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1 [SHORT COMMUNICATION]

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4 **Intra-specific downsizing of frugivores affects**
5 **seed germination of fleshy-fruited plant species**

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29 **Abstract**

30 The loss of largest-bodied individuals within species of frugivorous animals is one
31 of the major consequences of defaunation. The gradual disappearance of large-
32 bodied frugivores is expected to entail a parallel deterioration in seed dispersal
33 functionality if the remaining smaller-sized individuals are not so effective as seed
34 dispersers. While the multiple impacts of the extinction of large bodied species
35 have been relatively well studied, the impact of intraspecific downsizing (i.e. the
36 extinction of large individuals within species) on seed dispersal has rarely been
37 evaluated. Here we experimentally assessed the impact of body-size reduction
38 in the frugivorous lizard *Gallotia galloti* (Lacertidae), an endemic species of the
39 Canary Islands, on the seed germination patterns of two fleshy-fruited plant
40 species (*Rubia fruticosa* and *Withania aristata*). Seed germination curves and the
41 proportions of germinated seeds were compared for both plant species after
42 being defecated by large-sized individuals and small-sized individuals. The data
43 show that seeds of *W. aristata* defecated by larger-sized lizards germinated faster
44 and in a higher percentage than those defecated by small-sized lizards, while no
45 differences were found for *R. fruticosa* seeds. Our results suggest that
46 disappearance of the largest individuals of frugivorous species may impair
47 recruitment of some plant species by worsening seed germination. They also
48 warn us of a potential cryptic loss of seed dispersal functionality on defaunated
49 ecosystems, even when frugivorous species remain abundant.

50

51 **Keywords:** Defaunation, saurochory, seed dispersal, plant recruitment, Canary
52 Islands

53 Defaunation, the progressive disappearance of numerous vertebrate species and
54 populations, and declines in their local abundance is triggering a (mis)functioning
55 of increasingly depauperate ecosystems (Dirzo *et al.* 2014; Young *et al.* 2016).
56 This global change process has disproportional impacts on largest-bodied
57 species at community level (Hansen & Galetti 2009; Dirzo *et al.* 2014; Young *et al.*
58 *al.* 2016), and also on largest-sized individuals at the species level (Anderson *et al.*
59 *al.* 2011; Young *et al.* 2016; Pérez-Méndez 2016), resulting in skewed body size
60 distributions (Dirzo *et al.* 2014). Documented consequences range from shifts in
61 evolutionary regimes (e.g. reduction in seed sizes of fleshy-fruited plant species)
62 (Galetti *et al.* 2013) to notable deteriorations in key ecosystem functions such as
63 nutrient cycling, food and water provisioning, and animal-mediated seed
64 dispersal (Malhi *et al.* 2016). While the multiple impacts of downsizing at
65 community level (i.e. the extinction of largest bodied species) have been relatively
66 well studied, the impact of intraspecific downsizing (i.e. the extinction of large
67 individuals within species) has been rarely assessed.

68 Seed dispersal mediated by vertebrate animals is a crucial process in the
69 regeneration cycle of fleshy-fruited plants. The extinction of large frugivorous
70 species may thus impair natural regeneration, as they are usually more efficient
71 seed dispersers (quantitatively and qualitatively) than smaller species (Jordano
72 *et al.* 2007; Wotton & Kelly 2011; Anderson *et al.* 2011; Larsen & Burns 2012;
73 Pérez-Méndez *et al.* 2015, 2016; Costa-Pereira & Galetti 2015; Pérez-Méndez
74 2016). Large frugivores usually consume a greater number of fruits, and disperse
75 a wider range of seed sizes over much longer distances than smaller bodied
76 species (Jordano *et al.* 2007; Anderson *et al.* 2011; Larsen & Burns 2012; Chen
77 & Moles 2015; Pérez-Méndez *et al.* 2016, 2017). Furthermore, the gut retention

78 times of a seed in the digestive tract of frugivores until defecated or regurgitated,
79 can vary with body size, influencing seed germination (Karasov 1990). Many
80 studies have demonstrated that gut passage can enhance seed germination,
81 while others describe negative effects (de Barros Leite *et al.* 2012). Such positive
82 or negative effects may depend on morphological characteristics of both fruit
83 consumers and seeds (Traveset 1998). For example, the normally longer
84 retention times of larger digestive tracts, may enhance germination in those
85 seeds that are benefited by a more intense scarification process (e.g. hard-
86 coated seeds), or harm their viability in the opposite case (Nogales *et al.* 2015).
87 Only a few studies have assessed the impact of downsizing on this important
88 qualitative component of seed dispersal, all of them focussing on the loss of large-
89 sized species but not on intra-specific loss of the largest individuals.

90 Frugivorous lizards are important seed dispersers, especially in insular
91 ecosystems (Olesen & Valido 2003). In the Canary Islands, lizards of the endemic
92 genus *Gallotia* (Lacertidae) are pivotal seed dispersers of a wide range of fleshy-
93 fruited plant species in several ecosystems (e.g. Valido & Nogales 1994;
94 Rodríguez *et al.* 2008; Rumeu *et al.* 2015). The largest species and individuals
95 have however been decimated since the arrival of the first human settlers on the
96 islands (*ca.* 2,500 years ago). The current lizard fauna is composed therefore by
97 only a subset of smaller individuals when compared with the pre-human situation
98 (Barahona *et al.* 2000). This defaunation process had important consequences
99 on the demography and genetic characteristics of plants (Pérez-Méndez *et al.*
100 2015, 2016, 2017; Pérez-Méndez 2016). Similarly, the loss of the largest
101 individuals of a given *Gallotia* species may have marked impacts on these and

102 other components of the dispersal process such as germination of seeds.
103 However, as far as we know this question remains unstudied.

104 Here we experimentally assessed the impact of body-size reduction in the
105 species *Gallotia galloti* (endemic to Tenerife and La Palma, Canary Islands) on
106 the seed germination patterns of two fleshy-fruited plant species *Rubia fruticosa*
107 (Rubiaceae) and *Withania aristata* (Solanaceae). These two native plant species
108 are locally abundant at lowlands and are mainly dispersed by *Gallotia* lizards and
109 a few passerine bird species (*Sylvia atricapilla*, *S. melanocephala*, *Turdus merula*,
110 and *Erithacus rubecula*) (González-Castro *et al.* 2015). For testing the hypothesis
111 that intra-specific downsizing of *Gallotia* lizards may trigger negative impacts on
112 seed dispersal, seed germination curves and the germination percentage of
113 seeds defecated by large-bodied and small-bodied individuals were compared
114 for the two plant species.

115

116 **Methods**

117 *Rubia fruticosa* (Rubiaceae) is an endemic plant of Madeira, Selvagens and
118 Canary Archipelagos. It is a shrub 0.5-1.5 m in height that grows approximately
119 between 0-450 m a.s.l. in the threatened Macaronesian thermophilous woodland.
120 Flowering in January it produces translucent fruits with an average of 1.3 ± 0.1
121 seeds per fruit (mean \pm SD, $n = 30$ fruits) in early spring (March). The average
122 diameter of fruits is 7.5 mm (Valido & Nogales 1994), the average seed diameter
123 is 2.6 ± 0.32 mm (mean \pm SD; present study) and average seed mass is 0.0074
124 g (Valido & Nogales 1994). *Withania aristata* (Solanaceae) is a native shrub
125 reaching 3 m in height, which grows between approximately 0-300 m a.s.l. and is
126 widely distributed through North Africa. Its ripe red-yellow fruits are usually

127 present at the end of May (late spring) and contain an average of 13.3 ± 0.99
128 seeds (mean \pm SD, $n = 28$ fruits). Average diameter of fruits is 9.6 mm (Valido &
129 Nogales 1994), average seed diameter is 3.8 ± 0.36 mm (mean \pm SD; present
130 study) and seed mass is 0.01 g (Valido & Nogales 1994). Fruits of these two
131 species are often consumed by Canarian lizards in the lowland shrubs (Valido *et al.*
132 *et al.* 2003) and the thermophilous woodland of the Canaries (Rodríguez *et al.* 2008;
133 González-Castro *et al.* 2015).

134 The frugivorous Canarian lizards of the genus *Gallotia* are currently represented
135 by seven extant species. Those used for the experiments belong to *Gallotia*
136 *galloti*, which is endemic to Tenerife and La Palma, Canary Islands. *Gallotia*
137 *galloti* is a medium-sized species (maximum snout-vent length of 145 mm;
138 Hernández *et al.* 2000) that inhabits all ecosystems of these islands, although it
139 is more abundant in open, sunny habitats. Its diet is omnivorous throughout the
140 year, including an important fraction of fleshy fruits (Valido *et al.* 2003; Rodríguez
141 *et al.* 2008).

142 Eight *G. galloti* individuals with contrasting body sizes (small-sized lizards,
143 range of Snout- to Vent-Length = 82 - 94 mm, $n = 4$; large-sized lizards, range =
144 126-137 mm, $n = 4$) were captured during May 2006 in Buenavista del Norte,
145 Tenerife Island. Lizards were kept individually in eight cages (45 cm diameter)
146 under natural conditions of sun/shade. They were fed *ad libitum* on a diet
147 consisting of beetle larvae, tomatoes, bananas and apples; water was also
148 continuously available.

149 Ripe fruits were collected from five haphazardly chosen individuals of each
150 plant species. Fruits were randomly assigned to four different treatments: *i*)
151 consumption by large-sized lizards, *ii*) consumption by small-sized lizards, and

152 two control treatments: *iii*) manually depulped seeds (no lizard consumption), and
153 *iv*) intact fruits (non-depulped fruits, no lizard consumption). For *W. aristata* the
154 control *with pulp* treatment consisted in planting whole fruits with an unknown
155 number of seeds (fruits are opaque and the number of seeds per fruit could not
156 be counted without removing the pulp). Seed germination occurred in all pots with
157 the control *with pulp* treatment for *W. aristata*, i.e. with a fruit and multiple seeds.
158 Consequently, the proportion of germinated seeds was not assessed and we
159 decided not to include these results. Ripe fruits of both plant species were offered
160 around midday to small- and large-sized lizards from May to September. Cages
161 were inspected for faecal pellets every day. Seeds were kept inside the pellets
162 until sowing. All seeds belonging to the four treatments were separately and
163 randomly sown in 4 cm² pots at about 5 mm depth in a greenhouse with controlled
164 abiotic conditions (a standard substrate composed of 50% culture soil, 25% turf
165 and 25% volcanic sand; and watered every 2 days) and natural regime of light-
166 dark and temperature (20-25 °C). Overall, we sowed 3,895 seeds (*R. fruticosa*, *n*
167 = 2,213; *W. aristata*, *n* = 1,682, see Table 1 for a detailed account of the four
168 treatments). The germination test started on 1st October 2006, coinciding with
169 the arrival of the regular rainfall pattern of the wet season in the Canaries, and
170 monitoring seedling emergence every five days for six months. Germination was
171 considered as the emergence of any seedling part from the soil surface. The
172 germination curves and overall percentage of seeds germinated were compared
173 between treatments. We applied a Cox proportional hazard regression model
174 with Efron's approximation to deal with tied germination times and a post-hoc
175 Tukey test to assess differences in the germination curves. Finally, we fitted a
176 Generalized Linear Model with a binomial distribution of errors and a logit link

177 function with germination as response variable (0 = no germination, 1 =
178 germination) and seed treatments as a four-level fixed factor (with pulp, depulped,
179 small-sized lizard and large-sized lizard). To test for differences among seed
180 treatments, a post-hoc Tukey test was applied. Statistical analyses were carried
181 out with R software (version 3.4.0, R Foundation for Statistical Computing,
182 Vienna, Austria).

183

184 **Results and discussion**

185 We found significant differences in germination curves and percentage of
186 germinated seeds between the two lizard treatments in *W. aristata*, with seeds
187 defecated by large-sized lizards exhibiting a faster germination and
188 approximately a 10% higher germination than those defecated by small-sized
189 lizards (Table 1). No statistical differences were found for the same variables and
190 treatments in *R. fruticosus* (Table 1). Overall, seeds in control treatments
191 germinated faster ($p < 0.01$ for all comparisons) and showed a higher germinated
192 percentage than those defecated by lizards for both plant species (Table 1; Fig.
193 1).

194 Although sample size of experimental lizards is not very large ($n = 8$), our
195 experimental approach provided supports for the hypothesis that the loss of the
196 largest individuals within a given frugivorous species may entail negative impacts
197 on different components of the seed dispersal process. Extinction of the largest
198 individuals of the frugivorous *G. galloti* lizards may thus impair recruitment of
199 some plant species (e.g. *W. aristata*) by worsening seed germination, an
200 important qualitative component of plant dispersal.

201 Overall, our results suggest that fruit depulping by lizards is not an
202 important process enhancing seed germination ability of the studied plant species.
203 In fact, the effect of the gut passage was negative, as indicated by a faster
204 germination and a higher germination percentage for control seeds. This is not
205 surprising considering the similar results in previous studies for the same plant
206 species and vegetation (González-Castro *et al.* 2015; but see contrasting results
207 in Valido & Nogales 1994 for *W. aristata* in xerophytic shrublands). The observed
208 pattern may be explained as due to the digestive and mechanical action of lizard
209 guts on seed coats, reducing germinability. Despite not finding a positive effect
210 of gut passage, it is important to note that our experimental design did not include
211 monitoring seed fate under natural conditions. Survival of seeds that remain
212 beneath source plants without being consumed and dispersed may be
213 compromised, as seed/seedling mortality in maternal neighbourhoods is often
214 disproportionately high (Janzen 1970; Connell 1971). Therefore, seed dispersal by
215 lizards becomes essential to escape the maternal neighbourhood and reach
216 suitable sites for germination and seedling survival. Indeed, lizards have been
217 shown to be very efficient seed dispersers of *both R. fruticosa* and *W. aristata* in
218 moving a large quantity of seeds to suitable habitats for germination and seedling
219 establishment (González-Castro *et al.* 2015).

220 Body-size of *Gallotia* lizards is a key trait influencing seed dispersal
221 effectiveness in terms of effective seedling recruitment and long-distance
222 dispersal of seeds (Pérez-Méndez *et al.* 2015, 2016, 2017; Pérez-Méndez 2016).
223 Our results suggest that large individuals may also be more effective than small
224 individuals in terms of seed germination probability. In fact, *W. aristata* seeds
225 defecated by large-sized lizards germinated faster and showed a higher

226 germination percentage than those defecated by small-sized lizards. Intestine
227 length and gut retention times increase with body size in *G. galloti* (Valido &
228 Nogales 2003). The longer-lasting abrasive treatment given by the larger lizards
229 (longer retention times) ought to intensify the scarification of *W. aristata* seed
230 coats. This does not seem to explain the observed pattern as depulped seeds
231 (without scarification) reached higher germination rates than lizard-consumed
232 seeds. Furthermore, no association between germinability and retention time
233 differences were observed for *W. frutescens* fruits consumed by the lizard
234 *Podarcis lilfordi* on the Balearic Islands (Castilla 2000). It is important to note that
235 the disappearance of largest individuals may entail not only an important skew in
236 body size distribution of *Gallotia* lizards, but also in distribution of ontogenetic
237 stages; i.e., an overrepresentation of sub-adults. Thus, the differences in
238 germination of seeds consumed by large and small lizards could be related to
239 other factors such as thermoregulatory behaviour, endocrine and reproduction
240 status or inclusion of non-food items (e.g. stones or soil) in the diet (lizard cages
241 were placed on stony soils), which can vary with both body size and ontogenetic
242 stage of individuals.

243 Our findings have important implications for the natural regeneration of
244 plant species on defaunated or fragmented ecosystems. While small-sized
245 species/individuals are usually resilient to human disturbances, the largest ones
246 are rapidly extirpated from small patches. As shown here, the extinction of the
247 largest individuals of *G. galloti* might entail appreciable impacts on the seed
248 germination patterns of some plant species (e.g. *W. aristata*). In addition, this
249 study provides a warning about the cryptic loss (or deterioration) of important
250 ecological functions such as seed dispersal (McConkey & O’Farrill 2015, 2016),

251 associated with the extinction of the largest individuals of a given species. Marked
252 deteriorations in dispersal functioning may occur even when a species is quite
253 abundant within a given ecosystem. For example, as illustrated here, subtle
254 changes in the intra-specific distribution of frugivore body sizes may trigger a
255 substantial drop in seed germination, even when this species remains abundant.
256 This is of special relevance to insular ecosystems (islands, mountains, lakes,
257 etc.), where the very low functional redundancy of animal assemblages prevents
258 functional replacement after the extinction of large- bodied species or individuals
259 (McConkey & Brockelman 2011; McConkey & Drake 2015).

260 **Contribution of the authors**

261 N.P.-M., A.R., M.N. conceived the idea. A.R. and M.N. conducted the
262 experimental work, N.P.-M. performed statistical analyses and wrote a first draft
263 of the manuscript. A.R. and M.N. contributed critically to the drafts and all
264 authors gave final approval for publication.

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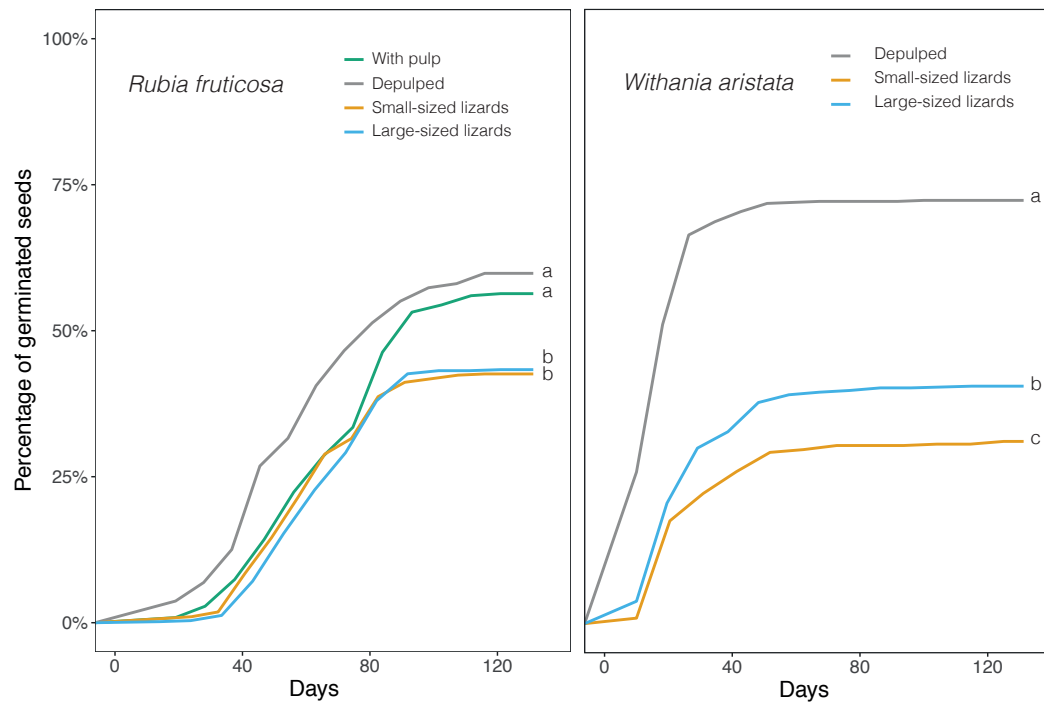
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371

72 **Fig.1** Seed germination curves: (A) *Rubia fruticosa* (Rubiaceae) and (B) *Withania aristata* (Solanaceae) ingested by large-sized
73 lizards, small-sized lizards, depulped seeds and control seeds (with pulp). The same letters represent non-significant differences in
74 germination curves between treatments, according to post-hoc Tukey tests. Accumulation curves were smoothed with the LOWEES
75 method.



76

77 **Table 1.** Seed germination percentages and sample sizes of *Rubia fruticosa* (Rubiaceae) and *Withania aristata* (Solanaceae) for the
 78 different treatments. Estimates and Standard Errors of the models are also indicated. The same letters as the curves in Figure 1
 79 represent non-significant differences among treatments according to post-hoc Tukey tests for germination percentage and
 80 germination curves.

81

Plant species	No. seeds	Germination percentage	Estimate ± SE (Germination percentage)	Estimate ± SE (Germination curve)
<i>Rubia fruticosa</i>				
<i>With pulp</i>	575	56.3	Intercept ^a	Intercept ^a
<i>Depulped</i>	575	59.8	0.14 ± 0.12 ^a	0.19 ± 0.08 ^a
<i>Large-sized lizard</i>	570	42.3	-0.52 ± 0.12 ^b	0.33 ± 0.09 ^b
<i>Small-sized lizard</i>	493	43.7	-0.55 ± 0.12 ^b	-0.33 ± 0.08 ^b
<i>Withania aristata</i>				
<i>Depulped</i>	575	72.3	Intercept ^a	Intercept ^a
<i>Large-sized lizard</i>	680	40.6	-1.75 ± 0.14 ^b	-1.01 ± 0.08 ^b
<i>Small-sized lizard</i>	427	31.1	-1.34 ± 0.12 ^c	-1.35 ± 0.10 ^c