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1 **Collapse of dispersal trait diversity across a long-term chronose-**  
2 **quence reveals a strong negative impact of frugivore extinctions on**  
3 **forest resilience**

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7 **Abstract**

8 **1.** Understanding how seed dispersal disruption may alter plant community diversity  
9 and dynamics over a large temporal scale remains a challenge. Here, we use a long-  
10 term chronosequence to compare changes in the richness and composition of different  
11 dispersal trait assemblages in communities established before and after human colo-  
12 nisation in the Mascarene archipelago.

13 **2.** Our study was located on Réunion on the slopes of the Piton de la Fournaise, one  
14 of the most active volcanoes worldwide. We analysed 151 vegetation surveys on lava  
15 flows dated between 1401-AD and 1956-AD and in tropical rainforests established on  
16 older substrata. We defined five classes of substratum age, according to the well-  
17 known chronology of native frugivore defaunation: “old substrata” and [1401,  
18 1665[ when frugivores were abundant and diverse before permanent human settle-  
19 ment; [1665, 1800[ when large-bodied frugivore populations were strongly reduced;  
20 [1800, 1900[ when large-bodied frugivores went extinct and small-bodied frugivores  
21 were still abundant; [1900, 1956] decline in the populations of small-bodied frugivores.

22 Based on dispersal traits, we categorised 146 native woody species as anemochorous,  
23 rous, small fleshy-fruited or large fleshy-fruited, *i.e.* plant of which fruit could not theo-  
24 retically be dispersed by extant frugivores.

25 **3.** Changes in dispersal trait diversity strongly correlated with the chronology of de-  
26 faunation. Species-rich communities settled before human colonisation were strongly  
27 dominated by fleshy-fruited species. Large fleshy-fruited plants in the oldest commu-  
28 nities settled after human colonisation declined markedly and almost disappeared af-  
29 ter 1800. The richness of small fleshy-fruited plants decreased less rapidly across the  
30 chronosequence, with medium levels on [1665, 1800[ and [1800, 1900[ lava flows and  
31 low levels on [1900, 1956] lava flows. Conversely, the richness of anemochorous  
32 plants remained unchanged. Communities settled before human colonisation had a  
33 similar composition. Fleshy-fruited assemblages showed strong species loss across  
34 the chronosequence, while anemochorous assemblages showed strong species turn-  
35 over, which was probably due to lower dispersal limitation.

36 **4. Synthesis.** Our results provide the first insights into the tremendous impact that  
37 frugivore extinction has on plant colonisation dynamics over 300 years. The dramatic  
38 loss of fleshy-fruited plant diversity on historical lava flows highlights the irreplaceable  
39 dispersal role played by frugivores, especially large-bodied species. The conservation  
40 of plant-animal mutualistic interactions is invaluable and refaunation efforts need to be  
41 undertaken in areas where frugivores have been extirpated.

## 42 **Résumé**

43 **1.** Comprendre comment la rupture des interactions de frugivorie peut altérer la diver-  
44 sité et la dynamique des communautés végétales sur une grande échelle temporelle  
45 demeure un défi. Ici, nous utilisons une chronoséquence de plus de six siècles pour  
46 comparer les changements dans la richesse et la composition de différents assem-  
47 blages basés sur les traits de dispersion au sein de communautés établies avant et  
48 après la colonisation humaine de l'archipel des Mascareignes.

49 **2.** Notre étude est située à La Réunion sur les pentes du Piton de la Fournaise, l'un  
50 des volcans les plus actifs au monde. Nous analysons 151 relevés de végétation sur  
51 des coulées de lave datées entre 1401-AD et 1956-AD, et en forêt tropicale humide  
52 sur des substrats plus anciens. Nous définissons cinq classes d'âge de substrat, selon  
53 la chronologie bien connue de la défaunation des frugivores indigènes : “vieux sub-  
54 trats” et [1401, 1665[ quand les frugivores étaient abondants et diversifiés avant la  
55 colonisation humaine permanente; [1665, 1800[ quand les populations des grands  
56 frugivores étaient fortement réduites; [1800, 1900[ quand les grands frugivores étaient  
57 éteints et les petits frugivores encore abondants; [1900, 1956] déclin des populations  
58 de petits frugivores. Nous caractérisons 146 espèces ligneuses indigènes selon leurs  
59 traits de dispersion : anémochores, à petits fruits charnus ou à gros fruits charnus, *i.e.*  
60 les fruits ne peuvent être théoriquement dispersés par les frugivores relictuels.

61 **3.** Les changements dans la diversité des traits de dispersion sont fortement corrélés  
62 à la chronologie de la défaunation. Les communautés avec une grande richesse spé-  
63 cifique établies avant la colonisation humaine sont largement dominées par les es-  
64 pèces à fruits charnus. Les plantes à gros fruits charnus dans les communautés éta-

65 blies peu après le début de la colonisation humaine déclinent très fortement et dispa-  
66 raissent quasiment après 1800. La richesse des plantes à petits fruits charnus diminue  
67 moins vite le long de la chronoséquence, avec des niveaux moyens sur les coulées  
68 de lave de [1665, 1800[ et [1800, 1900[, puis faibles sur les coulées de lave du 20<sup>ème</sup>  
69 siècle. En revanche, la richesse des plantes anémochores ne change pas de manière  
70 significative. Les communautés établies avant la colonisation humaine ont une com-  
71 position comparable. Les assemblages de plantes à fruits charnus montrent une forte  
72 perte d'espèces le long de la chronoséquence tandis que les assemblages anemo-  
73 chores montrent un fort remplacement, probablement en raison d'une faible barrière  
74 à la dispersion.

75 **4. Synthèse.** Nos résultats montrent pour la première fois l'impact considérable de  
76 l'extinction des frugivores sur la dynamique de colonisation des plantes sur plus de  
77 300 ans. L'effondrement de la diversité des plantes à fruits charnus sur les coulées de  
78 lave historiques souligne le rôle irremplaçable joué par les frugivores, en particulier  
79 les espèces de grande taille. La conservation des interactions mutualistes plantes-  
80 animaux est primordiale, et des efforts de refaunation doivent être entrepris dans les  
81 zones où les frugivores ont disparu.

## 82 **Keywords**

83 Anemochory; biodiversity loss; defaunation; island biology; plant-animal mutualistic  
84 interactions; seed dispersal disruption; succession; zoochory

## 85 **Abbreviations:**

86 AD: anno Domini; ADF: anemochorous dry-fruited; asl: above sea level; LFF: large  
87 fleshy-fruited; SFF: small fleshy-fruited;  $S_{st}$ : standardised richness

## 88 **Introduction**

89 The decline in large vertebrates is a global phenomenon (Blackburn, 2004; Dirzo et  
90 al., 2014; Hansen & Galetti, 2009; Steadman, 1995; Young, McCauley, Galetti, &  
91 Dirzo, 2016). For decades it has been raising serious concern with regard to the con-  
92 sequences for plant-animal mutualistic interactions (Bond, 1994; Emmons, 1989; Jan-  
93 zen, 1974). Notably, frugivore vertebrates (hereafter referred to as "frugivores") play a  
94 prominent role and their extirpation alters seed dispersal process (Babweteera &  
95 Brown, 2009; 2016; Jordano, Garcia, Godoy, & Garcia-Castano, 2007; McConkey &  
96 Drake, 2006; Meehan, McConkey, & Drake, 2002; Riera, Traveset, & Garcia, 2002;  
97 Wotton & Kelly, 2012; Young et al., 2016). Ecological and evolutionary consequences  
98 at plant population level include altered regeneration (Levi & Peres, 2013; Wotton &  
99 Kelly, 2011; Zeng, Swihart, Zhao, Si, & Ding, 2019), reduced connectivity (Pérez-Mén-  
100 dez, Jordano, & Valido, 2018), downsized dispersal traits (Galetti et al., 2013) and  
101 altered genetic diversity (Carvalho, Galetti, Colevatti, & Jordano, 2016). Recent stud-  
102 ies reported the transforming effects of frugivore loss on plant communities, by com-  
103 paring seedling recruitment between intact and defaunated sites (Effiom, Nunez-Iturri,  
104 Smith, Ottosson, & Olsson, 2013; Terborgh et al., 2008; Vanthomme, Bellé, & Forget,  
105 2010; Wandrag, Dunham, Duncan, & Rogers, 2017; Wright et al., 2007). However, to  
106 our knowledge, no study has yet examined how seed dispersal disruption may jeop-  
107 ardise whole tree communities over a period exceeding thirty years. Our research uses  
108 a long-term chronosequence of lava flows that spans a frugivore defaunation time  
109 range of 300 years on Réunion, an oceanic island that belongs to the Mascarenes. It  
110 has been one of the latest tropical archipelagos to be colonised by humans in the 17<sup>th</sup>  
111 century, which makes it a unique study system, particularly since: (1) the kinetics of  
112 frugivore extinction is well documented by subfossil records (Hume, 2013; Mourer-

113 Chauvire, Bour, Ribes, & Moutou, 1999) and historical archives (Cheke & Hume, 2008;  
114 Loughnon, 2005); and (2) high volcanic activity has produced numerous lava flows,  
115 which provide an ideal natural experiment to date and explain patterns of plant com-  
116 munity changes (Fig. 1).

117         Seed dispersal is a key process for ecosystem recovery after disturbance, such  
118 as lava flows. Dispersal is the only possible pathway by which plant colonise disturbed  
119 areas where the living biomass, including soil seed banks, has been totally destroyed  
120 (Walker & Moral, 2003). In relation to seed dispersal strategies, fruit traits are im-  
121 portant for understanding plant colonisation mechanisms: plants with large or small  
122 fleshy fruits mainly depend on frugivores for their dispersal, whereas most plants with  
123 dry fruits depend on abiotic dispersal vectors, *e.g.* wind (Howe & Smallwood, 1982;  
124 van der Pijl, 1982). In most tropical rainforests, frugivorous vertebrates are key com-  
125 ponents of forest succession, since they play a far greater role than wind in dispersing  
126 woody plants (González-Castro, Yang, & Carlo, 2019; Ingle, 2003; Whittaker, Bush, &  
127 Richards, 1989). Hence, past and present frugivore defaunation probably has severe  
128 consequences on ecosystem recovery and forest dynamics after disturbance. This is  
129 especially the case on tropical oceanic islands, where a mass extinction of frugivore  
130 vertebrates has frequently followed human colonisation (Blackburn, 2004; Heinen, van  
131 Loon, Hansen, & Kissling, 2017; Steadman, 1995). Therefore, we would expect drastic  
132 changes in the diversity and composition of fleshy-fruited plant assemblages on lava  
133 flows, before and after human colonisation, compared to anemochorous dry-fruited  
134 (ADF) plant assemblages, which remain unaffected.

135         The fruit of fleshy-fruited plants varies considerably in size, typically ranging  
136 from a few millimetres to over 50 cm (Guimarães, Galetti, & Jordano, 2008). This sug-  
137 gests that different sized frugivores are required for effective dispersal (Hansen &

138 Galetti, 2009; Naniwadekar, Chaplod, Datta, Rathore, & Sridhar, 2019). Critical fruit  
139 size thresholds exist among plant communities: for example, the early extinction of  
140 megafauna limited the dispersal of many large-seeded plants (Federman et al., 2016;  
141 Guimarães et al., 2008). Fruit size of ca 13 mm is documented as a critical threshold,  
142 both on the mainland (Dowsett-Lemaire, 1988; Galetti et al., 2013) and on oceanic  
143 islands (McConkey & Drake, 2015). As defaunation primarily extirpates large verte-  
144 brates (Dirzo et al., 2014), most oceanic islands are strongly depauperate in large-  
145 bodied frugivores (McConkey & Drake, 2015; Schleuning, Böhning-Gaese, Dehling, &  
146 Burns, 2014). In some places, including Réunion, they have been totally extirpated  
147 and therefore absent for several centuries (Heinen et al., 2017). In addition to the con-  
148 trast between ADF vs fleshy-fruited species, we would also expect to see dramatic  
149 changes in diversity and composition within fleshy-fruited species given that large  
150 fleshy-fruited (LFF) plant assemblages are likely to have been impacted for a longer  
151 period (since human colonisation) than small fleshy-fruited (SFF) plant assemblages.

152         In this paper, we use a comparative approach to investigate whether dispersal  
153 failure caused by defaunation leads to severe diversity loss in plant communities stud-  
154 ied across a long-term chronosequence of lava flows. We focus on changes in the  
155 richness and composition of ADF, SFF and LFF plant assemblages settled on sub-  
156 strata belonging to five age classes, which we consider as a proxy of dispersal agent  
157 availability (Fig. 1). We compare plant communities settled before permanent human  
158 settlement in 1665-AD, when frugivores were abundant and diverse, to more recent  
159 communities established after the extinction of large-bodied frugivores and the decline  
160 in the population of small-bodied frugivores began. First, we test whether changes in  
161 richness relate to the availability of frugivores. We expect the richness of LFF and SFF  
162 plant to be high on ancient lava flows that were colonised when frugivores were still

163 abundant. In theory, LFF plant richness should decrease faster across the chronose-  
164 quence (from oldest to youngest lava flows) than SFF plant richness because large-  
165 bodied frugivores became extinct sooner than small frugivores. On the contrary, dis-  
166 persal limitation for ADF plants is low, therefore, variation in ADF plant richness should  
167 be independent of the defaunation history. It may even increase across the chronose-  
168 quence because early primary successional stages are often dominated by ADF spe-  
169 cies (Walker & Moral, 2003). Second, we analyse  $\beta$ -diversity and its two components,  
170 *i.e.* nestedness and turnover, which respectively result from the loss (or gain) of taxa  
171 and from the replacement of taxa (Baselga, 2010), to detect variation in plant commu-  
172 nity composition across the chronosequence. We expect strong dispersal limitation in  
173 fleshy-fruited species to lead to a significant increase of nestedness across the chron-  
174 osequence, especially for LFF plants. On the contrary, if ADF species suffer no major  
175 dispersal limitation and can all reach lava flows, we should detect higher species re-  
176 placement or species gain on recent lava flows (Wandrag et al., 2017).

## 177 **Material and methods**

### 178 **Study area**

179 Réunion (2512 km<sup>2</sup>) is the largest island in the Mascarene archipelago. It is located in  
180 the biodiversity hotspot that characterises the South-West Indian Ocean islands (Mit-  
181 termeier et al., 2004) (Fig. 2). The study site is located in the South-East of Réunion  
182 on the slopes of the Piton de la Fournaise. This shield volcano is one of the most active  
183 in the world. More than 238 eruptions have been recorded since the second half of the  
184 17th century (Morandi et al., 2016). For 5000 years, most lava flows have occurred in  
185 the most recent caldera of the Piton de la Fournaise. Eruptions have also occurred

186 outside the caldera along three rift zones (Morandi et al., 2016). The Piton de la Four-  
187 naise area has a humid tropical climate throughout the year below 750 m asl, *i.e.* an-  
188 nual mean temperature ranges from 19 to 25°C and precipitation in the driest month  
189 ranges from 75 to 350 mm, with large inter- and intra- annual variations (Jumeaux,  
190 Quetelard, & Roy, 2011). This area shelters almost all that remains of the tropical  
191 rainforest on Réunion and represents the last sanctuary of its kind in the Mascarene  
192 archipelago (Strasberg et al., 2005).

### 193 **Data collecting**

#### 194 *Vegetation sampling and frugivore guild characterisation*

195 We used a historical dataset sampled in the 1970s by the French botanist Cadet  
196 (1977). It is invaluable because it includes forests that have since been destroyed  
197 (Appendix Fig. S1). We retained 151 vegetation plots sampled in pristine or relatively  
198 undisturbed habitats, where alien plants were rare or had little overall cover (Fig. 2).  
199 Twenty-eight plots were settled on well-developed soils as reported by Cadet (1977)  
200 in his technical notes. We did not have proper dating for these substrata, but based  
201 on the very likely slow pedogenesis, we assumed that they were at least 1000 years  
202 old (Meunier et al., 2010). One-hundred and twenty-three plots were located on 27  
203 lava flows dated between 1401 AD and 1956 AD: (i) three lava flows were dated by  
204 <sup>14</sup>C (Morandi et al., 2016), (ii) sixteen lava flows were known from historical sources  
205 (Cadet, 1977; Stieltjes, 1986) and (iii) eight lava flows were dated using an indirect  
206 approach based on the size distribution of long-lived ADF pioneer trees found on lava  
207 flows (Strasberg, Michon, Daux, & Muro, 2012). Because <sup>14</sup>C dating could not be used

208 in several areas such as the caldera that, however, hosted isolated old remnant for-  
209 ests, the tree size method allowed to expand the chronosequence and to add some  
210 heterogeneity in the sampled ecological situations.

211 We assigned the 151 vegetation plots to five substrata age classes, defined  
212 according to the availability of dispersal agents, as documented by subfossils records  
213 (Hume, 2013; Mourer-Chauvire et al., 1999) and historical archives (Cheke & Hume,  
214 2008) (Fig.1). Namely, the first class was “old substrata” on which plant communities  
215 assembled when frugivores were numerous and where pedological conditions were  
216 supposed to be more favorable. This class therefore included our reference control  
217 plots (n = 28 plots); the second class was [1401, 1665[, when frugivores were still  
218 numerous and diverse (n = 36 plots); the third class was [1665, 1800[, when large-  
219 bodied frugivore populations were severely reduced, while small-bodied frugivore pop-  
220 ulations were less impacted (n = 23 plots); the fourth class was [1800, 1900[, when  
221 large-bodied frugivores were extinct and small-bodied frugivores, especially the native  
222 bulbul (*Hypsipetes borbonicus*) and the hoopoe starling (*Fregilupus varius*), were still  
223 abundant (n = 37 plots); the fifth and most recent class was [1900, 1956], when pop-  
224 ulations of extant small-bodied frugivores further declined to extremely low densities  
225 (n = 27 plots) (Fig.1).

226 Spatial distribution of study plots was not random given the volcanic eruption  
227 pattern, as well as difficulties in accessing some remote locations (Fig. 2 & Appendix  
228 Fig. S2). All plots on “old substrata” were outside the caldera; plots on [1401,  
229 1665[ lava flows were all located in the southern half of the Fournaise area, whereas  
230 those on [1665, 1800[ lava flows showed a wider distribution; plots located on [1800,  
231 1900[ and [1900, 1956] lava flows were respectively located in south-central Fournaise  
232 area and in the caldera. In the latter area, old growth native forests were already rare

233 and very fragmented in 1975. Cadet (1977) also used different sampling areas ranging  
234 from 500 to 1000 m<sup>2</sup> on pre-defaunation lava flows and from 100 to 1000 m<sup>2</sup> on his-  
235 torical lava flows (Fig. 2).

236 For each plot, Cadet (1977) recorded the cover of tree, shrub and herbaceous  
237 *strata* and maximum canopy height. For each *stratum*, he recorded the list of trache-  
238 ophyta at species level, including seedlings with the Braun-Blanquet semi-quantitative  
239 method. These data allowed us to quantify species richness, composition and vege-  
240 tation structure. We focused on woody species, *i.e.* woody angiosperms and arbores-  
241 cent ferns because they were taxonomically well known in the 1970s, unlike herba-  
242 ceous species. In addition, they contribute significantly to the structure of plant com-  
243 munities from the early stages of vegetation development on (Cadet, 1977).

#### 244 *Dispersal traits of woody species*

245 Woody species were assigned to three functional groups based on dispersal traits.  
246 Fleshy-fruited plants that were originally dispersed by a rich native frugivore fauna  
247 (Fig. 1 & Appendix Tab. S1) were assigned to two dispersal trait groups based on fruit  
248 size (Izhaki, 2002; McConkey & Drake, 2015): small fleshy-fruited (SFF) and large  
249 fleshy-fruited (LFF) species. These two groups were defined according to the mean  
250 value for fruit (or arillate seed) diameter, *i.e.* above or below 13 mm, which is the max-  
251 imum gape width of *Hypsipetes borbonicus*, the largest extant frugivore on Réunion  
252 (body mass = 55 g) (Cheke, 1987). Plants that use wind dispersal mechanisms and  
253 do not depend on animal dispersal were categorised as anemochorous dry-fruited  
254 (ADF). Dry-fruited plant species whose dispersal strategy remained unclear were in-  
255 cluded in the overall analysis of diversity, but not assigned to a specific dispersal trait  
256 group. These species are not common in lowland forests on Réunion.

257 **Statistical analyses**

258 We constructed a presence-absence matrix for each plot and each dispersal trait  
259 group based on species presence at any growth stage, *i.e.* in any vegetation *stratum*.  
260 Species could thus be present at seedling or sapling stage only.

261 *Plant species richness across the chronosequence*

262 We modeled plant species richness across the chronosequence using a multiple re-  
263 gression approach to take into account the relative influence of plot area, elevation,  
264 precipitation of driest month and isolation that substantially varied across study plots  
265 (Appendix Fig. S2). To assess plot isolation, we used a habitat map to construct a  
266 binary raster of native closed-canopy forests at 100 m resolution and calculated the  
267 proportion of native forests in the 100 hectares surrounding each plot. The five varia-  
268 bles used for analyses showed moderate collinearity with maximum variance inflation  
269 factors < 4.

270 The relationship between count data responses (species richness of all woody  
271 plants, ADF, SFF, LFF and not-assigned plants) and explanatory variables including  
272 the five variables and four interaction terms, *i.e.* age of lava flow x (isolation + elevation  
273 + precipitation + area), were analysed using generalized linear models (GLMs) with a  
274 Poisson distribution (O'Hara & Kotze, 2010). Using a type-II analysis of deviance, we  
275 dropped the non-significant terms for each GLM. We used the Moran eigenvector fil-  
276 tering function (R package "spdep") to account for possible effects of spatial autocor-  
277 relation on parameter estimates (Bivand et al., 2015). Pseudo- $R^2$  of GLMs were cal-  
278 culated by the relationship "1 – residual deviance/null deviance". We finally estimated  
279 the standardised values of species richness ( $S_{st}$ ) across the chronosequence by fixing

280 the four other variables to their mean value (sampling area = 591 m<sup>2</sup>, elevation = 354  
281 m asl, precipitation of driest month = 226 mm, isolation = 46 % of native forests).

## 282 *Community composition across the chronosequence*

283 We performed pairwise dissimilarity analyses between vegetation plots and used the  
284 *beta.pair* function (R package *betapart*) to decompose total  $\beta$ -diversity (measured by  
285 Sorensen dissimilarity) into its two components, nestedness and turnover (measured  
286 by Simpson dissimilarity) (Baselga & Orme, 2012). We then constructed six distance  
287 matrices by calculating the absolute values of the difference between each pair of plots  
288 for age of lava flow, sampling area, elevation, precipitation of driest month and isola-  
289 tion. Because age of lava flow was an ordinal variable, we converted the five age  
290 classes to numerical values from 1 (old substrata) to 5 ([1900; 1956]). We also calcu-  
291 lated the Euclidean geographical distance for each plot pair. To take into account the  
292 influence of sampling area, elevation, precipitation of driest month, isolation and Eu-  
293 clidean distance on dissimilarities across the chronosequence, we could not use a  
294 multiple regression as we did for species richness because of obvious violation of the  
295 assumption on independence (Anderson et al., 2011). Consequently, we performed  
296 partial Mantel tests with 1000 permutations (R package *ecodist*) to examine the influ-  
297 ence of age of lava flow on each dissimilarity while controlling for other variables, and  
298 vice versa (Goslee & Urban, 2007).

## 299 **Results**

### 300 **Species richness across the chronosequence**

301 The age of lava flow was by far the best predictor of species richness for woody plants  
302 overall ( $n = 151$ ,  $p = 1.7e-27$ ; pseudo- $R^2 = 0,87$ ), small fleshy-fruited (SFF) plants ( $p =$

303 4.7e-27; pseudo-R<sup>2</sup> = 0,84) and large fleshy-fruited LFF plants (p = 6.2e-41; pseudo-  
304 R<sup>2</sup> = 0,87) (Appendix Tab. S2 & Fig. S3). Conversely, elevation was the best predictor  
305 for anemochorous dry-fruited (ADF) plant richness (p = 3.7e-16; pseudo-R<sup>2</sup> = 0,70).  
306 Isolation also had a strong influence on the richness of the four groups, but only on  
307 post-defaunation lava flows for all woody plants, SFF and LFF plants.

308         The estimated standardised species richness ( $S_{st}$ ) for woody plants overall de-  
309 creased considerably across the chronosequence, *i.e.* with decreasing substrata age  
310 (Fig. 3):  $S_{st}$  was similar on pre-defaunation substrata, *i.e.* 32.9 and 35.4 in “old sub-  
311 strata” and [1401; 1665] respectively, then declined markedly to 17.6 in [1665;  
312 1800[ and [1800; 1900[, and dropped down to 11.5 species in [1900; 1956]. This gen-  
313 eral downward trend across the chronosequence concealed very different changes  
314 that were evidenced when dispersal trait groups were considered separately (Fig.3).  
315  $S_{st}$  for ADF plants ranged from 4.8 to 6.2 species and showed no significant trend  
316 across the chronosequence. Changes in species richness of fleshy-fruited plants  
317 drove the general trend of woody plant species.  $S_{st}$  for SFF plants was similar on pre-  
318 defaunation substrata, *i.e.* 20.9 and 22.5 in “old substrata” and [1401; 1665], respec-  
319 tively, then strongly decreased in [1665; 1800[ to 10.8 species. It was similar in [1800;  
320 1900[ with 11.3 species and dropped down to 5.4 species in [1900; 1956].  $S_{st}$  for LFF  
321 plants followed a similar pattern to SFF plants, although their decline was more abrupt:  
322 LFF plant richness was similar on pre-defaunation substrata, *i.e.* 6.1 and 7.3 in “old  
323 substrata” and [1401; 1665], respectively. It showed a strong decrease to 1.1 species  
324 in [1665; 1800[, fell to 0.4 species in [1800; 1900[ and 0 in [1900; 1956]. The inde-  
325 pendently standardized estimated richness across dispersal trait groups overall  
326 summed to the overall richness of woody species with a low average relative differ-  
327 ence of 0.5%, which suggested a good accuracy of the separate estimates (Appendix

328 Fig. S4). Lastly, we also performed statistical analyses without taking into account lava  
329 flows whose dating was based on pioneer trees development and obtained similar  
330 conclusions (Appendix Fig. S5).

### 331 **Community composition across the chronosequence**

332 The total  $\beta$ -diversity measured by Sorensen dissimilarity with control plots as reference  
333 (“old substrata”) showed a highly significant increase across the chronosequence for  
334 woody plants overall (from 0.35 to 0.90), as well as within each dispersal trait group  
335 (ADF, from 0.35 to 0.78; SFF, from 0.35 to 0.89; LFF, from 0.33 to 0.62) when other  
336 variables were controlled (partial Mantel test,  $p < 0.001$ ) (Fig. 4 & Appendix Fig. S6).  
337 For woody plants overall, turnover and nestedness increased significantly across the  
338 chronosequence (partial Mantel tests,  $p < 0.001$  &  $p < 0.001$ ). However, turnover was  
339 the main driver of composition changes, in relation with fleshy-fruited (both LFF and  
340 SFF) and ADF species dominating assemblages on old and recent lava flows, respec-  
341 tively (Fig. 3). Within dispersal trait groups, the general increase in Sorensen dissimi-  
342 larity concealed very different situations evidenced when the two components of  $\beta$ -  
343 diversity were considered separately.

344 For ADF assemblages, the turnover strongly increased across the chronose-  
345 quence from 0.26 to 0.64 (partial Mantel test,  $p < 0.001$ ), whereas nestedness was low  
346 and stable (partial Mantel test, NS) and mostly influenced by elevation and isolation  
347 (Fig. 4 & Appendix Fig. S6). For SFF assemblages, the turnover was mostly influenced  
348 by elevation and showed a weak increase from 0.26 to 0.32 across the chronose-  
349 quence (partial Mantel test,  $p = 0.04$ ), whereas nestedness strongly increased from  
350 0.09 to 0.57 (partial Mantel test,  $p < 0.001$ ). For LFF assemblages, dissimilarity anal-  
351 yses involve a shorter chronosequence, given that LFF plants are totally absent on

352 [1900; 1956] lava flows, and showed similar trends as SFF assemblages. The turnover  
353 was mostly influenced by elevation and remained stable between 0.19 and 0.29 (par-  
354 tial Mantel test, NS), whereas nestedness strongly increased from 0.12 to 0.37 (partial  
355 Mantel test,  $p < 0.001$ ). Overall, species replacement was the main phenomenon driv-  
356 ing species composition of ADF assemblages across the chronosequence, while SFF  
357 and LFF plant assemblages that remained on recent lava flows constituted a subset  
358 of the communities found on “old substrata”.

## 359 **Discussion**

### 360 **Frugivory disruption as a major cause of fleshy-fruited plant diversity loss**

361 Plant dispersal trait diversity is strongly related to the availability of dispersal agents  
362 across a long-term chronosequence on the Piton de la Fournaise volcano. This sug-  
363 gests that the extinction of large-bodied frugivores has severely limited dispersal for  
364 many plant species since the early 18<sup>th</sup> century, *i.e.* less than a century after the first  
365 human settlements. It appears to be a major cause of the fleshy-fruited plant diversity  
366 loss on historical lava flows. The negative impact of frugivore defaunation on tree re-  
367 cruitment has already been shown at community level (Effiom et al., 2013; Terborgh  
368 et al., 2008; Vanthomme et al., 2010; Wright et al., 2007). Nevertheless, to our  
369 knowledge, our study is the first to reveal such a dramatic collapse of dispersal trait  
370 diversity of the temporal scale of several centuries. Our research was made possible  
371 because frugivore defaunation in the Mascarene archipelago has been well docu-  
372 mented (Cheke & Hume, 2008; Lougnon, 2005) and because the high volcanic activity  
373 on Réunion provides numerous lava flows that constitute a natural experiment acting  
374 as a “time machine”.

375           Forests on old substrata and lava flows that occurred before permanent human  
376 settlements are widely dominated by fleshy-fruited species (Albert, Flores, Rouget,  
377 Wilding, & Strasberg, 2018). They include LFF plants, that are usually big trees (Diaz  
378 et al., 2004; Thompson & Rabinowitz, 1989) with an important structural role in native  
379 forests (Appendix Fig. S7 & Fig. S8). LFF plants are far less present on lava flows that  
380 occurred while the large-bodied frugivores were strongly decreasing in number.  
381 Hence, it is likely that effective dispersal at ecosystem level was disrupted before the  
382 dispersers of most LFF species actually went extinct, as shown elsewhere (McConkey  
383 & O’Farrill, 2016). LFF plants, including seedlings, are very scarce on lava flows that  
384 occurred after the extinction of all large-bodied frugivores in 1800. This shows that the  
385 latter play an extremely important role because they can swallow large fruits and are  
386 more likely to deposit seeds away from the parent tree (Naniwadekar et al., 2019;  
387 Wotton & Kelly, 2012). This also suggests that potential dispersal alternatives are very  
388 unreliable, *e.g.* secondary dispersal by introduced vertebrates or cyclone-mediated  
389 seed dispersal (Babweteera & Brown, 2009; Federman et al., 2016). The richness of  
390 SFF plants also decreases on lava flows that occurred after 1665, despite the abun-  
391 dance of several important frugivores for this species group, the native bulbul and the  
392 hoopoe starling. Large-bodied frugivores do not just eat LFF plants and also play an  
393 important role in SFF plant dispersal (Bollen & Elsacker, 2002; Florens et al., 2017;  
394 Oleksy, Giuggioli, McKetterick, Racey, & Jones, 2017). In fact, their extinction has  
395 probably led to a decrease in the dispersal efficiency of most fleshy-fruited plants (Ba-  
396 bweteera & Brown, 2009; Carvalho et al., 2016) and to the inability of many SFF plants  
397 to reach isolated post-defaunation lava flows (Jordano et al., 2007; Wotton & Kelly,  
398 2012). We show that SFF richness eventually collapses on lava flows from the 20<sup>th</sup>  
399 century, as already suggested (Chevennement, 1990; Strasberg, 1994; Thébaud &

400 Strasberg, 1997). We also reveal that the few fleshy-fruited species that colonise these  
401 areas are usually present on older substrata. Conversely, ADF plant richness remains  
402 unchanged across the chronosequence, despite strong species replacement. This  
403 finding suggests that successional changes occur within ADF assemblages across the  
404 chronosequence, but only rarely in fleshy-fruited assemblages (Wandrag et al., 2017).

#### 405 **Potential post-dispersal limitations**

406 The pattern that we detected could partly be explained by post-dispersal factors, such  
407 as environmental filtering, e.g. light requirements, depth soil, or biotic interactions, e.g.  
408 seed predation (Wang & Smith, 2002).

409 We have consistent evidence that the total absence of many fleshy-fruited plant  
410 species, even at early life stages, on lava flows dating from [1665; 1800[ and [1800;  
411 1900[ is not a consequence of environmental filtering. Although shade tolerance or  
412 light requirements were not considered in our analyses, it is likely that some SFF un-  
413 derstorey shrubs have difficulty germinating in open canopy vegetation, especially on  
414 the most recent lava flows. However, the proportions of LFF and SFF plants do not  
415 depend on canopy cover (Appendix Fig. S9). Many vegetation plots on historical lava  
416 flows show a well-developed canopy, but totally lack a LFF tree that is very common  
417 on pre-defaunation lava flows (*Labourdonnaisia calophylloides*, Sapotaceae, Appen-  
418 dix Fig. S10). Moreover, the presence of long-lived pioneer trees across the chrono-  
419 sequence provides relevant insights: a SFF pioneer tree (*Sideroxylon borbonicum*,  
420 Sapotaceae) is common on lava flows that occurred when small frugivores were abun-  
421 dant, but is much less prevalent on [1900; 1956] lava flows, despite favorable light  
422 conditions. On the contrary, an ADF pioneer tree (*Agarista salicifolia*, Ericaceae) is  
423 present across the entire chronosequence (Appendix Fig. S10). Finally, soil type is

424 another factor that might limit recruitment, but our analyses show a standardised rich-  
425 ness as high on old substrata as on [1401, 1665[ lava flows and a low  $\beta$ -diversity  
426 between these categories. Hence, most big trees found on well-developed soils are  
427 able to establish and develop on [1401, 1665[ lava flows that usually display a very  
428 thin soil on continuous rock (Meunier et al., 2010) (Appendix Fig. S11).

429         Seed predation may also be an important mechanism that limits plant recruit-  
430 ment (Forget, 2005; Hubbell, 1980; Janzen, 1970). Rats are usually the main seed  
431 predators on oceanic islands (Shiels & Drake, 2015) and probably reached high den-  
432 sities in the late 17<sup>th</sup> century, after their introduction on Réunion (Cheke & Hume,  
433 2008). Since then, rat populations may have remained at high levels. It is however  
434 unlikely that seed predation by rats could explain the temporal shift observed between  
435 LFF and SFF plants across the chronosequence. A few LFF plants are common at all  
436 growth stages in extant mature rainforest on pre-defaunation lava flows, despite the  
437 abundance of rats (Strasberg, 1996), whereas they are totally absent from post-1800  
438 lava flows. Hence, seed predation may play a secondary role in limiting recruitment,  
439 as shown by Wotton & Kelly (2011) in New Zealand.

#### 440 **Primary succession disruption and implications for conservation**

441 Our analyses show that, in less than five centuries, primary succession on lava flows  
442 has led to plant assemblages of woody plants similar in richness and composition to  
443 those found on old substrata. The fact that LFF plants probably lost their dispersal  
444 capacity after 1800 shows that they were already present on historical lava flows in  
445 1800. Hence, well under 200 years might have been enough for the establishment of  
446 most shade-tolerant tree species. This temporal scale is consistent with Thornton

447 (1997), who documents the assembly of the Krakatau Islands ecosystem after its de-  
448 struction in 1886, *i.e.* three years after the islands' sterilisation: despite the sea barrier  
449 (12 km from the closest source and 40 km from mainland Java and Sumatra), six  
450 zoochorous plants were recorded as soon as 1896, 23 in 1905, 35 in 1920, 68 in 1934  
451 and 124 species in 1992. In the case of the Krakatau Islands, Whittaker & Jones (1994)  
452 emphasise the crucial role played by fruit pigeons able to transport large-seeded  
453 plants that became established in the decades following the initial disturbance.

454         The absence of many native species on historical lava flows has probably had  
455 severe consequences on succession processes. For instance, the absence of LFF  
456 tree species may have caused competition release (Hurt & Pacala, 1995), possibly  
457 benefiting alien plants with low dispersal limitation. Recent surveys on post-1800 lava  
458 flows reveal the presence of the same native plant communities as those surveyed by  
459 Cadet (1977), as well as the generally low or absent regeneration of native species  
460 (Albert, Flores, Franc, & Strasberg, 2019), suggesting arrested succession (Cohen,  
461 Singhakumara, & Ashton, 1995). Together, these findings demonstrate that plant com-  
462 munities of different ages do not follow the same trajectory and that the vegetation  
463 stages originally described by Cadet (1977) do not represent successional seres  
464 (Walker, Wardle, Bardgett, & Clarkson, 2010). Therefore, it is unlikely that the structure  
465 and diversity of native plant communities on historical lava flows will ever be as rich  
466 as the tropical rainforests on pre-defaunation substrata.

467         The persistently high LFF plant richness on pre-defaunation lava flows supports  
468 the fact that, despite the loss of all large-bodied frugivores since 1800, plant commu-  
469 nities can display a high level of resilience *in situ*, but a very low level of resilience by  
470 migration (Grubb, 1987). The plant communities on pre-defaunation lava flows are

471 among the most important and well-preserved testimony of Mascarenes' lowland eco-  
472 systems (Strasberg, 1996), and their protection is considered crucial (Mittermeier et  
473 al., 2004). Our results confirm that their loss would be particularly dramatic because  
474 these ecosystems have lost their resilience. Although most of the remaining lowland  
475 ecosystems are protected as part of the Réunion National Park, the high frequency of  
476 lava flows in this area of Réunion may lead to their gradual destruction. In 2007, for  
477 example, the last fragment of tropical rainforest at sea level was destroyed (Appendix  
478 Fig. S1). Moreover, the apparent maintenance of diversity on pre-defaunation lava  
479 flows is probably due to the fact that our study uses presence/absence data and does  
480 not take into account a potential failure of local recruitment for many species of the  
481 canopy. Several shade-tolerant long-lived trees hardly regenerate (Strasberg, 1996)  
482 and long-lived pioneer trees are often unable to reach gaps nearby, which makes them  
483 particularly sensitive to local extinction in the near future (Wandrag et al., 2017).

484 Today, frugivory disruption combined with alien plant invasion (see Potgieter,  
485 Wilson, Strasberg, & Richardson, 2014) leads to the development of novel ecosystems  
486 with extremely low taxonomic and functional diversity. Given the dramatic loss of na-  
487 tive fleshy-fruited plant diversity on recent lava flows, conservation strategies should  
488 include the lack of native vegetation recovery as a matter of urgency. Restoring the  
489 seed dispersal function will be necessary in defaunated ecosystems (Correia,  
490 Timóteo, Rodríguez-Echeverría, Mazars-Simon, & Heleno, 2017), as has already  
491 been done on several islands in the Indo-Pacific region (Griffiths, Hansen, Jones, Zuël,  
492 & Harris, 2011; Pedrono et al., 2013). The fact that there will be no altitudinal escape  
493 for most fleshy-fruited plants in the context of climate change makes the situation even  
494 more urgent (McConkey et al., 2012).

495 **Conclusion**

496 Defaunation can cause negative impacts on ecosystem functioning comparable with  
497 those from major drivers of global change (Young et al., 2016). However, its long term  
498 impact on dynamics of very long-lived trees is not sufficiently documented. Our study  
499 brings a first evidence of frugivore defaunation effect at community level over a tem-  
500 poral scale of 300 years. The studied chronosequence of lava flows acting as a “time  
501 machine” and harboring plant communities settled before and after human colonisa-  
502 tion provides a natural experiment on one of the last tropical islands colonised by hu-  
503 mans. To our knowledge, this is the first time that such a collapse of dispersal trait  
504 diversity has been shown. It strongly argues in favour of restoration programs targeting  
505 the re-establishment of seed dispersal interactions by promoting native frugivore pop-  
506 ulations and rewilding projects focusing on large vertebrates.

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519 **Authors' contributions**

520 Sébastien Albert, Olivier Flores and Dominique Strasberg developed the ideas for the  
521 research and collected data. Sébastien Albert and Olivier Flores analysed the data.  
522 All authors contributed critically to the drafts of the paper and have given their approval  
523 for publication.

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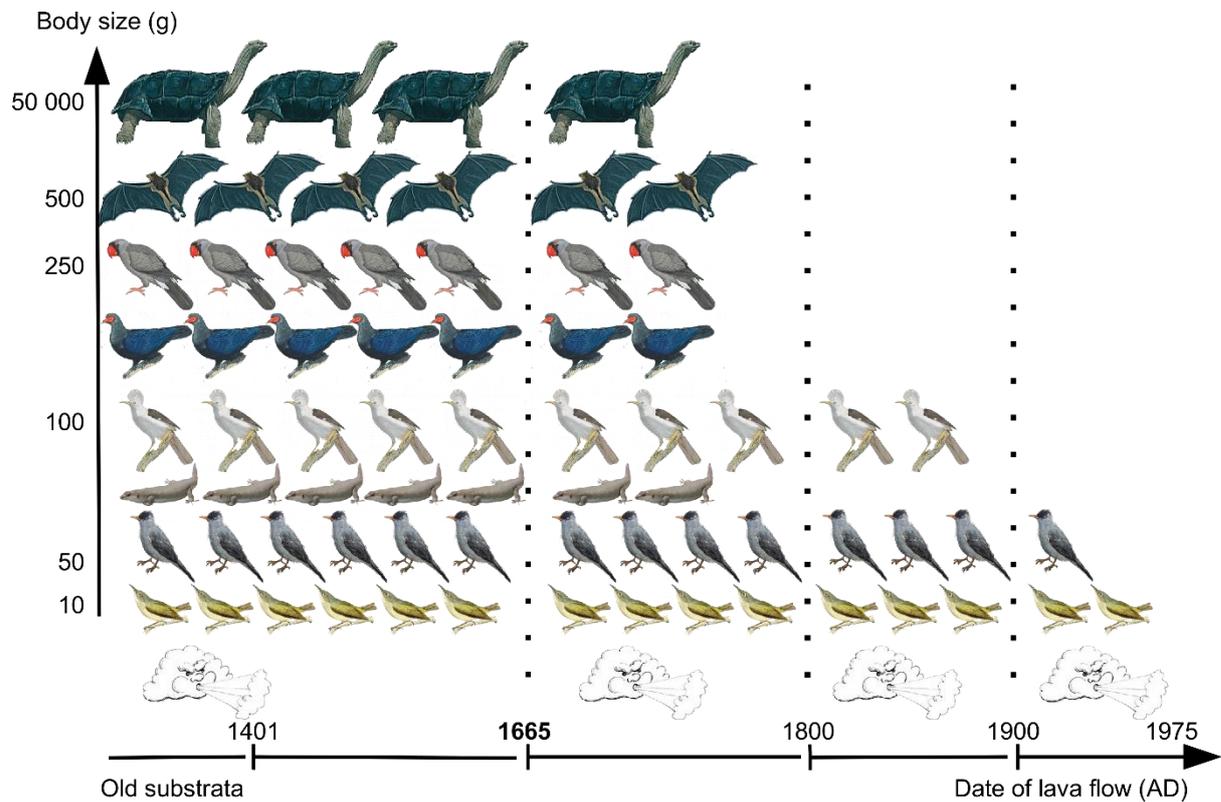
## 525 **Supporting information**

526 Appendix. This appendix includes Table (S1) and Figures (S1, S2), presenting additional  
527 information on methods, and Table (S2) and Figures (S3 to S11), presenting  
528 additional results related to species richness, species composition and vegetation  
529 structure across the chronosequence.

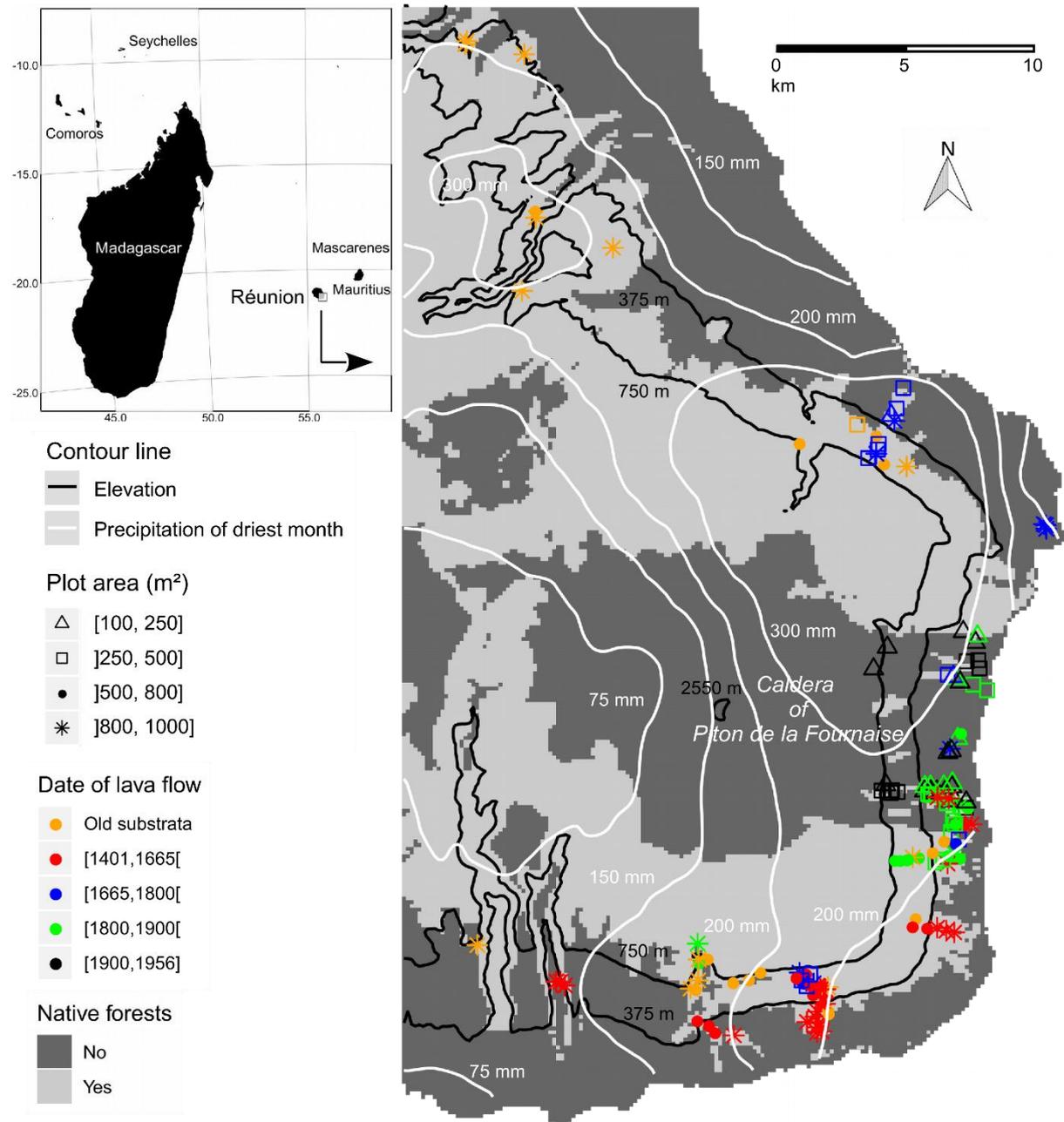
## 530 **Data accessibility**

531 Data available from the Dryad Digital Repository:  
532 <https://doi.org/10.5061/dryad.2v6wwpzhm> (Albert, Flores, & Strasberg, 2019)

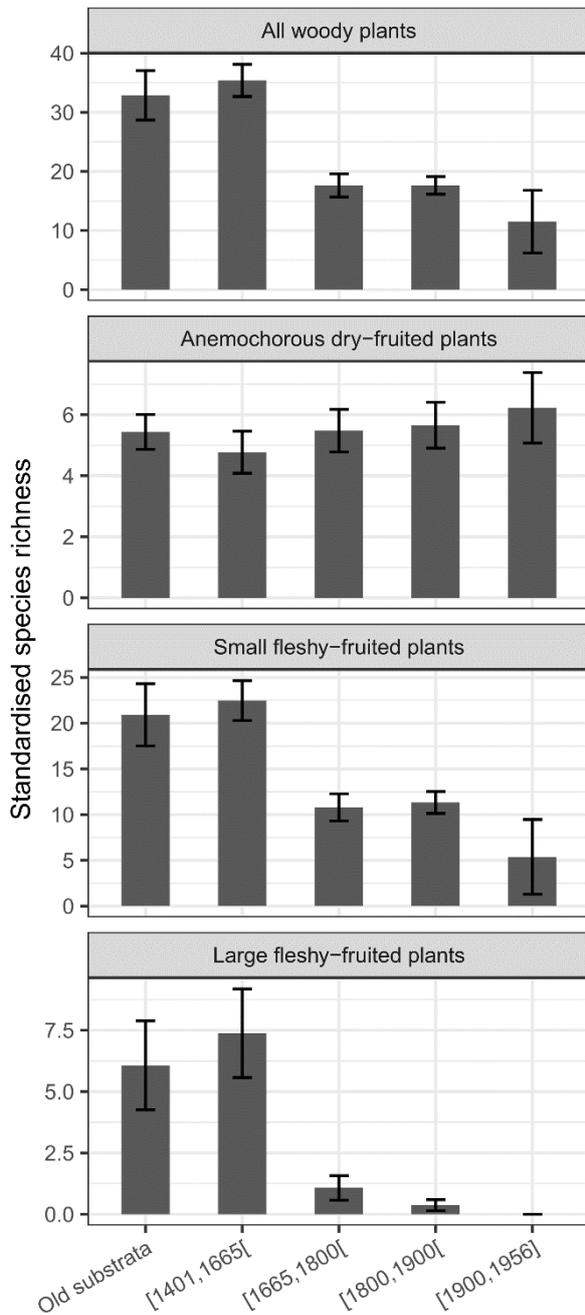
## Figures



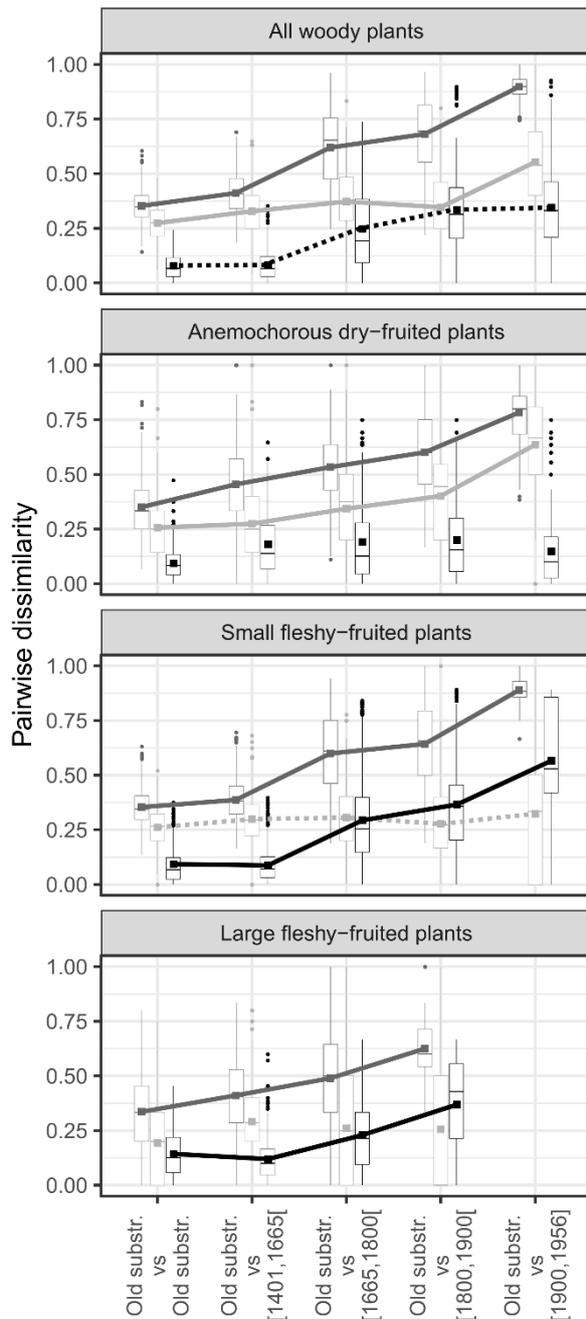
**Fig. 1.** Historical milestones in relation to availability of dispersal agents on Réunion across a long-term chronosequence of lava flows. Availability through time in native frugivores (from top to bottom: giant tortoises, flying foxes, parrots, fruit pigeons, starlings, skinks, bulbuls and white-eyes) is inferred from Cheke and Hume (2008) and Lounnon (2005). Native frugivore assemblages were diversified and oversized until the first human settlements were established in 1665 AD. After 135 years of human settlement throughout the lowlands, habitat destruction and overharvesting led to the extinction of large-bodied frugivores by 1800. The Réunion bulbul was abundant until the beginning of the 20<sup>th</sup> century, when populations declined sharply. They have remained at low levels throughout the 20<sup>th</sup> century until Cadet's sampling in 1975. Wind is assumed to be constantly present across the chronosequence. The giant tortoises, flying foxes, parrots, fruit pigeons and starlings were illustrated by Julian Hume, the white-eyes by John Gerrard Keulemans, the skinks by Josh Noseworthy and the bulbuls by Dominique Strasberg. For more details about frugivores, see Appendix Tab. S1.



**Fig. 2.** The study site on Réunion in the Piton de la Fournaise area. Réunion is an oceanic island in the South-West Indian Ocean, situated between Madagascar and Mauritius in the Mascarenes. The massif of the Piton de la Fournaise extends across the South-Eastern third of the island (white rectangle). The 151 vegetation plots are located on the windward side below 750 m asl and shown according to lava flow dating: 123 plots in four classes are located on lava flows that occurred between 1401 and 1956; and 28 plots are found on old substrata, i.e. over 1000 years old.



**Fig. 3.** *Estimated standardised richness of native woody plants at any growth stage across the chronosequence (sampling area fixed at 591 m<sup>2</sup>, elevation at 354 m asl, precipitation of driest month at 226 mm, isolation at 46% of native forests). Richness is independently assessed for woody plants overall and for three dispersal trait groups: anemochorous dry-fruited, small fleshy-fruited and large fleshy-fruited plants that respectively depend on wind, frugivores of various size and large-bodied frugivores. Confidence intervals at 95% on estimated standardised richness are given by error bars. Note that large fleshy-fruited plants are completely absent on the most recent lava flows.*



**Fig. 4.** Pairwise Sorensen (dark grey), turnover (light grey) and nestedness (black) dissimilarities between native plant assemblages on old substrata (used as reference) and native plant assemblages in each lava flow age class. Pairwise dissimilarities are independently assessed for woody plants overall and for three dispersal trait groups: anemochorous dry-fruited, small fleshy-fruited and large fleshy-fruited plants that respectively depend on wind, frugivores of various size and large-bodied frugivores. Boxplots and squares respectively display raw and mean values for each age class. Solid lines are displayed when the age of lava flow is the most explanatory variable

*apart the effect of area, elevation, precipitation of driest month, isolation and geographical distance (Appendix Fig. S2). Dotted lines are displayed when the age of lava flow has a significant effect, but is not the most explanatory variable. Note that large fleshy-fruited plants are completely absent on the most recent lava flows.*