130 Rainfall is concentrated mainly between December and July (Héritier 2011). Granitic inselbergs are
131 mostly concentrated in southern and eastern parts of the territory (Fig. 1). In the extreme south, groups
132 of elevated dome-shaped inselbergs border the Brazilian Amazon basin. The peneplain in the southern

133 half of French Guiana is characterised by low elevation and slightly slanting rocky slabs in a semi-
134 open forest matrix. The northern half of French Guiana is covered with a dense rain forest with
135 isolated dome-shaped inselbergs (Gond et al. 2011).

136 **Vegetation data**

137 We first carried out vegetation surveys in 20 inselbergs from 1988 to 2011. A comprehensive
138 inventory of the vascular flora was undertaken on each inselberg. However, we excluded from the
139 analysis species growing in the ecotone zone between rock-savanna and the surrounding forested
140 matrix, and species growing in summit forests (when present). Consequently, the analysis was
141 restricted to the “rock savanna” facies *sensu stricto* characterized by vegetation patches on bare rock.
142 Each inselberg was sampled only once due to financial constraints. Given the difficult conditions for
143 field work, the sites were only reached by helicopter. Nouragues was sampled in 1988, Dachine and
144 Mont Chauve in 1997, Trinité A in 1998, Mitaraka in 2001, Bakra, Arawa and Saint Marcel in 2002,
145 Wanapi and Marouini in 2004. Our goal was to carry the most exhaustive inventories possible during
146 our presence on the field, with a unique methodology. The period from March to July was chosen
147 because previous work showed it harboured a maximum of flowering plants (Sarhou 1992). Sampling
148 effort was adapted to area and environmental heterogeneity of each site, and was included in the form
149 of the number of person-days devoted to sampling.

150 The data set was completed for Trinité B (1981) and Virginie (1991) through an extraction from the
151 Cayenne Herbarium data base available at <http://publish.plantnet-project.org/project/caypub>. The
152 sampling effort devoted to Trinité B and Virginie by the collectors allowed us to consider these
153 additional records as comprehensive and fully reliable.

154 The final data set comprised 391 species, including 73 epiphytes and 318 terrestrial plant species.
155 Voucher specimens were deposited in the Cayenne Herbarium (CAY) and were registered in the
156 Cayenne Herbarium database. Plant identification was performed according to Funk et al. (2007).

157 We studied plant diversity as the species richness for the whole community but also of specific
158 ecological groups, such as terrestrial (growing directly on bare rock or on shallow soils), epiphytic

159 (growing on shrubs), small-scale dispersal (autochorous and barochorous), and large-scale dispersal
160 (wind- and animal-dispersed) plant species.

161 **Ecological drivers**

162 The area of rock-savanna vegetation was measured directly in the field or calculated from aerial
163 photographs for the smallest inselbergs ($< 0.1 \text{ km}^2$). The number of terrestrial habitats available on
164 each inselberg was based on the list published by Porembski et al. (2000a) after refinement from field
165 observations (Sarhou et al. 2017). For epiphyte species, the number of habitats on each inselberg was
166 estimated by measuring the number of woody species. The number of person-days spent was used as a
167 measure of sampling effort.

168 Mean annual rainfall values were interpolated for each site from the isoline map published by
169 Héritier (2011). Maximum summital altitude of inselbergs (here called 'altitude') was measured
170 during field survey using a GPS device with an integrated high-resolution barometer. Inselberg density
171 was estimated by the percent surface occupied by inselbergs within a 15 km radius, using the GIS
172 program Mapinfo® version 9.0.

173 Canopy openness of the forest matrix surrounding each inselberg was calculated from remote-
174 sensing data (Gond et al. 2011). We pooled categories RSLC 20, 21 and 22 of open and semi-open
175 canopy forests, and measured their cover percentage within a 15 km radius.

176 **Statistical analyses**

177 We conducted all analyses separately for the richness of all plants, terrestrial and epiphytic as well
178 as small and large-scale dispersal plant species. Bivariate relationships between plant diversity and
179 ecological drivers were assessed using Spearman's correlation coefficients (Table S1) as well as
180 simple regression linear models with either linear, quadratic or power relationships (Table S2). Power
181 regressions were modelled using log-log transformation. The selection of the set of terms yielding the
182 best model goodness-of-fit was conducted by comparing models based on adjusted r^2 .

183 We performed structural equation modelling (SEM) to investigate which ecological drivers
184 influence species richness of inselberg rock-savanna vegetation. We used eight parameters as potential
185 direct or indirect drivers of plant diversity (Table 1): rock-savanna vegetation area, habitat diversity,
186 sampling effort, inselberg density, mean annual rainfall, maximum altitude, distance to the Atlantic
187 coast and openness of the surrounding forest matrix. A causal diagram was first built based on
188 ecological theories and our *a priori* knowledge of the system (Fig. 2). We used the number of
189 terrestrial habitats as a measure of habitat diversity for all ecological groups except epiphytic species,
190 for which the number of woody species was used as a measure of habitat diversity instead.

191 We adopted a local-estimation approach based on piecewise fitting of component linear models.
192 Normal distribution and homogeneity of variances of the residuals of each component model of the
193 global path model were checked graphically. We adopted a model-selection approach using
194 information-theoretic methods. First, we selected the best set of plant diversity predictors by
195 comparing multiple regression models comprising all possible combinations of predictors using the
196 Akaike Information Criteria corrected for small sample size (AICc). This allowed us to establish a
197 confidence set of models with $\Delta\text{AICc} < 2$ from all possible combination of the 7 factors (Burnham and
198 Anderson 2002). To avoid multicollinearity, models with variance inflation factors (VIF) > 10 were
199 excluded from the confidence models set (Dormann et al. 2013). Then, we removed all the paths
200 toward plant richness representing factors not included in the best multiple regression model selected
201 during the initial step (Table S3). All variables no longer related to plant diversity and their paths were
202 also removed as well as non-significant paths. At each removal step, SEM model goodness-of-fit was
203 assessed by Shipley's d-sep test (Shipley 2009) and the AICc computed following Shipley (2013). We
204 applied this selection procedure until we found the most parsimonious SEM model.

205 All statistical analyses were performed using R software version 3.1.2 with the packages
206 *MuMIn* and *piecewiseSEM*. All statistical tests were realized with $\alpha = 5\%$.

207

208 **Results**

209 **Total plant species richness**

210 In accordance with hypothesis H₁, the best fit SEM model showed that the species richness of all
211 plants was exclusively explained by the size of inselberg rock-savanna vegetation patches (Fig. 3a),
212 which explained 79.9 % of variation (Fig. 4). Total plant species richness increased linearly with rock-
213 savanna vegetation area (Fig. 3b). Direct size effect (H_{1a}) was not supported by the model. This size
214 effect was indirect and mediated by habitat diversity and heterogeneity (H_{1b}). The number of terrestrial
215 habitats increased with rock-savanna vegetation area following a power function (Fig. 3c, Table S2).
216 In turn, total plant species richness was positively associated with the number of terrestrial habitats
217 following a power function (Fig. 3d, Table S2), even after accounting for the linear increase in
218 sampling effort (H_{1a}, Fig. 3a, Fig. S1a). In contrast with hypothesis H₂, total plant species richness was
219 not related to inselberg density (Fig. 3e).

220 **Terrestrial *versus* epiphytic species richness**

221 Terrestrial species richness followed the general trend depicted by total plant species richness, with
222 78.6 % of variation explained by rock-savanna vegetation area (Figs. 4, 5a). Terrestrial plant species
223 richness increased with rock-savanna vegetation area following a power function (Fig. S2a). The
224 positive effect of inselberg size was mediated mostly by the increase in habitat diversity (H_{1b}, number
225 of terrestrial habitats), which was positively associated with terrestrial plant species richness following
226 a power function (Fig S2b).

227 Epiphytic species richness was explained by both inselberg size and environmental factors (Fig.
228 5b), to which environmental filtering contributed most (65.0 %, Fig. 4). In accordance with hypothesis
229 H₃, rainfall (H_{3a}) and altitude (H_{3b}) had a direct positive relationship with epiphytic species richness.
230 As expected, rainfall was negatively influenced by distance to the Atlantic coast following a power
231 function (Fig. S1b). Rainfall and altitude also had an indirect positive effect on epiphytic species
232 richness through their positive relationship with woody plant species richness, which had a direct
233 positive effect on epiphyte plant species richness (Fig. S3a). We also observed a positive relationship
234 between the proportion of woody and epiphytic species within the community (Fig. S3b). Epiphytic

235 plant species richness increased linearly with rock-savanna vegetation area (Fig. S2c). The positive
236 effect of island size was both related to a direct stochastic size effect (H_{1a}), but also to an indirect
237 effect through the increase of woody plant species richness with rock-savanna vegetation area (H_{1b} ,
238 Fig. 5b). The effect of forest matrix openness (H_4) was not supported by the model.

239 **Large-scale *versus* small-scale dispersal species richness**

240 The richness of large-scale and small-scale dispersal species was explained by both size and
241 environmental filtering (Figs. 4, 6). The species richness of both classes of dispersal ability was
242 affected by the size of rock-savanna vegetation area, with a positive indirect effect mediated by the
243 number of habitats (H_{1b}) and by sampling effort (H_{1c}), similarly to total plant species richness (Fig.
244 3a). Altitude and rainfall contributed to a significant extent to the total variation in species richness,
245 but in opposite direction whether dispersal occurred over large or small distances. Altitude and rainfall
246 had negative effects on the richness of small-scale dispersal species (Fig. 6a), while they had positive
247 effects on the richness of large-scale dispersal species (Fig. 6b), in accordance with hypothesis H_3 .

248 In order to better explain the above-mentioned discrepancy between the classes of species
249 dispersal ability, we analysed the correlation between altitude and rainfall with the contribution of
250 each of the four dispersal syndromes to the total plant species richness (Fig. S4). We focused on
251 terrestrial species only, because they are dominant (90% of total plant species richness per inselberg
252 on average) and better studied in the literature. The proportion of autochorous (small-scale dispersal)
253 species within the community decreased when altitude increased (Fig. S4a), while that of
254 anemochorous (large-scale dispersal) species increased (Fig. S4b). The proportion of species of the
255 two other large-scale dispersal types (zoochorous and hydrochorous) remained unchanged (Figs.
256 S4c,d). Similarly, the proportion of autochorous species decreased when annual rainfall increased (Fig.
257 S4e), while the proportion zoochorous species increased (Fig. S4g). The proportion of species of the
258 two other large-scale dispersal types (anemochorous and hydrochorous) remained unchanged (Figs.
259 S4f,g).

260

261 Discussion

262 The primary aim of our study was to investigate the drivers shaping plant diversity in island-like
263 neotropical inselberg ecosystems by testing multiple hypothesis related to island size (H_1) and
264 isolation (H_2) as well as environmental and dispersal filtering (H_3 and H_4 , Fig. 2).

265 In accordance with hypothesis H_1 , we found here that total plant species richness was positively
266 related to the area of rock-savanna vegetation on inselbergs (Figs. 3a,b), even after controlling for
267 sampling effort (H_{1c}). This positive size effect was observed whether plants considered are terrestrial
268 or epiphytic (Fig. 5) and able to disperse over small or large-scale (Fig. 6), showing that island size
269 was a major determinant of plant diversity (Fig. 4). This result is in agreement with ecological theories
270 (MacArthur and Wilson 1967, Hanski 1989, Leibold et al. 2004) and is largely shared by many studies
271 on isolated patches of vegetation (Price 2004, Pepler-Lisbach et al. 2015), especially on inselbergs
272 (Porembski et al. 1996, Meirelles et al. 1999, Porembski et al. 2000b). Further, we showed that this
273 positive size effect on species richness was not explained by a direct stochastic size effect (H_{1a})
274 (Connor and McCoy 1979), except for epiphytic species. For terrestrial species, the positive size effect
275 was rather mediated by the increase in the diversity of terrestrial habitats present on a given inselberg
276 (H_{1b} , Figs. 3c, d), in line with various studies on vegetation patches (Auerbach and Shmida 1987,
277 Honnay et al. 1999, Dufour et al. 2006). The effect of habitat diversity was here related to floristic
278 differences between habitats typical of rock-savanna vegetation, such as continuous rock surfaces,
279 temporary ponds, crevices with their variants according to the presence of soil, rock or woody debris
280 (Sarhou and Villiers 1998, Gröger and Huber 2007, Parmentier and Hardy 2009). For epiphytic
281 species, the indirect size effect was mediated by the diversity of shrubs and lianas (Fig. 5b). Epiphytes
282 need the bark of woody species as supports (Benzing 1981), and the degree of epiphytism is in direct
283 proportion to the contribution of woody flora.

284 In contrast to hypothesis H_2 , we found that the density of surrounding inselbergs did not affect the
285 species richness of rock-savanna plants covering a given inselberg (Fig. 3e), suggesting that inselberg
286 plant species richness was not affected by the geographic isolation of inselbergs from others.

287 Similarly, the cover of open-canopy forest matrix was never selected as a predictor of inselberg plant
288 species richness, in contrast to the hypothesis H₄ that higher openness of the surrounding forest matrix
289 would increase plant diversity by increasing permeability to immigration from the surroundings. This
290 might indicate that rescue and mass effects (Shmida and Wilson 1985, Hanski 1991, Moritz et al.
291 2013) are here negligible. It means that whatever the presence of other inselbergs and the cover of
292 open-canopy forest in the vicinity of a given inselberg (for instance within the so-called archipelagos),
293 only its size and size-related factors (habitat diversity and sampling effort), as well as environmental
294 filters (rainfall and altitude), contribute to increase or decrease the total number of plant species it
295 harbours. While several studies showed that during drier periods of the Holocene savanna-like
296 vegetation covered large areas of the Guianan Shield (Servant et al. 1993, Freycon et al. 2010, Rull
297 and Montoya 2017), present-day rock-savanna vegetation should be considered as a relict constellation
298 of isolated fragments of xeric vegetation embedded in a more or less continuous rain-forest cover (de
299 Granville 1982, Prance 1996). Even inselbergs distributed in archipelagos do not seem to exchange
300 diaspores to a significant extent (Barbará et al. 2007, Pinheiro et al. 2014). The absence of any effects
301 of inselberg density on floristic richness was valid whatever the ecological group considered
302 (terrestrial *versus* epiphytic vegetation, small-scale *versus* large-scale dispersal types), pointing to the
303 paucity of dispersal and related mass/rescue effects (Leibold et al. 2004). This result supports at
304 community-level the results obtained at species level, showing poor gene flow among inselbergs
305 (Sarhou et al. 2001, Boisselier-Dubayle et al. 2010, Pinheiro et al. 2014). This was also apparent in
306 floristic composition. The flora of each inselberg located within Wanapi, Haut Marouini, Monts Bakra
307 and Trinité archipelagos was not influenced (either positively or negatively) by that of other members
308 of the same archipelago (Sarhou et al. 2017). However at local-scale, dispersal is an important driver
309 of biodiversity when in the presence of a patchwork of habitats and successional stages of the same
310 habitat (Porembski et al. 1997, Sarhou and Villiers 1998, Bruun et al. 2008). In inselbergs, where
311 disturbances occur at a high rate (lightning fires, violent storms, alternating phases of drought and
312 flooding), vegetation patches are submitted to rapid and pronounced changes, implying the
313 reconstruction of disturbed habitats through primary or secondary successional processes (Whitehouse

314 1933, Shure and Ragsdale 1977, Sarthou et al. 2009). All these successional processes require seed
315 dispersal for species establishment in safe sites (Houle and Phillips 1989, Biedinger et al. 2000).

316 In accordance with hypothesis H₃, we found that environmental filtering was also a major
317 determinant of species richness for epiphytic plants, explaining a larger portion of variance relative to
318 the effect of size (65.0 versus 25.1 % respectively, Fig. 4). The notion of environmental filtering (H₃)
319 encompasses here how the local abiotic environment can filter the species pool directly by impeding
320 species survival and persistence, and also indirectly by affecting dispersal agents and/or biotic
321 interactions (Cadotte and Tucker 2017). Epiphytic species richness was strongly affected by both
322 altitude and rainfall, itself determined by distance to the Atlantic Ocean (Fig. 5b). We observed that
323 taller inselbergs with higher rainfall harboured more epiphytic species. Epiphytes are known to fulfil
324 their moisture requirements through taking up water from mist, canopy drip and/or stem flow
325 (Veneklaas and Van Ek 1990), and thus thrive at higher elevation and in higher-rainfall areas (Wolf
326 and Flamenco-S 2003; Cardelús et al. 2006, Obregon et al. 2011). Further, we found that higher
327 elevation and rainfall similarly favoured woody-plant richness, which had a beneficial effect on
328 epiphytic species richness by increasing the diversity of their habitats (Fig. 5b). Given that rainfall and
329 altitude have been shown to influence inselberg floristic composition (Sarthou et al. 2017), it can be
330 argued that the absence of any effects of rainfall and altitude on terrestrial species richness (Fig. 5a)
331 can be due to a balance between addition and deletion of species under the influence of these factors,
332 without any resulting shift of terrestrial species richness (Ricklefs 1987). Indeed, we showed that
333 altitude and rainfall exerted contrasting effects on plant diversity depending on species dispersal
334 modes (Fig. 6). Autochorous (small-scale dispersal) species were disfavoured by higher rainfall and
335 altitude. The negative influence of rainfall on small-scale dispersal plant species richness can be
336 explained by the higher intensity of water flows on inselberg slopes under high rainfall, sweeping
337 recently fallen seeds downslope during intense storm events (Isichei et al. 1990). The negative effect
338 of altitude can be explained by the steeper slopes of dome-shaped taller inselbergs (Bremer and Sander
339 2000), with similar negative consequences on seed fate. On the contrary, large-scale dispersal plant
340 species richness was favoured by these two factors. The favourable effect of altitude can be explained

341 by its positive effect on atmospheric turbulence, which could be beneficial for anemochorous (wind-
342 dispersing) species (Horn et al. 2012). The favourable influence of a more rainy climate can be
343 explained by its positive effect on seed-dispersing animals such as bats, birds and monkeys, in turn
344 benefitting zoochorous species (Tabarelli et al. 2003, Almeida-Neto et al. 2008, Correa et al. 2015).

345 In conclusion, our study disentangled how multiple drivers related to island biogeography and
346 environmental filtering contribute directly or indirectly to the plant species richness of island-like
347 rock-savanna vegetation patches covering neotropical inselbergs. Considering all plants, the effect of
348 size was the most important factor, while isolation and environmental filtering had no detectable
349 effect. However, when plants were separated according to their growth form or dispersal ability,
350 environmental filtering also appeared as a influential factor, even largely outweighing size effect in the
351 case of epiphytic species (Fig. 4). The species richness of all plants as well as of all ecological groups
352 increased with higher rock-savanna vegetation area and this size effect was mostly mediated by an
353 increase in habitat diversity, even after accounting for increased sampling effort. Higher rainfall and
354 altitude favoured epiphytic richness, as well as that of large-scale dispersal plant species, while it was
355 detrimental for small-scale dispersal plant species.

356

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361

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367

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- 545

546 **Table 1.** Description of the variables studied on the 22 inselbergs.

Variable name	Nature and unit	Range	Mean	Coefficient of variation (%)
Distance to Atlantic coast	continuous - km	60 - 380	247	39.36
Rock-savanna vegetation area	continuous - km ²	0.013 - 0.663	0.198	77.03
Number of terrestrial habitats	discrete	3 - 10	7.26	26.02
Sampling effort	discrete ¹ - person-days	1 - 40	5.64	153.56
Inselberg density	continuous ² - %	0.000 - 0.686	0.321	71.71
Rainfall	continuous - mm	2182 - 3767	2494	15.95
Altitude	continuous - m	110 - 670	313.63	50.37
Open-canopy forest matrix cover	continuous ³ - %	2.45 - 100.00	73.47	49.69
Plant species richness	discrete	32 - 137	76.23	30.94
Terrestrial plant species richness	discrete	31 - 107	67.91	28.13
Epiphytic plant species richness	discrete	0 - 30	8.32	89.69
Small-scale dispersal plant species richness	discrete	3 - 29	13.86	42.78
Large-scale dispersal plant species richness	discrete	25 - 124	61.82	34.95
Woody plant species richness	discrete	8 - 35	18.45	38.37

547 ¹Number of person-days spent on sampling548 ²Proportion of surface occupied by surrounding inselbergs within a 15 km circle549 ³Proportion of surface occupied by open-canopy forest within a 15 km circle

550

551 **Figure captions**

552 **Fig. 1.** Map of inselbergs in French Guiana. The 22 studied inselbergs are indicated by large red
 553 triangles with the name of their respective inselberg cluster and a letter of the alphabet. Small
 554 black dots indicate unstudied inselbergs. For more details see Sarthou et al. (2017).

555 **Fig. 2.** Conceptual model of the hypotheses representing how multiple ecological drivers can shape
 556 plant diversity of island-like neotropical inselberg ecosystems. Arrows represent the flow of
 557 causality. We studied plant diversity as the species richness for the whole community but also
 558 of specific ecological groups, such as terrestrial (growing directly on bare rock or on shallow
 559 soils), epiphytic (growing on shrubs), small-scale dispersal (autochorous and barochorous),
 560 and large-scale dispersal (wind- and animal-dispersed) plant species. We used the number of
 561 terrestrial habitats as a measure of habitat diversity for all ecological groups except epiphytic
 562 species, for which the richness of woody species was used as a measure of habitat diversity
 563 instead. See the end of the introduction for the details of hypotheses and Table 1 for the
 564 description of the variables used.

565 **Fig. 3.** Drivers of plant diversity in island-like inselberg ecosystems ($n = 22$). (a) Selected path model
 566 explaining the species richness of all species. The model was well supported by the data
 567 (Fisher's $C = 3.88$, $df = 4$, $P = 0.423$). None of the independence claims implied by the model
 568 was statistically significant at $P = 0.05$. Path coefficients are (partial) range-standardized
 569 regression coefficients (effect sizes). Arrow widths are proportional to path coefficients.
 570 Coefficients of determination (r^2) of each endogenous variable are reported. (b-d) Selected
 571 pairwise relationships between open-rock vegetation area, inselberg density, number of
 572 habitats and plant species richness. β_{st} is the range-standardized regression coefficient. ** and
 573 *** indicate statistical significance at $P = 0.01$ and 0.001 , respectively. ^{ns}: not significant.

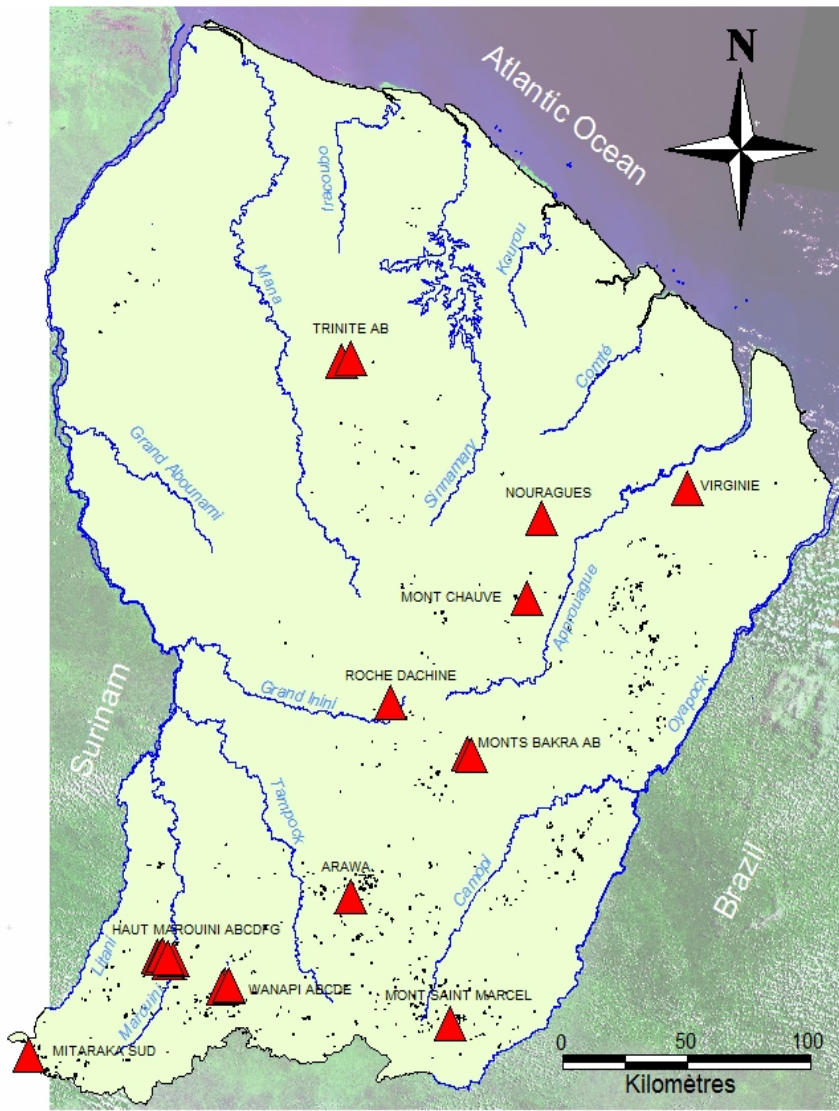
574 **Fig. 4.** Variance partitioning of plant species richness across ecological drivers related to island size
 575 (rock-savanna vegetation area, H_1), island isolation (inselberg density, H_2), environmental
 576 filtering (rainfall and altitude, H_3) and dispersal filtering (forest matrix openness, H_4). The

577 proportion of variance of each class of factors is derived from the sum of squares of the
578 multiple regression of species richness according to the SEM model selected (see Figures 3, 5
579 and 6).

580 **Fig. 5.** Selected path models explaining the species richness of terrestrial (a) and epiphytic (b) plant
581 species richness (n = 22). Both models were well supported by the data (model a: Fisher's C =
582 2.2, df = 4, P = 0.692; model b: Fisher's C = 28.3, df = 28, P = 0.446). None of the
583 independence claims implied by the model was statistically significant at P = 0.05 (Table S2).
584 For further details, see Figure 3. †, *, ** and *** indicate statistical significance at P = 0.10,
585 0.05, 0.01 and 0.001, respectively.

586 **Fig. 6.** Selected path models explaining the species richness of small-scale (a, autochorous) and large-
587 scale (b, anemochorous, zoochorous, hydrochorous) dispersal plant species richness (n = 22).
588 Both models were well supported by the data (model a: Fisher's C = 22.5, df = 22, P = 0.430;
589 model b: Fisher's C = 21.1, df = 22, P = 0.512). None of the independence claims implied by
590 the model was statistically significant at P = 0.05. For further details, see Figure 3. *, ** and
591 *** indicate statistical significance at P = 0.05, 0.01 and 0.001, respectively.

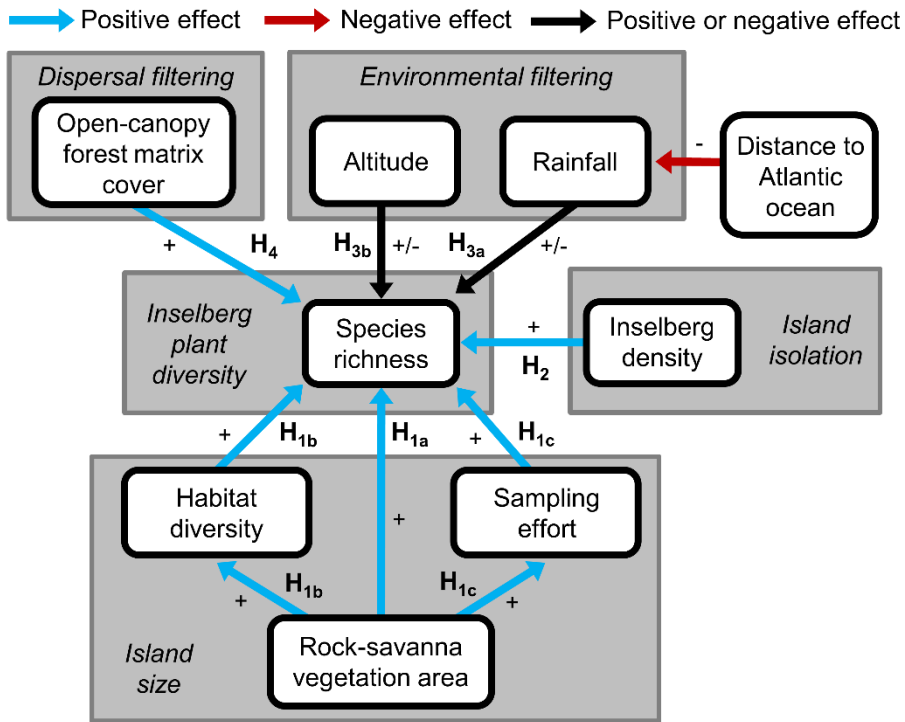
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594 Fig. 1

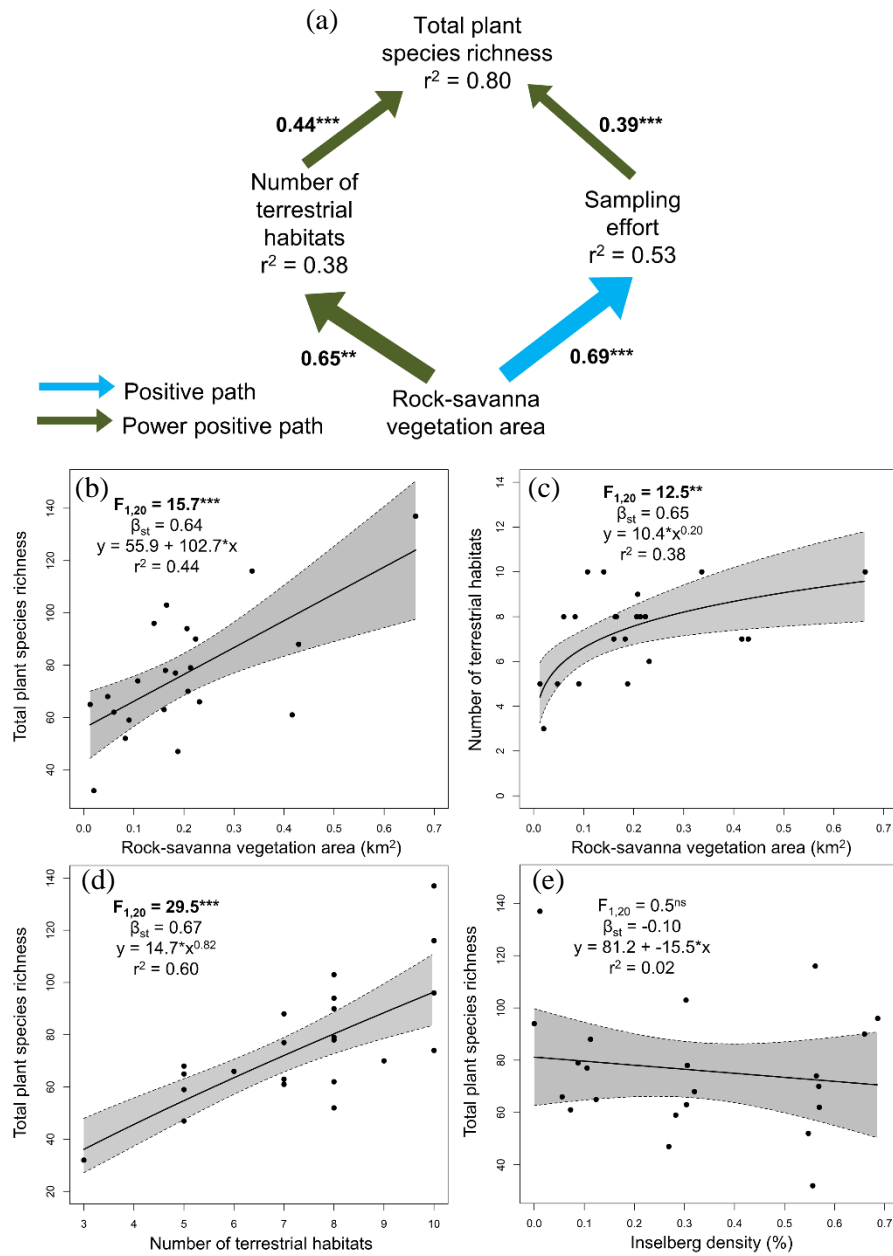
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597 Fig. 2

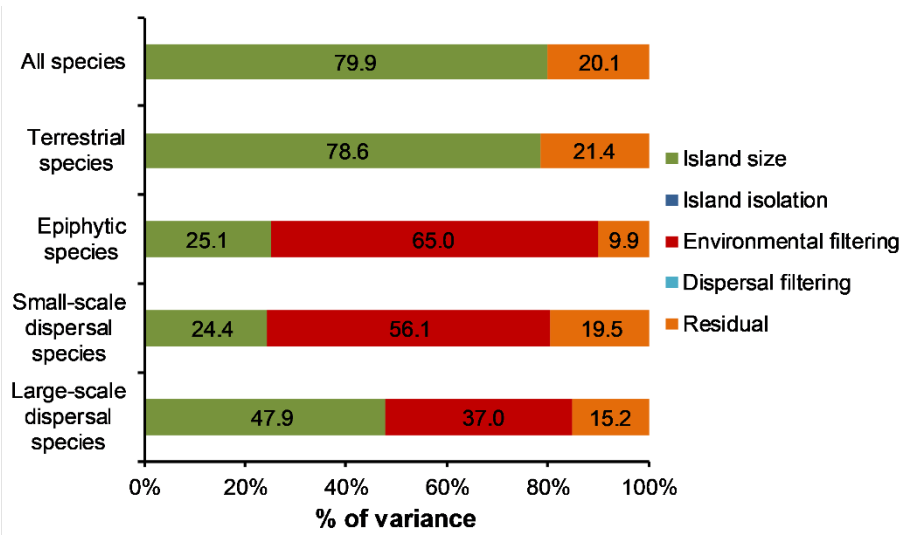
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600 Fig. 3

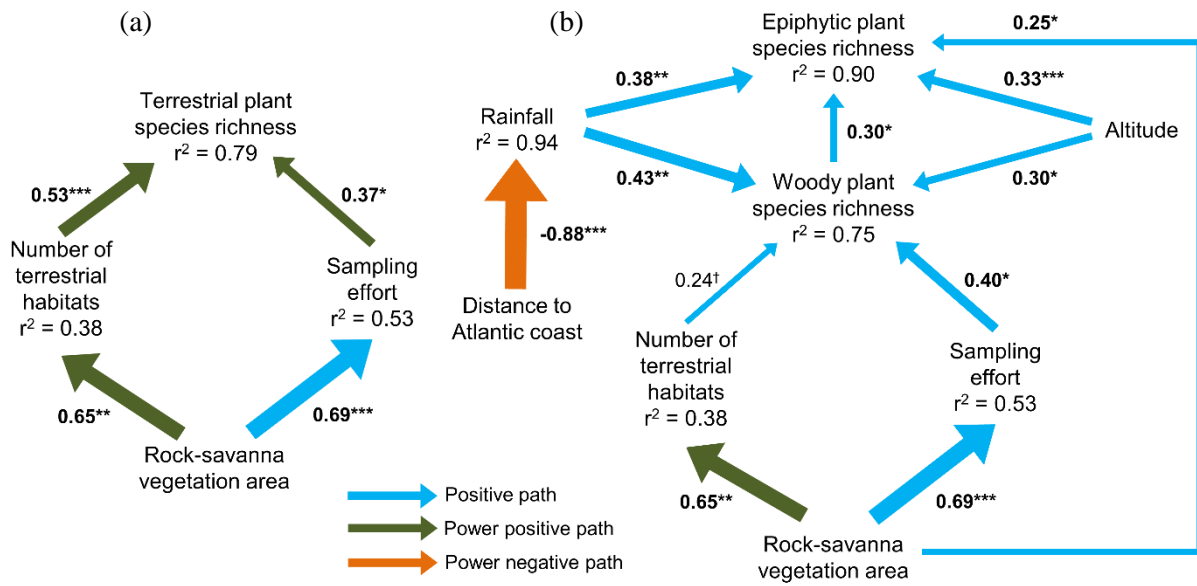
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603 Fig. 4

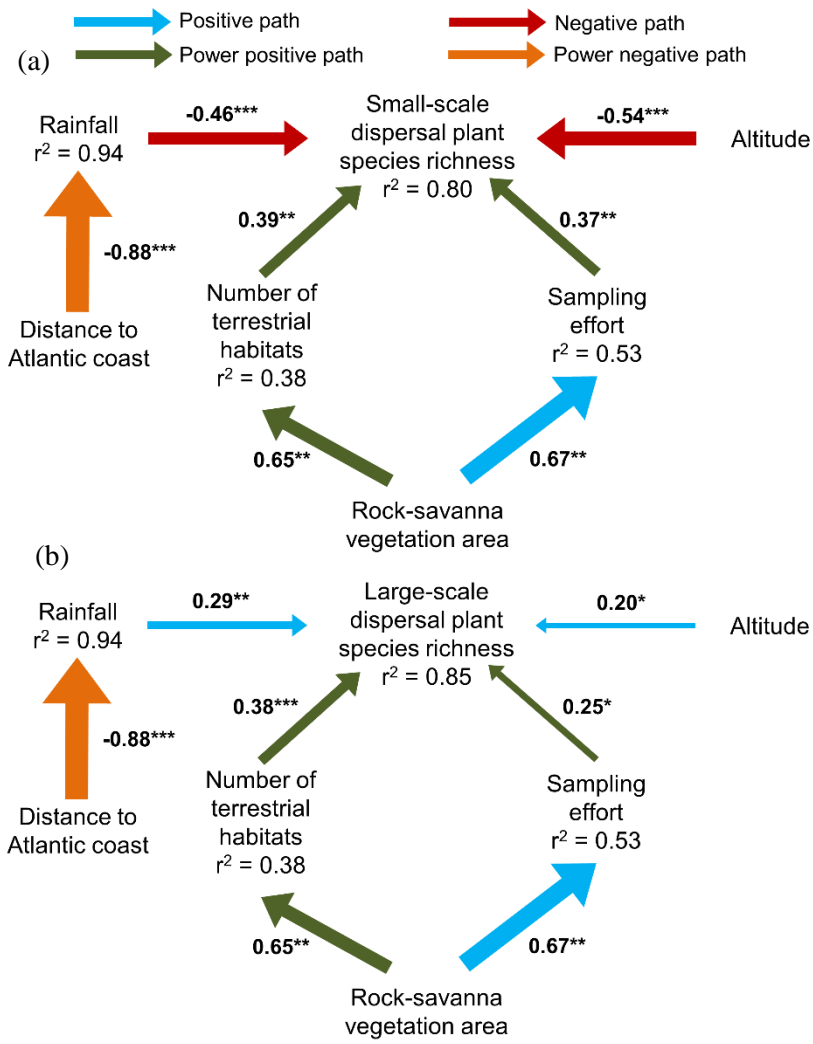
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605

606 Fig. 5

607



608

609 Fig. 6

Appendix

Table S1. Correlation structure of the variables studied. Spearman's correlation coefficients are shown with values significant at P = 0.05 in bold.

Open-rock vegetation area	-0.55												
Number of habitats	-0.07	0.35											
Sampling effort	-0.17	0.48	0.48										
Inselberg density	0.62	-0.43	0.31	-0.10									
Rainfall	-0.80	0.63	-0.14	0.33	-0.83								
Altitude	-0.32	0.41	0.18	0.26	-0.12	0.22							
Open-canopy forest matrix cover	0.79	-0.53	-0.19	-0.30	0.46	-0.66	-0.57						
Plant species richness	-0.25	0.52	0.69	0.82	-0.06	0.36	0.22	-0.37					
Terrestrial plant species richness	-0.09	0.41	0.74	0.79	0.08	0.21	0.03	-0.21	0.96				
Epiphytic plant species richness	-0.69	0.60	0.31	0.53	-0.44	0.68	0.59	-0.83	0.67	0.47			
Small-scale dispersal plant species richness	0.45	0.08	0.47	0.43	0.45	-0.28	-0.33	0.48	0.46	0.61	-0.24		
Large-scale dispersal plant species richness	-0.46	0.57	0.57	0.75	-0.22	0.53	0.43	-0.62	0.93	0.82	0.86	0.16	
Woody plant species richness	-0.50	0.51	0.42	0.73	-0.29	0.61	0.42	-0.65	0.85	0.74	0.84	0.09	0.92
	Distance to Atlantic coast	Open-rock vegetation area	Number of habitats	Sampling effort	Inselberg density	Rainfall	Altitude	Open-canopy forest matrix cover	Plant species richness	Terrestrial plant species richness	Epiphytic plant species richness	Small-scale dispersal plant species richness	Large-scale dispersal plant species richness

Table S2. Comparison of model's goodness-of-fits for different regression functions.

Curve	Function	F-value	P-value	Adjusted r^2
Plant species richness (Y)				
<i>Rock-savanna vegetation area (X)</i>				
Linear	Y = a+bX	F_{1,20} = 15.7	0.0008	0.41
Quadratic	Y = a+bX+cX ²	F _{1,19} = 7.5	0.0040	0.38
Power	Y = a*X ^b	F _{1,20} = 12.0	0.0024	0.34
<i>Terrestrial habitat number (X)</i>				
Linear	Y = a+bX	F _{1,20} = 21.8	0.0002	0.50
Quadratic	Y = a+bX+cX ²	F _{1,19} = 10.4	0.0009	0.47
Power	Y = a*X^b	F_{1,20} = 29.5	< 0.0001	0.58
Terrestrial plant species richness (Y)				
<i>Rock-savanna vegetation area (X)</i>				
Linear	Y = a+bX	F _{1,20} = 22.4	0.0001	0.51
Quadratic	Y = a+bX+cX ²	F _{1,19} = 3.8	0.0398	0.51
Power	Y = a*X^b	F_{1,20} = 9.6	0.0057	0.29
<i>Terrestrial habitat number (X)</i>				
Linear	Y = a+bX	F _{1,20} = 26.6	< 0.0001	0.55
Quadratic	Y = a+bX+cX ²	F _{1,19} = 12.74	0.0003	0.51
Power	Y = a*X^b	F_{1,20} = 34.4	< 0.0001	0.61
Epiphytic plant species richness (Y)				
<i>Rock-savanna vegetation area (X)</i>				
Linear	Y = a+bX	F_{1,20} = 22.4	0.0001	0.51
Quadratic	Y = a+bX+cX ²	F _{1,19} = 12.3	0.0004	0.51
Power	Y = a*X ^b	F _{1,20} = 4.78	0.0409	0.15
<i>Woody species richness (X)</i>				
Linear	Y = a+bX	F_{1,20} = 51.15	< 0.0001	0.70
Quadratic	Y = a+bX+cX ²	F _{1,19} = 25.85	< 0.0001	0.70
Power	Y = a*X ^b	F _{1,20} = 14.3	0.0013	0.38

Table S3. Results of the selection procedure of multiple regression models relating plant diversity to ecological drivers (n = 22). All models with $\Delta\text{AICc} < 2$ and variance inflation factor (VIF) < 4 were included in the confidence models set. ω_i is the model weight indicating the relative support of the model. *, ** and *** indicate statistical significance at P = 0.05, 0.01 and 0.001, respectively. ^{ns}: not significant.

Open-rock vegetation area	Number of habitats	Woody plant species richness	Sampling effort	Inselberg density	Rainfall	Altitude	Open-canopy forest matrix cover	ΔAICc	w_i	r^2
<i>Richness of all plant species</i>										
	0.44***		0.39***					0.00	0.43	0.80
	0.49***		0.34**	-0.12 ^{ns}				0.39	0.34	0.83
	0.45**		0.35**		0.13 ^{ns}			1.26	0.23	0.82
<i>Richness of terrestrial plant species</i>										
	0.53***		0.37**					0.00	1.00	0.78
<i>Richness of epiphytic plant species</i>										
0.25*		0.30*			0.38**	0.33***		0.00	0.70	0.90
		0.40**			0.45***	0.33**		1.74	0.30	0.87
<i>Richness of small-scale dispersal plant species</i>										
	0.39**		0.37**		-0.46***	-0.54***		0.00	1.00	0.80
<i>Richness of large-scale dispersal plant species</i>										
	0.38**		0.25*		0.29**	0.20*		0.00	1.00	0.85

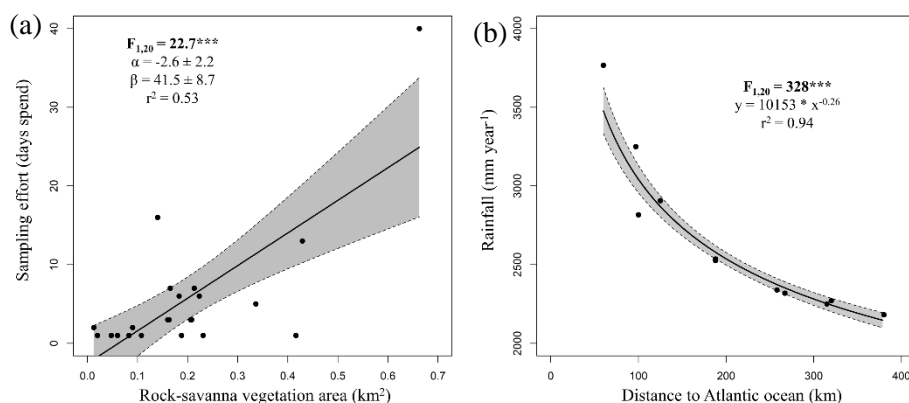


Figure S1. Pairwise relationships between open-rock vegetation area and sampling effort (a), and between distance to the Atlantic Ocean and rainfall (b). α and β represent the intercept and slope of linear regression models, respectively (\pm standard error). *** indicate statistical significance at P = 0.001, respectively. ^{ns}: not significant.

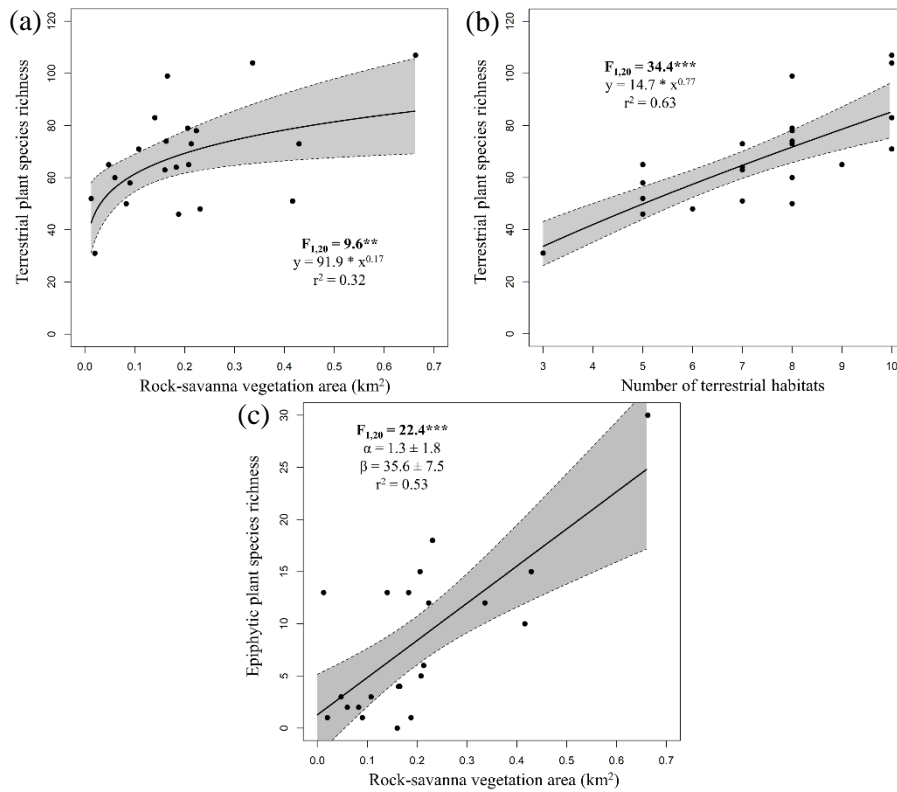


Figure S2. Pairwise relationships between open-rock vegetation area and terrestrial plant species richness (a), between terrestrial habitat number and terrestrial plant species richness (b), and open-rock vegetation area and epiphytic plant species richness (c). α and β represent the intercept and slope of linear regression models, respectively (\pm standard error). ** and *** indicate statistical significance at $P = 0.010$ and 0.001 , respectively..

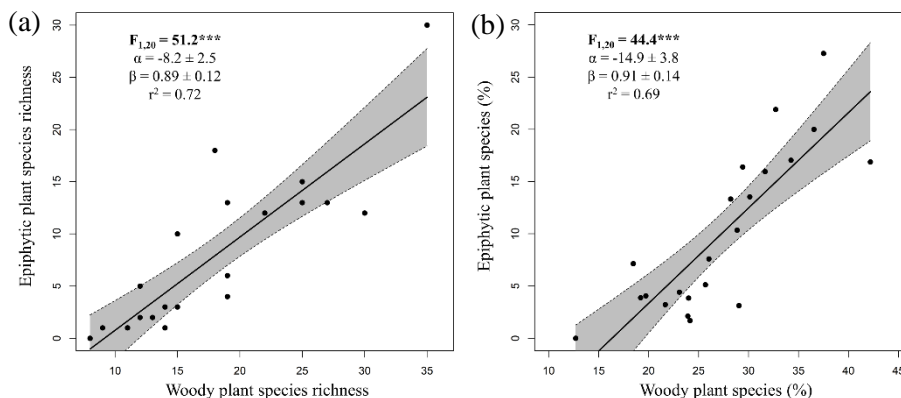


Figure S3. Pairwise relationships of the species richness of woody and epiphytic plants (a), as well as the proportion of woody and epiphytic species within the community (b). α and β represents the intercept and slope of linear regression models, respectively (\pm standard error). *** indicate statistical significance at $P = 0.001$.

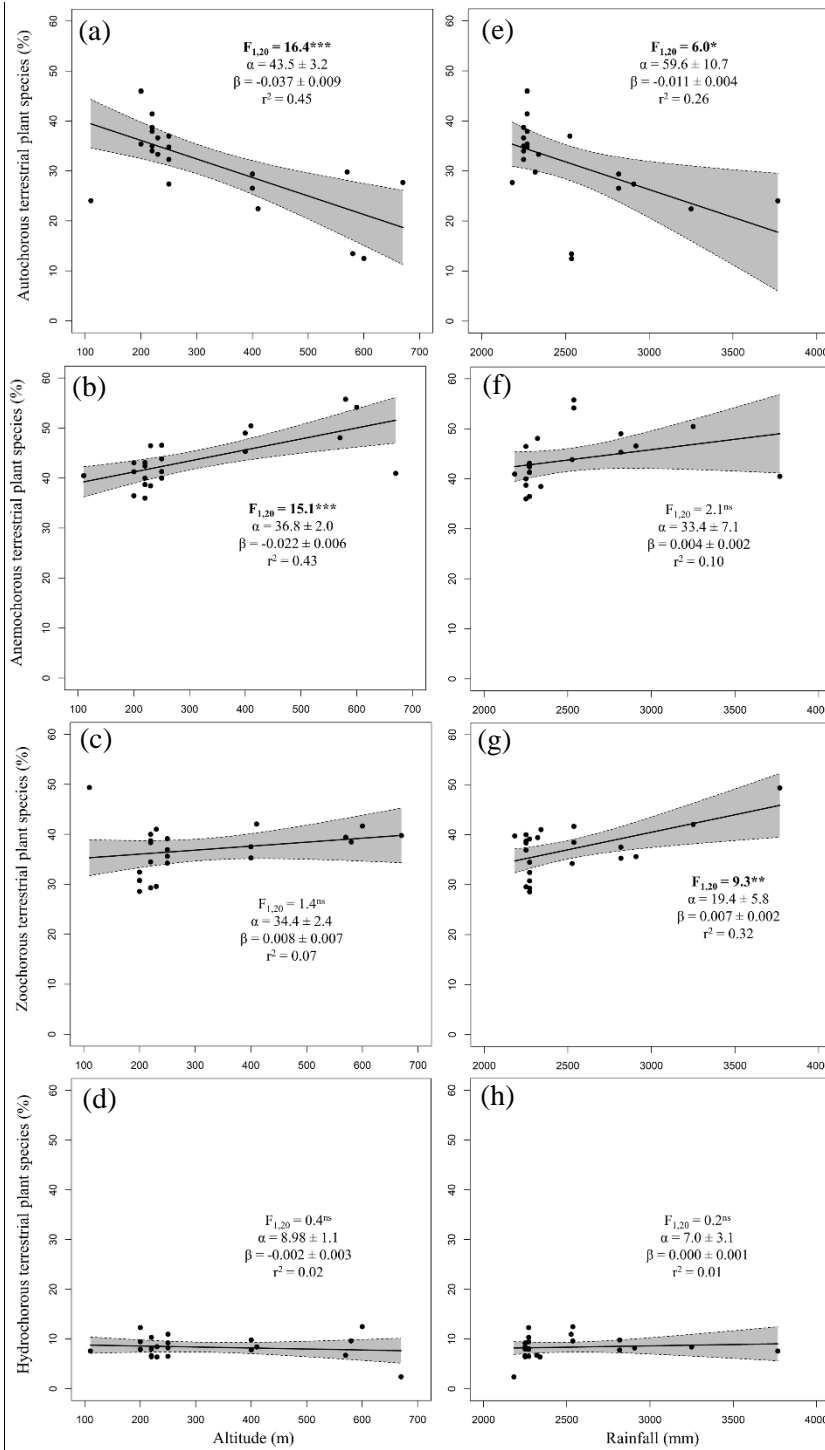


Figure S4. Pairwise relationships of altitude (a, c, e and g) and rainfall (b, d, f and h) with the proportion of species with contrasting dispersal type within the community. α and β represents the intercept and slope of linear regression models, respectively (\pm standard error). *, ** and *** indicate statistical significance at $P = 0.05, 0.01$ and 0.001 , respectively. ^{ns}: not significant.