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1 **Defaunated and invaded insular tropical rainforests will not recover alone: recruitment**
2 **limitation factors disentangled by hierarchical models of spontaneous and assisted**
3 **regeneration**

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8 **SUMMARY**

9 **1.** Most tropical forests are now severely degraded and their ability to recover is highly dependent
10 on frugivores which ensure seed dispersal for most woody plants. The global collapse of large
11 vertebrates therefore raises major concerns about tropical forest succession, but few field studies
12 have been conducted to disentangle recruitment limitations during disrupted succession.

13 **2.** This study took place on Réunion (Mascarenes) where all large native frugivores have been
14 extinct since human colonisation in 1665 and where multiple invasions threaten native
15 ecosystems. We set up 20 experimental blocks on a lava flow dated back to 1800, in plant-
16 impoverished post-defaunation vegetation bordered by old-growth forests. We assessed
17 fecundity, seed dispersal and seedling recruitment of the complete fleshy-fruited plant community
18 and used Bayesian analyses to disentangle the impact of multiple factors on these key processes.
19 In the same blocks, we sowed four native trees assumed to be disperserless to test their capacity
20 to establish, controlling for two additional post-dispersal limitations (seed predation and
21 competition with invasive plants).

22 **3.** On the flow, small-seeded native plants were fairly dispersed but did not recruit, probably due
23 to strong competition with invasive plants; the few native species that recruited somehow were
24 mostly medium-seeded plants that were still dispersed; large-seeded plants were absent from
25 seed rain (which shows that invasive frugivores did not replace extinct ones) and subsequently

26 from spontaneous recruitment. Instead, some alien plants, notably the tiny-seeded highly-
27 dispersed *Clidemia hirta* and the medium-seeded *Psidium cattleianum* largely dominated seedling
28 recruitment. Native plants recruited better at the forest margin, including some large-seeded
29 species nearby mother trees.

30 **4.** Sown large-seeded species were able to emerge and survive in all plots whatever the
31 treatment, which demonstrates that dispersal loss was the primary cause of regeneration failure
32 on the flow.

33 **Synthesis.** The strong modulation of the establishment capacity of native plants by seed mass
34 shows that invasive plants win by forfeit of large-seeded plants after native frugivores loss. Our
35 study emphasises the fundamental role of dispersal loss and competition with invasive plants in
36 the disruption of ecological succession, as well as the urgency of restoring seed dispersal and
37 strengthening biosecurity regulations.

38 **KEY-WORDS**

39 Bayesian analyses; community ecology; ecological filters; field experiment; island biology; seed
40 dispersal loss; vertebrate extinction; winning-by-forfeit

41 **ABBREVIATIONS**

42 *CalTac*, *Calophyllum tacamahaca*; *CliHir*, *Clidemia hirta*; *DicLin*, *Dicranopteris linearis*; DF, dry-
43 fruited; *DioBor*, *Diospyros borbonica*; FF, fleshy-fruited; HBM, Hierarchical Bayesian model;
44 *PsiCat*, *Psidium cattleianum*; RGR, relative growth rate; *SidBor*, *Sideroxylon borbonicum*;
45 *SyzCym*, *Syzygium cymosum*.

46 1. INTRODUCTION

47 Tropical forests are mainly secondary or severely degraded and are increasingly threatened year
48 after year (Hoang & Kanemoto, 2021). Because most tropical forest regeneration occurs through
49 natural forest succession, it is critical to analyse the resilience of fragmented ecosystems in the
50 matrix of disturbed habitats (Rozendaal et al., 2019). After complete destruction by landslides,
51 lava flows, or for agriculture development, forest regeneration cannot rely anymore on formerly
52 active soil seed banks, seedling or sapling cohorts (Quintana-Ascencio et al., 1996; Walker &
53 Moral, 2003). Under such conditions, the seed dispersal function is particularly essential (Carlo &
54 Morales, 2016; Tabarelli & Peres, 2002; Whittaker et al., 1997).

55 Frugivorous vertebrates play an important role in transporting seeds from old-growth
56 forests to degraded areas (Caves et al., 2013; Ingle, 2003), sometimes crossing long distances
57 (Oleksy et al., 2019; Whittaker et al., 1997). Because tropical forests worldwide are dominated by
58 fleshy-fruited species (Turner, 2001), the global decline of frugivores raises deep concern for the
59 consequences of the breakdown of seed dispersal mutualism (Dirzo et al., 2014; Guimarães et
60 al., 2008; Heinen et al., 2017; Young et al., 2016). Several studies have shown that frugivore loss
61 limits recruitment at the community level in the understory of old-growth forests (Effiom et al.,
62 2013; Harrison et al., 2013; Terborgh et al., 2008). However, the negative impact of frugivore loss
63 on plant colonisation may be much more pronounced (Caves et al., 2013; Costa et al., 2012;
64 Wijdeven & Kuzee, 2000) with dramatic consequences in heavily defaunated ecosystems such
65 as oceanic islands (Albert, Flores, & Strasberg, 2020; Wandrag et al., 2017). However, field
66 experiments testing how frugivory disruption affects plant community assembly during primary
67 succession are still lacking (but see Carlo & Morales, 2016). This is especially true when forest
68 ecosystems are subject to other major threats such as plant invasions (Liebhold et al., 2017;
69 Pyšek et al., 2020).

70 Here, we assess the effects of ecological filters acting before, during, and after seed
71 dispersal to limit recruitment in a species-rich protected area on Réunion where concerns about

72 the recovery of native ecosystems have been growing over the past decades (Albert et al., 2021;
73 Albert, Flores, & Strasberg, 2020; Cuénin et al., 2019; Strasberg et al., 2005). We focus in
74 particular on the filters of dispersal limitation, and biotic interactions. We choose as a study system
75 a two-hundred-year-old lava flow dated back to 1800 that bears a depauperate plant community
76 established after the extinction of all large-bodied native frugivores; this flow is bordered on both
77 sides by old-growth tropical rainforest fragments that act as pseudo-controls (**Fig.1**). In this
78 setting, we build two complementary empirical approaches to evaluate recruitment limitation
79 through both observations of spontaneous processes and experimental sowing.

80 First, we monitor fecundity, seed dispersal, and seedling recruitment to understand how
81 these processes contribute to the regeneration of the plant community (Wang & Smith, 2002). We
82 expect the active seed rain and subsequent recruitment to be depleted in native plants, especially
83 large-seeded species, regardless of their seed availability in the vicinity. We also expect seed rain
84 and recruitment to be dominated by alien plants that have been reported to be very attractive for
85 native/alien frugivores and highly invasive in native ecosystems (Kueffer et al., 2009; Vizentin-
86 Bugoni et al., 2019). Second, we sow several large-seeded plant species particularly threatened
87 by the strong downsizing of the native frugivore guild. Hypothesising that large-seeded trees do
88 not benefit from novel frugivory interactions (Sperry et al., 2021), we restore their seed dispersal
89 on the flow through direct sowing, which is relevant to assess additional post-dispersal limitations
90 (Poulsen et al., 2012). We expect seed predation by introduced rodents known for their potential
91 strong negative impact (Carpenter et al., 2020) and therefore test an enclosure treatment.
92 Likewise, the flow is mainly a fernland where we expect strong competition with ferns (Cohen et
93 al., 1995; Kato-Noguchi et al., 2012; but see Yang et al., 2021) and alien angiosperms known for
94 their invasiveness on Réunion (Macdonald et al., 1991), as elsewhere (Kueffer et al., 2010;
95 Vizentin-Bugoni et al., 2019). Therefore, we test an uprooting treatment to reduce allelopathy and
96 competition for nutrients.

97 2. METHODS

98 2.1 Study site

99 The study was carried out on Réunion on the lower flanks (350 m asl) of the *Piton de la Fournaise*
100 volcano at Le Tremblet (374,330 N; 7,644,500 W) (**Fig.1**). Annual rainfall averages 400 cm per
101 year at Le Tremblet (Réchou et al., 2019), where the habitat is classified as lowland tropical
102 rainforest (Strasberg et al., 2005). This area belongs to one of the last native forest corridors from
103 sea level to subalpine shrublands in the Afrotropical realm and is part of the Réunion national
104 park. The study system consisted of a historical 'A'ā lava flow dated back to 1800 bordered on
105 both sides by a Pāhoehoe lava flow that occurred around 1565 (Albert, Flores, Michon, et al.,
106 2020). The 1800 and 1565 lava flows host a depauperate open-canopy landscape and a species-
107 rich old-growth forest, hereafter referred to as 'flow' and 'forest', respectively (Appendix S1
108 Fig.S1). On the flow, the native fern *Dicranopteris linearis* (*DicLin*) forms thickets whose density
109 increases with distance from the forest.

110 2.2 Experimental design

111 In August 2018, we set up 20 experimental blocks along a track through the flow for the
112 observational assessment and the experimental sowing (**Fig. 1**). Sixteen blocks were located on
113 the flow and four beneath the forest margin, near isolated trees that were used as natural perches
114 for flying or arboreal frugivores. We expected trees emerging from the dense surrounding
115 vegetation to be all the more attractive to frugivores as they are tall. We thus measured the tree
116 height above the canopy (noted h_{tree}) to account for this possible influence on dispersal. We also
117 measured the distance from each block to the nearest forest edge (d_{forest}) as we expected dispersal
118 to be distance-limited.

119 2.2.1 Observational assessment

120 2.2.1.1 Fecundity

121 In order to assess community composition, we surveyed the local species pool in the 2.25
122 hectares (150×150 m) surrounding the blocks (**Fig.1**). We established an 800-metre track to
123 monitor fruiting fleshy-fruited species monthly between 12/2018 and 06/2020 (**Fig.1**). The fruit
124 track was divided into three spatially homogeneous zones in terms of plant composition: forest
125 north, flow, and forest south. Fruit production was assessed per species and per zone using a
126 semiquantitative scale: 0: 0; 10: 1-100; 100: 101-1000; 1000: >1000 fruits. We then quantified
127 species fecundity as the cumulative seed production over the whole study period:

$$128 \quad fecundity = \sum_{i=1}^3 \sum_{j=1}^{18} f_{i,j} * n$$

129 where 'f' was the fruit production for the month 'j' in the monitoring zone 'i' and 'n' the mean number
130 of seeds per fruit.

131 2.2.1.2 Active seed rain

132 In each block, we set up two circular seed traps (diameter=52 cm, area=0.21 m²) per block under
133 dry-fruited (DF) or fleshy-fruited (FF) perch trees to sample the seed rain between 12/2018 and
134 06/2020. The seed traps were covered with metal mesh (2×2 cm) to keep introduced mammals
135 out. This mesh size was large enough to allow almost all seeds in the community to go through.
136 Therefore, seeds trapped under heterospecific perch trees were considered actively dispersed
137 (biotically or abiotically).

138 Using nylon fabric, we collected the contents of the seed traps once a month and dried
139 them to separate seeds from debris. To identify trapped seeds, we built a seed catalogue of the
140 plant community (Appendix S2); the phylogenetic overdispersion of the latter (Albert et al., 2018)
141 minimised the difficulties of seed identification at the species level due to phylogenetic
142 conservatism of seed traits. We identified and counted seeds with diameter (D_{seed}) > 0,2 mm,
143 which was the lower threshold for fleshy-fruited plants known at the study site. For small seeds

144 ($D_{seed} < 0,8$ mm), the numbers were estimated using a binocular loupe by area-based
145 extrapolation.

146 2.2.1.3 Seedling recruitment and invasion level

147 At the end of the survey period (07/2020), we identified and counted all seedlings (2-25 cm)
148 present in 1 m² recruitment plots located at the foot of perch trees used for seed rain survey
149 (**Fig.1**). To assess the impact of invasive plants on recruitment, we calculated the number of
150 stems (height > 25 cm) belonging to the 8 invasive plants present at the study site (see Macdonald
151 et al., 1991).

152 2.2.2 Sowing experiment

153 We tested the influence of three factors on recruitment (sown species, enclosure, and vegetation
154 treatment) over two different monitoring periods in a cross-factorial design set up in 2x1 m² sowing
155 plots and located close to spontaneous recruitment plots (**Fig.1**).

156 First, in December 2018, we collected fruits at the foot of mother trees for four fleshy-fruited
157 species including 3 large-seeded shade-tolerant trees completely absent on the flow, *Calophyllum*
158 *tacamahaca* (*CalTac*), *Diospyros borbonica* (*DioBor*), *Syzygium cymosum* (*Syzcym*), and 1
159 medium-seeded pioneer tree, rare at the study site, *Sideroxylon borbonicum* (*SidBor*) (Appendix
160 S1 Fig.S2). For each species, 1440 seeds were hand-cleaned and sown on 12/2018 using 18
161 seeds per modality (**Fig.1**).

162 Second, to understand the impact of seed predators, we tested an enclosure treatment in
163 half of the plots (size: 100x50x25 cm, metal mesh: 0.8x0.8 cm; **Fig.1**). Because the substrata
164 were rough and exclusion difficult to obtain, the effectiveness of enclosure was tested prior to
165 sowing (Appendix S1 Fig.S3). We maintained enclosures for six months after sowing, after which
166 they were removed to allow seedlings to grow unconstrained.

167 Third, to understand the impact of competition with invasive plants, we uprooted them in
168 one sowing plot out of two in each block on the flow (**Fig.1**). For the 'no-uprooting' modality, dense

169 low vegetation had to be cut to settle exclosures, but involved invasive plants were able to
170 resprout quickly. The experimental blocks at the forest margin were located in the understory
171 without a root mat and considered as a pseudo-control.

172 We evaluated seedling emergence and survival based on counts between February 2019
173 and September 2022. Likewise, we assessed seedling growth using maximum height for each
174 modality between May 2020 and September 2022. We calculated relative growth rates (RGR)
175 adapted for discrete time intervals (Hastwell & Facelli, 2003):

$$176 \quad RGR = \frac{MaxHeight_t - MaxHeight_{(t-1)}}{MaxHeight_{(t-1)} * time}$$

177 with 'time' as the duration of the period in weeks.

178 2.3 Analyses

179 All statistical analyses were conducted in R ver. 4.0.3 (R core team, 2020). We analysed
180 observational and experimental data separately under Hierarchical Bayesian Models (HBM)
181 implemented using the greta modelling framework (Golding, 2019a).

182 2.3.1 Observational assessment

183 We incorporated all collected data in a hierarchical Bayesian model (obs-HBM) of processes
184 involved in the seed dispersal loop (Wang & Smith, 2002), and more generally in forest
185 regeneration, from fecundity to seedling recruitment (**Fig.2 & Appendix S3**).

186 For each plot and each fleshy-fruited species, we calculated the responses 'dispersal' and
187 'recruitment' as the number of seeds and the number of seedlings cumulated over the study
188 period, respectively. These numbers were considered as random variables serving as responses
189 in the model for which we considered all the species that fruited in the monitoring area and/or
190 were dispersed and/or recruited at least once. We thus obtained community tables with 50 fleshy-

191 fruited species in rows and 40 plots in columns; finally, we removed the 20 observations
192 associated with conspecific FF perch trees resulting in 1980 observations.

193 Both responses were strongly zero-inflated and seed dispersal was highly overdispersed
194 and varying over five orders of magnitudes, so that we could not use models based on quantitative
195 discrete responses. We consequently transformed both responses as four-level ordered factors
196 (null, low, medium, high) balancing levels of non-zero observations:
197 $0 < [1:8] < [9:61] < [62:101727]$ for dispersal and $0 < 1 < [2:5] < [6:153]$ for recruitment (**Fig.2**).
198 We modelled both responses using an ordered multilogit distribution (Golding, 2019b). We applied
199 on predictors usual transformations (logarithm, square root, quadratic) to maximise linearity of
200 statistical relationships with responses and retained predictors to minimise collinearity: h_{tree} , d_{forest} ,
201 invasion (block variables); D_{seed} , status (plant variables); fecundity and dispersal (processes),
202 dispersal served both as response variable and predictor of recruitment (**Fig.2 & Appendix S1**
203 Fig.S4). We also included block and species identity to account for non-independence in the data
204 and unobserved variables at these observation levels. Continuous predictors were scaled prior to
205 analyses. We based parameter estimates on $4 \times 10,000$ Markov chain Monte Carlo iterations,
206 following an equal warm-up period. All covariate estimates converged acceptably (Rhat statistics
207 < 1.015 , rank-normalized ESS > 400 [Vehtari et al., 2021]; Appendix S3 Tab.S1). For variable
208 selection, we calculated 95% posterior credible intervals to only include terms for which the
209 intervals did not contain zero in the model (Gabry & Mahr, 2022). We performed intense variable
210 selection to detect interactions between predictors with non-null effects. We eventually assessed
211 if the final obs-HBM fitted the observed data using posterior predictive checks (Appendix S3
212 Fig.S5).

213 2.3.2 Experimental sowing

214 We modelled the emergence, survival, and growth of seedlings after direct sowing in two different
215 HBM.

216 First, we estimated the emergence of seedlings over a period when a maximum number
217 of seedlings emerged, that was, from sowing (t_0) to 27 weeks after (t_{27}), and survival on the
218 following survey period, from t_{27} to 194 weeks after sowing (t_{194} ; Appendix S1 Fig.S5). We used
219 these two periods in a two-level 'time' predictor. We calculated the emergence and survival of
220 seedlings as $\text{number}_{\text{seedlings-}t_{27}} / \text{number}_{\text{seeds-}t_0}$ and $\text{number}_{\text{seedlings-}t_{194}} / \text{number}_{\text{seedlings-}t_{27}}$,
221 respectively. We used seedling ratios as responses that we modelled depending on four factors,
222 'sown species', 'vegetation treatment', 'exclosure' and 'time' using a binomial distribution (Tab.1).

223 Second, with three dates available for seedling maximum height (60, 92 and 194 weeks
224 after sowing), we calculated two RGR values and used the two associated periods (60-92 and
225 92-194 weeks) in a 'time' predictor. We then modelled the RGR depending on 'sown species',
226 'vegetation treatment', 'exclosure' and 'time' using a Gaussian distribution (Tab.1). In both HBMs,
227 we included block identity to account for potential autocorrelation. We based parameter estimates
228 on 4x5,000 Markov chain Monte Carlo iterations, following an equal warm-up period. We used
229 the same methods as in 2.3.1 for model validation.

230 3. RESULTS

231 3.1 *Observational assessment*

232 Regarding the mother plant community, FF trees constituted the bulk of woody plant richness at
233 the study site (33 species of 58 in total, Fig.3A). Large-seeded and medium-seeded trees were
234 absent and uncommon on the flow, respectively, which explains the richness gap with the close
235 neighbouring forest. Alien fleshy-fruited plants comprised 13 species, including several perennial
236 herbs.

237 Among the 50 FF species analysed in the obs-HBM, 45 species fruited at the study site,
238 31 species were dispersed, and 33 species recruited as seedlings (Appendix S1 Fig.S6). No
239 seeds belonging to mature native plants absent from the study site were trapped, unlike 2 alien
240 species; moreover, the seeds of 10 - probably alien - taxa remained unidentified (Appendix S2).

241 Although native species produced the bulk of fleshy fruits, fecundity was largely dominated
242 by the alien shrub *Clidemia hirta* (*CliHir*) (Fig.3B). Considering dispersal, *CliHir* accounted
243 for >90% of the total number of seeds dispersed, but the 5 next most dispersed species were
244 native (Appendix S1 Fig.S7). Considering recruitment, the alien *CliHir* and *Psidium cattleianum*
245 (*PsiCat*) accounted for 27% and 33% of the total number of seedlings, respectively (Fig.3B).

246 The most influential predictors of dispersal, as shown by posterior parameter estimates in
247 the obs-HBM, were D_{seed} , far ahead of *fecundity*, *fecundity* \times d_{forest} , D_{seed} \times d_{forest} and h_{tree} (Fig.4A
248 & Appendix S1 Tab.S1). Species status revealed no particular effect, as shown by the 'Native'
249 coefficient that was not different from 0. The model also highlights large specific species effects
250 (high $\sigma_{Species}$), *i.e.* large differences in dispersal levels in relation with species identity; by contrast,
251 blocks showed little effects (low σ_{block}). Posterior predictions showed that the cumulative median
252 probability 'P' (*i.e.* $1 - P_{zero}$) of dispersal was null for a randomly selected plant with $D_{seed} > 8$ mm
253 (Fig.5A), which was the size of the largest seeds trapped at the study site (Appendix S1 Fig.S8A).
254 The cumulative probability of dispersal increased strongly with decreasing D_{seed} below 3 mm; only
255 small-seeded plants were dispersed at high levels. Medium-seeded plants were better dispersed
256 on average at the forest margin than at the flow centre (Fig.5A); however, the species effect with
257 the strongest absolute value in the obs-HBM was related to an alien medium-seeded plant that
258 was exclusively dispersed on the flow (Appendix S1 Fig.S9). The cumulative probability of
259 dispersal increased strongly with increasing *fecundity* and this effect was all the stronger the lower
260 d_{forest} was (Fig.5A). Lastly, h_{tree} had a weak positive influence on dispersal probability.

261 The most influential predictors of recruitment were D_{seed}^2 , $D_{seed}^2 \times Native$, $D_{seed} \times d_{forest}$,
262 d_{forest} and *invasion* \times *Native* (Fig.4B & Appendix S1 Tab.S1); as for dispersal, $\sigma_{species}$ was very
263 strong. The cumulative median probability of recruitment for a randomly selected plant was hump-
264 shaped in relation to D_{seed} ($P \approx 0.25$ maximum at $D_{seed} \approx 5$ mm, Fig.5B). The smaller d_{forest} (and
265 so the fern cover), the greater the recruitment probability; in the forest, the peak of probability
266 occurred at larger D_{seed} , which was notably due to the recruitment of dispersal-limited plants in

267 the vicinity of mother trees (Appendix S1 Fig.S8B). On the flow, the probability of recruitment of
268 native small-seeded plants was surprisingly null, and that of large-seeded plants was expectedly
269 null due to the absence of mother plants and seed dispersal; accordingly, alien large-seeded
270 plants did not recruit on the flow, but alien small-seeded ones were more likely to recruit than
271 native plants. Lastly, *invasion* had a limited, negative impact on the recruitment of native plants
272 (Fig.5B).

273 Behind the low recruitment of most native FF plants on the flow, one would expect a higher
274 recruitment of DF plants. Although some species such as the native small-seeded *Agarista*
275 *salicifolia* reached very high levels of seed dispersal on the flow, DF plants accounted for only
276 1.6% of seedlings (Appendix S1 Fig.S10).

277 3.2 Experimental sowing

278 As expected, the 4 species sown were neither dispersed (except a single seed of *SidBor* at the
279 forest margin) nor recruited once (Appendix S1 Fig.S7). Once dispersal was reinstated, the 3
280 large-seeded species could emerge and survive sometimes at very high levels in all blocks,
281 without enclosure or root mat uprooting, among invasive alien plants that we did not control after
282 sowing (Fig.6 & Appendix S1 Fig.S11). On the contrary, only nine *SidBor* seedlings emerged in
283 total, this species was therefore excluded from the modelling analyses. Note, however, that
284 *SidBor* had the highest observed RGR on the flow (Fig.7B).

285 The most influential predictors of seedling ratios were 'sown species', before 'sown
286 species x time' and 'sown species x time x vegetation treatment'; other factors and interactions
287 had a weak influence (Fig.6A). For *CalTac*, the posterior median of emergence (ratio=0.82, during
288 the first survey period, 0-27 w) and survival (ratio=0.92, second survey period, 27-194 w) were
289 much higher than that of *DioBor* and *SyzCym* (Fig.7A). *DioBor* emerged less well than *SyzCym*
290 (ratio=0.21 versus ratio=0.45), but survived better (ratio=0.77 versus ratio=0.49). Regarding
291 vegetation treatment, *DioBor* and *SyzCym* emerged and survived less at forest margin than on

292 the flow, respectively; a weak positive impact of uprooting was mainly observed on *DioBor*.
293 Exclosure had a weak positive impact on the emergence of *CalTac* and *DioBor*, which did not
294 occur for survival rates. On the contrary, the impact of exclosure was surprisingly negative on the
295 emergence as well as on survival of *SyzCym*.

296 The most influential predictors of relative growth rate (RGR) were 'sown species', ahead
297 of 'vegetation treatment', 'sown species x vegetation treatment' and 'time' (Fig.6B). The posterior
298 median of *CalTac* was much higher (RGR=0.0038 mm.mm⁻¹.week⁻¹) than that of *DioBor*
299 (RGR=0.0013) and *SyzCym* (RGR=0.0014; Fig.7B), as was the maximum height 194 weeks after
300 sowing (Appendix S1 Fig.S12). *CalTac* and *DioBor* grew better at the forest margin (RGR=0.0052;
301 RGR=0.0027) than on the flow (Fig.7B). However, while *CalTac* and, to a lesser extent, *SyzCym*
302 have continued to grow so far on the flow, the RGR of *DioBor* was almost null during the second
303 survey period. Lastly, uprooting on the flow had a weak positive influence on the RGR as well as
304 on the maximum height, except for *SyzCym*, for which the uprooting effect was a little stronger.

305 4. DISCUSSION

306 Combining observational and experimental approaches, we provide one of the first
307 comprehensive assessments of multiple limitations acting on the assembly of an insular plant
308 community (but see Carlo & Morales, 2016). Although the vegetation of the 1800 lava flow has
309 been thought for decades to be a typical stage of plant succession in tropical rainforest (Cadet,
310 1977), our evaluation of the recruitment limitations acting before, during, and after seed dispersal
311 shows that the low diversity of the plant community settled after the loss of every large native
312 frugivore is primarily the consequence of strong dispersal limitation and high competition with
313 some invasive plants that, nowadays, dominate seed rain and overwhelm spontaneous
314 recruitment. Reinstating the seed dispersal of 3 large-seeded trees also shows they can emerge
315 and survive over the flow regardless of the treatment, which suggests that invasive plants win by
316 forfeit in areas that lost their native frugivore populations (see Hurtt & Pacala, 1995). Given the

317 growing threats to tropical forests (Hoang & Kanemoto, 2021), the ongoing defaunation (Dirzo et
318 al., 2014; Young et al., 2016) and the increasing numbers of invasions in forest ecosystems
319 worldwide (Liebhold et al., 2017), our study emphasises once again the urgent need to maintain
320 and even restore seed dispersal of native plants (Fricke et al., 2022) and to strengthen biosecurity
321 regulations to avoid dramatic invasions (Pyšek et al., 2020).

322 *The seed rain depleted in native plants, especially on the flow*

323 The seed rain is particularly depauperate in medium- and large-seeded native plants despite the
324 high fecundity of multiple plant species in the nearby forest. The largest seeds are mainly
325 dispersed by frugivorous birds that can swallow fruits up to 1.2 cm in diameter and subsequently
326 seeds of a lower diameter (8 mm), a threshold very close to that documented by Sperry et al.
327 (2021) in Hawaii. The absence of large seeds in the seed rain also shows that alien vertebrates
328 larger than the native bulbul (*Hypsipetes borbonicus*) do not play a functional replacement of
329 extinct large-bodied frugivores (Carpenter et al., 2020), despite rare short-distance synzoochory
330 events in nearby old-growth forest (Appendix S1 Tab.S2). Hence, most native large-seeded plants
331 can be considered as 'anachronisms', as well as some alien plants (e.g. *Artocarpus heterophyllus*)
332 introduced by humans in old-growth forest (Guimarães et al., 2008).

333 Dispersal of FF plants is modulated by the distance to old-growth forest, which probably
334 results from differing movements of the main frugivores at the study site; the native bulbul, more
335 restricted to native forests, would disperse most native plants at forest margin; in contrast, the
336 red-whiskered bulbul (*Pycnonotus jocosus*) would disperse most plants on the flow and more
337 often over long distances, notably alien species (Appendix S1 Fig.S9). Indeed, we also monitored
338 frugivory interactions and showed that the native bulbul and the red-whiskered bulbul mainly feed
339 on native and alien FF plants, respectively (Appendix S1 Tab.S2). Obviously, native frugivores
340 also disperse alien plants. For example, *CliHir*, absent from native forests 45 years ago (Cadet,
341 1977), is now fed by all frugivores throughout the year due to its palatability (Kueffer et al., 2009)

342 and overwhelms the seed rain at the study site, as in Hawaii (Vizentin-Bugoni et al., 2019).
343 However, this shrub was only able to invade native ecosystems from gardens after the spread of
344 the red-whiskered bulbul on Réunion (Simberloff & Von Holle, 1999), which strikingly shows the
345 crucial role of highly mobile alien frugivores in the propagation of new plant invasions (Sperry et
346 al., 2021; Spotswood et al., 2012; Vizentin-Bugoni et al., 2019). Finally, since the seed
347 morphology of the about 250 FF native species is well known, unidentified seeds in the seed rain
348 probably belong to alien plants (more than 2000 species have been introduced on Réunion
349 [Strasberg et al., 2005]). Therefore, the seed dispersal capacity of alien plants may be
350 underestimated in our model.

351 *The spontaneous recruitment overwhelmed by some alien fleshy-fruited plants*

352 Known for their invasiveness worldwide (Pyšek et al., 2020; Vizentin-Bugoni et al., 2019), *PsiCat*
353 and *CliHir* represent 60% of seedlings at the study site. These species show very high fecundity,
354 are able to recruit at the foot of mother plants, and to be dispersed everywhere on the flow (even
355 though dispersal levels are much higher for the latter, which also shows higher germination levels
356 after gut passage [Mandon-Dalger et al., 2004]). The few native FF species that recruit well on
357 the flow are medium-seeded dispersed plants; but ongoing field experiments show that most of
358 these seedlings cannot survive and grow on the flow regardless of their light demand. Likewise,
359 multiple small-seeded well-dispersed plants cannot germinate on the flow, including FF and DF
360 species that sometimes recruit on recent less invaded lava flows (Albert, Flores, & Strasberg,
361 2020); this is also true for many alien plants that are dispersed at the study site, but cannot recruit.
362 These examples show that strong post-dispersal limitations are at work at Le Tremblet (Wang &
363 Smith, 2002).

364 Seed predation is usually stronger the larger the seeds are (Carpenter et al., 2020), but its
365 weak impact on sown species suggests that rats play a minor role in the failure of germination of
366 native still-dispersed plants. Rather, invasive plants probably lead to strong competition that may

367 not only prevent the germination of various species through allelopathy (Kalisz et al., 2021; Kato-
368 Noguchi et al., 2012), but also cause high mortality of most seedlings through resource hoarding
369 (Tng et al., 2016). In addition to competition with invasive angiosperms, competition with ferns
370 may play a crucial role since *DicLin* (and occasionally *Pteridium aquilinum*) dominates the open-
371 canopy landscape on the flow. The difficulty for native woody plants to settle in fernlands is
372 documented elsewhere (Cohen et al., 1995; Kato-Noguchi et al., 2012) and uprooting revealed
373 that the roots of native trees generally do not prospect this upper soil horizon (Appendix S1
374 Fig.S13). On the contrary, *PsiCat* that can thrive in this root mat has considerably invaded the
375 flow for 45 years (Cadet, 1977). Thus, *DicLin* does not improve biotic resistance to alien plant
376 invasions as expected (Russell et al., 1998; Yang et al., 2021), but rather prevents the emergence
377 and survival of still-dispersed native plants.

378 Our study shows that most spontaneous recruitment of native plants occurs at the forest
379 margin where disperserless large-seeded plants are sometimes able to recruit in the vicinity of
380 mother trees. Large-seeded plants are particularly threatened in fragmented landscapes on
381 Réunion (Albert, Flores, & Strasberg, 2020), as elsewhere (Costa et al., 2012); nevertheless, we
382 demonstrate that the restoration of their seed dispersal is an effective way to restore their
383 recruitment during succession.

384 *Establishment of large-seeded plants in all experimental plots after sowing*

385 After direct sowing, we demonstrate that three large-seeded trees can establish on the flow where
386 they have been absent to date: dispersal loss is indeed the major recruitment limitation. The
387 variability of survival and growth is primarily related to species. Emergence rates range from
388 medium-low (0.2-0.4 for *DioBor*) to very high (0.75-0.87 for *CalTac*) on the flow, and survival rates
389 are higher on average, especially for *DioBor*. Contrary to what was expected (Carpenter et al.,
390 2020), seed predation by introduced rodents has a weak negative impact and remains a
391 secondary recruitment limitation (Wotton & Kelly, 2011); the cause underlying the paradoxical

392 negative impact of exclosure on the establishment of *SyzCym* is unclear. As expected, *CalTac*
393 and *DioBor* seedlings grow better at the forest margin, where environmental conditions are
394 buffered (Hastwell & Facelli, 2003): *CalTac* reaches 1.1 m in some plots and *DioBor*, a slow-
395 growing endangered ebony tree, shows numerous healthy seedlings. On the contrary, *SyzCym*
396 grows as fast on the flow as it does at the forest margin and even faster where the root mat has
397 been uprooted, probably due to competition release (Cohen et al., 1995). However, the overall
398 impact of uprooting on plant growth remains weak, which might result from strong soil legacies
399 (Kalisz et al., 2021; Kato-Noguchi et al., 2012). This could also explain why most dispersed native
400 and alien plants did not benefit from a competition release after uprooting (Appendix S1 Fig.S11).
401 As an alternative hypothesis, the area of the uprooting treatment (1 m²) might be inadequate. The
402 recolonisation of *DicLin* through its rhizomes is indeed potentially rapid (Yang et al., 2021), which
403 may have considerably reduced the expected positive effect.

404 Only a few *SidBor* seedlings emerged and survived after direct sowing; however, they
405 display the highest RGR value on the flow, which was expected because *SidBor* is a light-
406 demanding tree (Cadet, 1977). Because we believed that strong seed dormancy might explain
407 germination failure, we used chemical scarification treatments in a parallel experiment but could
408 not obtain significantly higher recruitment (S. Albert, unpublished data). Rather, the germination
409 of *SidBor* may be severely impeded by a pathogenic agent, as already suggested in related
410 congeneric species on Mauritius (Wyse Jackson et al., 1988). Our inability to document the factors
411 underlying the lack of regeneration of this once structuring tree is a reminder that key recruitment
412 limitations remain unclear for many native species.

413 *Key perspectives*

414 The capacity to establish in invaded vegetation which is positively modulated by seed mass shows
415 that depleted recruitment of native plants may also result from winning-by-forfeit (see Hurtt &
416 Pacala, 1995). Since the most defaunated islands (Hawaiian Islands, Society Islands, The

417 Mascarenes [Heinen et al., 2017]) are also those known for the severity of plant invasions (Kueffer
418 et al., 2010), winning-by-forfeit following frugivore loss might have increased the severity of plant
419 invasions (for the role of other ecological interactions in biotic resistance, see Levine et al. [2004]).
420 Failure to consider the disruption of seed dispersal may have led to an overestimation of the
421 negative impact of plant invasions on native plant communities.

422 Lastly, our study demonstrates that the collapse of native plant diversity is not a fatality on
423 historical lava flows on Réunion and that massive direct sowing of large-seeded plants could
424 enrich large areas, as elsewhere (Shaw et al., 2020). However, these human-led sowing actions
425 should not hinder our efforts to rewild native ecosystems (Griffiths et al., 2011), as nothing will
426 ever replace large effective frugivores in their perpetual search for food and space.

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432 experiment. We appreciated the referee's relevant comments which have notably improved the
433 manuscript.

434 **CONFLICT OF INTEREST**

435 Authors have no conflict of interest to disclose.

436 **AUTHOR'S CONTRIBUTIONS**

437 Sébastien Albert, Olivier Flores, and Dominique Strasberg developed the ideas. Sébastien Albert,
438 Olivier Flores, Charlène Franc, and Raphaël Solesse collected data. Sébastien Albert and Olivier
439 Flores analysed the data. All authors contributed critically to the drafts of the article and have
440 given their approval for publication.

441 **SUPPORTING INFORMATION**

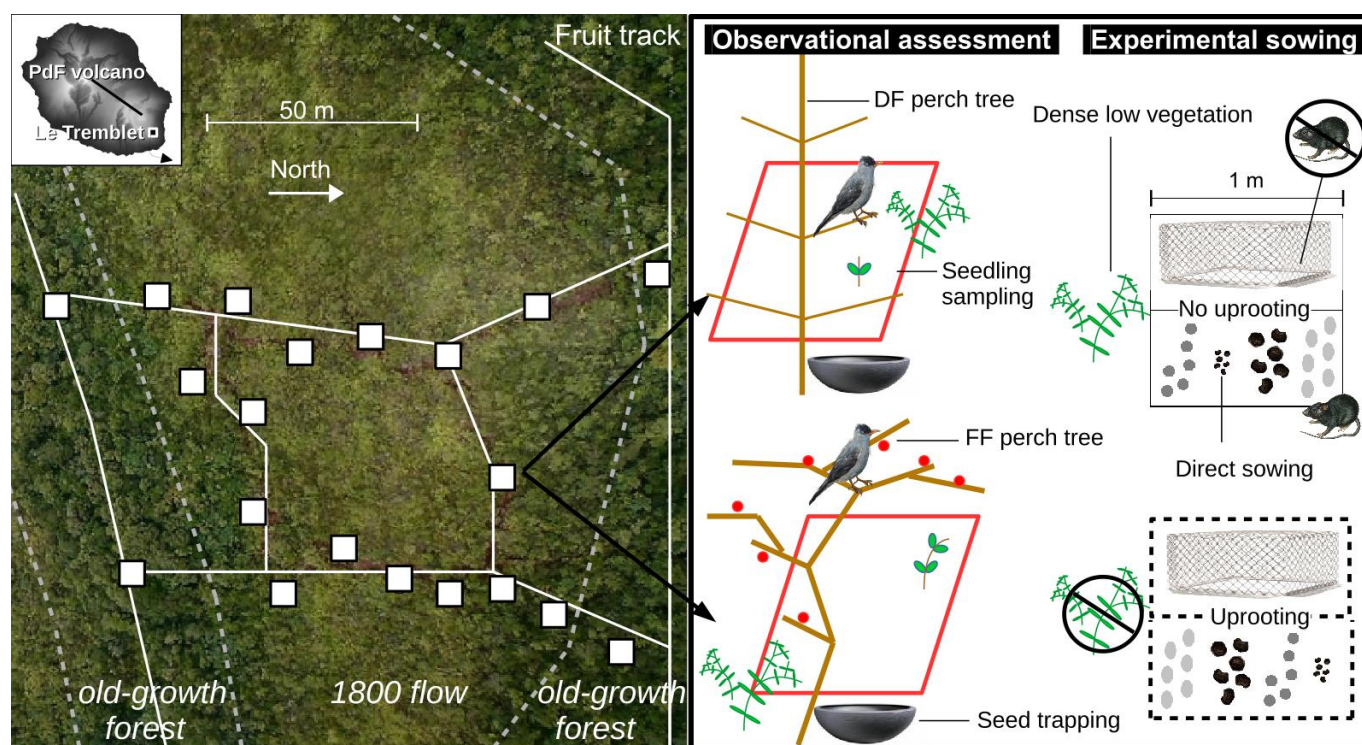
442 Appendix S1. This Appendix includes 2 Tables and 13 Figures presenting additional information
 443 on methods, results and discussion.

444 Appendix S2. This Appendix presents the seed catalogue for the plant community studied.

445 Appendix S3. This Appendix describes in detail the obs-HBM and its evaluation.

446 **DATA ACCESSIBILITY**

447 Data available from the Zenodo Repository: <https://doi.org/10.5061/dryad.sj3tx96b5> (Albert et al.,
 448 2023).

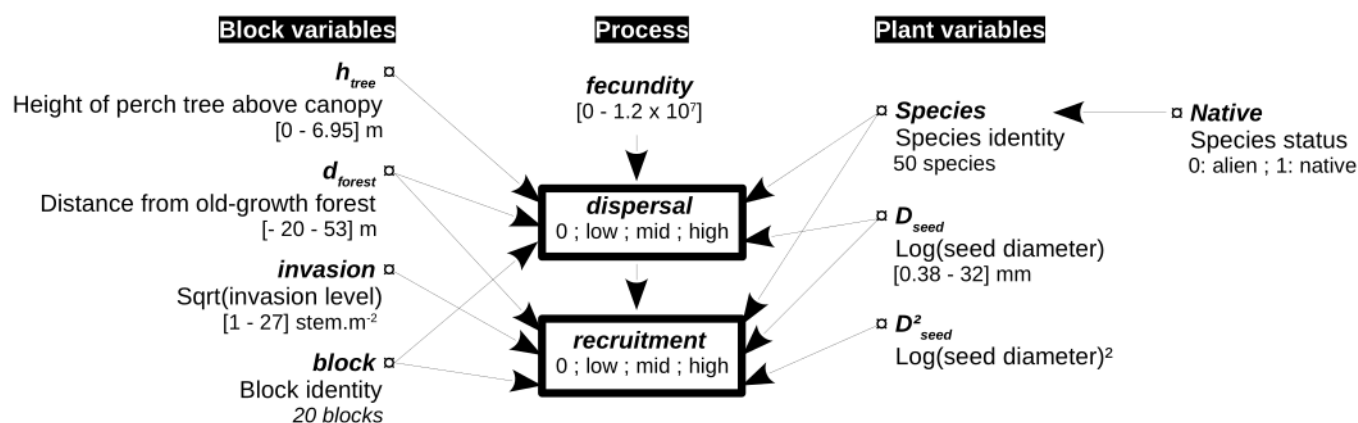
449 **FIGURES & TABLE**

450
 451 **Fig.1 Study site.** Our experiment was located at Le Tremblet on the windward south-east of
 452 Réunion 1 km south of the caldera of the *Piton de la Fournaise* (PdF). The experiment was set
 453 up over the 1800 flow between two old-growth forest areas. Fruit production was estimated
 454 monthly along an 800 m track (white lines). Sixteen and four experimental blocks (white disks)
 455 were set up on the flow and in the understory beneath the forest margin, respectively. Each block

456 on the flow consisted of (i) two seed traps set up under dry-fruited and fleshy-fruited perch trees
 457 to measure active seed rain, (ii) 2x1 m² area to sample spontaneous seedling recruitment,
 458 (iii) 2x1 m² area for the sowing experiment testing three factors: 'sown species', 'vegetation
 459 treatment' and 'exclosure'. The main native frugivore (*Hypsipetes borbonicus*) and alien seed
 460 predator (*Rattus* spp.) at the study site are shown. Drone image: H. Santacreu.

461

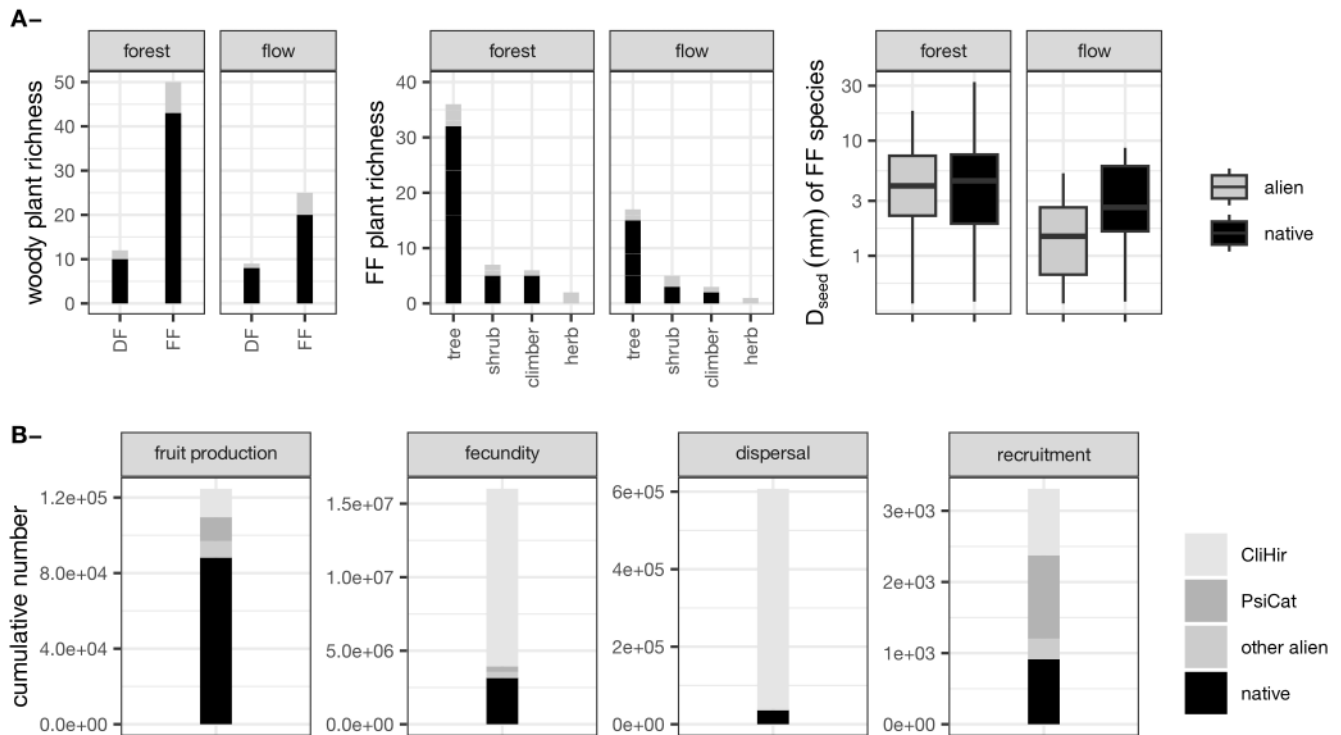
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463

464 **Fig.2 Directed acyclic graph representing the ecological model (obs-HBM).** Arrows and
 465 rectangles display selected predictors and statistical responses, respectively. Predictors are
 466 presented in three groups related to blocks, processes, and plants. Raw range levels are
 467 described below each variable ('[-]' and ';' are used for continuous and categorical variables,
 468 respectively). Note that 'Native' is nested within 'Species'. Pairwise interactions are not shown to
 469 lighten the figure; refer to the Appendix S3 for more details.

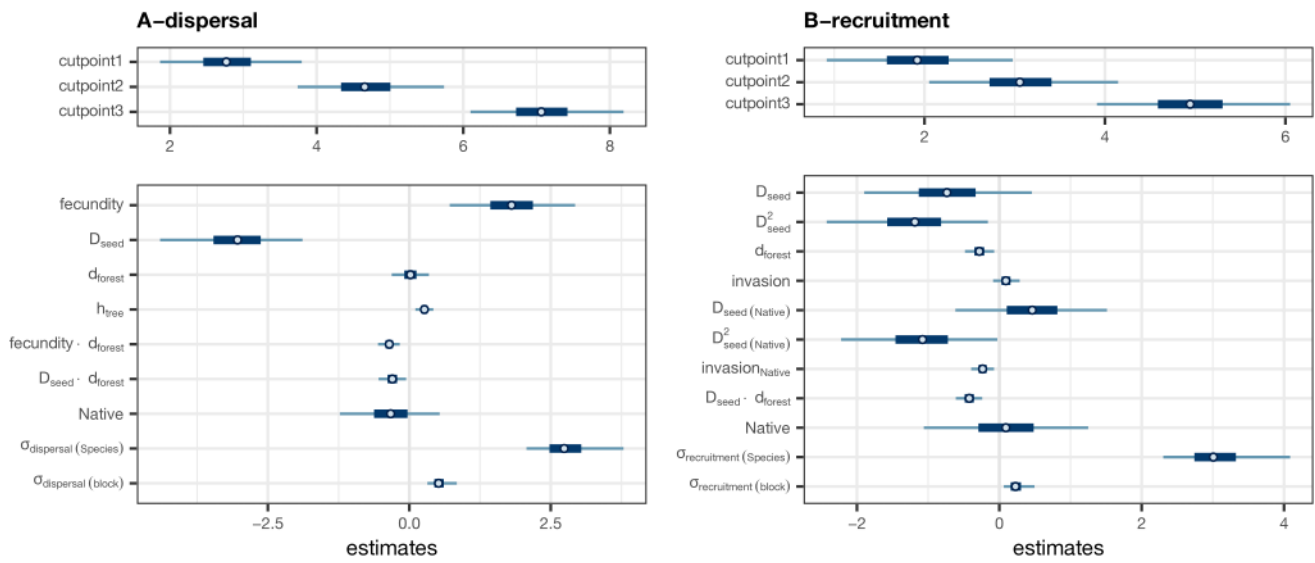
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471

472 **Fig.3 Overview of the plant community at the study site. (A)** Diversity of mother plants at the
 473 study site depending on plant status (black: native; grey: alien), fruit type (DF: dry-fruited; FF:
 474 fleshy-fruited), monitoring zone (forest *versus* flow) and growth form. Note the log-scale for the
 475 box plot of D_{seed} . **(B)** Cumulative assessment of fruit production, fecundity, dispersal and
 476 recruitment for native and alien plants; details are given for the two invasive *CliHir* and *PsiCat*.

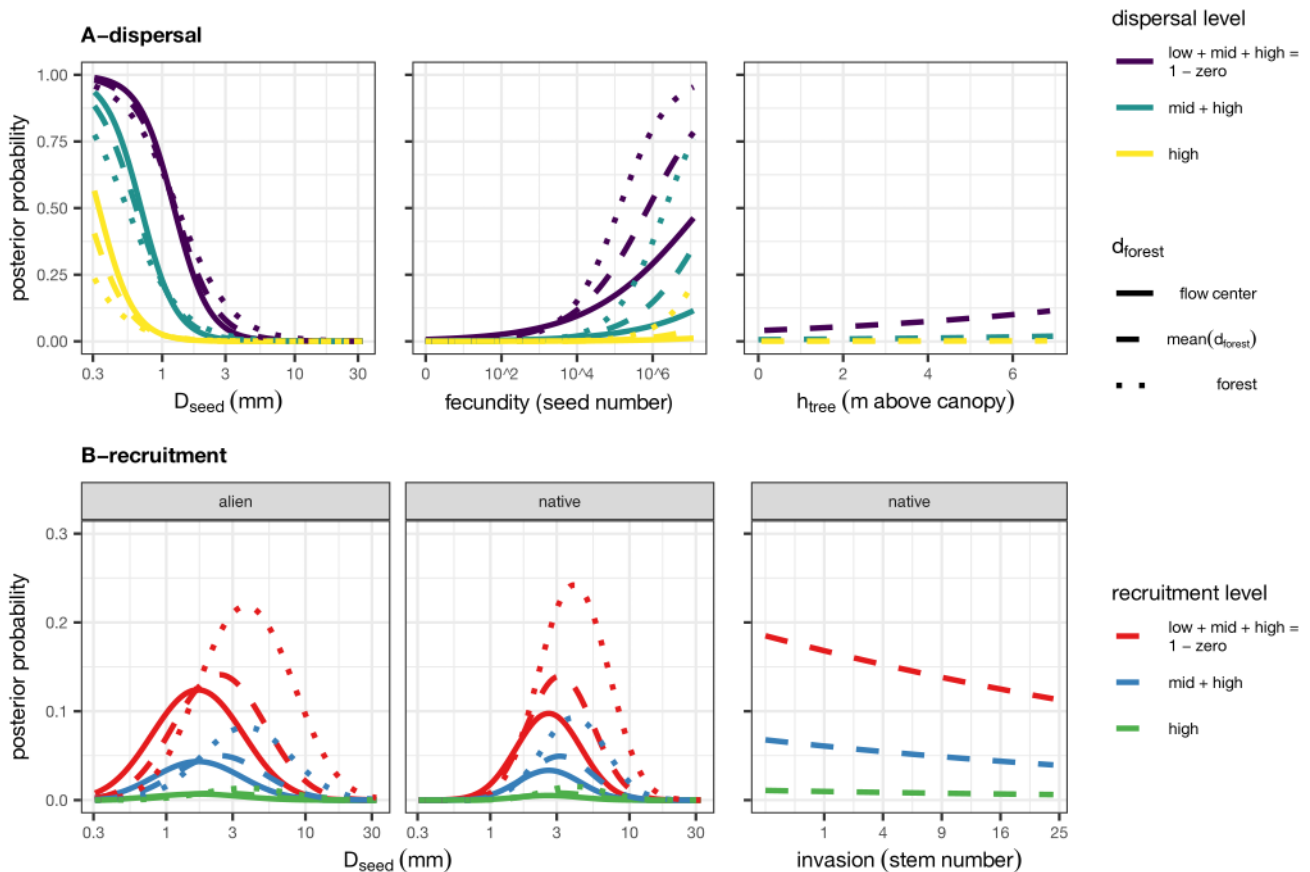
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478

479 **Fig.4 Estimates of the obs-HBM.** For each four-level response (A-seed dispersal and B-
 480 recruitment), the graph of median estimates (dots) with 50% (rectangles) and 95% (lines) credible
 481 intervals is displayed. Note the different scale for the estimates of cutpoints; 'x' indicates
 482 interacting terms. Report to Fig.2 for the detail of predictors.

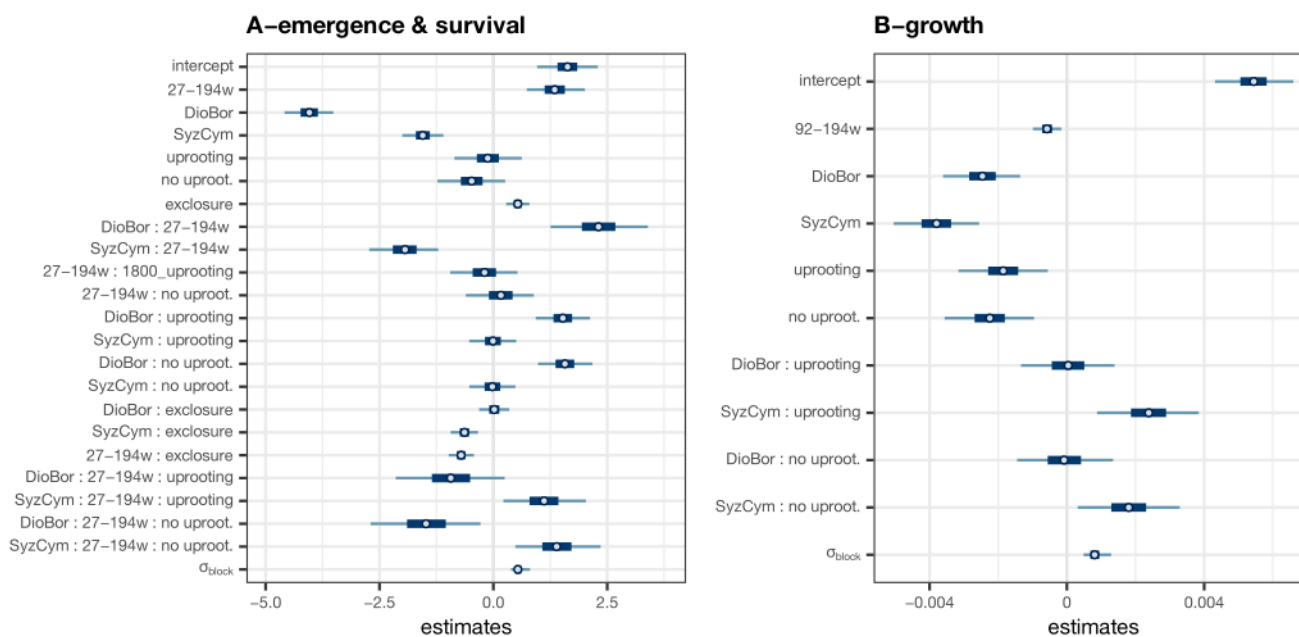
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484

485 **Fig.5 Posterior probabilities of the most influential predictors of the obs-HBM.** For each
 486 four-level response (A-seed dispersal and B-recruitment), the three curves display three stacked
 487 posterior median probabilities P , from bottom to top: (1) $P_{high-level}$, (2) $P_{high-level} + P_{mid-level}$ and
 488 (3) $P_{high-level} + P_{mid-level} + P_{low-level} = 1 - P_{0-level} =$ 'cumulative probability' in the main text. Note the
 489 different scale on the y-axis and predictions for d_{forest} using discrete values to account for
 490 interactions between continuous predictors. Covariates were set to their mean value for
 491 continuous predictors. Raw data can be viewed in Appendix S1 Fig.S8.

492



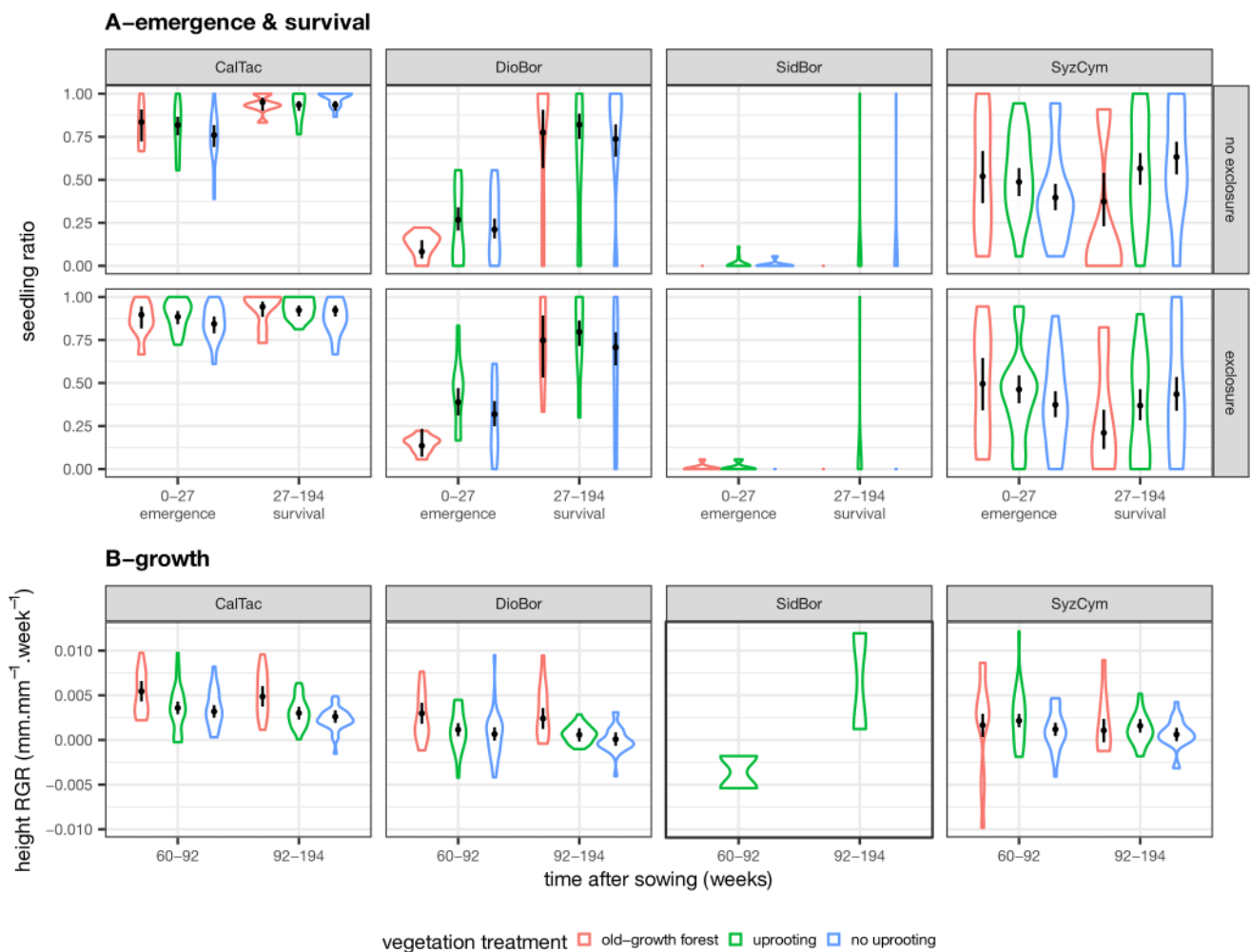
493

494 **Fig.6 Estimates of the HBM for (A) emergence & survival and (B) growth of seedlings after**495 **direct sowing.** The graph of median estimates (dots) with 50% (rectangles) and 95% (lines)

496 credible intervals is displayed. Colons indicate interacting terms. Report to Tab.1 for the detail of

497 predictors.

498



499

500 **Fig.7 Raw data and posterior probabilities of the predictors for (A) emergence & survival**501 **and (B) growth of seedlings after direct sowing.** Violin plots display raw data; dots and error

502 bars display related posterior median values and credibility intervals, respectively. The predictors

503 were 'sown species' (horizontal facets), 'enclosure' (vertical facets in A- only), 'time' (x-axis) and

504 'vegetation treatment' (colours). *SidBor* was excluded from the modelling due to insufficient data.

505

506 **Tab.1 Overview of the factors tested in the sowing experiment.** 'Vegetation treatment', 'sown

507 species' and 'enclosure' were the same predictors of both HBM. For the 'time' factor, the

508 modalities '0-27 weeks' and '27-194 weeks' were used as proxies for emergence and survival of
 509 seedlings, respectively.

HBM	emergence & survival ; growth				emergence & survival	growth
Factor name	vegetation treatment	sown species	exclosure	block identity	time	
Factor modalities	old-growth forest (pseudo-control)	CalTac	exclosure	1	0-27w	60-92w
	uprooting	DioBor	no exclosure	...	27-194w	92-194w
	no uprooting	SidBor		20		
		Syzcym				

510

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