[SHORT COMMUNICATION]

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

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Abstract

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

Keywords: Defaunation, saurochory, seed dispersal, plant recruitment, Canary Islands

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

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

& Moles 2015; Pérez-Méndez *et al.* 2016, 2017). Furthermore, the gut retention times of a seed in the digestive tract of frugivores until defecated or regurgitated, can vary with body size, influencing seed germination (Karasov 1990). Many studies have demonstrated that gut passage can enhance seed germination, while others describe negative effects (de Barros Leite *et al.* 2012). Such positive or negative effects may depend on morphological characteristics of both fruit consumers and seeds (Traveset 1998). For example, the normally longer retention times of larger digestive tracts, may enhance germination in those seeds that are benefited by a more intense scarification process (e.g. hard-coated seeds), or harm their viability in the opposite case (Nogales *et al.* 2015). Only a few studies have assessed the impact of downsizing on this important qualitative component of seed dispersal, all of them focussing on the loss of large-sized species but not on intra-specific loss of the largest individuals.

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

components of the dispersal process such as germination ~~patterns of seeds~~.

However, as far as we know this question remains unstudied.

Here we experimentally assessed the impact of body-size reduction in the species *Gallotia galloti* (endemic to Tenerife and La Palma, Canary Islands) on the seed germination patterns of ~~the~~ two fleshy-fruited plant species *Rubia fruticosa* (Rubiaceae) and *Withania aristata* (Solanaceae). ~~Both plant species are native from these habitats located at the island~~ These two native plant species ~~are abundant at~~ lowlands ~~and are mainly dispersed by~~ *Gallotia* lizards and a few passerine bird species (*Sylvia atricapilla*, *S. melanocephala*, *Turdus merula*, and *Erithacus rubecula*) (González-Castro *et al.* 2015). For ~~this testing the hypothesis that intra-specific downsizing of~~ *Gallotia* lizards may trigger negative impacts on ~~seed dispersal~~, seed germination curves and the ~~overall proportion germination percentage of seeds defecated by large-bodied and small-bodied individuals of these plant species~~ were compared ~~after being defecated by large-sized individuals vs. small-sized individuals of this lizard species~~ for the two plant species.

Comentado [a1]: No sé si esto lo sugirió algún revisor, peor creo que así está más claro. Evalúalo tú

Con formato: Fuente: Cursiva

Methods

Rubia fruticosa (Rubiaceae) is an endemic plant of Madeira, Selvagens and Canary Archipelagos. It is a shrub 0.5-1.5 m in height that grows approximately between 0-450 m a.s.l. in the threatened Macaronesian thermophilous woodland. Flowering in January it produces translucent fruits with an average of 1.3 ± 0.1 seeds per fruit (mean $\pm$ SD, $n = 30$ fruits) in early spring (March). The average diameter of fruits is 7.5 mm (Valido & Nogales 1994), the average seed diameter is 2.6 ± 0.32 mm (mean $\pm$ SD; present study), and average seed mass is 0.0074

g (Valido & Nogales 1994). *Withania aristata* (Solanaceae) is a native shrub reaching 3m in height, which grows between approximately 0-300 m a.s.l. and is widely distributed through North Africa. Its ripe red-yellow fruits ~~ripen during spring and summer~~ are usually present at the end of May (late spring) and contain an average of 13.3 ± 0.99 seeds (mean $\pm$ SD, $n = 28$ fruits). Average diameter of fruits is 9.6 (Valido & Nogales 1994), average seed diameter is 3.8 ± 0.36 mm (mean $\pm$ SD; present study) and seed mass is 0.01 g (Valido & Nogales 1994). Fruits of these two species are often consumed by Canarian lizards in the lowland shrubs (Valido *et al.* 2003) and the thermophilous woodland of the Canaries (Rodríguez *et al.* 2008; González-Castro *et al.* 2015).

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

Eight *G. galloti* individuals with contrasting body sizes (small-sized lizards, range of Snout- to Vent-Length = 82 - 94 mm, $n = 4$; large-sized lizards, range = 126-137 mm; 4 individuals, SL < 10 mm; 4 individuals, SL > 12 mm), ~~captured during 2008~~ ~~Burrián~~ ~~et al.~~ ~~2008~~ Tenerife Island. Lizards were kept individually in eight cages (45 cm diameter) under natural conditions of sun/shade. They were fed *ad libitum* on a diet consisting of beetle larvae, tomatoes, bananas and apples; water was also continuously available.

Comentado [a2]: Con mis limitados conocimientos de inglés, yo diría que aquí va un "that", pues sólo usamos una especie de lagarto. Por tanto la "s" de belongs sería correcta. Those es para el plural (si fueran varias especies)

Comentado [a3]: Desheché esta eliminación. No sé si algún referee lo propuso, pero creo que sería bueno decir que buena parte de la dieta son frutos (o al menos eso es lo reportado por los estudios de dieta basados en fecal pellets)

Ripe fruits were collected from five ~~haphazardly chosen random~~ individuals of each plant species. Fruits were randomly assigned to four different treatments: i) consumption by large-sized lizards, ii) consumption by small-sized lizards, and two control treatments: iii) manually depulped seeds (no lizard consumption), and iv) ~~intact fruits (non depulped fruits, no lizard consumption). We did not include the control with pulp treatment for *W. aristata* because it consisted in planting whole fruits with an unknown number of seeds (fruits are opaque and the number of seeds per fruit could not be counted without removing the pulp). Seed germination occurred in all pots with the control with pulp treatment for *W. aristata*, i.e. with a fruit and multiple seeds. C, consequently, the number of seeds per fruit could not be counted without removing the pulp, and thus its proportion of germinated seeds was not assessed and we decided not to include these results.~~ Ripe fruits of both plant species were offered around midday to small- and large-sized lizards ~~from (desde que empezó el experimento) to (hasta que acabó; no sé si parece algo de esto en el excel).~~ Cages were inspected for faecal pellets every day. Seeds were kept inside the pellets until sowing. All seeds belonging to the four treatments were separately and randomly sown in 4 cm² pots ~~at about 5 mm depth~~ in a greenhouse with controlled abiotic conditions ~~controlled (soil a standard substrate composed of 50% culture soil, 25% turf and 25% volcanic sand; and watered every 2 days, water and temperature) and natural regime of light-dark and temperature (20-25 °C).~~ Overall, we sowed 3,895 seeds (*R. fruticosa*, *n* = 2,213; *W. aristata*, *n* = 1,682, see Table 1 for a detailed account of the four treatments). The germination test started on 1st October 2006, coinciding with the arrival of the regular rainfall pattern of the wet season in the Canaries, and monitoring seedling emergence every five days for six months. Germination was considered as the emergence of

Comentado [a4]: Aquí yo pondría lo siguiente o algo así. Si quieren podemos incluir la curva en las gráficas poniendo un pie de figura diciendo que hay múltiples semillas en ese tratamiento "control with pulp". Aquí ya decimos que el porcentaje de germinación es 100% sólo faltaría la información de la velocidad de germinación. Y si no tal y como he puesto aquí no ponemos la info porque nos parece engañosa.

any seedling part from the soil surface. The germination curves and overall percentage of seeds germinated were compared between treatments. We applied a Cox proportional hazard regression model with Efron's approximation ~~for dealing to deal~~ with tied germination times and a post-hoc Tukey test ~~to assess~~ ~~for assessing~~ differences in the germination curves. Finally, we fitted a Generalized Linear Model with a binomial distribution of errors and a logit link function with germination as response variable (0 = no germination, 1 = germination) and seed treatments as a four-level fixed factor (with pulp, depulped, small-sized lizard and large-sized lizard). To test for differences among seed treatments, a post-hoc Tukey test was applied. Statistical analyses were carried out with R software (version 3.4.0, R Foundation for Statistical Computing, Vienna, Austria).

Results and discussion

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

Although sample size of experimental lizards is not very large ($n = 8$), This
our experimental approach provided supports for the hypothesis that the loss of

the largest individuals within a given frugivorous species may entail negative impacts on different components of the seed dispersal process. Extinction of the largest individuals of the frugivorous *G. galloti* lizards may thus impair recruitment of some plant species (e.g. *W. aristata*) by worsening seed germination, an important qualitative component of plant dispersal.

Overall, our results suggest that fruit depulping by lizards is not an important process enhancing seed germination ability of the studied plant species.

In fact, the effect of the gut passage was negative, as indicated by a faster germination and a higher germination percentage for control ~~vs. defecated~~ seeds.

This is not surprising considering the similar results in previous studies for the same plant species and vegetation (González-Castro *et al.* 2015; but see contrasting results in Valido & Nogales 1994 for *W. aristata* in xerophytic shrublands). The observed pattern may be explained as due to the digestive and mechanical action of lizard guts on seed coats, reducing germinability. Despite not finding a positive effect of gut passage, it is important to note that our experimental design did not include monitoring seed fate under natural conditions.

~~The future~~Survival of seeds that remain beneath source plants without being consumed and dispersed may be compromised, as seed/seedling mortality in maternal neighbourhoods is often disproportionately high (Janzen 1970; Connell 1971). Therefore, seed dispersal by lizards becomes essential to escape the maternal neighbourhood and reach suitable sites for germination and seedling survival. Indeed, lizards have been shown to be very efficient seed dispersers of both *R. fruticosa* and *W. aristata* in moving a large quantity of seeds to suitable habitats for germination and seedling establishment (González-Castro *et al.* 2015).

Body-size of *Gallotia* lizards is a key trait influencing seed dispersal effectiveness in terms of effective seedling recruitment and long-distance dispersal of seeds (Pérez-Méndez *et al.* 2015, 2016, 2017; Pérez-Méndez 2016). Our results suggest that large individuals may also be more effective than small individuals in terms of seed germination probability. In fact, *W. aristata* seeds defecated by large-sized lizards germinated faster and showed a higher germination percentage than those defecated by small-sized lizards. Intestine length and gut retention times increase with body size in *G. galloti* (Valido & Nogales 2003). The longer-lasting abrasive treatment given by the larger lizards (longer retention times) ought to intensify the scarification of *W. aristata* seed coats. This does not seem to explain the observed pattern as depulped seeds (without scarification) reached higher germination rates than lizard-consumed seeds. Furthermore, no association between germinability and retention time differences were observed for *W. frutescens* fruits consumed by the lizard *Podarcis lilfordi* on the Balearic Islands (Castilla 2000). It is important to note that the disappearance of largest individuals may entail not only an important skew in body size distribution of *Gallotia* lizards, but also in distribution of ontogenetic stages; i.e., an overrepresentation of sub-adults. Thus, the differences in germination of seeds consumed by large and small lizards could be related to other factors such as thermoregulatory behaviour, endocrine and reproduction status or inclusion of non-food items (e.g. stones or soil) in the diet (lizard cages were placed on stony soils), which can vary with both body size and ontogenetic stage of individuals.

Our findings have important implications for the natural regeneration of plant species on defaunated or fragmented ecosystems. While small-sized

species/individuals are usually resilient to human disturbances, the largest ones are rapidly extirpated from small patches. As shown here, the extinction of the largest individuals of *G. galloti* might entail appreciable impacts on the seed germination patterns of some plant species (e.g. *W. aristata*). In addition, this study provides a warning about the cryptic loss (or deterioration) of important ecological functions such as seed dispersal (McConkey & O’Farrill 2015, 2016), associated with the extinction of the largest individuals of a given species. Marked deteriorations in dispersal functioning may occur even when a species is quite abundant within a given ecosystem. For example, as illustrated here, subtle changes in the intra-specific distribution of frugivore body sizes ~~of *G. galloti* body~~ sizes may trigger a substantial drop in seed germination, even when this species remains abundant. This is of special relevance to insular ecosystems (islands, mountains, lakes, etc.), where the very low functional redundancy of animal assemblages prevents functional replacement after the extinction of large-bodied species or individuals (McConkey & Brockelman 2011; McConkey & Drake 2015).

Comentado [a5]: Body sizes está repetido y lo de *G. galloti* no creo que sea necesario aquí pues tratas de dar un mensaje más amplio, no? A estas alturas el lector debería saber que hemos trabajado con *G. galloti*. Quizás habría que introducir “frugivore”, es decir, “...of frugivore body sizes...”

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§ 74 ~~Article IV, State Personnel Law (SP) Employment and Compensation Board By-Products~~ 235

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

379

380 **Table 1.** Seed germination percentages and sample sizes of *Rubia fruticosa* (Rubiaceae) and *Withania aristata* (Solanaceae) for the
381 different treatments. Estimates and Standard Errors of the models are also indicated. The same letters as the curves in Fig.1 represent
382 non-significant differences among treatments according to post-hoc Tukey tests for germination percentage and germination curves.
383

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