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1 ~~With or without frugivores? Flying foxes sustain woody plant~~  
2 ~~regeneration~~ **Differing severity of frugivore loss contrasts the fate of native**  
3 **forests on the land of the Dodo (Mascarene archipelago)**

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# 1 Differing severity of frugivore loss contrasts the fate of native forests on the 2 land of the Dodo (Mascarene archipelago)

## 3 **ABSTRACT**

4 Frugivore loss has the potential to alter the regeneration of tropical hyperdiverse forests. However, no  
5 study has investigated tree diversity maintenance within old-growth protected forests on tropical  
6 oceanic islands where conservation stakes are considerable. In the Mascarenes, the largest frugivores  
7 including the Dodo went extinct after human colonization in the 17<sup>th</sup> century. Mauritius, today devoid of  
8 almost all its native habitats, retains an important population of flying foxes, while Réunion, largely  
9 covered by native habitats, has lost all but one of its native frugivores, a bulbul. Using census data of  
10 130 woody species from 3-ha permanent plots from Mauritius (MAU-BF) and Réunion (REU-ML), we  
11 show that most fleshy-fruited species regenerate poorly at REU-ML, in contrast to MAU-BF, although  
12 large-seeded fleshy-fruited species regenerate poorly at both sites. The difference in recruitment is all  
13 the more striking because local woody plant diversity at MAU-BF is double that at REU-ML. Changes  
14 observed in the understory will probably lead to a strongly impoverished canopy at REU-ML, and to  
15 canopy shift composition at MAU-BF. Hence, the protected but highly fragmented forests on Mauritius  
16 are likely more resilient than those on Réunion usually considered best preserved within the ecoregion.  
17 Although processes other than seed dispersal might also be at work, flying foxes probably ensure  
18 effective dispersal of numerous native fleshy-fruited plants on Mauritius, contrary to only bulbuls on  
19 Réunion. To efficiently protect tropical rainforests on islands and continents alike, there is an urgent  
20 need to protect extant frugivores populations and reinstate seed dispersal function wherever necessary.

## 21 **KEYWORDS**

22 Frugivore extinction; island biology; Janzen-Connell effect; plant diversity loss; protected tropical forest;  
23 seed dispersal disruption

## 24 **INTRODUCTION**

25 Vertebrates play an important role as mutualistic pollinators or seed dispersers in most tropical forests  
26 worldwide (Dirzo et al., 2014; Turner, 2001). Recently, it has become clear that their loss has the  
27 potential to deeply alter tropical forest composition (Albert et al., 2020b; Dirzo et al., 2014; Effiom et al.,  
28 2013; Terborgh et al., 2008; Trolliet et al., 2019; Wandrag et al., 2017). Most conservation strategies  
29 have for decades involved integrating forest habitats into protected areas. However, preserving forests  
30 in which mutualistic vertebrates are absent or at low density might be ineffective when their functioning  
31 highly depends on plant-animals interactions (Laurance et al., 2012).

32 The various life-history strategies of trees complicate the assessment of the impact of frugivore  
33 extirpation, but studies at community level indicate an alteration of the recruitment for numerous fleshy-  
34 fruited plants in defaunated protected forests of the Neotropics (Terborgh et al., 2008), Central Africa  
35 (Effiom et al., 2013; Trolliet et al., 2019) and Borneo (Harrison et al., 2013). Changes in recruitment  
36 were detected just a few decades after frugivore decline or loss, being mainly the consequence of the  
37 negative distance- and/or density-dependent effects on germination or seedling survival close to  
38 maternal trees (Comita et al., 2014; Connell, 1971; Janzen, 1970). Other works have also shown how  
39 fruit consumption by frugivores may enhance the recruitment of fleshy-fruited plants by removing  
40 potential physical/chemical dormancy (Soltani et al., 2018; Traveset et al., 2008) or more simply, by  
41 cleaning the seed of flesh that could attract pathogens and seed predators causing propagule mortality  
42 (Levi and Peres, 2013). Hence, frugivores play a central role in closing the loop of dispersal in habitats  
43 largely dominated by fleshy-fruited plants (Wang and Smith, 2002).

44 In theory, the decline and extirpation of frugivores threaten tropical forests not only on  
45 continents, where they can be hyperdiverse (Terborgh et al., 2008), but also on oceanic islands

46 (Hansen et al., 2008). Despite their isolation and small areas, oceanic islands can indeed host  
47 substantial richness in fleshy-fruited species, e.g. one forest patch on Mauritius harbours more than 60  
48 tree species per hectare of which 89% are fleshy-fruited (Florens et al., 2017a, 2012). This relative  
49 diversity is comparable to some African continental tropical rainforests (Turner, 2001). Hence, one may  
50 expect a higher negative impact of frugivore loss on diversity maintenance on tropical oceanic islands  
51 since numerous frugivores went extinct after human colonization (Hansen and Galetti, 2009; Heinen et  
52 al., 2017), and having no options of alternative seed dispersal systems (Guimarães et al., 2008).

53 Fleshy-fruited plant species vary in their vulnerability following the extinction of frugivores  
54 (Guimarães et al., 2008). Plants with large fruits and/or large seeds are particularly at risk because  
55 large vertebrates often constitute the first guild to be extirpated (Dirzo et al., 2014; Hansen and Galetti,  
56 2009; Heinen et al., 2017). Several studies have shown that insular large-seeded tree species  
57 experience recruitment failure at plant population level due to disperser loss (Carpenter et al., 2018;  
58 Hansen et al., 2008; Wotton and Kelly, 2011). Although large-seeded species are reputedly well  
59 adapted to the strong competition encountered in tropical understory (Leishman et al., 2000), their  
60 seedlings/saplings can be strongly depleted at community level in defaunated sites (Effiom et al., 2013;  
61 Harrison et al., 2013; Terborgh et al., 2008; Trolliet et al., 2019). To our knowledge however, the  
62 relationship between recruitment patterns inferred from size-distributions and defaunation has never  
63 been carried out before on islands, where one may expect a strong negative impact of large-bodied  
64 frugivore extinction on large-seeded plant recruitment.

65 This study aims to assess the impact of frugivore extinction on forest regeneration by comparing  
66 diameter cohorts of native woody species within two islands sharing a close biogeographic history, but  
67 with different trajectories since human colonization (Fig.1 ). Mauritius and Réunion had lowland  
68 species-rich forests dominated by fleshy-fruited species (Albert et al., 2018; Florens et al., 2017a;  
69 Strasberg, 1996). On Réunion, the extirpation of large frugivores from Réunion dates back two  
70 centuries (Fig.1). Consequently, primary succession dynamics have been severely altered after  
71 frugivore extinctions and great uncertainty remains about the capacity of established forests to maintain  
72 their diversity in the near future (Albert et al., 2020b). On Mauritius by contrast, *Pteropus niger* still  
73 exists in large populations and is a keystone species which feeds fruits of at least 53% of woody plants  
74 (Florens et al., 2017a; Fig.1). With a mean body mass of 450 g, this flying-fox is about nine times larger  
75 than the bulbul *Hypsipetes borbonicus*, the largest extant frugivorous bird on Réunion (Cheke and  
76 Hume, 2008). This critical difference in the defaunation history between the islands provides a relevant  
77 opportunity to use these two main islands of the Mascarenes as pseudo-replicates, and to isolate the  
78 effects of seed dispersal from other factors on plant recruitment. Although this biogeographical setting  
79 is relevant to address the effects of defaunation on forest regeneration, we note that Mauritius cannot  
80 be considered as a strict control in terms of frugivory interaction. Indeed, Mauritius also lost its largest  
81 frugivore species that were able to swallow large fruits (Fig.1) and their extirpation has probably not  
82 been fully compensated for by the surviving fauna (Howe, 2016; Meehan et al., 2002; Trolliet et al.,  
83 2019).

84 Using census data from permanent plots at Brise Fer on Mauritius (MAU-BF) and Mare Longue  
85 on Réunion (REU-ML), we address three complementary hypotheses in response to differential  
86 alteration of seed dispersal networks. First, we assume that plant diversity is better maintained at MAU-  
87 BF than at REU-ML. In particular, at community level, we expect that the diversity among juveniles  
88 should be similar or greater than that of adults at MAU-BF, whereas it should be lower at REU-ML.  
89 Second, within species, we assume a higher number of juveniles relative to adults at MAU-BF than at  
90 REU-ML. Indeed, few juveniles in proportion at a given time may indicate a declining population (Condit  
91 et al., 1998). Third, we hypothesize seed size to have a strong influence on plant diversity and juveniles  
92 ratio. The extinction of all Mascarene frugivores able to swallow fruit >13 mm in diameter probably led  
93 to recruitment failure of large-seeded fleshy-fruited plants on both islands, although the extant flying  
94 foxes might have, to some extent, carried out the function of these extinct large frugivores on Mauritius.

95 However, some plants, especially small-seeded species, might also have difficulties in regenerating in  
96 the understory independently of their ability to be dispersed, because of adverse establishment  
97 conditions, including competition and shade (Howe and Smallwood, 1982; Leishman et al., 2000). This  
98 could be particularly true at REU-ML where the canopy is higher and the understory darker than at  
99 MAU-BF.

## 100 **METHODS**

### 101 **Study sites**

102 Réunion (2512 km<sup>2</sup>, 2-3 million years) and Mauritius (1865 km<sup>2</sup>, 7.8 million years), the two largest  
103 islands of the Mascarene archipelago in the tropical Indian Ocean, are respectively 750 and 900 km  
104 east of Madagascar (Fig.1). They are part of the biodiversity hotspot of South-West Indian Ocean  
105 islands (Mittermeier et al., 2004). The Mascarene islands share most of their animal and plant lineages,  
106 with a great number of endemic species given their relatively small terrestrial area (Kier et al., 2009).  
107 Mauritius and Réunion host 691 native flowering plant species (273 single island endemic and 150  
108 Mascarene endemic) and 550 species (165 single-island endemic and 140 Mascarene endemic),  
109 respectively (Baider et al., 2010). Extinct and threatened species make 10.9% and 81.7% on Mauritius,  
110 while 1.2% and 50.9% on Réunion (Baider et al., 2010). Lower rates of plant extinction and threat on  
111 Réunion is attributed to its higher native cover (30%) than on Mauritius (4.4%), although lowland  
112 habitats have been almost completely transformed on Réunion (Florens et al., 2012; Strasberg et al.,  
113 2005). In that context, permanent plots at Brise Fer on Mauritius (MAU-BF) and Mare Longue on  
114 Réunion (REU-ML) are used for conservation purposes to monitor the remnants of evergreen wet  
115 tropical rainforest in the Mascarenes (Cadet, 1977; Florens et al., 2012; Safford, 1997; Strasberg et al.,  
116 2005).

#### 117 *Mare Longue (Réunion)*

118 The three 1-ha plots at REU-ML (centred around 21°21'13" S, 55°44'40" E) were in reserve (68  
119 hectares), now included in the National park of Réunion (Fig.1). This site is at the lower reaches of the  
120 last continuous corridor of vegetation in the Mascarenes running from 100 m asl to the volcano caldera  
121 at 2400 m. This forest corridor is surrounded by secondary vegetation and sugar cane fields at lower  
122 elevations. The studied plots are situated between 130 and 340 m asl and receive ca 4000 mm of mean  
123 annual rainfall (Réchou et al., 2019; Tab.1). The forest at REU-ML is classified as a lowland tropical  
124 rainforest with no deciduous species (Cadet, 1977) and is little invaded by alien plants . It is set on  
125 pahoehoe basaltic lava flow estimated at ca 430 years old (Albert et al., 2020a) and not yet significantly  
126 altered. Emergent trees can reach 25 m high and canopy is about 15-20 m, with an average of ca 900  
127 stems >10 cm dbh per hectare and basal area over 70 m<sup>2</sup>.ha<sup>-1</sup> (Tab.1).

#### 128 *Brise Fer (Mauritius)*

129 The three 1-ha plots at MAU-BF (centred around 20°22'20" S, 57°26'10" E) are near the western edge  
130 of Mauritius central plateau, in the Black River Gorges National Park (Fig.1). This National Park has the  
131 largest remnants of native forests on Mauritius (Florens, 2013). The studied plots are located at 560-  
132 600 m asl and receive ca 2400 mm of mean annual rainfall (Tab.1). The forest at MAU-BF is classified  
133 as a tropical rainforest (Lorence and Sussman, 1986). Trees can reach 18 m high and canopy is about  
134 12-15 m. MAU-BF has 1000-1600 stems >10 cm dbh per hectare but lower basal area than REU-ML  
135 (Tab.1). The area has been weeded of alien plant species since 1996 (Baider and Florens, 2011) .

### 136 **Sampling**

137 Monitoring of permanent plots began in the 1990s (at REU-ML), but we used the data sampled between  
138 2010 and 2014 to avoid temporal bias. We used saplings reaching 1 cm diameter at breast high (dbh,

139 measured at 1.3 m), as this was the threshold for measurements at REU-ML. We calculated an  
140 equivalent dbh for plants that had multiple stems.

#### 141 *Growth forms*

142 We categorized the growth form of each woody species as either tree, shrub or climber according to the  
143 description in the *Flore des Mascareignes* (Bossier et al., 1976–ongoing) or newer publication, and  
144 expert knowledge of the local floras. Shrubs could reach up to 15 cm dbh, while trees reached a  
145 maximum of 94 cm at MAU-BF and 148.8 cm dbh at REU-ML.

#### 146 *Diameter cohorts*

147 We excluded climbers and species without secondary growth (e.g. Monocots, fern trees) from the  
148 analyses and defined “young”, “intermediate” and “adult” cohorts as stems with dbh of [1; 3[ cm, [3; 10]  
149 cm and >10 cm, respectively for trees, and [1; 1.5[ cm, [1.5; 3] cm and >3 cm, respectively for shrubs  
150 (Fig.2). For each site, we extracted the number of young, intermediate and adult cohorts for each  
151 species.

#### 152 *Dispersal traits*

153 We categorized the fruit type of each woody species as either fleshy (FF) or dry (DF), using the *Flore*  
154 *des Mascareignes* (Bossier et al., 1976-ongoing), and expert knowledge of the local floras when  
155 information was missing or incomplete. Fruits were classified as fleshy if they had noticeable fleshy  
156 pericarps or fleshy appendages when mature. In the Mascarenes, most DF plants rely on abiotic agents  
157 for their dispersal.

158 We used seed length as a proxy for seed size as this trait was known for all species, based on  
159 the *Flore des Mascareignes* (Bossier et al., 1976-onwards) and authors' field measurements. At MAU-  
160 BF and REU-ML, seed length of woody species ranged from 0.06 cm (*Weinmannia tinctoria*,  
161 Cunoniaceae) to 5.3 cm (*Elaeocarpus integrifolius*, Elaeocarpaceae), which represented an order of  
162 magnitude of  $10^6$  in seed mass. We assigned seed length to three size classes (Appendix Fig.A1):  
163 small-seeded plants [0.06; 0.6] cm, medium-seeded plants [0.6; 1.5] cm and large-seeded plants [1.5;  
164 5.3] cm (following Corlett and Primack, 2006; Costa et al., 2012). Large seeds cannot be swallowed by  
165 the extant frugivores in the Mascarenes, but can be dispersed by flying foxes over short distances at  
166 MAU-BF (Florens et al., 2017a). Because there were no large-seeded and few medium-seeded DF  
167 species, we combined both classes to create a “dispersal trait” factor with four classes: (1) all DF  
168 species; and FF species that were (2) small-seeded, (3) medium-seeded, and (4) large-seeded.

## 169 **Analyses**

#### 170 *Dominance-diversity across diameter cohorts*

171 To analyze changes in woody species dominance-diversity across diameter cohorts (i.e. from adults to  
172 young), we used a rank-abundance distribution approach. Rank-abundance distributions display log-  
173 transformed species abundance ranked in declining order of species abundance. This approach,  
174 recommended by Matthews and Whittaker (2015), allows to describe the full distribution of  
175 commonness and rarity for the whole woody community and according dispersal traits at each site.

#### 176 *Diversity indices across diameter cohorts*

177 We first used the Shannon diversity index ( $I_{shannon}$ ) to synthetically characterize changes in diversity  
178 highlighted with rank-log abundance plots. We then assessed changes in phylogenetic diversity using  
179 the function *pla* (R package 'adiv') that generalizes PD index of Faith (1992) to account for species  
180 abundance (Pavoine, 2020). In this respect, we constructed phylogenetic trees for woody plant  
181 communities based on the phylogeny from Zanne et al. (2013) (R package 'brranching').

182 Phylogenetic decoupling can show whether changes in diversity affect particular lineages.  
183 Phylogenetic decoupling was calculated as  $(p_{a=1, adult} / p_{a=1, young}) / (I_{shannon, adult} / I_{shannon, young})$  and  $(p_{a=1, adult} / p_{a=1, int.}) / (I_{shannon, adult} / I_{shannon, int.})$  for “adult vs young cohorts” and “adult vs intermediate cohorts”  
184 respectively. We assume values  $>1.1$  and  $<0.9$  would reveal stronger and weaker changes in  
185 phylogenetic diversity than in Shannon diversity, respectively.  
186

### 187 *Demographic status assessment*

188 The demographic status of a tree population can be assessed via the ratio of juveniles to adults (Condit  
189 et al., 1998), hereafter called recruitment index. We therefore calculated the recruitment index of each  
190 woody species:  $n_{young} / (n_{young} + n_{adult})$  for youngs and  $n_{int} / (n_{int} + n_{int})$  for intermediate cohorts, including  
191 rare species, e.g. a single canopy tree without any conspecific individual in the understory. Finally, we  
192 estimated, at each site, the distribution of the recruitment index within classes of dispersal traits and  
193 growth forms (shrubs vs. trees). Analyses were done in R ver. 4.0.2 (R Core Team).

## 194 **RESULTS**

195 Total woody species richness was higher at Brise Fer (MAU-BF, 100 species: 65 trees, 35 shrubs) than  
196 at Mare Longue (REU-ML, 51 species: 42 trees, 9 shrubs). Woody plants were overwhelmingly fleshy-  
197 fruited (FF) (91% at MAU-BF; 88% at REU-ML). MAU-BF and REU-ML shared only 20 of the 130  
198 species studied in total, but shared 35 genera (51% of those at MAU-BF and 81% at REU-ML; Tab.A2).  
199 Eight other genera present at REU-ML, but absent at MAU-BF do exist on Mauritius. Among the 31  
200 genera present at MAU-BF but absent at REU-ML, 19 were present on Réunion (often in subhumid  
201 habitats, e.g. *Pleurostyliia*, *Pyrostria*, *Securinega*, *Scutia*) and 12 only occurred on Mauritius (Tab.A2).  
202 MAU-BF showed 1.47 species per genus on average against 1.16 species per genus at REU-ML, as a  
203 result of the existence of various radiated plant species at MAU-BF.

### 204 **Dominance-diversity across diameter cohorts**

205 Across diameter cohorts (from adults, to intermediate cohorts and youngs), woody species richness  
206 strongly decreased from 47, to 40 and 35 species at REU-ML, whereas it slightly decreased at MAU-BF  
207 from 87, to 84 and 80 species (Fig.3). We detected a strong increase in the steepness of the  
208 dominance-diversity curves of woody species overall at REU-ML. Some species excessively dominated  
209 young cohorts, and rare species were more numerous among intermediate and young cohorts despite  
210 depauperate richness. On the contrary, we detected no increase in steepness in the dominance-  
211 diversity curves at MAU-BF, but a tailing-off of rare species (Fig.3).

212 Considering dispersal traits (DF plants, FF small-, medium- and large-seeded plants), all groups  
213 were negatively impacted at REU-ML, seen by a noticeable decline in species richness across diameter  
214 cohorts (Fig.3). The increase in steepness curves of FF plants was related to one or several species  
215 becoming more dominant, e.g. the shrub *Chassalia corallioides* (Rubiaceae) and the tree  
216 *Labourdonnaisia calophylloides* (Sapotaceae) among medium-seeded and large-seeded plants,  
217 respectively. Actually, most ranks among young cohorts at REU-ML showed a strong deficit of  
218 abundance in comparison to adults, whatever dispersal traits (Fig.3).

219 At MAU-BF, FF small- and medium-seeded plants showed stability and a slight increase of  
220 species richness across diameter cohorts, respectively. Both groups had higher juvenile abundance on  
221 most ranks (Fig.3). Conversely, the strong increase in the steepness of dominance-diversity curve of FF  
222 large-seeded plants was accompanied by an important decline in species richness (-8 species; Fig.3).  
223 Large-seeded species were diverse in the canopy of MAU-BF with five species exceeding 100 stems  
224 (surprisingly, only one species at REU-ML), but their stem proportion strongly decreased across  
225 diameter cohorts from 0.37 to 0.21. Hence, the tailing-off of the overall dominance-diversity curve at  
226 MAU-BF was mainly due to diversity loss of large-seeded plants.

227 Dry-fruited plants showed low species richness at both REU-ML and MAU-BF, but they were

228 nevertheless fairly well represented in the canopies of both forests (Fig.3). While dominance-diversity  
229 curves were relatively similar across diameter cohorts at MAU-BF, dry-fruited plants were rare among  
230 juveniles at REU-ML. This shows that these plants could not be involved in any replacement in the  
231 understory at both sites and, therefore, were not studied further below.

### 232 **Diversity indices across diameter cohorts of fleshy-fruited plants**

233 Similarly to dominance-diversity curves, Shannon indices of small and medium-seeded plants strongly  
234 decreased across diameter cohorts at REU-ML, while they increased at MAU-BF (Fig.4). The Shannon  
235 index of large-seeded plants, which was already low for adults at REU-ML, declined further, and  
236 steadily decreased at MAU-BF. Phylogenetic diversity showed broadly similar trends across diameter  
237 cohorts for most dispersal traits at both sites. However, phylogenetic decoupling, i.e. values  $> 1.1$  and  $<$   
238  $0.9$  (Fig.4), was observed for medium-seeded plants at REU-ML and large-seeded plants at MAU-BF.  
239 At MAU-BF, the lower decrease in phylogenetic diversity of large-seeded plants was actually  
240 associated with the decline among young of several radiated large-seeded species within  
241 *Eugenia* / *Syzygium* (Myrtaceae), *Labourdonnaisia* (Sapotaceae) and *Diospyros* (Ebenaceae; Fig.A2).  
242 Conversely, the higher decrease in phylogenetic diversity of medium-seeded plants at REU-ML came  
243 from the high dominance of few medium-seeded Rubiaceae among young and from species of *Ocotea*  
244 (Lauraceae), *Xylopia* (Annonaceae) and *Tambourissa* (Monimiaceae) showing very few individuals,  
245 leading to low occurrence of Magnoliidae in the understory.

### 246 **Demographic status assessment of fleshy-fruited plants**

247 The median recruitment index of small- and medium-seeded FF trees was between three and five times  
248 higher at MAU-BF (between 0.7 & 0.8, Fig.5) than at REU-ML (between 0.15 & 0.26). In other words,  
249 half of small- and medium-seeded tree species had at least three times as many adults as juveniles at  
250 REU-ML and at least three juveniles for every adult at MAU-BF. For large-seeded FF trees, the median  
251 recruitment index was low at both sites (between 0.11 & 0.43), and the situation was paradoxically  
252 better at REU-ML than at MAU-BF for young. If this result has to be tempered by the low diversity of  
253 large-seeded trees at REU-ML, the collapse of the recruitment index observed in this group at MAU-BF  
254 was particularly striking.

255 The median recruitment index of small- and medium-seeded FF shrubs was relatively similar at  
256 MAU-BF and REU-ML (between 0.57 & 0.69 and between 0.45 & 0.58 for young and intermediate  
257 cohorts, respectively, Fig.5). The median recruitment index of shrubs at REU-ML was thus four times  
258 higher than that of trees with the same dispersal traits, despite the low number of shrub species.  
259 Conversely, although not low at MAU-BF, the median recruitment index of small- and medium-seeded  
260 shrubs was slightly lower than for juvenile trees. The few large-seeded shrubs in this study were only  
261 encountered at MAU-BF and showed a particularly low median recruitment index ( $< 0.09$ ). For details of  
262 the results for each woody species, please report to the dataset (available at  
263 <http://dx.doi.org/10.17632/r3x9hxt98s.1#file-2e500bfd-9b67-4bee-adac-e21e2d55f06c>).

## 264 **DISCUSSION**

265 Comparing three one-hectare plots of Mare Longue on Réunion (REU-ML) and Brise Fer on Mauritius  
266 (MAU-BF), famous for being the land of the Dodo, is a unique opportunity to explore the consequences  
267 of frugivores extinctions on the maintenance of diversity within tropical forests, as initiated by Terborgh  
268 et al. (2008) in Peru. On Réunion, all large-bodied native frugivores went extinct 200 years ago and the  
269 largest extant frugivore, the bulbul *Hypsipetes borbonicus*, weighs just over 50 g (Cheke and Hume,  
270 2008). On Mauritius, all frugivores above 600 g (including the Dodo), are also extinct, but MAU-BF still  
271 hosts a sister species of bulbul, but also a parakeet and more importantly a population of flying foxes  
272 (*Pteropus niger*) which weighs up to 540 g (Fig.1 & Tab.A1). Our results support three assumed  
273 differences between REU-ML considered as treatment (defaunated forest) and MAU-BF as pseudo-



274 control: (1) diversity is better preserved at MAU-BF than at REU-ML; (2) number of juveniles relative to  
275 adults is larger at MAU-BF than at REU-ML, indicating stronger forest regeneration at MAU-BF;  
276 (3) large-seeded plants have difficulties in regenerating in the understory at both sites. Our results  
277 therefore indicate that the loss of frugivores likely has a severe impact on the regeneration of lowland  
278 tropical forests in the Mascarenes. Hence, even protected forests on oceanic islands would be just as  
279 much at risk as tropical forests in Neotropics (Terborgh et al., 2008), in Central Africa (Effiom et al.,  
280 2013; Trollet et al., 2019) and in Borneo (Harrison et al., 2013).

### 281 **Concern about strong diversity loss at REU-ML, encouraging situation at MAU-BF**

282 Overall woody species richness is about twice as high at MAU-BF than at REU-ML, and if the  
283 associated factors are beyond the scope of this study, the maintenance of diversity across diameter  
284 cohorts (from adult to young) at MAU-BF compared to REU-ML is noteworthy. Over a third (ca 35%) of  
285 woody species do not have even a single sapling in the understory at REU-ML, compared to less than a  
286 fifth (ca 18%) at MAU-BF, especially large-seeded FF plants. In accordance, the recruitment is notably  
287 higher at MAU-BF than at REU-ML, except for large-seeded FF species, for which it is low at both sites.  
288 Although REU-ML forest is considered as the best preserved tropical rainforest in Mascarene islands  
289 (Strasberg, 1996), the extent of diversity loss in the understory and the poor recruitment of saplings for  
290 most species, questions the long-term sustainability of native forests on Réunion (Albert et al., 2020b).  
291 On the contrary, the important regeneration of numerous species at MAU-BF shows that weeding of  
292 invasive alien plants since the mid-1990s (Lorence and Sussman, 1986; Monty et al., 2013), has  
293 allowed this today promising recruitment (Fig.A3). Moreover, these observed differences between sites  
294 are remarkable as invasive alien mammals as pigs, deer or macaques are present at MAU-BF and  
295 absent at REU-ML (Florens, 2013). However, while the situation is encouraging at MAU-BF, our results  
296 indicate that when immediate threats are removed, there are still ongoing problems, as most large-  
297 seeded plants cannot recover despite conservation actions (Krivek et al., 2020). Therefore, it is likely  
298 that MAU-BF forest will probably experience a shift in composition in the future with considerably less  
299 large-seeded plants present in the canopy, as predicted elsewhere (Effiom et al., 2013; Harrison et al.,  
300 2013; Terborgh et al., 2008). This would be all the more problematic as this loss would affect structural  
301 tree species derived from the largest radiations, e.g. within *Eugenia*, *Syzygium* or *Diospyros* genera.

302 One might argue that we did not study community dynamics, and that caution must be taken  
303 about the demographic status of plants, as few juveniles at a given time would not necessarily translate  
304 in a population decline (Condit et al., 1998). Indeed, the non left-skewed diametric distribution might  
305 reflect the normal depletion in the understory of a fast-growing species sampled at an unfavourable  
306 time window. However, fast-growing species are very rare in the Mascarene flora (Cadet, 1977; Florens  
307 et al., 2017b), and the lack of recruitment of numerous large-seeded plants that are theoretically  
308 adapted to deeply shaded understory with strong competition (Leishman et al., 2000) suggests that  
309 anomalies in static diameter distribution truly derive from failure in forest regeneration because of  
310 strong dispersal limitation. Taking into account all dbh (and not only >1 cm) at MAU-BF shows, for  
311 example, that the recruitment of large-seeded plants remains very low, contrary to small- and medium-  
312 seeded FF plants which show a (very) large number of saplings with dbh < 1cm (Fig.A4). The difficulty  
313 now lies in disentangling the mechanisms underlying this pattern of diversity, particularly since factors  
314 other than the availability in frugivores, such as vegetation structure or other post-dispersal limitations,  
315 fluctuate between the two sites.

### 316 **The likely crucial role of flying foxes in woody plant dispersal on Mauritius**

317 Diversity loss at both sites primarily involves FF plants that make the bulk of woody plants at both sites.  
318 The disparities observed in the results between REU-ML and MAU-BF may be strongly influenced by a  
319 more or less significant alteration of mutualism networks at archipelago scale (Schleuning et al., 2014).  
320 Such a discrepancy in diversity maintenance and sapling recruitment of FF plants, except for large-

321 seeded ones, may be mainly due to the persistence of an important population of flying foxes on  
322 Mauritius. Indeed, this bat is today the most important keystone species at MAU-BF due to the  
323 extinction of all other large-bodied frugivores. Flying foxes are known to feed upon numerous native  
324 species on Mauritius (Florens et al., 2017a; Nyhagen et al., 2005) and the role of Pteropodidae as  
325 effective seed dispersers of small- and medium-seeded plants is well-known throughout the  
326 Paleotropics (Bollen and Elsacker, 2002; McConkey and Drake, 2006; Muscarella and Fleming, 2007;  
327 Oleksy et al., 2017; van Toor et al., 2019). Flying foxes probably ensure island-scale mobility for  
328 numerous small-seeded native species that are sometimes absent from MAU-BF canopies (Oleksy et  
329 al., 2019), ultimately allowing maintenance of local diversity. At REU-ML, the largest frugivore is the  
330 Réunion bulbul, which occurs at a relative small density since the beginning of the 20th century (Cheke  
331 and Hume, 2008), and might not ensure effective dispersal of many plant species even though it can  
332 theoretically swallow their fruits (McConkey and O’Farrill, 2016). In fact, the good recruitment of FF  
333 shrubs that the Réunion bulbul preferentially disperse (Albert, 2020) suggests that it still plays an  
334 important role in the understory of old-growth forests. Similarly, the high increase in density of several  
335 FF shrubs after weeding at MAU-BF (Baider and Florens, 2011) might be explained by consumption of  
336 their fruits by the Mauritius bulbul. The population levels of this bird nevertheless remain relatively low  
337 (< 600 individuals, Cheke and Hume, 2008).

338 Unlike other FF woody plants, large-seeded plants do not regenerate any better at MAU-BF  
339 than they do at REU-ML on average. The weak increase of large-seeded tree recruitment at REU-ML  
340 relative to smaller-seeded plants might be counterintuitive because of the extinction of all large native  
341 frugivores since 1800, but it might also be an artifact. Indeed, several endangered large-fruited trees  
342 might have already died out within permanent plots, e.g. *Sideroxylon majus* (Sapotaceae), *Hernandia*  
343 *mascarensis* (Hernandiaceae), *Scolopia heterophylla* (Salicaceae). This would explain why there is so  
344 low diversity among adults, and this would also lead to the overestimation of median recruitment of  
345 extant species. Isolated large-seeded trees that still survive near the plots, hardly regenerate and might  
346 go locally extinct, thus further impoverishing local diversity, and at the same time, increasing beta  
347 diversity at larger spatial scale (Wandrag et al., 2017). Exceptions exist, as the large-seeded  
348 *Labourdonnaisia calophylloides* that dominates plots at REU-ML and regenerates well, because  
349 invasive rats may act as secondary seed dispersers (Shiels and Drake, 2011). However, while rats  
350 could occasionally move large fruits, they are poor effective dispersers because their potential dispersal  
351 distance is limited, but more importantly, they do destroy most seeds, and those hoarded are usually  
352 clumped inside trees. Another possible contribution to this species regeneration are bird poachers that,  
353 for centuries, have made glue from the fruit flesh (Cheke and Hume, 2008), reproducing to some extent  
354 the behavior of extinct frugivores. Indeed, flesh persistence has a strong negative impact on the  
355 regeneration of this species (Albert, 2020), as already demonstrated elsewhere in the Sapotaceae  
356 family (Levi and Peres, 2013).

357 At MAU-BF, flying foxes feed upon large-seeded plants (Florens et al., 2017a), but fail to recruit  
358 in the understory. Despite their relative large body mass allowing them to move large fruits, flying foxes  
359 cannot swallow large seeds. This incapacity has two major implications as already demonstrated at  
360 MAU-BF for the endangered endemic shrub *Syzygium mamillatum* (Myrtaceae): (1) seeds are  
361 dispersed close from parents trees resulting in increased Janzen-Connell effects on seedlings and  
362 saplings; (2) seeds are not cleaned properly, leading to the persistence of potential dormancy-inducing  
363 or pathogen-attracting compounds, or increased attraction of introduced mammals (Hansen et al.,  
364 2008). Anyhow, the effectiveness of large-seeded plant dispersal by extinct large-bodied frugivores was  
365 probably much higher in the past. Entire lineages that had likely complementary functional roles in  
366 frugivory went extinct at both sites: fruit pigeons including the dodo (Meehan et al., 2002; Whittaker and  
367 Jones, 1994; Wotton and Kelly, 2011, 2012), parrots with the exception of the extant endangered  
368 parakeet (Sebastián-González et al., 2019; Tella et al., 2020), skinks (Zuël et al., 2012) or giant  
369 tortoises (Hansen et al., 2008). Their absence probably plays a major role in recruitment failure of  
370 numerous large-seeded plants at both sites.

## 371 **Potential post-dispersal factors: seed predation, herbivory and light availability**

372 Recruitment failure in some large-seeded species may also be due to seed predation, such as in the  
373 large tree *Canarium paniculatum* (Burseraceae) of which seeds are often predated by introduced rats at  
374 MAU-BF (Auchoybur and Florens, 2005). However, seed predation by invasive mammals may be a  
375 secondary cause of recruitment failure as already shown at MAU-BF (Hansen et al., 2008), on Réunion  
376 (Albert, 2020) or in New Zealand (Wotton and Kelly, 2011). Furthermore, seedlings and saplings are  
377 impacted by invasive herbivores, such as macaques or deers, as already reported by Thompson in the  
378 late 19th century (Cheke and Hume, 2008). Large-seeded plants such as Sapotaceae or *Diospyros*  
379 spp. may have specific vegetative traits which would make them more palatable than other plants  
380 (Cheke and Hume, 2008). Again, herbivory might be a secondary limitation on large-seeded plants that  
381 would primarily have difficulty establishing because of strong dispersal limitation.

382 One may argue that some species are shade-intolerant and have major difficulties in  
383 regenerating under closed canopy where competition for light is strong. This is especially true for most  
384 DF trees that include the smaller-seeded woody plants in the Mascarenes, as elsewhere (Leishman et  
385 al., 2000). The fact that saplings of anemochorous long-lived pioneer species such as *Agarista*  
386 *salicifolia* (Ericaceae), *Homalium paniculatum* (Salicaceae) or *Nuxia verticillata* (Stilbaceae) are absent  
387 or very rare at REU-ML reinforces this hypothesis (Cadet, 1977; Strasberg, 1996), and contributes to  
388 the observed decline in diversity. This influence of light availability is shown at MAU-BF where DF  
389 plants such as *Homalium integrifolium* or *N. verticillata*, only regenerate well where canopy cover is the  
390 lowest (Fig.A5). Canopy tree species with large, wind-dispersed seeds are absent in the Mascarenes, a  
391 common feature of oceanic islands (Whittaker et al., 1997). Therefore, a gradual replacement of large-  
392 seeded FF plants in the understory, as shown in continental tropical forests (Harrison et al., 2013;  
393 Terborgh et al., 2008), is not possible.

394 Finally, native large-fruited light-demanding trees are usually absent in gaps at REU-ML  
395 because they are not dispersed to such areas (Wandrag et al., 2017) and most native tree species do  
396 not have a seedling/sapling bank prior to disturbance. These gaps are often occupied by alien FF small-  
397 seeded plants that benefit from high levels of dispersal by small frugivores (Albert, 2020; Baret et al.,  
398 2008; Mandon-Dalger et al., 2004), indicating the importance of seed dispersal in forest dynamics.

## 399 **RECOMMENDATIONS FOR CONSERVATION**

400 The protected tropical rainforest of REU-ML shows insufficient regeneration of most of its species  
401 because of large-bodied frugivore loss, while that of MAU-BF shows an important recruitment of FF  
402 plants, indicating their capacity of being effectively dispersed. There is consequently an urgent need to  
403 protect flying foxes that face repeated mass culling on Mauritius (Florens and Baider, 2019) and to  
404 promote the recolonization of larger forested areas by this species, which has now only a small  
405 population on Réunion, after over 200 years of absence. While the ideal would be to rewild ecosystems  
406 with large-gape frugivores as already undertaken in several South-West Indian Ocean islands (Griffiths  
407 et al., 2011; Pedrono et al., 2013), direct sowing actions of large-seeded species should nevertheless  
408 be considered to support their recruitment. Ultimately, we provide additional evidence of a bleak future  
409 for diverse tropical rainforest if seed dispersal networks are not restored wherever necessary.

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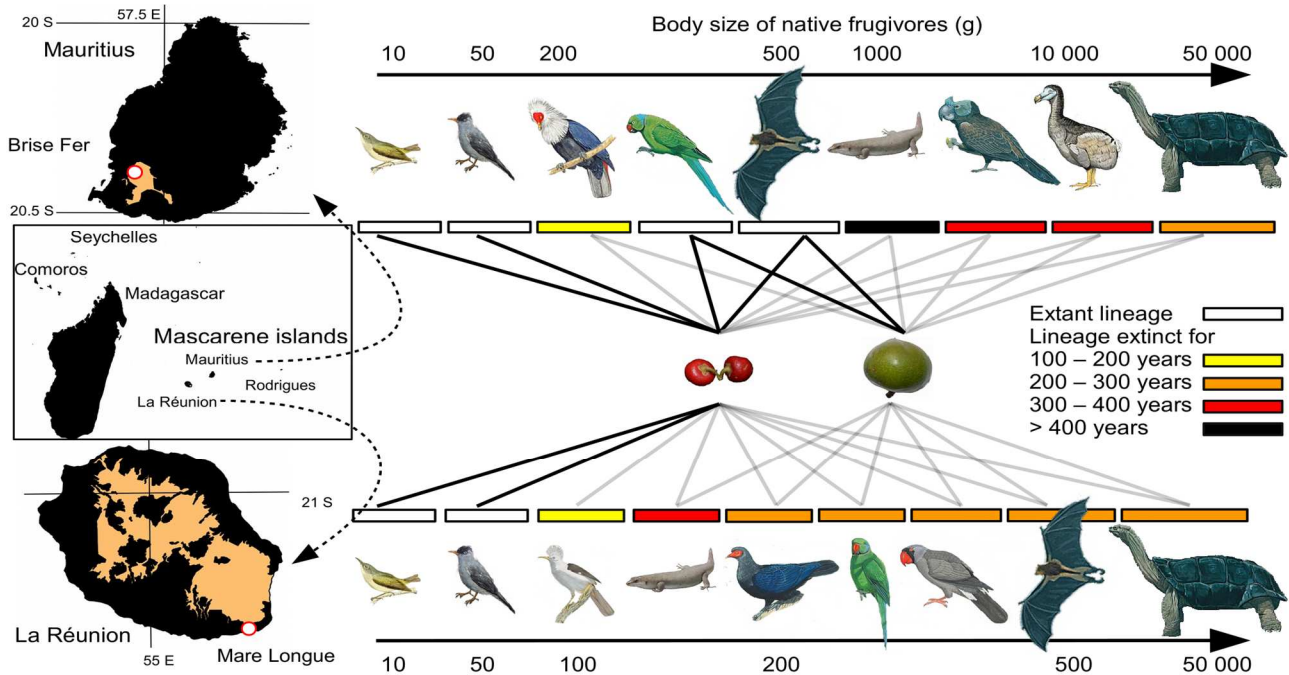
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- 613 **DATA ACCESSIBILITY**
- 614 Data associated with this study will be archived in the *Mendeley Data*. DOI:  
615 <http://dx.doi.org/10.17632/r3x9hxt98s.1#file-2e500bfd-9b67-4bee-adac-e21e2d55f06c>





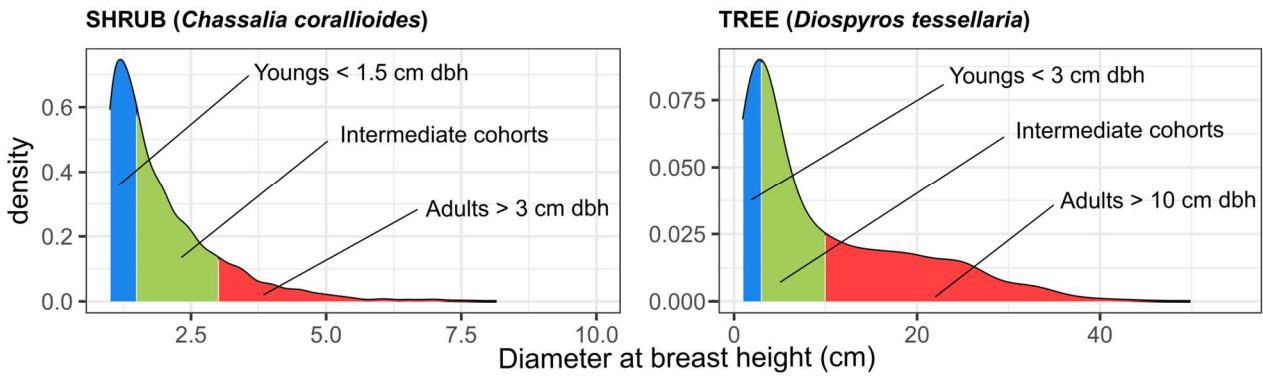
617  
 618 **Fig.1** Overview of native frugivore guild at study sites. Réunion and Mauritius are the two main islands of the  
 619 Mascarenes. Permanent plots of Mare Longue and Brise Fer (red circles) are located in the National Parks of  
 620 Réunion and Mauritius, respectively (in orange). Réunion and Mauritius hosted a diverse and plethoric fauna  
 621 of frugivores until the 17<sup>th</sup> century (from right to left, in descending order of body size): giant tortoises, dodo  
 622 (Mauritius only), broad-billed parrot (Mauritius only), giant skink (Mauritius only), flying foxes, Mascarin parrot  
 623 (Réunion only), parakeets, fruit pigeons, skinks, starlings (Réunion only), bulbuls and white-eyes. The  
 624 extinction period of frugivore lineages is indicated by the rectangle colour. Extant and extinct frugivory  
 625 interactions are given by black and grey lines, respectively. The red and green berries symbolize several  
 626 hundred woody species with small and large fleshy fruits, large fleshy-fruited plants being theoretically not  
 627 dispersible by small frugivores. Actually, the Mascarenes initially showed highly asymmetric dispersal  
 628 networks with relatively few species of frugivores compared to the diversity of plants (see Schleuning et al.,  
 629 2014). Illustrations: giant tortoises, dodo, flying foxes, parrots, fruit pigeons, starling by J. Hume; white-eyes  
 630 by J.G. Keulemans; skinks by J. Noseworthy; bulbuls by D. Strasberg. For more details, see Appendix  
 631 Tab.A1.

632  
 633 **Tab.1** Descriptors of permanent plots at MAU-BF and REU-ML. Main environmental factors are shown:  
 634 elevation (“asl”: above sea level) and annual precipitation (“Precip.”). Basal area and number of stems are  
 635 also displayed depending on diameter cohorts. Basal area and number of stems account for all woody  
 636 species.

Site	Plot	Elevation (m asl)	Precip. (mm)	Sampling year	Basal area dbh>1 cm (m <sup>2</sup> .ha <sup>-1</sup> )	Basal area dbh>10 cm (m <sup>2</sup> .ha <sup>-1</sup> )	Number of stems with dbh>1 cm	Number of stems with dbh>10 cm
Mauritius	BF1	560-600	2400	2011	41.6	34.8	6369	1026
	BF2	560-600	2400	2011	58.9	48.7	8003	1631
	BF3	560-600	2400	2010	65.2	58.4	5799	1463
Réunion	ML1	310-320	4540	2012	74.6	69.6	5807	984
	ML2	300-310	4520	2012	80.1	76.7	4580	935
	ML3	140-150	4375	2014	60.8	57.9	3098	814

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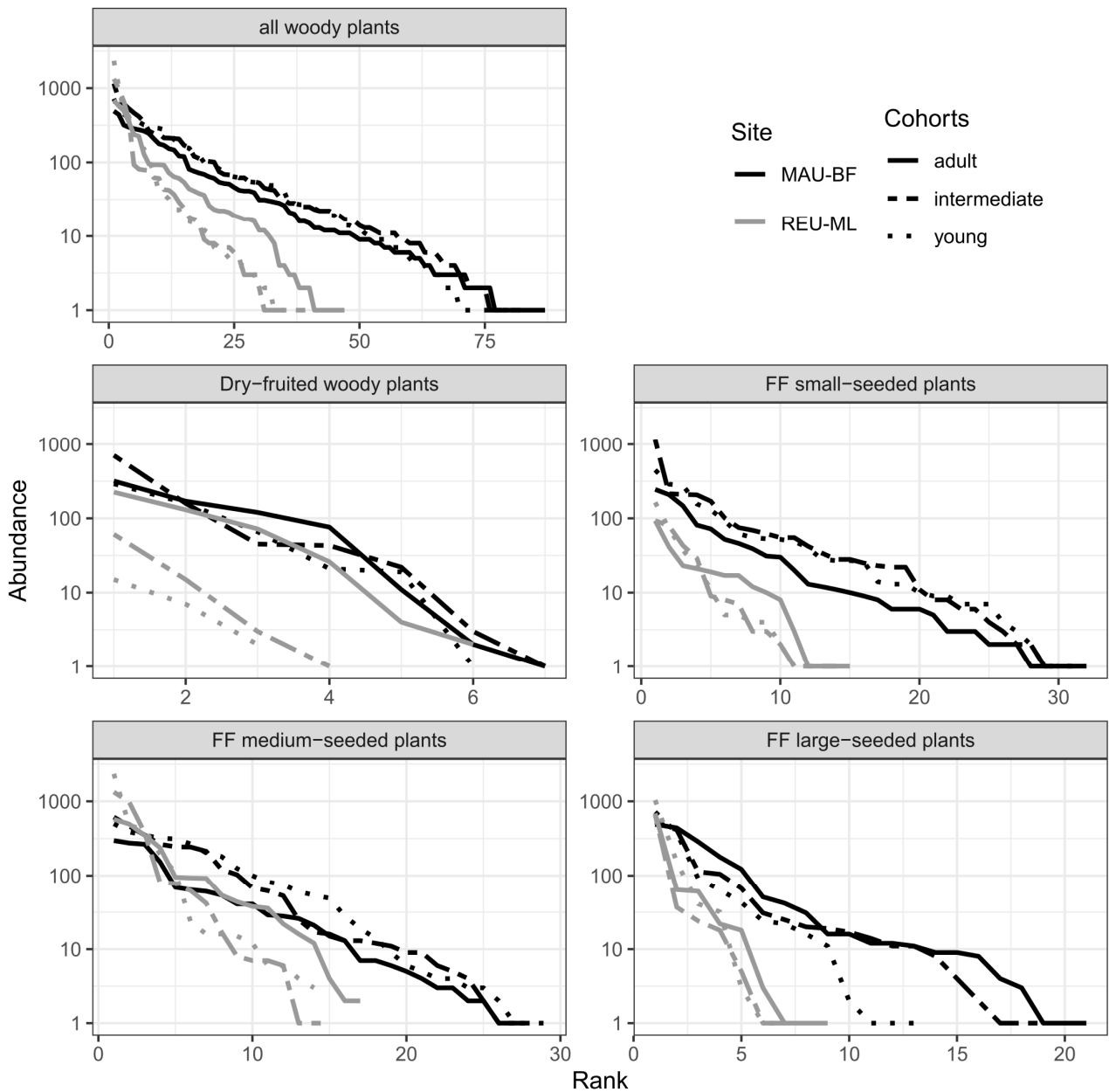
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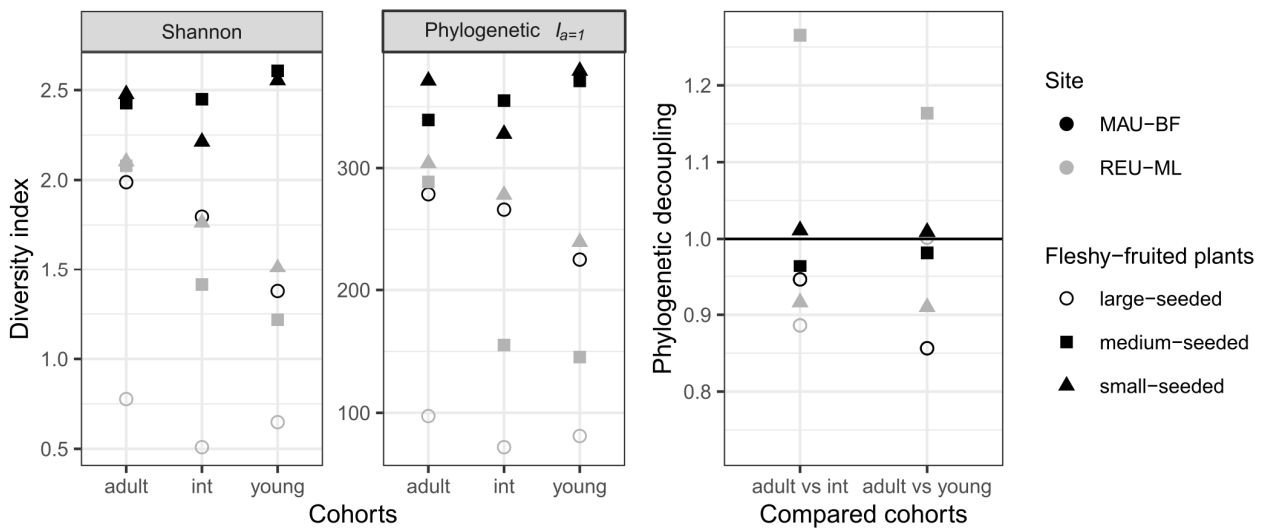
640 **Fig.2** Definition of diameter cohorts according to growth forms. Young cohorts of shrubs and trees show a  
 641 diameter at breast height (dbh) of [1; 1.5[ cm and [1; 3[ cm (blue), respectively. Intermediate cohorts of  
 642 shrubs and trees have a dbh of [1.5; 3[ cm and [3; 10[ cm (green), respectively. Adult cohorts of shrubs and  
 643 trees have a dbh>3 cm and >10 cm (red), respectively. Two species with a left-skewed diametric distribution  
 644 illustrate the assignment.

645

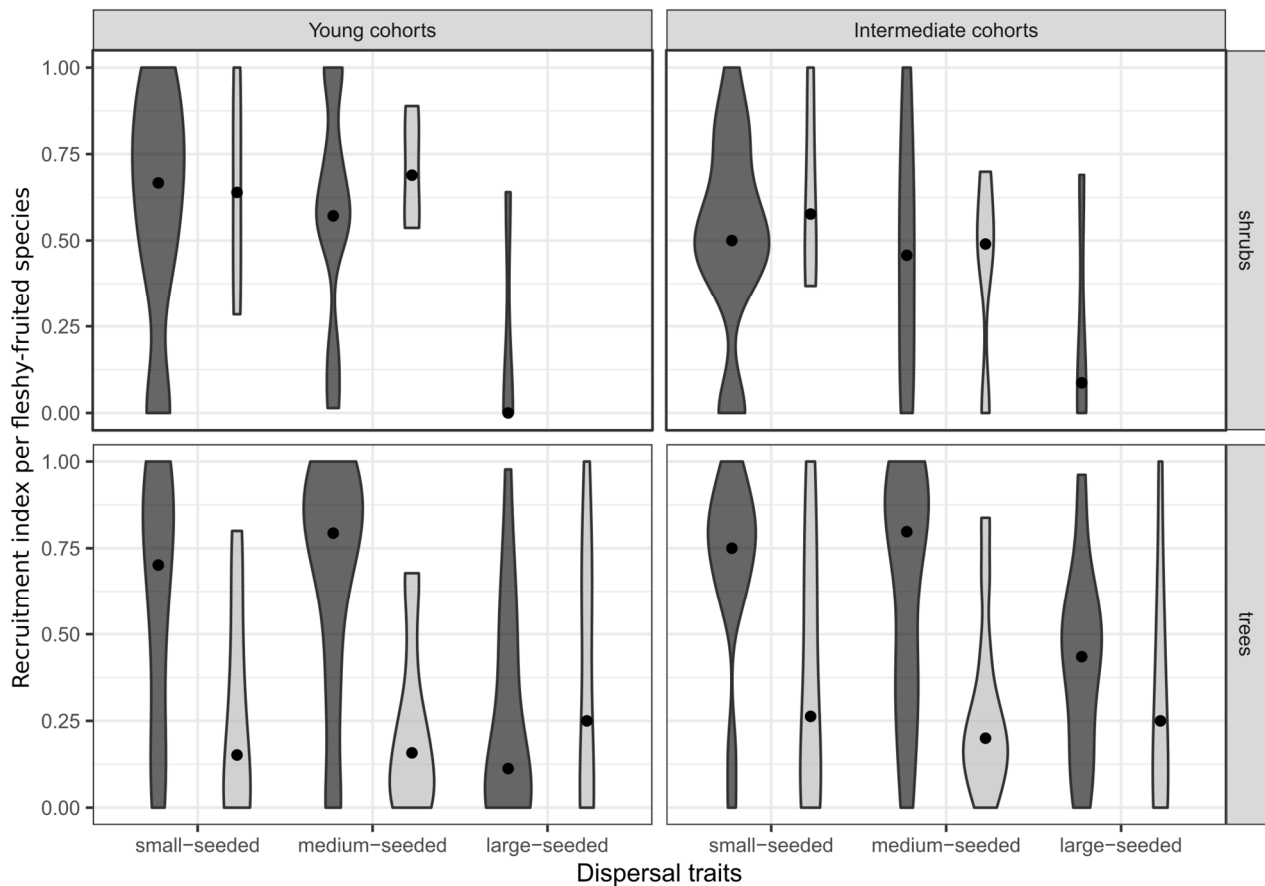


646 **Fig.3** Rank-abundance diagrams at MAU-BF (black) and REU-ML (grey) for woody species overall and  
 647 according to dispersal traits: dry-fruited plants that were mainly anemochorous at both sites and fleshy-fruited  
 648 (FF) small-seeded, medium-seeded and large-seeded plants of which mean seed length was [0.06; 0.6],  
 649 [0.6; 1.5] and [1.5; 5.3] cm, respectively. Solid, dashed-dotted and dotted lines respectively displayed adult,  
 650 intermediate and young cohorts. Note the different scale for the x-axis.

652



653  
 654 **Fig.4** Changes in diversity indices of fleshy-fruited plant assemblages across diameter cohorts at MAU-BF  
 655 (black) and REU-ML (grey). Left, Shannon diversity index; Center, phylogenetic diversity index  $p_{l_{a=1}}$  of  
 656 Pavoine (2020); Right, phylogenetic decoupling, e.g. for “adult vs young” ( $p_{l_{a=1}, \text{adult}} / p_{l_{a=1}, \text{young}} / (I_{\text{shannon}, \text{adult}} /$   
 657  $I_{\text{shannon}, \text{young}}$ ). Values of phylogenetic decoupling  $> 1$  and  $< 1$  indicated stronger and lower changes in  
 658 phylogenetic diversity than in Shannon diversity across diameter cohorts, respectively. Circles, squares and  
 659 triangles displayed large-, medium- and small-seeded fleshy-fruited plants, respectively. Note the different  
 660 scale for the y-axis.



661  
 662 **Fig.5** Violin plots of recruitment index of fleshy-fruited plants calculated as  $n_{\text{young}} / (n_{\text{young}} + n_{\text{adult}})$  and  $n_{\text{int}} / (n_{\text{int}}$   
 663  $+ n_{\text{adult}})$  per species at MAU-BF (black) and REU-ML (grey) in relation to dispersal traits and growth forms. A  
 664 value of 0.5 and 0.25 for young cohorts means that a species has as many youngs as adults and three times  
 665 as many adults as youngs, respectively. Black dots display the median of observed distributions. Note that  
 666 areas of violins are scaled proportionally to the number of species.