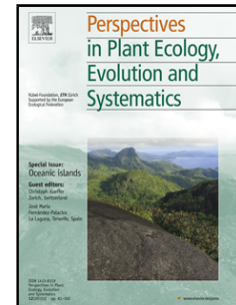


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**Downsized mutualisms: consequences of seed dispersers' body-size
reduction for early plant recruitment**

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26 **Summary**

27 Extinction-driven, body-size reduction of seed dispersers (i.e. an ecological downsizing resulting
28 from severe defaunation) can entail the loss of unique ecological functions, and impair plant
29 regeneration. However, the manner in which the downsizing of mutualistic animals affects seed
30 dispersal and plant recruitment remains understudied. Here, we took advantage of a natural
31 experiment in the Canarian archipelago to document the consequences of lizards body-size
32 reduction (*Gallotia*, Lacertidae) on the recruitment of *Neochamaelea pulverulenta* (Rutaceae),
33 which relies exclusively on these frugivores for seed dispersal. Subsequent to the arrival of humans
34 (ca. 2000-2500 yr BP), the extinction of large-bodied lizards generated a gradient of increasing
35 defaunation on the three islands inhabited by this plant. We hypothesized a significant reduction,
36 and eventually collapse, of early seedling recruitment mirroring the defaunation intensity of the
37 frugivores. We sampled 42 populations spanning the whole geographic range of the plant to
38 examine the quantitative (age structure pattern) and qualitative components (proportion of seedlings
39 growing outside the canopy, number of seedlings established outside the canopy relative to the
40 number of adults -effective recruitment rate-, and seedling vigour) of plant regeneration. Our results
41 show that the age structure patterns did not differ among the three contrasted insular scenarios.
42 However, we found significant reductions in seedling recruitment outside the canopy, effective
43 recruitment rate, and delayed negative effects on seedling vigour in populations hosting small- to
44 medium-sized lizard species. Thus, extirpation of large seed-dispersers did not cause substantial
45 reductions in quantitative components of seed dispersal, but determined declines in qualitative
46 aspects impairing dispersal effectiveness. Our study highlights the importance of examining all
47 components of the dispersal and recruitment process to properly document the regeneration
48 outcomes of plants in defaunated, downsized ecological scenarios.

49 **Keywords:** Canary Islands, defaunation, *Gallotia*, lizard extinction, *Neochamaelea pulverulenta*,
50 seed dispersal.

51 **Introduction**

52 Extinction of vertebrate species has been a recurrent and taxonomically non-random pattern
53 throughout the Earth's history (Raup, 1986; Shodhi et al., 2009). Mass extinction events have
54 reduced, in most cases, the number of large-bodied species (e.g. the disappearance of dinosaurs in
55 the Cretaceous-Tertiary transition, Sheehan et al., 1991 or the demise of megafauna in the Late
56 Pleistocene, Alroy, 2001) ending up with present-day defaunation scenarios in the anthropocene
57 (Barnosky et al., 2011). This phenomenon often results in transitions from pristine communities,
58 where large species are relatively abundant, to downsized communities dominated by small- to
59 medium-bodied vertebrate species (Peres and Dolman, 2000), a pattern of ecological downgrading
60 entailing the loss of unique ecological functions (Estes et al., 2011; Dirzo et al., 2014). Since the
61 large species have are disproportionately important ecological roles in ecosystem dynamics
62 (Cordeiro and Howe, 2001, 2003; Woodward et al., 2005; Wright et al., 2007; Johnson, 2009), the
63 effect of their extinction is expected to cascade through the remainder of the biota and produce deep
64 shifts in the composition, structure and function of downsized communities (Redford and
65 Feinsinger, 2001; Rule et al., 2012; Harrison et al., 2013). A critical issue is thus to develop
66 research frameworks potentially enabling a better forecasting of cascading effects and the potential
67 for delayed consequences of extinction-driven body size reduction and the deterioration of their
68 associated ecological functions (Dirzo et al., 2014).

69 Animal-mediated seed dispersal is a crucial process in the life cycle of many flowering
70 plants. It allows seeds and seedlings to not only escape the higher mortality frequently associated
71 with the adult neighbourhood (Janzen, 1970) but also colonize new sites (Howe, 1982), and it
72 promotes gene flow within and among populations (Hamrick et al., 1993). Large frugivores have an
73 important role in all of these components of seed dispersal because they can consume a larger
74 amount of fleshy fruits, disperse larger seeds and move them further away than smaller species in
75 mutualistic assemblages (Jordano et al., 2007; Muller-Landau, 2007; Wotton and Kelly, 2011).
76 Thus, there are numerous ways in which natural regeneration, especially of large seeded plants, can
77 be impaired by a body size reduction in frugivore assemblages. For example, if frugivores become

78 smaller, plants bearing large fruits can have strong seed dispersal limitations because frugivore gape
79 width constrains the maximum fruit size animals can successfully handle and swallow
80 (Wheelwright, 1985). Late-acting, post-dispersal effects may unfold, preventing or severely limiting
81 seedling recruitment, and leaving defaunated ecosystems dominated by living-dead adult plants
82 (Janzen, 1986) or with highly clumped regeneration within the neighbourhood of parent plants
83 (Cordeiro and Howe, 2001). In addition, the extinction of large frugivores may trigger rapid
84 evolutionary responses, given that extant small frugivores promote selection for reduced seed size
85 (Galetti et al., 2013). Reduction of seed size may in turn negatively impact plant recruitment since it
86 frequently correlates with reduced seed reserves and seedling size which result in reduced seedling
87 survival under stress conditions (Howe and Richter, 1982; Moles and Westoby, 2004). Therefore,
88 the downsizing of mutualistic frugivores can affect multiple scales of their interaction with plants,
89 yet most of these cascading influences remain largely undocumented.

90 The effects of large frugivore declines are expected to be much more pervasive in
91 species-poor systems such as oceanic islands. Firstly, extinction or body-size reduction of
92 frugivore species has been pronounced on islands (Hansen and Galetti, 2009) and quite often
93 preceded by the loss of their functional roles associated with the reduced population size
94 (McConkey and Drake, 2006; Boyer and Jetz, 2014). Secondly, insular environments
95 frequently present low functional redundancy of dispersal agents (e.g. Woodward et al.,
96 2005; Wotton and Kelly, 2011; González-Castro et al., 2014). Thus, seed dispersal may
97 collapse in defaunated insular scenarios, causing substantial reductions of plant recruitment
98 due to loss of efficient mutualistic dispersers. Previous studies have addressed the
99 demographic consequences for plants when disruption of seed dispersal occurs (Meehan et
100 al., 2002; Traveset and Riera, 2005; Rodríguez-Pérez and Traveset, 2009; Wotton and Kelly,
101 2011, 2012; Traveset et al., 2012). However, as far as we know, none of these investigations
102 tracked the demographic consequences of impaired seed dispersal as a result of the
103 downsizing of interacting animal species.

104 Lizard-mediated seed dispersal has been described as a widespread mutualism on oceanic
105 islands (Olesen and Valido, 2003; Valido and Olesen, 2007). In the Canary Islands, endemic
106 lacertid lizards (*Gallotia* spp.) are significant seed dispersers (Valido and Nogales, 1994; Valido,
107 1999; Valido and Nogales, 2003; Valido et al., 2003; Rodríguez et al., 2008). However, the arrival
108 of humans (ca. 2000-2500 yr BP) triggered a process of lizard species extinction and body size
109 reduction on these islands (e.g. Barahona et al., 2000). The pattern and magnitude of this extinction
110 has been markedly different on each island, related to differences in predation intensity by
111 introduced mammals, habitat disturbances, and life-history traits (Machado, 1985; see also
112 Appendix S1 for details). As a result, a gradient of defaunation-mediated lizard downsizing ranging
113 from subtle (Gran Canaria) to noticeable (Tenerife), to quite marked (La Gomera; see Fig.1 and Fig.
114 S1 for island-specific scenarios), exists in present-day environments of the archipelago.

115 Here, we document the effects of body size reduction of Canarian lizards on the early
116 recruitment of a plant species which relies exclusively on these reptiles for seed dispersal. We
117 selected *Neochamaelea pulverulenta* (Rutaceae), an endemic large-seeded treelet, as it is dispersed
118 exclusively by medium- to large-sized frugivorous lizards and, accordingly, it represents a
119 potentially useful model species to test downsizing effects (Valido, 1999). Our approach is a
120 comparative analysis among the unique three islands where *N. pulverulenta* is distributed (Gran
121 Canaria, Tenerife and La Gomera). These islands define a gradient of extinction-driven lizard body
122 size reduction: Gran Canaria preserves the largest extant lizard species, i.e. *G. stehlini*; Tenerife has
123 abundant medium-sized *G. galloti* lizards, whereas La Gomera hosts the smallest species *G.*
124 *caesaris* (Fig.1; see also Appendix S1 and Fig. S1 for further details). Since larger lizards consume
125 bigger and a greater amount of fruits (Valido, 1999), we hypothesize that the extinction-driven body
126 size reduction will negatively affect both quantitative and qualitative components of *N. pulverulenta*
127 recruitment. Among the former we considered the amount of seedlings established; among the latter
128 we analysed the proportion of those that effectively established outside adult plants and the
129 reduction in seedling vigour estimated resulting from reduced seed sizes being dispersed. We expect

130 the downsized scenarios will determine: *i*) differences among islands in overall recruitment patterns
131 as indicated by differences in the age structure (i.e. the relative abundance of seedlings), *ii*) a
132 decrease in the proportion of seedlings recruiting outside the canopy of adult plants, *iii*) a reduction
133 of the effective recruitment rate of seedlings (per capita of adult plants), and *iv*) a reduced vigour of
134 seedlings, resulting from a lack of consumption of large fruits (with large seeds; Howe and Ritcher,
135 1982; Valido, 1999).

136

137 **Material and methods**

138 *Study species*

139 *Neochamaelea pulverulenta* (Rutaceae) (Vent) Erdtman is an endemic treelet distributed in the dry
140 lowlands (< 400 m a.s.l.) of Gran Canaria, Tenerife and La Gomera (Canary Islands). In these
141 areas the average annual temperature and precipitation are around 21°C and 200 mm, respectively
142 (AEMET-IP, 2012). The resulting lowland vegetation is dominated by *Euphorbia* spp.
143 (Euphorbiaceae), *Lavandula* spp. (Labiatae), *Lycium intricatum* (Solanaceae), *Periploca laevigata*
144 (Asclepiadaceae), *Plocama pendula*, and *Rubia fruticosa* (Rubiaceae), among others. Adult plants
145 of *N. pulverulenta* average 1.1 ± 0.49 m in height but some individuals can reach 2.7 m ($n = 2132$
146 from all sampled populations). Plants can bloom almost all year round, with a peak in winter and
147 spring. The main pollinators are ants, solitary bees and flies. Fruits include 1 to 4 ‘cocci’ ($11.1 \pm$
148 1.6 mm in diameter each; Valido, 1999). Each coccus can be considered to be functionally a drupe
149 composed of fleshy pulp containing invariably one hard-coated seed (8.6 ± 1.0 mm in diameter;
150 Valido, 1999).

151 Only medium- and large-bodied lizards eat these fruits, adequately handling and swallowing
152 individual cocci, acting as legitimate seed dispersers (Valido and Nogales, 1994; Valido, 1999;
153 Valido et al., 2003). Secondary seed dispersal by raptor predators on lizards containing seeds of *N.*
154 *pulverulenta* has also been documented (Padilla et al., 2012). Subsequent to human colonization
155 (ca. 2000-2500 yr BP, Appendix S1), different extinction scenarios emerged on each island

156 generating a gradient of lizard body-size reduction (Fig. 1). On Gran Canaria lizard downsizing
157 has been relatively minor, from the large forms of *G. stehlini* sub-fossils (maximum snout-vent
158 length, max SVL = 367 mm) to the extant *G. stehlini* (max SVL = 280 mm). In contrast, lizard
159 size reduction has been intense on La Gomera, where the extant widespread species (*G. cae*
160 *saris*, max SVL = 111 mm) is 4 times smaller than their extinct relatives (*G. goliath*, max SVL = 466
161 mm). In turn, on Tenerife *G. goliath* (max SVL = 502 mm) became extinct and currently only the
162 medium-sized species *G. galloti* (max SVL = 145 mm) is widely distributed. Moreover, the large
163 species *G. intermedia* (max SVL = 174 mm) and *G. bravoana* (max SVL = 212 mm) are present
164 on Tenerife and La Gomera respectively, but they are critically endangered, surviving only in
165 extremely reduced populations on highly localized, inaccessible cliffs (Fig. S1 and references
166 therein for details).

167

168 ***Plant demography***

169 To carry out a comparative study on plant recruitment under different seed dispersal scenarios, we
170 sampled 42 *N. pulverulenta* populations from the three islands. We deliberately choose
171 populations spanning the range of environmental conditions where the species occurs: Gran
172 Canaria ($n = 11$), Tenerife ($n = 19$), and La Gomera ($n = 12$) (Table S1, Fig. S2). In each
173 population we haphazardly set up 3-6 linear transects (25-100 m length; 5 m wide) depending on
174 plant population size. Along these transects we counted and measured all individual plants, except
175 for seedlings, for which only a subset were measured ($n = 637$ seedlings; sampling, on average,
176 29.3% of seedlings recorded in each population). The individual plant measurements included the
177 maximum basal trunk/stem diameter at ground level (using a digital caliper), the maximum
178 stretched height (except for adults; non-stretched height), and the two major diameters of the
179 vertical canopy projection (using a measuring tape). Moreover, all individual plants were
180 categorized according to their size-related age class (seedling, sapling, juvenile, adult). Seedlings
181 were identified as plants with < 1 mm of basal diameter and with less than four leaves; individuals

182 not branched, with 1-7 mm basal diameter were recorded as saplings; plants with 7-15 mm basal
183 diameter and no evidence of reproduction (absence of floral buds and/or seeds beneath the plant)
184 were considered juveniles; otherwise they were recorded as adults. On average we collected data
185 from 228 plants per population (range: 102-571), with a total of 9402 plants sampled. We used
186 this dataset to describe the age structure of populations.

187 For a subset of 32 populations (Table S1, Fig. S2), we also kept information on the
188 proportion of seedlings outside the canopy of *N. pulverulenta* plants and the effective recruitment
189 rate of seedlings along the transects. For the first variable, we recorded the number of seedlings
190 located within the transects and >1 m away from the canopy of the nearest adult plant relative to
191 the total seedlings recruited. The effective recruitment rate was calculated as the number of
192 seedlings outside the canopy relative to the number of adult plants. This demographic parameter
193 represents the per-adult number of seedlings successfully recruiting away from adults, i.e.
194 recruiting from effectively dispersed seeds.

195 Finally, for the analyses of seedling vigour, as reflected by stem diameter, we selected 22
196 populations with at least six seedlings measured (6-93 seedlings, depending on seedling
197 abundance; Table S1).

198

199 *Plant densities, climatic variation, and lizard abundance*

200 To obtain an estimate of plant density per population we set up two perpendicular 100 m x 4 m
201 transects, for which we counted all *N. pulverulenta* adult plants rooted within the transect. These
202 data were independent of the adult plants censused in the age structure sampling. In addition, we
203 gathered climatic data from meteorological stations located within a 7 km distance (1 to 4
204 stations), with long temporal data series available (range = 6–53 years). For each population we
205 recorded the average annual precipitation (pp), the mean maximum temperature of the hottest
206 month (t_{max}), and the mean minimum temperature of the coldest month (t_{min}). Then, we calculated
207 the Emberger index (Emberger, 1955) defined as $Q = (2000 pp)/(t_{max}^2 - t_{min}^2)$, which we log-

208 transformed ($-\ln Q$; Tieleman et al., 2003) for statistical analyses.

209 We obtained an index of relative abundance of medium- to large-bodied lizards in the 32
210 populations selected for the detailed analyses of seedling recruitment. Given that lizard body-size
211 and diameter of their droppings are positively correlated (Valido and Nogales, 2003), we recorded
212 the number of medium- to large-sized droppings in 50 quadrats (0.5 x 0.5 m), regularly spaced 5
213 m apart along five linear transects (spaced 10 m apart) per population.

214

215 *Statistical analyses*

216 Quantitative plant recruitment

217 To examine differences in the age structure pattern (relative frequencies of each age class) among
218 islands we fitted two generalized linear models (GLMs) with a binomial distribution of errors and
219 a log link function. We included 'island' as a fixed factor using data from all sampled populations
220 ($n = 42$). In the first model we tested for island differences in the proportion of subadults (pooled
221 number of seedlings, saplings and juveniles) vs. the proportion of adult plants. In the second
222 model, we tested for differences in the proportion of seedlings relative to the rest of the pooled age
223 classes (saplings, juveniles, adults).

224

225 Qualitative plant recruitment

226 To assess the effect of the ecological scenarios (islands) on the proportion of seedlings outside the
227 canopy we applied a GLM with a binomial distribution of errors and a logit link function. We used
228 'island' as the main fixed factor and both the density of *N. pulverulenta* adult plants and the
229 Emberger index as covariates. Among-island differences in the effective recruitment rate of
230 seedlings were tested by fitting a GLM with a Poisson distribution of errors and a log link
231 function. The number of seedlings was used as a response variable, while 'island' was used as a
232 fixed factor, the Emberger index as a covariate and the number of adults per population as an
233 offset of the model. The stem diameter of sampled seedlings was used as an estimate of seedling

234 size and vigour. We tested variation in seedling vigour among islands by fitting a linear mixed
235 model (LMM) using ‘island’ as the main fixed factor with population identity as a random factor
236 nested within it and the Emberger index as a covariate.

237 In order to assess differences in all measured demographic parameters among pairs of
238 islands we used post-hoc contrasts (Tukey test). In addition, we checked for spatial autocorrelation
239 among model residuals by performing multivariate Mantel correlograms. Given that spatial
240 autocorrelation was not detected for any of the above demographic variables, we did not include
241 spatial information in the abovementioned models (details in Appendix S2, Fig. S3).

242 Finally, we tested for island effects on the density of large- to medium-sized droppings, as
243 a proxy of the relative density of large- to medium-sized lizards. We used an ANOVA with post-
244 hoc contrasts (Tukey test) to test for differences among islands. All statistical analyses were
245 carried out with R (R Development Core Team, 2014).

246

247 **Results**

248 Quantitative plant recruitment

249 The age structure pattern of *N. pulverulenta* was highly variable among populations within each
250 island, ranging from aged populations, where most individuals were adults (e.g. Montaña de
251 Tabaiba, Gran Canaria), to relatively younger stands where many censused plants were subadults
252 (e.g. Barranco de la Negra, La Gomera) (Table S1). When considering the frequencies of
253 subadults (pooling seedlings, saplings, and juveniles) relative to adult plants, differences were not
254 detected among the three insular scenarios (GLM, $p > 0.05$; Fig. 2), suggesting similar overall
255 amount of recruitment. In turn, the average percentage of seedlings was consistently similar
256 among islands, varying from $31.0 \pm 27.8\%$ in Tenerife to $25.1 \pm 20.7\%$ in Gran Canaria (GLM, p
257 > 0.05 ; Fig. 2).

258

259 Qualitative plant recruitment

260 The proportion of seedlings outside the canopy of adult plants was significantly different among
261 islands: Gran Canaria (12.7%), Tenerife (17.7%) and La Gomera (2.8%) (Table 1, Fig. 3). In the
262 model, the effect of *N. pulverulenta* adult plant density was statistically significant ($Z = -3.19$, $p <$
263 0.001). However, variation in climatic conditions did not account for these differences.

264 Regarding the effective recruitment rate of seedlings, we detected significant differences
265 for all the possible pairwise comparisons (Table 1, Fig. 4a). Populations on La Gomera recruited
266 significantly fewer seedlings per adult (0.01 seedlings/adult) than those on Gran Canaria (0.06
267 seedlings/adult) and Tenerife (0.39 seedlings/adult). In this case, the Emberger index (i.e. aridity
268 index) showed a significant effect ($Z = 6.05$, $p < 0.001$), indicating higher effective recruitment in
269 more arid populations.

270 The observed differences among islands in the proportion of seedlings outside the canopy
271 and the effective recruitment rate of seedlings match the variability detected in the abundance of
272 medium-to-large lizard droppings. In the particular case of La Gomera, large droppings were
273 totally absent in the sampled populations (Fig. 4b). Also, we recorded a significantly lower density
274 of lizard droppings on Gran Canaria than on Tenerife ($t = 2.58$, $p < 0.05$).

275 Finally, we found seedlings with consistently smaller basal stem diameter in Tenerife, with
276 no differences between Gran Canaria and La Gomera (Fig. 5, Table 1). Variation in stem diameter
277 across populations was unrelated to the Emberger index.

278

279 **Discussion**

280 *Scenarios of downsized mutualisms*

281 By using a natural island-based field experiment from the Canary Islands we found support for the
282 observation that defaunation-mediated downsizing of frugivorous lizards critically hampers
283 recruitment of *N. pulverulenta*, an endemic shrub strictly dependent on these seed dispersers.
284 Unexpectedly, our results suggest that a reduction of lizard body size has no effect on the
285 quantitative component of seed dispersal (age structure pattern) in the different insular scenarios,

286 with similar overall amount of recruits (juveniles, saplings, and seedlings pooled) relative to the
287 number of adult plants. However, we detected critical effects on the qualitative components, such
288 as a significant reduction of seedling establishment away from adult plants, and delayed negative
289 effects on seedling vigour. First, there was a marked reduction in recruitment beyond the
290 neighbourhood of adult plants on La Gomera, where a drastic reduction of lizard body-size has
291 occurred. Second, even a relatively small decline of lizard body-size may result in less vigorous
292 seedlings as exemplified by the contrast between populations hosting medium-sized lizards
293 (Tenerife) and giant lizards (Gran Canaria) (see below for the specific case of La Gomera, with
294 extinct seed disperser). These differences are not attributable to variation in climatic factors or soil
295 characteristics, but appear closely associated with the downsizing pattern. Our results broadly
296 support the patterns reported in previous studies in which plant–frugivore mutualism disruption
297 affected the quantity and/or the quality of plant regeneration (e.g. Chapman and Chapman, 1995;
298 Cordeiro and Howe, 2003; Traveset and Riera, 2005; Galetti et al., 2013). Yet our study highlights
299 the fact that situations with reduced or collapsed dispersal services can remain undocumented if
300 not all the components of dispersal effectiveness are studied, as indicated by the significant
301 reductions in both effective dispersal and seedling vigour in the downsized scenarios.

302

303 *Quantitative consequences for plant demography*

304 We found a similar proportion of established seedlings despite the marked differences in lizard
305 body sizes among islands. In fact, we found high values (>25%) in most populations. These
306 populations do not differ in soil type (volcanic substrate) or climatic conditions (i.e. aridity index;
307 Table S1), so the similarity of the demographic pattern across islands cannot be attributed to
308 compensatory effects of abiotic conditions (e.g. favourable conditions for establishment in areas
309 with limited dispersal by lizards). Biotic interactions could also have associated compensatory
310 effects, for instance, if differences in competition, herbivory and/or post-dispersal seed predation
311 intensities counterbalance the effect of dispersers, yet we have no evidence supporting this, e.g.

312 we have no records of herbivory on seedlings. The lack of differences in overall recruitment
313 contrasts with previous studies indicating reductions of recruit density in systems hosting non-
314 effective seed dispersers (e.g. Cordeiro and Howe, 2003; Traveset and Riera, 2005, but see Bleher
315 and Böhning-Gaese, 2001 for similar results).

316 In our study system, several factors might explain the large proportion of seedlings of *N.*
317 *pulverulenta* observed on the three islands. A very large fraction of the fully-developed fruit crop
318 falls beneath parents, usually during early summer. Thus, it is common to find a large amount of
319 *N. pulverulenta* seeds without pulp beneath conspecific plants. Small lizards can bite and tear off
320 the pulp without removing the fruit, thus not acting as legitimate dispersers but potentially
321 enabling seed germination (Fig. S4). In addition, we have evidence that rodents consume the pulp
322 and leave seeds accumulating beneath adult plants, but most of them are also predated (pers. obs.).
323 Besides, both lizards and rodents can move a minor proportion of these seeds away from mother
324 plants. Thus, seed movement by runoff, or haphazard dispersal by seed predators and/or small
325 lizards is most likely contributing to early establishment even in situations with limited or absent
326 legitimate dispersal (La Gomera).

327

328 ***Qualitative consequences for plant demography***

329 Despite the absence of differences in the age structure pattern among islands, a clear inter-insular
330 trend emerges when considering several qualitative components of seed dispersal effectiveness
331 (Schupp et al., 2010), i.e. proportion of seedlings outside the canopy of adult plants, effective
332 recruitment rate of seedlings, and seedling vigour.

333 At one extreme of the defaunation and downsizing gradient at La Gomera, we found the
334 lowest values for both the proportion of seedlings outside the canopy and the effective recruitment
335 rate of seedlings. These results, together with an absolute absence of seeds of *N. pulverulenta* in
336 Gomeran lizard droppings, indicate the collapse of the lizard-mediated dispersal interactions on
337 this island. This contrasts with data recorded from islands hosting medium- and large-bodied

338 lizards (Tenerife and Gran Canaria, respectively). The human-driven extinction of the largest
339 known species on La Gomera (*G. goliath*) and the marginal presence of the extant giant lizard *G.*
340 *bravoana* only in an isolated remnant population (Valle Gran Rey; Valido et al., 2000), have
341 actually deprived *N. pulverulenta* of effective seed dispersers throughout the island. The
342 remaining abundant species *G. caesaris* is unable to effectively handle fruits and seeds due to
343 marked morphological restrictions, i.e. fruit size considerably exceeds gape width of the lizard
344 (Valido, 1999), a factor potentially impairing fruit removal and effective seed dispersal.
345 Significant reductions of seeds dispersed away from adult parents have been reported in other
346 defaunated scenarios (Chapman and Chapman, 1995; Cordeiro and Howe, 2003) where the lack of
347 efficient dispersal agents leads to seed accumulations beneath the mother plants.

348 The plant populations from La Gomera, however, still preserve a marginal effective
349 recruitment. We recorded approximately 3% of seedlings recruiting beyond the vicinity of adult
350 plants and a very low (but non-zero) effective recruitment rate. Small-sized *G. caesaris*, which
351 frequently take the fleshy pulp from fruits of the undispersed crop, can sporadically move some
352 fruits and remove the pulp away from adult plants where a minor fraction of seeds may likely
353 germinate. In addition, *N. pulverulenta* populations are usually distributed on ravine slopes, where
354 these seeds without pulp can be dispersed by rain or gravity. Lastly, although rodents mostly act as
355 seed predators they can also disperse some seeds infrequently. Similar results have been reported
356 for other plants (Traveset and Riera, 2005; Guimarães et al., 2008) where vertebrate-mediated
357 seed dispersal has been disrupted and plants rely solely on haphazard, marginal dispersal. In fact, a
358 recent study tracking seed fates (Jansen et al., 2012) showed that scatter-hoarding rodents provide
359 effective seed dispersal to widowed plants, acting as substitutes of an extinct megafauna.

360 We would expect the largest fraction of seeds being dispersed away from maternal plants
361 on Gran Canaria, whose populations currently host the largest-sized lizards (*G. stehlini*). However,
362 contrary to this expectation, the probability of finding seedlings recruiting beyond the parent
363 plants and the effective recruitment rate of seedlings was higher on the island (Tenerife) hosting

364 medium-sized lizards (*G. galloti*). Neither abiotic factors nor differential enemy-mediated
365 mortality of seeds or seedlings, as discussed above, help explain this difference between the Gran
366 Canaria and Tenerife scenarios. A more plausible explanation is related to the variation in
367 abundance of Canarian lizards on both islands. It is known that larger lizards are relatively less
368 abundant than small ones (Buckley et al., 2008). In this respect, our estimates (density of lizard
369 droppings) indicate that *G. galloti* on Tenerife is 6-fold more abundant than *G. stehlini* on Gran
370 Canaria. This result suggests that increased abundance of the less-effective, medium-sized lizards
371 on Tenerife may explain the large number of seedlings found beyond maternal plants, i.e. a type of
372 compensatory mass effect directly favouring higher fruit removal rates and dispersal. This
373 supports the idea that the contribution of less-effective animal mutualists to the reproductive
374 success of plants may frequently be overcompensated by their abundance (Vázquez et al., 2005).

375 A key variable driving the outcome of mutualistic interactions with gape-limited frugivores
376 is fruit size (Wheelwright, 1985). Small-bodied frugivores do not adequately handle and process
377 large fruits or seeds. Large-bodied frugivores usually disperse larger seeds and a wider range of
378 seed sizes, thus potentially favouring large seeds (Valido, 1999; Galetti et al., 2013) which results
379 in larger seedlings (Howe and Richter, 1982; Moles and Westoby, 2004). We hypothesized that
380 body-size reduction of mutualistic lizards could entail a late-acting reduction of seedling vigour of
381 *N. pulverulenta* due to consistent size reductions of successfully removed seeds. Our results
382 partially support this hypothesis. On the one hand, we found a consistent and significant reduction
383 of seedling stem diameter in populations hosting medium-sized lizards (Tenerife) compared to
384 populations with large-sized lizards (Gran Canaria). On the other hand, seedling stems on La
385 Gomera were unexpectedly thicker than those on Tenerife, and similar to those on Gran Canaria.
386 As previously discussed, these differences are not related to climatic conditions or soil type
387 differences. Thus, the large seed sizes and vigorous seedlings currently observed on La Gomera
388 may reflect the phenotypic selection pattern on fruit size exerted by giant lizards in the recent past
389 (Valido, 1999) and the more recent extinction events.

390 In summary, our comparative approach included three contrasting ecological scenarios along
391 a gradient of progressive reduction of frugivore body size due to extinction-driven downsizing.
392 After controlling for variation in abiotic conditions, differences in the early recruitment of a plant
393 species mirrored this defaunation-mediated downsizing gradient. At one extreme, Gran Canaria
394 populations illustrate a scenario of preserved interactions; whereas Tenerife represents an
395 intermediate suboptimal scenario, and La Gomera exemplifies a scenario in which both the seed
396 dispersal process and the regeneration away from maternal plants have collapsed. The example of
397 La Gomera is paradigmatic since plant populations have persisted for a long period without their
398 effective seed disperser partners, as reported for other widowed megafaunal-dispersed plant
399 species surviving more than 10,000 years (Janzen and Martin, 1982; Guimarães et al., 2008).
400 Reliance on secondary dispersal has been proposed as a key mechanism underlying this
401 persistence of widowed plant species (Guimarães et al., 2008; Jansen et al., 2012). Accordingly,
402 our results suggest that in the case of *N. pulverulenta* the very limited secondary dispersal
403 mediated by abiotic and biotic vectors in combination with apparently low seedling mortality
404 under parent plants may be allowing the long-term local persistence of the plant populations on La
405 Gomera.

406

407 **Conclusions**

408 Anthropogenic impact is causing a very fast decline of frugivore size on islands worldwide, where
409 the projected downsizing in the future is up to three orders of magnitude above mainland
410 ecosystems (Hansen and Galetti, 2009). Despite the limitations (number of insular replicates)
411 associated with this natural-based experiment, our results highlight a number of effects that such
412 downsizing may entail in relation to plant demography and population recruitment. Extirpation of
413 large-bodied frugivores may not cause a marked decline in some quantitative components of
414 dispersal (Markl et al., 2012), but it will certainly determine a reduction in qualitative aspects
415 critical for ensuring dispersal effectiveness. It remains unknown if this downsizing pattern also

416 drives reduced gene flow via seed dispersal within and among populations, with a lasting signal on
417 the genetic structure both at local and regional scales. Meanwhile, our results highlight the
418 importance of conserving the full range of functional processes (qualitative and quantitative
419 components) involved in mutualistic interactions crucial for the persistence of local regeneration
420 and plant population dynamics in a changing world.

421

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433

434 **Appendix A. Supplementary data**

435 The following are the supplementary data to this article:

436 **Appendix S1.** Natural history of Canarian lizards (g. *Gallotia*, Lacertidae).

437 **Appendix S2.** Additional information for the statistical analyses.

438 **Table S1.** Information about the sampled *N. pulverulenta* populations.

439 **Figure S1.** Distribution of *Gallotia* species in the Canary Islands.

440 **Figure S2.** Distribution map of sampled *N. pulverulenta* populations.

441 **Figure S3.** Autocorrelograms of the model residuals.

442 **Figure S4.** Photo-collage illustrating the study system.

443

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618 **Table 1.** Demographic parameters and results of multiple comparisons (Tukey test) among islands.

619 The number of sampled populations is indicated within brackets. Post-hoc analyses were conducted

620 after application of GLM¹ with a binomial distribution and a logit link function, GLM² with a621 Poisson distribution and a log link function, and LMM³. Non-shared, superscript letters indicate622 significant differences among islands. Data are mean \pm SE.

623

Demographic parameters	Gran Canaria	Tenerife	La Gomera
Proportion of seedlings outside canopy ¹	12.70 \pm 6.79 ^a (9)	17.71 \pm 6.58 ^b (13)	2.76 \pm 2.12 ^c (10)
Effective recruitment rate of seedlings ²	0.06 \pm 0.03 ^a (9)	0.39 \pm 0.22 ^b (13)	0.01 \pm 0.00 ^c (10)
Seedling stem diameter ³ (mm)	0.74 \pm 0.06 ^a (7)	0.47 \pm 0.05 ^b (7)	0.81 \pm 0.05 ^a (8)

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632 **Fig. 1.** Schematic representation of the maximum snout-vent length (max SVL) reduction of
633 Canarian giant lizards (g. *Gallotia*, Lacertidae) from the past (light-grey silhouettes) to the present
634 day (black silhouettes). Silhouettes are scaled to the max SVL. Only the islands hosting
635 *Neochamaelea pulverulenta* populations are shown (see Fig. S1 for details of the other islands):
636 Gran Canaria (from *G. stehlini* sub-fossils to extant *G. stehlini*), Tenerife (from *G. goliath* to *G.*
637 *galloti*) and La Gomera (from *G. goliath* to *G. caesaris*).

638

639 **Fig. 2.** Age-structure patterns (distribution of age classes) for the 42 analysed populations of
640 *Neochamaelea pulverulenta* in Gran Canaria (11 populations), Tenerife, (19), and La Gomera (12).
641 Data were pooled at the island level. Age classes: Ad (Adults), Juv (Juveniles), Sap (Saplings),
642 Seedl (Seedlings). Bars indicate mean \pm SE.

643

644 **Fig. 3.** Proportion of *Neochamaelea pulverulenta* seedlings growing outside (grey bars) and beneath
645 the canopy (black bars). Each bar represents a sampled population, sorted within islands in
646 decreasing order of the proportion of seedlings recruiting beneath the canopy (see Table S1, Fig. S2
647 for population codes and locations). Grey boxplots show the median as well as the upper and the
648 lower quartile of the proportion of seedlings outside the canopy on each island (the whiskers are 1.5
649 times the interquartile range of the box). Dots outside of the whiskers are considered outliers.

650

651 **Fig. 4.** (a) Effective recruitment rate of seedlings on each island (no. of seedlings outside the
652 canopy \cdot no. of adult plants⁻¹). Data are shown on the $\log(x+1)$ scale. (b) Density of medium to large

653 droppings of lizards on each island (no. of lizard droppings $\cdot 0.25 \text{ m}^2$). In both panels, population
654 parameters are represented with points. Boxplots show the median as well as the upper and the
655 lower quartile, the whiskers are 1.5 times the interquartile range of the box. Dots outside of the
656 whiskers are considered outliers. Gran Canaria, $n = 9$ populations; Tenerife, $n = 13$ populations; La
657 Gomera, $n = 10$ populations.

658

659 **Fig. 5.** Variation in seedling stem diameter within and among islands. Data are population mean \pm
660 SE (unfilled circles). At the island level, dotted lines and grey shadows indicate mean and SE
661 respectively. Population codes along the abscissa are as in Table S1 and Fig. S2. Populations are
662 ordered as in Fig. 3.

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