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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 frugivorous animals is one of the major consequences of defaunation. The gradual disappearance of large-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 and 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.

Defaunation, the progressive disappearance of vertebrate species and populations, and declines in their local abundance, is triggering a (mis)functioning of increasingly depauperate ecosystems (Dirzo et al., 2014; Young et al., 2016). This global change process has disproportional impacts on largest-bodied species at community level (Hansen and Galetti, 2009; Dirzo et al., 2014; Young et al., 2016), and also on largest-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 reproduction 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 and Kelly, 2011; Anderson et al., 2011; Larsen and Burns, 2012; Pérez-Méndez et al., 2015, 2016; Costa-Pereira and 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 and Burns, 2012; Chen and 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

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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., 2005). 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 and 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 and 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.* 2500 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, 2017; Pérez-Méndez, 2016). Similarly, the loss of the largest individuals of a given *Gallotia* species may have marked impacts on these and other components of the dispersal process such as germination 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 two fleshy-fruited plant species *Rubia fruticosa* (Rubiaceae) and *Withania aristata* (Solanaceae). These two native plant species are locally 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 testing the hypothesis that intra-specific downsizing of *Gallotia* lizards may trigger negative impacts on seed dispersal, seed germination curves and the germination percentage of seeds defecated by large-bodied and small-bodied individuals were compared for the two plant species.

1. 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 and 450 m a.s.l. In the threatened Macaronesian thermophilous woodland. It flowers in January and produces translucent fruits with an average of 1.3 ± 0.1 seeds per fruit (mean ± SD, $n = 30$ fruits) in early spring (March). The average diameter of fruits is 7.5 mm (Valido and Nogales, 1994), the average seed diameter is 2.6 ± 0.32 mm (mean ± SD; present study) and average seed mass is 0.0074 g (Valido and Nogales, 1994). *Withania aristata* (Solanaceae) is a native shrub reaching 3 m in height, which grows between approximately 0-300 m a.s.l. and is widely distributed through North Africa. Its ripe red-yellow fruits are usually present at the end of May (late spring) and contain an average of 13.3 ± 0.99 seeds (mean ± SD, $n = 28$ fruits). Average diameter of fruits is 9.6 mm (Valido and Nogales, 1994), average seed diameter is 3.8 ± 0.36 mm (mean ± SD; present study) and seed mass is 0.01 g (Valido and 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 belong to *Gallotia galloti*, which is endemic to Tenerife and La Palma, Canary Islands. *Gallotia 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 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, $n = 4$) were captured during May 2006 in Buenavista del Norte, 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.

Ripe fruits were collected from five haphazardly chosen 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). For *W. aristata* the control *with pulp* treatment 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. Consequently, the 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 May to September. 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 $4\ cm^2$ pots at about 5 mm depth in a greenhouse with controlled abiotic conditions (a standard substrate composed of 50% culture soil, 25% turf and 25% volcanic sand; and watered every 2 days) and natural regime of light-dark and temperature (20–25 °C). Overall, we sowed 3,895 seeds (*R. fruticosa,* $n = 2{,}213$; *W. aristata*, $n = 1{,}682$,

Table 1

Seed germination percentages and sample sizes of *Rubia fruticosa* (Rubiaceae) and *Withania aristata* (Solanaceae) for the different treatments. Estimates and Standard Errors of the models are also indicated. Different letters (a, b, c) as the curves in Fig. 1 represent significant differences among treatments according to post-hoc Tukey tests for germination percentage and germination curves (p-values < 0.05).

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

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 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 to deal with tied germination times and a post-hoc Tukey test to assess 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).

2. Results and discussion

We found significant differences in germination curves and 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). No statistical differences were found for the same variables and treatments in *R. fruticosa* (Table 1). Overall, seeds in control treatments germinated faster ($p < 0.01$ for all comparisons) and showed a higher germinated percentage than those defecated by lizards for both plant species (Table 1; Fig. 1).

Although sample size of experimental lizards is not very large ($n = 8$), 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 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 and 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. 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 disproportionally 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

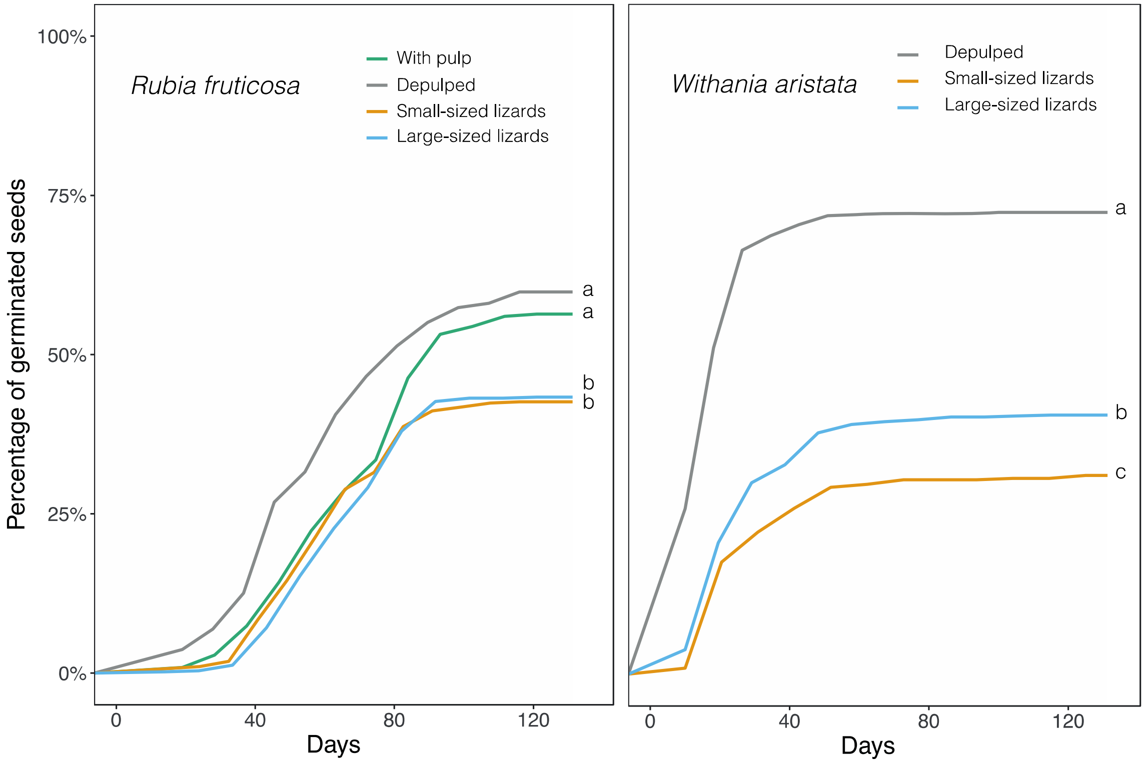

Fig. 1. Seed germination curves: (A) *Rubia fruticosa* (Rubiaceae) and (B) *Withania aristata* (Solanaceae) ingested by large-sized lizards, small-sized lizards, depulped seeds and control seeds (with pulp). The same letters represent non-significant differences in germination curves between treatments,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

retention times increase with body size in *G. galloti* (Valido and 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 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 and Brockelman, 2011; McConkey and Drake, 2015).

Contribution of the authors

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

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