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## Research article

# Downsized mutualisms: Consequences of seed dispersers' body-size reduction for early plant recruitment



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## ABSTRACT

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

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## Introduction

Extinction of vertebrate species has been a recurrent and taxonomically non-random pattern throughout the Earth's history (Raup, 1986; Shodi et al., 2009). Mass extinction events have reduced, in most cases, the number of large-bodied species (e.g. the disappearance of dinosaurs in the Cretaceous-Tertiary transition, Sheehan et al., 1991 or the demise of megafauna in the Late Pleistocene, Alroy, 2001) ending up with present-day defaunation scenarios in the anthropocene (Barnosky et al., 2011). This phenomenon often results in transitions from pristine communities, where large species are relatively abundant, to downsized communities dominated by small- to medium-bodied vertebrate species (Peres and Dolman, 2000), a pattern of ecological downgrading

entailing the loss of unique ecological functions (Estes et al., 2011; Dirzo et al., 2014; Valiente-Banuet et al., 2014). Since the large species have disproportional important ecological roles in ecosystem dynamics (Cordeiro and Howe, 2001, 2003; Woodward et al., 2005; Wright et al., 2007; Johnson, 2009), the effect of their extinction is expected to cascade through the remainder of the biota and produce deep shifts in the composition, structure and function of downsized communities (Redford and Feinsinger, 2001; Rule et al., 2012; Harrison et al., 2013). A critical issue is thus to develop research frameworks potentially enabling a better forecasting of cascading effects and the potential for delayed consequences of extinction-driven body size reduction and the deterioration of their associated ecological functions (Dirzo et al., 2014).

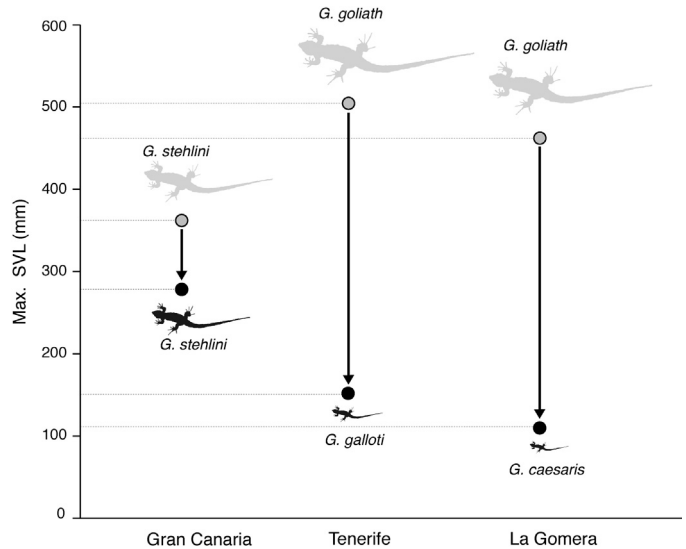
Animal-mediated seed dispersal is a crucial process in the life cycle of many flowering plants. It allows seeds and seedlings to not only escape the higher mortality frequently associated with the adult neighbourhood (Janzen, 1970) but also colonize new sites (Howe, 1982), and it promotes gene flow within and

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among populations (Hamrick et al., 1993). Large frugivores have an important role in all of these components of seed dispersal because they can consume a larger amount of fleshy fruits, disperse larger seeds and move them further away than smaller species in mutualistic assemblages (Jordano et al., 2007; Muller-Landau, 2007; Wotton and Kelly, 2011). Thus, there are numerous ways in which natural regeneration, especially of large seeded plants, can be impaired by a body size reduction in frugivore assemblages. For example, if frugivores become smaller, plants bearing large fruits can have strong seed dispersal limitations because frugivore gape width constrains the maximum fruit size animals can successfully handle and swallow (Wheelwright, 1985). Late-acting, post-dispersal effects may unfold, preventing or severely limiting seedling recruitment, and leaving defaunated ecosystems dominated by living-dead adult plants (Janzen, 1986) or with highly clumped regeneration within the neighbourhood of parent plants (Cordeiro and Howe, 2001). In addition, the extinction of large frugivores may trigger rapid evolutionary responses, given that extant small frugivores promote selection for reduced seed size (Galetti et al., 2013). Reduction of seed size may in turn negatively impact plant recruitment since it frequently correlates with reduced seed reserves and seedling size which result in reduced seedling survival under stress conditions (Howe and Richter, 1982; Moles and Westoby, 2004). Therefore, the downsizing of mutualistic frugivores can affect multiple scales of their interaction with plants, yet most of these cascading influences remain largely undocumented.

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

Lizard-mediated seed dispersal has been described as a widespread mutualism on oceanic islands (Olesen and Valido, 2003; Valido and Olesen, 2007). In the Canary Islands, endemic lacertid lizards (*Gallotia* spp.) are significant seed dispersers (Valido and Nogales, 1994, 2003; Valido, 1999; Valido et al., 2003; Rodríguez et al., 2008). However, the arrival of humans (ca. 2000–2500 yr BP) triggered a process of lizard species extinction and body size reduction on these islands (e.g. Barahona et al., 2000). For example, in La Gomera the decline of giant lizard populations began 1230–2344 years ago coinciding with the human colonization (González et al., 2014). The pattern and magnitude of this extinction has been markedly different on each island, related to differences in predation intensity by introduced mammals, habitat disturbances, and life-history traits (Machado, 1985; see also Appendix S1 for details). As a result, a gradient of defaunation-mediated lizard downsizing ranging from subtle (Gran Canaria) to noticeable (Tenerife), to quite marked (La Gomera; see Fig. 1 and Fig. S1 for island-specific scenarios), exists in present-day environments of the archipelago.



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

Here, we document the effects of body size reduction of Canary lizards on the early recruitment of a plant species which relies exclusively on these reptiles for seed dispersal. We selected *Neochamaelea pulverulenta* (Rutaceae), an endemic large-seeded treelet, as it is dispersed exclusively by medium- to large-sized frugivorous lizards and, accordingly, it represents a potentially useful model species to test downsizing effects (Valido, 1999). Our approach is a comparative analysis among the unique three islands where *N. pulverulenta* is distributed (Gran Canaria, Tenerife and La Gomera). These islands define a gradient of extinction-driven lizard body size reduction: Gran Canaria preserves the largest extant lizard species, i.e. *Gallotia stehlini*; Tenerife has abundant medium-sized *Gallotia galloti* lizards, whereas La Gomera hosts the smallest species *Gallotia caesaris* (Fig. 1; see also Appendix S1 and Fig. S1 for further details). Since larger lizards consume bigger and a greater amount of fruits (Valido, 1999), we hypothesize that the extinction-driven body size reduction will negatively affect both quantitative and qualitative components of *N. pulverulenta* recruitment. Among the former we considered the amount of seedlings established; among the latter we analyzed the proportion of those that effectively established outside adult plants and the reduction in seedling vigour estimated resulting from reduced seed sizes being dispersed. We expect the downsized scenarios will determine: (i) differences among islands in overall recruitment patterns as indicated by differences in the age structure (i.e. the relative abundance of seedlings), (ii) a decrease in the proportion of seedlings recruiting outside the canopy of adult plants, (iii) a reduction of the effective recruitment rate of seedlings (per capita of adult plants), and (iv) a reduced vigour of seedlings, resulting from a lack of consumption of large fruits (with large seeds; Howe and Richter, 1982; Valido, 1999).

## Materials and methods

### Study species

*N. pulverulenta* (Rutaceae) (Vent) Erdtman is an endemic treelet distributed in the dry lowlands (<400 m a.s.l.) of Gran Canaria,

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

Only medium- and large-bodied lizards eat these fruits, adequately handling and swallowing individual cocci, acting as legitimate seed dispersers (Valido and Nogales, 1994; Valido, 1999; Valido et al., 2003). Secondary seed dispersal by raptor predators on lizards containing seeds of *N. pulverulenta* has also been documented (Padilla et al., 2012). Subsequent to human colonization (ca. 2000–2500 yr BP, Appendix S1), different extinction scenarios emerged on each island generating a gradient of lizard body-size reduction (Fig. 1). On Gran Canaria lizard downsizing has been relatively minor, from the large forms of *G. stehlini* sub-fossils (maximum snout-vent length, max SVL = 367 mm) to the extant *G. stehlini* (max SVL = 280 mm). In contrast, lizard size reduction has been intense on La Gomera, where the extant widespread species (*G. caesaris*, max SVL = 111 mm) is four times smaller than their extinct relatives (*G. goliath*, max SVL = 466 mm). In turn, on Tenerife *G. goliath* (max SVL = 502 mm) became extinct and currently only the medium-sized species *Gallotia galloti* (max SVL = 145 mm) is widely distributed. Moreover, the large species *Gallotia intermedia* (max SVL = 174 mm) and *Gallotia bravoana* (max SVL = 212 mm) are present on Tenerife and La Gomera respectively, but they are critically endangered, surviving only in extremely reduced populations on highly localized, inaccessible cliffs (Fig. S1 and references therein for details).

#### Plant demography

To carry out a comparative study on plant recruitment under different seed dispersal scenarios, we sampled 42 *N. pulverulenta* populations from the three islands. We deliberately choose populations spanning the range of environmental conditions where the species occurs: Gran Canaria ( $n=11$ ), Tenerife ( $n=19$ ), and La Gomera ( $n=12$ ) (Table S1, Fig. S2). In each population we haphazardly set up 3–6 linear transects (25–100 m length; 5 m wide) depending on plant population size. Along these transects we counted and measured all individual plants, except for seedlings, for which only a subset were measured ( $n=637$  seedlings; sampling, on average, 29.3% of seedlings recorded in each population). The individual plant measurements included the maximum basal trunk/stem diameter at ground level (using a digital calliper), the maximum stretched height (except for adults; non-stretched height), and the two major diameters of the vertical canopy projection (using a measuring tape). Moreover, all individual plants were categorized according to their size-related age class (seedling, sapling, juvenile, adult). Seedlings were identified as plants with <1 mm of basal diameter and with less than four leaves; individuals not branched, with 1–7 mm basal diameter were recorded as saplings; plants with 7–15 mm basal diameter and no evidence of reproduction (absence of floral buds and/or seeds beneath the plant) were considered juveniles; otherwise they were recorded as adults. On average we collected data from 228 plants per

population (range: 102–571), with a total of 9402 plants sampled. We used this dataset to describe the age structure of populations.

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

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

#### Plant densities, climatic variation, and lizard abundance

To obtain an estimate of plant density per population we set up two perpendicular 100 m  $\times$  4 m transects, for which we counted all *N. pulverulenta* adult plants rooted within the transect. These data were independent of the adult plants censused in the age structure sampling. In addition, we gathered climatic data from meteorological stations located within a 7 km distance (1–4 stations), with long temporal data series available (range = 6–53 years). For each population we recorded the average annual precipitation ( $pp$ ), the mean maximum temperature of the hottest month ( $t_{\max}$ ), and the mean minimum temperature of the coldest month ( $t_{\min}$ ). Then, we calculated the Emberger index (Emberger, 1955) defined as  $Q = (2000 pp) / (t_{\max}^2 - t_{\min}^2)$ , which we log-transformed ( $-\ln Q$ ; Tieleman et al., 2003) for statistical analyses.

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

#### Statistical analyses

##### Quantitative plant recruitment

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

##### Qualitative plant recruitment

To assess the effect of the ecological scenarios (islands) on the proportion of seedlings outside the canopy we applied a GLM with a binomial distribution of errors and a logit link function. We used ‘island’ as the main fixed factor and both the density of *N. pulverulenta* adult plants and the Emberger index as covariates. Among-island differences in the effective recruitment rate of seedlings were tested by fitting a GLM with a Poisson distribution of errors and a log link function. The number of seedlings was used as a response variable, while ‘island’ was used as a fixed

**Table 1**  
Demographic parameters and results of multiple comparisons (Tukey test) among islands. The number of sampled populations is indicated within brackets. Post hoc analyses were conducted after application of GLM<sup>1</sup> with a binomial distribution and a logit link function, GLM<sup>2</sup> with a Poisson distribution and a log link function, and LMM<sup>3</sup>. Non-shared, superscript letters indicate significant differences among islands. Data are mean  $\pm$  S.E.

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

factor, the Emberger index as a covariate and the number of adults per population as an offset of the model. The stem diameter of sampled seedlings was used as an estimate of seedling size and vigour. We tested variation in seedling vigour among islands by fitting a linear mixed model (LMM) using 'island' as the main fixed factor with population identity as a random factor nested within it and the Emberger index as a covariate.

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

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

## Results

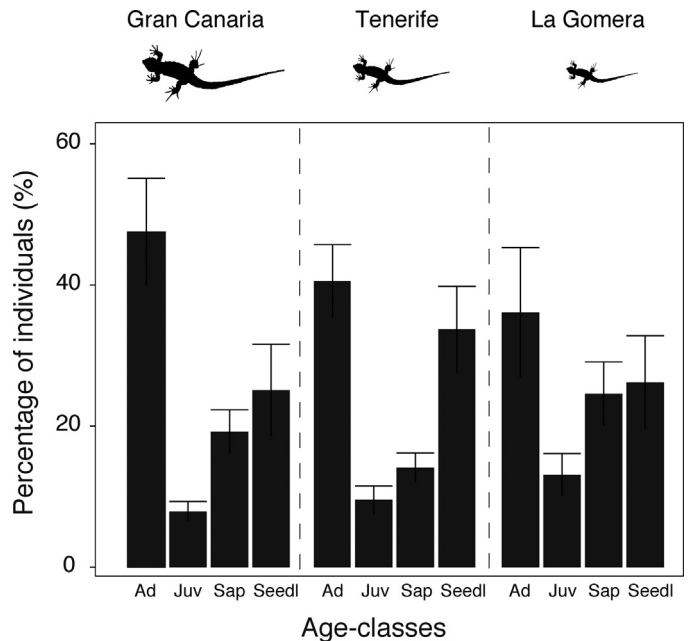
### Quantitative plant recruitment

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

### Qualitative plant recruitment

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

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



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

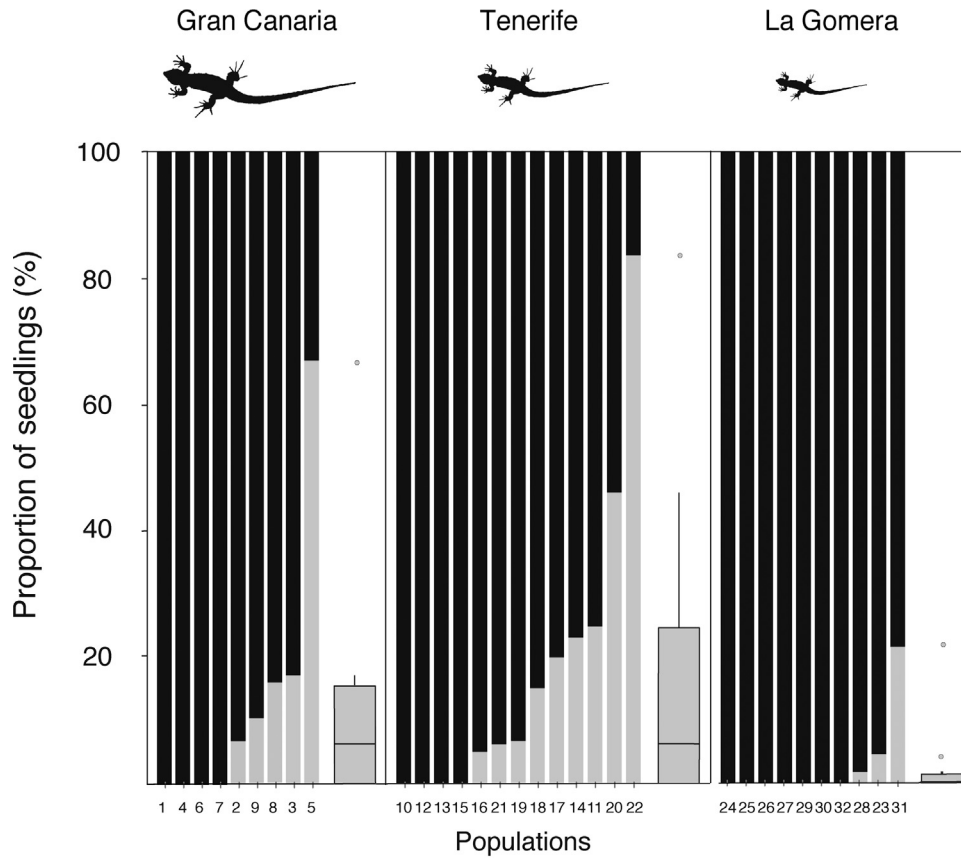
The observed differences among islands in the proportion of seedlings outside the canopy and the effective recruitment rate of seedlings match the variability detected in the abundance of medium-to-large lizard droppings. In the particular case of La Gomera, large droppings were totally absent in the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

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

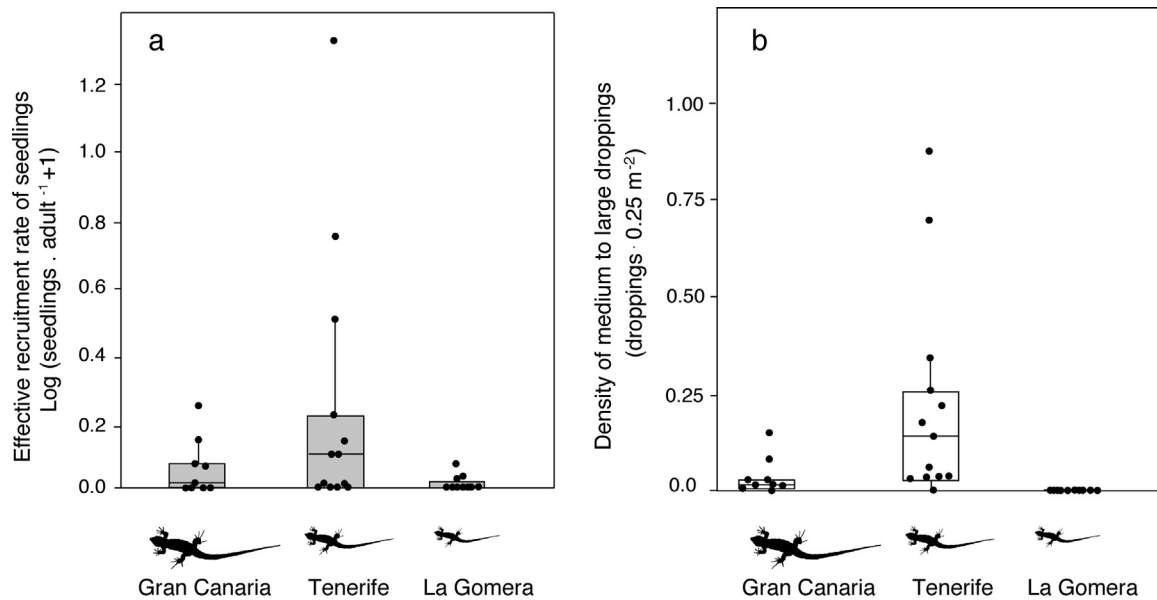
## Discussion

### Scenarios of downsized mutualisms

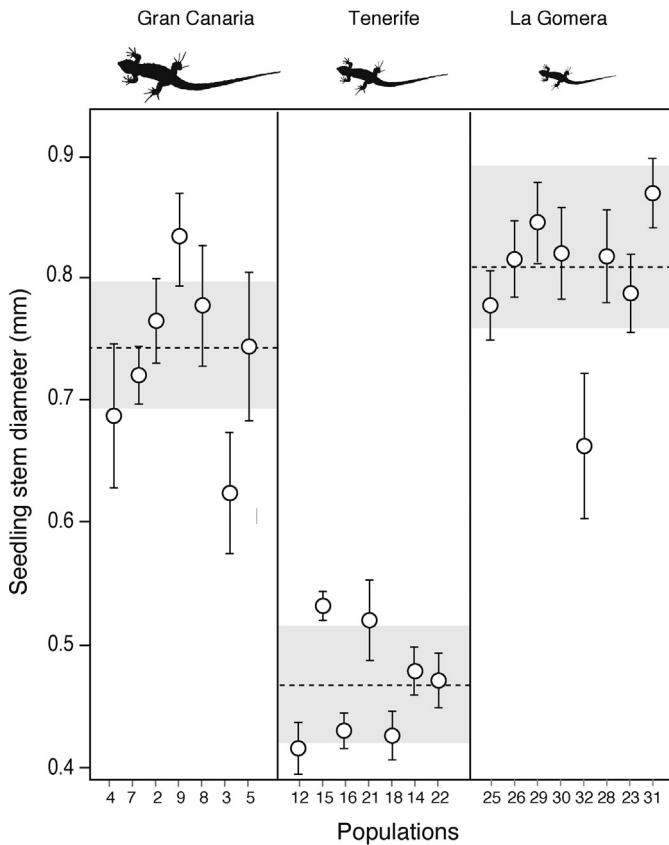
By using a natural island-based field experiment from the Canary Islands we found support for the observation that defaunation-mediated downsizing of frugivorous lizards critically hampers recruitment of *N. pulverulenta*, an endemic shrub strictly dependent on these seed dispersers. Unexpectedly, our results suggest that a reduction of lizard body size has no effect on the quantitative component of seed dispersal (age structure pattern) in the different insular scenarios, with similar overall amount of recruits (juveniles, saplings, and seedlings pooled) relative to the number of adult plants. However, we detected critical effects on the



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



**Fig. 4.** (a) Effective recruitment rate of seedlings on each island (no. of seedlings outside the canopy no. of adult plants<sup>-1</sup>). Data are shown on the  $\log(x + 1)$  scale. (b) Density of medium to large droppings of lizards on each island (no. of lizard droppings 0.25 m<sup>-2</sup>). In both panels, population parameters are represented with points. Boxplots show the median as well as the upper and the lower quartile, the whiskers are 1.5 times the interquartile range of the box. Dots outside of the whiskers are considered outliers. Gran Canaria,  $n = 9$  populations; Tenerife,  $n = 13$  populations; La Gomera,  $n = 10$  populations.



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

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

#### Quantitative consequences for plant demography

We found a similar proportion of established seedlings despite the marked differences in lizard body sizes among islands. In fact, we found high values (>25%) in most populations. These populations do not differ in soil type (volcanic substrate) or climatic conditions (i.e. aridity index; Table S1), so the similarity of the

demographic pattern across islands cannot be attributed to compensatory effects of abiotic conditions (e.g. favourable conditions for establishment in areas with limited dispersal by lizards). Biotic interactions could also have associated compensatory effects, for instance, if differences in competition, herbivory and/or post-dispersal seed predation intensities counterbalance the effect of dispersers, yet we have no evidence supporting this, e.g. we have no records of herbivory on seedlings. The lack of differences in overall recruitment contrasts with previous studies indicating reductions of recruit density in systems hosting non-effective seed dispersers (e.g. Cordeiro and Howe, 2003; Traveset and Riera, 2005, but see Bleher and Böhning-Gaese, 2001 for similar results).

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

#### Qualitative consequences for plant demography

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

At one extreme of the defaunation and downsizing gradient at La Gomera, we found the lowest values for both the proportion of seedlings outside the canopy and the effective recruitment rate of seedlings. These results, together with an absolute absence of seeds of *N. pulverulenta* in Gomeran lizard droppings, indicate the collapse of the lizard-mediated dispersal interactions on this island. This contrasts with data recorded from islands hosting medium- and large-bodied lizards (Tenerife and Gran Canaria, respectively). The human-driven extinction of the largest known species on La Gomera (*G. goliath*) and the marginal presence of the extant giant lizard *G. bravoana* only in an isolated remnant population (Valle Gran Rey; Valido et al., 2000), have actually deprived *N. pulverulenta* of effective seed dispersers throughout the island. The remaining abundant species *G. caesaris* is unable to effectively handle fruits and seeds due to marked morphological restrictions, i.e. fruit size considerably exceeds gape width of the lizard (Valido, 1999), a factor potentially impairing fruit removal and effective seed dispersal. Significant reductions of seeds dispersed away from adult parents have been reported in other defaunated scenarios (Chapman and Chapman, 1995; Cordeiro and Howe, 2003) where the lack of efficient dispersal agents leads to seed accumulations beneath the mother plants.

The plant populations from La Gomera, however, still preserve a marginal effective recruitment. We recorded approximately 3% of seedlings recruiting beyond the vicinity of adult plants and a very low (but non-zero) effective recruitment rate. Small-sized *G. caesaris*, which frequently take the fleshy pulp from fruits of the undispersed crop, can sporadically move some fruits and

remove the pulp away from adult plants where a minor fraction of seeds may likely germinate. In addition, *N. pulverulenta* populations are usually distributed on ravine slopes, where these seeds without pulp can be dispersed by rain or gravity. Lastly, although rodents mostly act as seed predators they can also disperse some seeds infrequently. Similar results have been reported for other plants (Traveset and Riera, 2005; Guimarães et al., 2008) where vertebrate-mediated seed dispersal has been disrupted and plants rely solely on haphazard, marginal dispersal. In fact, a recent study tracking seed fates (Jansen et al., 2012) showed that scatterhoarding rodents provide effective seed dispersal to widowed plants, acting as substitutes of an extinct megafauna.

We would expect the largest fraction of seeds being dispersed away from maternal plants on Gran Canaria, whose populations currently host the largest-sized lizards (*G. stehlini*). However, contrary to this expectation, the probability of finding seedlings recruiting beyond the parent plants and the effective recruitment rate of seedlings was higher on the island (Tenerife) hosting medium-sized lizards (*G. galloti*). Neither abiotic factors nor differential enemy-mediated mortality of seeds or seedlings, as discussed above, help explain this difference between the Gran Canaria and Tenerife scenarios. A more plausible explanation is related to the variation in abundance of Canarian lizards on both islands. It is known that larger lizards are relatively less abundant than small ones (Buckley et al., 2008). In this respect, our estimates (density of lizard droppings) indicate that *G. galloti* on Tenerife is 6-fold more abundant than *G. stehlini* on Gran Canaria. This result suggests that increased abundance of the less-effective, medium-sized lizards on Tenerife may explain the large number of seedlings found beyond maternal plants, i.e. a type of compensatory mass effect directly favouring higher fruit removal rates and dispersal. This supports the idea that the contribution of less-effective animal mutualists to the reproductive success of plants may frequently be overcompensated by their abundance (Vázquez et al., 2005).

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

In summary, our comparative approach included three contrasting ecological scenarios along a gradient of progressive reduction of frugivore body size due to extinction-driven downsizing. After controlling for variation in abiotic conditions, differences in the early recruitment of a plant species mirrored this defaunation-mediated downsizing gradient. At one extreme, Gran Canaria populations illustrate a scenario of preserved interactions; whereas Tenerife represents an intermediate suboptimal scenario, and La Gomera exemplifies a scenario in which both the seed dispersal

process and the regeneration away from maternal plants have collapsed. The example of La Gomera is paradigmatic since plant populations have persisted for a long period without their effective seed disperser partners, as reported for other widowed megafaunal-dispersed plant species surviving more than 10,000 years (Janzen and Martin, 1982; Guimarães et al., 2008). Reliance on secondary dispersal has been proposed as a key mechanism underlying this persistence of widowed plant species (Guimarães et al., 2008; Jansen et al., 2012). Accordingly, our results suggest that in the case of *N. pulverulenta* the very limited secondary dispersal mediated by abiotic and biotic vectors in combination with apparently low seedling mortality under parent plants may be allowing the long-term local persistence of the plant populations on La Gomera.

## Conclusions

Anthropogenic impact is causing a very fast decline of frugivore size on islands worldwide, where the projected downsizing in the future is up to three orders of magnitude above mainland ecosystems (Hansen and Galetti, 2009). Despite the limitations (number of insular replicates) associated with this natural-based experiment, our results highlight a number of effects that such downsizing may entail in relation to plant demography and population recruitment. Extirpation of large-bodied frugivores may not cause a marked decline in some quantitative components of dispersal (Markl et al., 2012), but it will certainly determine a reduction in qualitative aspects critical for ensuring dispersal effectiveness. It remains unknown if this downsizing pattern also drives reduced gene flow via seed dispersal within and among populations, with a lasting signal on the genetic structure both at local and regional scales. Meanwhile, our results highlight the importance of conserving the full range of functional processes (qualitative and quantitative components) involved in mutualistic interactions crucial for the persistence of local regeneration and plant population dynamics in a changing world.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2014.12.001>.

## References

- AEMET-IP, 2012. *Climate atlas of the archipelagos of the Canary Islands, Madeira and the Azores*. Agencia Estatal de Meteorología, Madrid.

- Alroy, J., 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* 292, 1893–1896, <http://dx.doi.org/10.1126/science.11059342>.
- Barahona, F., Evans, S.E., Mateo, J.A., García-Márquez, M., López-Jurado, L.F., 2000. Endemism, gigantism and extinction in island lizards: the genus *Gallotia* on the Canary Islands. *J. Zool.* 250, 373–388, <http://dx.doi.org/10.1111/j.1469-7998.2000.tb00781.x>.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57, <http://dx.doi.org/10.1038/nature09678>.
- Bleher, B., Böhning-Gaese, K., 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia* 129, 385–394, <http://dx.doi.org/10.1007/s004420100747>.
- Boyer, A.G., Jetz, W., 2014. Extinctions and the loss of ecological function in island bird communities. *Glob. Ecol. Biogeogr.* 23, 679–688, <http://dx.doi.org/10.1111/geb.12147>.
- Buckley, L.B., Rodda, G.H., Jetz, W., 2008. Thermal and energetic constraints on ectotherm abundance: a global test using lizards. *Ecology* 89, 48–55, <http://dx.doi.org/10.1890/05-0386>.
- Chapman, C.A., Chapman, L.J., 1995. Survival without dispersers: seedling recruitment under parents. *Conserv. Biol.* 9, 675–678, <http://dx.doi.org/10.1046/j.1523-1739.1995.09030675.x>.
- Cordeiro, N.J., Howe, H.F., 2001. Low recruitment of trees dispersed by animals in African forest fragments. *Conserv. Biol.* 15, 1733–1741, <http://dx.doi.org/10.1046/j.1523-1739.2001.99579.x>.
- Cordeiro, N.J., Howe, H.F., 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proc. Natl. Acad. Sci. U. S. A.* 100, 14052–14056, <http://dx.doi.org/10.1073/pnas.2331023100>.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345, 401–406, <http://dx.doi.org/10.1126/science.1251817>.
- Emberger, L., 1955. *Une classification biogéographique des climats, vol. 7. Recueil des Travaux de l'Institut Botanique de l'Université de Montpellier*, pp. 3–43.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet Earth. *Science* 333, 301–306, <http://dx.doi.org/10.1126/science.1205106>.
- Galetti, M., Guevara, R., Córtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labacca, F., Ribeiro, T., Carvalho, C.S., Collevatti, R.G., Pires, M.M., Guimarães Jr., P.R., Brancalion, P.H., Ribeiro, M.C., Jordano, P., 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340, 1086–1090, <http://dx.doi.org/10.1126/science.1233774>.
- González, E., Cerón-Souza, I., Mateo, J.A., Zardoya, R., 2014. Island survivors: population genetic structure and demography of the critically endangered giant lizard of La Gomera, *Gallotia bravoana*. *BMC Genetics* 15, 121, <http://www.biomedcentral.com/1471-2156/15/121>
- González-Castro, A., Calviño-Cancela, M., Nogales, M., 2014. Comparing seed dispersal effectiveness at the community level. *Ecology*, <http://dx.doi.org/10.1890/14-0655.1> (in press).
- Guimarães Jr., P.R., Galetti, M., Jordano, P., 2008. Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS ONE* 3, e1745, <http://dx.doi.org/10.1371/journal.pone.0001745>.
- Hamrick, J.L., Murawski, D.A., Nason, J.D., 1993. The influence of seed dispersal on the genetic structure of tropical trees populations. In: Fleming, T.H., Estrada, A. (Eds.), *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects*. Springer, Dordrecht, Netherlands, pp. 281–297, <http://dx.doi.org/10.1007/978-94-011-1749-4>.
- Hansen, D.M., Galetti, M., 2009. The forgotten megafauna. *Science* 324, 42–43, <http://dx.doi.org/10.1126/science.1172393>.
- Harrison, R.D., Tan, S., Plotkin, J.B., Slik, F., Detto, M., Brenes, T., Itoh, A., Davies, S.J., 2013. Consequences of defaunation for a tropical tree community. *Ecol. Lett.* 16, 687–694, <http://dx.doi.org/10.1111/ele.12102>.
- Howe, H.F., 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13, 201–228, <http://dx.doi.org/10.1146/annurev.es.13.110182.001221>.
- Howe, H.F., Richter, W.M., 1982. Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia* 53, 347–351, <http://dx.doi.org/10.1007/BF00389011>.
- Jansen, P.A., Hirsch, B.T., Emsens, W., Zamora-Gutierrez, V., Wikelski, M., Kays, R., 2012. Thieving rodents as substitute dispersers of megafaunal seeds. *Proc. Natl. Acad. Sci. U. S. A.* 109, 12610–12615, <http://dx.doi.org/10.1073/pnas.1205184109>.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528, <http://dx.doi.org/10.1086/282687>.
- Janzen, D.H., 1986. The future of tropical ecology. *Annu. Rev. Ecol. Syst.* 17, 305–324, <http://dx.doi.org/10.1146/annurev.es.17.110186.001513>.
- Janzen, D.H., Martin, P.S., 1982. Neotropical anachronisms: the fruits the gomphotheres ate. *Science* 215, 19–27, <http://dx.doi.org/10.1126/science.215.4528.19>.
- Johnson, C.N., 2009. Ecological consequences of Late Quaternary extinctions of megafauna. *Proc. R. Soc. B* 276, 2509–2519, <http://dx.doi.org/10.1098/rspb.2008.1921>.
- Jordano, P., García, C., Godoy, J.A., García-Castaño, J.L., 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proc. Natl. Acad. Sci. U. S. A.* 104, 3278–3282, <http://dx.doi.org/10.1073/pnas.0606793104>.
- Machado, A., 1985. *Hypothesis on the reasons for the decline of the large lizards in the Canary Islands*. *Bonn. Zool. Beitr.* 36, 563–575.
- Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J., Böhning-Gaese, K., 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conserv. Biol.* 26, 1072–1081, <http://dx.doi.org/10.1111/j.1523-1739.2012.01927.x>.
- McConkey, K.R., Drake, D.R., 2006. Flying seeds cease to function as seed dispersers long before they become rare. *Ecology* 87, 271–276, <http://dx.doi.org/10.1890/05-0386>.
- Meehan, H.J., McConkey, K.R., Drake, D.R., 2002. Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. *J. Biogeogr.* 29, 695–712, <http://dx.doi.org/10.1046/j.1365-2699.2002.00718.x>.
- Moles, A.T., Westoby, M., 2004. Seedling survival and seed size: a synthesis of the literature. *J. Ecol.* 92, 372–383, <http://dx.doi.org/10.1111/j.0022-0477.2004.00884.x>.
- Muller-Landau, H.C., 2007. Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica* 39, 372–384, <http://dx.doi.org/10.1111/j.1744-7429.2007.00290.x>.
- Olesen, J.M., Valido, A., 2003. Lizards as pollinators and seed dispersers: an island phenomenon. *Trends Ecol. Evol.* 18, 177–181, [http://dx.doi.org/10.1016/S0169-5347\(03\)00004-1](http://dx.doi.org/10.1016/S0169-5347(03)00004-1).
- Padilla, D.P., González-Castro, A., Nogales, M., 2012. Significance and extent of secondary seed dispersal by predatory birds on oceanic islands: the case of the Canary archipelago. *J. Ecol.* 100, 416–427, <http://dx.doi.org/10.1111/j.1365-2745.2011.01924.x>.
- Peres, C.A., Dolman, P.M., 2000. Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* 122, 175–189, <http://dx.doi.org/10.1007/PL00008845>.
- R Development Core Team, 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raup, D.M., 1986. Biological extinction in Earth history. *Science* 231, 1528–1533, <http://dx.doi.org/10.1126/science.11542058>.
- Redford, K.H., Feinsinger, P., 2001. *The half-empty forest: sustainable use and the ecology of interactions*. In: Reynolds, J.D., Mace, G.M., Redford, K.H., Robinson, J.G. (Eds.), *Conservation of Exploited Species*. Cambridge University Press, Cambridge, pp. 370–399.
- Rodríguez, A., Nogales, M., Rumeu, B., Rodríguez, B., 2008. Temporal and spatial variation in the diet of the endemic lizard *Gallotia galloti* in an insular Mediterranean scrubland. *J. Herpetol.* 42, 213–222, <http://dx.doi.org/10.1670/07-0752.1>.
- Rodríguez-Pérez, J., Traveset, A., 2009. Seed dispersal effectiveness in a plant–lizard interaction and its consequences for plant regeneration after disperser loss. *Plant Ecol.* 207, 269–280, <http://dx.doi.org/10.1007/s11258-009-9671-7>.
- Rule, S., Brook, B.W., Haberle, S.G., Turney, C.S.M., Kershaw, A.P., Johnson, C.N., 2012. The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia. *Science* 335, 1483–1486, <http://dx.doi.org/10.1126/science.1214261>.
- Schupp, E.W., Jordano, P., Gómez, J.M., 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytol.* 188, 333–353, <http://dx.doi.org/10.1111/j.1469-8137.2010.03402.x>.
- Sheehan, P.M., Fastovsky, D.E., Hoffman, R.G., Berghaus, C.B., Gabriel, D.L., 1991. Sudden extinction of the dinosaurs: Latest Cretaceous Upper Great Plains U.S.A. *Science* 254, 835–839, <http://dx.doi.org/10.1126/science.11536489>.
- Shodi, N.S., Brook, B.W., Bradshaw, C.A.J., 2009. *Causes and consequences of species extinctions*. In: Levin, S.A. (Ed.), *Princeton Guide to Ecology*. Princeton University Press, Princeton, pp. 514–520.
- Tieleman, B.I., Williams, J.B., Bloomer, P., 2003. Adaptation of metabolism and evaporative water loss along an aridity gradient. *Proc. R. Soc. B* 270, 207–214, <http://dx.doi.org/10.1098/rspb.2002.2205>.
- Traveset, A., Riera, N., 2005. Disruption of a plant–lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. *Conserv. Biol.* 19, 421–431, <http://dx.doi.org/10.1111/j.1523-1739.2005.00019.x>.
- Traveset, A., González-Varo, J.P., Valido, A., 2012. Long-term demographic consequences of a seed dispersal disruption. *Proc. R. Soc. B* 279, 1–6, <http://dx.doi.org/10.1098/rspb.2012.0535>.
- Valiente-Banuet, A., Aizen, M., Alcántara, J., Arroyo, J., Cocucci, A., Galetti, M., García, M., García, D., Gómez, J., Jordano, P., Medel, R., Navarro, L., Obeso, J., Oviedo, R., Ramírez, N., Rey, P., Traveset, A., Verdú, M., Zamora, R., 2014. Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, <http://dx.doi.org/10.1111/1365-2435.12356> (in press).
- Valido, A., (Ph.D. thesis) 1999. *Ecología de la dispersión de semillas por los lagartos endémicos canarios (g. Gallotia, Lacertidae)*. University of La Laguna, Tenerife.
- Valido, A., Nogales, M., 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* 70, 403–411, <http://dx.doi.org/10.2307/3545778>.
- Valido, A., Nogales, M., 2003. Digestive ecology of two omnivorous Canarian lizard species (*Gallotia Lacertidae*). *Amphibia-Reptilia* 24, 331–344, <http://dx.doi.org/10.1163/156853803322440790>.
- Valido, A., Olesen, J.M., 2007. The importance of lizards as frugivores and seed dispersers. In: Dennis, A., Green, R., Schupp, E.W., Wescott, D. (Eds.), *Frugivory and*



- seed dispersal: theory and its application in a changing world. CAB International, Wallingford, UK, pp. 124–147.
- Valido, A., Rando, J.C., Nogales, M., Martín, A., 2000. Fossil lizard found alive in the Canary Islands. *Oryx* 34, 75–76.
- Valido, A., Nogales, M., Medina, F.M., 2003. Fleshy fruits in the diet of Canarian lizards *Gallotia galloti* (Lacertidae) in a xeric habitat of the island of Tenerife. *J. Herpetol.* 37, 741–747, <http://dx.doi.org/10.1670/15-02AN>.
- Vázquez, D.P., Morris, W.F., Jordano, P., 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.* 8, 1088–1094, <http://dx.doi.org/10.1111/j.1461-0248.2005.00810.x>.
- Wheelwright, N.T., 1985. Fruit-size, gape width, and the diets of fruit-eating birds. *Ecology* 66, 808–818, <http://dx.doi.org/10.2307/1940542>.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., Warren, P.H., 2005. Body size in ecological networks. *Trends Ecol. Evol.* 20, 402–409, <http://dx.doi.org/10.1016/j.tree.2005.04.005>.
- Wotton, D., Kelly, D., 2011. Frugivore loss limits recruitment of large-seeded trees. *Proc. R. Soc. B* 278, 3345–3354, <http://dx.doi.org/10.1098/rspb.2011.0185>.
- Wotton, D.M., Kelly, D., 2012. Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. *J. Biogeogr.* 39, 1973–1983, <http://dx.doi.org/10.1111/jbi.12000>.
- Wright, S.J., Stoner, K.E., Beckman, N., Corlett, R.T., Dirzo, R., Muller-Landau, H.C., Nuñez-Iturri, G., Peres, C.A., Wang, B.C., 2007. The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica* 39, 289–291, <http://dx.doi.org/10.1111/j.1744-7429.2007.00293.x>.

Supplementary Data for

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

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

The Canarian lacertid lizards are included into the endemic genus *Gallotia* (Arnold, 1973). Currently, it comprises seven extant species (Arechavaleta et al., 2010; Cox et al., 2010): *G. atlantica* (Peters and Doria, 1882) from Lanzarote and Fuerteventura, *G. stehlini* (Schenkel, 1901) from Gran Canaria, *G. galloti* (Oudart, 1839) from Tenerife and La Palma, *G. intermedia* (Hernández et al., 2000) from Tenerife, *G. caesaris* (Lehrs, 1914) from La Gomera and El Hierro, *G. bravoana* Hutterer, 1985 from La Gomera, and *G. simonyi* (Steindachner, 1889) from El Hierro (Figure S1). However, the western islands were inhabited in the past by other giant taxa, considered extinct nowadays: *Gallotia simonyi* (Steindachner, 1889; Tenerife, La Gomera and La Palma), *G. goliath* (Mertens, 1942; Tenerife, La Gomera, La Palma and El Hierro), and *G. auaritae* (Mateo et al., 2001; La Palma) (Figure S1). The taxonomic status of these extinct taxa is certainly controversial. Some authors consider that just one giant species inhabited each of the western islands in the past (Mateo et al., 2011; but see Maca-Meyer et al., 2003). According to this, some of the recently discovered species in these islands surviving in very restricted and isolated populations i.e., *G. simonyi* (discovered in 1975 in El Hierro; Böhme and Bings, 1975), *G. intermedia* (1995 in Tenerife; Hernández et al., 1997, 2000) and *G. bravoana* (1999 in La Gomera; Valido et al., 2000; Nogales et al., 2001) are considered as dwarf individuals of the giant taxa already described from fossil/subfossil giant specimens (Rando et al., 1997; Bischoff, 1998; Barahona et al., 2000; Mateo et al., 2001, 2011). Therefore, until the taxonomic position of these extinct lizards is resolved by sequencing ancient DNA, we can say that each of these islands was inhabited in the past by giant lizards. These recently discovered species are closely related to extinct giant taxa, but currently restricted to small and

isolated populations. In turn, the medium- to smaller-bodied species (*G. galloti* and *G. caesaris* respectively) are abundant and widespread within each of the western islands. The resulting downsize gradient caused by the extinction process is summarized in Fig. 1 and Fig. S1.

The origin of this monophyletic group of lizards goes back to the Miocene (ca. 17 - 20 Mya), when a common ancestor of *Psammmodromus* and *Gallotia* colonized the older, easternmost islands (Lanzarote/Fuerteventura) from Southern Europe or Northwest Africa (Cox et al., 2010). Subsequent stepping-stone colonization and diversification processes were occurring from eastern to western islands. Therefore, in the Middle Miocene (ca. 13 - 10 Mya) three genetic lineages had been already formed: *G. atlantica* in Lanzarote/Fuerteventura, *G. stehlini* in Gran Canaria, and a different genetic lineage in Tenerife. The latter, during the Pliocene and Pleistocene (6 - 0.6 Mya), evolved in two lineages: small- to medium and giant bodied lizards. These lizards colonized the rest of western islands and formed a new species/subspecies in each island. Thus, by the mid-Pleistocene, Tenerife, La Gomera, La Palma and El Hierro each hosted a giant lizard coexisting with a small- or medium-sized species (Barahona et al., 2000; Cox et al., 2010).

Gigantism on oceanic islands is a recurrent evolutionary pattern among vertebrates (Lomolino, 2005), including lizards (Pregill, 1986; Meiri, 2008). Body-sizes of the *Gallotia* giant lizards are the largest (max. SVL = 502 mm) within the Lacertidae family, and they are considered a paradigmatic example of gigantism on islands (Barahona et al., 2000; Lomolino, 2005; Whittaker and Fernández-Palacios, 2007; Meiri, 2008). It is likely that the absence of large predators and the expansion of ecological niches (e.g. to herbivorous diets) enabled these lizards to reach giant sizes and diverge from smaller species (Maca-Meyer et al., 2003; Cox et al., 2010).

According to paleontological records, giant *Gallotia* lizards were widely distributed within these islands until the arrival of the first settlers, approximately 2000-2500 yr BP (García-Cruz and Marrero-Rodríguez, 1978; López-Jurado, 1985; Mateo and López-Jurado, 1992; Castillo et al., 1994; López-Jurado and Mateo, 1999; Castillo et al., 2001; Mateo 2007). The discovery of giant lizard bones in shell deposits (e.g. Alberto, 1999), together with results obtained from stable isotopes analysis of aboriginal bones (Arnay-de-la-Rosa et al., 2010, 2011) suggest that the first human colonization marked the beginning of the decline of giant lizard populations in these islands. In addition, a recent genetic study performed with giant lizards from La Gomera indicates that the drastic reduction of *G. bravoana* populations coincided with the arrival of humans to the island (1230-2344 years ago; González et al., 2014). Therefore, subsequent to colonization by Europeans ca. 500-600 yr BP, introduced predators and competitors (e.g. rats, cats, dogs and goats), habitat destruction, and some life-history components (e.g. low reproductive rate), finally resulted in the extinction and the body size reduction of the giant lizard species in these islands (Machado, 1985a; Mateo and López-Jurado, 1992; Barahona et al., 2000).

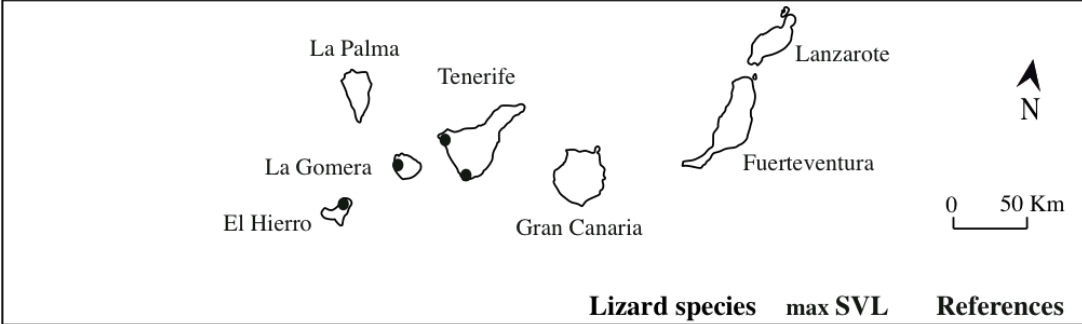





















Despite the extinction process and/or the resulting downsize of lizards occurred in all central and western islands (Figure S1), its intensity was not homogeneous among them (Figures 1, S1). For example, a subtle size reduction (according to max SVL recorded) took place in Gran Canaria, from 350 mm to 280 mm (*G. stehlini*). Tenerife experienced an intermediate reduction of lizard body sizes, as it still preserves the medium-sized *G. galloti* (145 mm) after the extinction of *G. goliath* (502 mm). In contrast, the extinction process resulted in a drastic downsize of lizards in La Gomera, from 466 mm (*G. goliath*) to 110 mm (*G. caesaris*). This allowed us defining three well-contrasted eco-evolutionary scenarios, providing an interesting natural experiment

to evaluate how the progressive reduction of lizard body-sizes affected the early recruitment of the large-seeded treelet *Neochamaelea pulverulenta* (Rutaceae), an endemic species whose seeds are dispersed exclusively by the large-to medium Canarian lizards (Valido, 1999).

All *Gallotia* lizard species present a marked omnivorous diet, with fleshy fruits being an important component year round. Thus, they legitimately disperse seeds of many fleshy-fruited plant species in different habitats and islands (Barquín-Díez and Wildpret, 1975; Machado, 1985b; Barquín-Díez et al., 1986; Naranjo et al., 1991; Valido and Nogales, 1994; Valido, 1999; Pérez-Mellado et al., 1999; Valido and Nogales, 2003; Valido et al., 2003; Martín et al., 2005; Carretero et al., 2006; Nogales et al., 2007; Rodríguez et al., 2008; Padilla et al., 2009, 2012; Carretero et al., 2014; González-Castro et al., 2014). Nevertheless, the quantitative importance of the vegetarian components in the diet positively covary with lizard body sizes both within- and among species. Larger lizards are more vegetarian and/or frugivores than the smaller ones (Mateo and López-Jurado, 1992; Valido et al., 2003; Carretero et al., 2006). These results, and a paleodiet study of *G. goliath* in Tenerife (Bocherens et al., 2003), suggest that extinct giant species might be even more vegetarian/frugivores than the extant largest species. Thus, it is assumed that these extinct lizards were also important seed dispersers of *N. pulverulenta* (Valido, 1999).

The geographical distribution of *N. pulverulenta* before the arrival of humans to the Canary Islands is undocumented. However, some archaeological studies indicate the presence of seed remains in many aboriginal burials (Del Arco, 1976, 1993; Machado, 2007; Morales, 2010; Morales and Gil, 2014), matching with actual distribution of this plant species within island. These results suggest non-important changes in the insular distribution of *N. pulverulenta* after the defaunation of giant lizards.

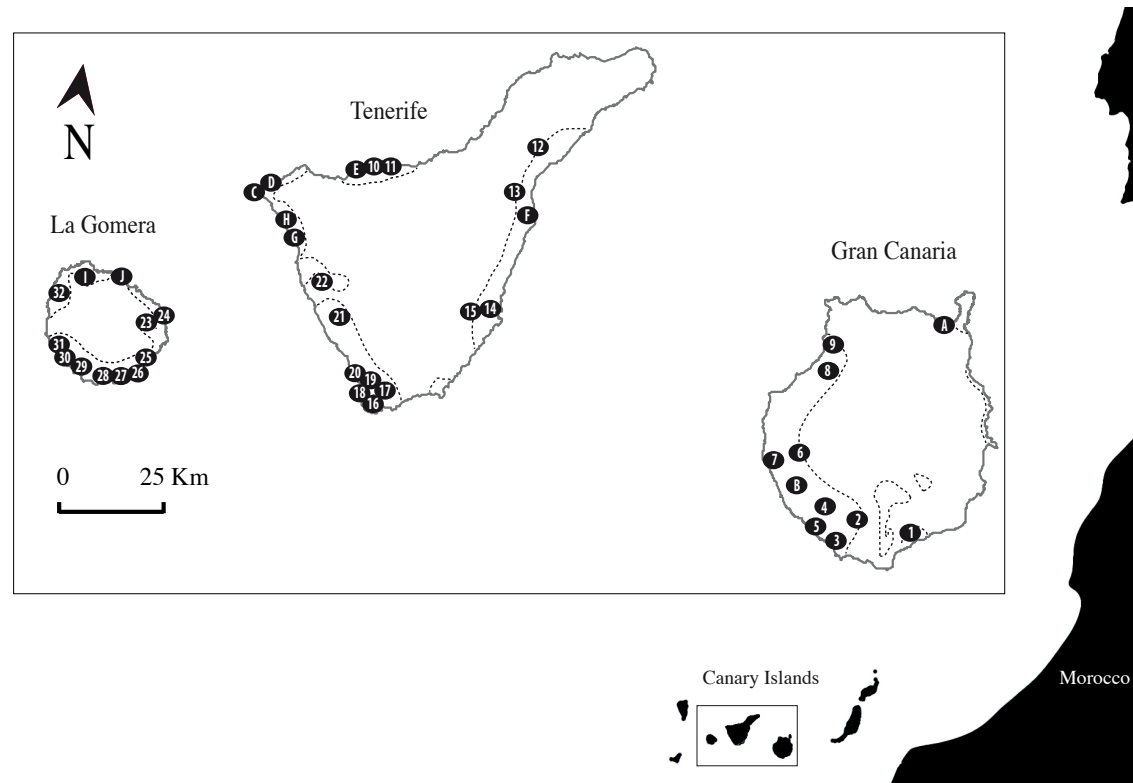
**Figure S1.** Distribution of *Gallotia* (Lacertidae) species in the Canary Islands and their maximum snout-vent length (max. SVL). Silhouettes are scaled to the max. SVL. Light-grey silhouettes (†) represent extinct lizards. Dark-grey silhouettes (\*) represent critically-endangered species with very restricted and isolated populations (dots on the maps). Black silhouettes represent extant, widely distributed species. Max. SVL of fossil *G. atlantica* has not been estimated, although López-Jurado and Mateo (1992) suggest a similar length to extant conspecifics according to data reported by Michaux et al. (1991). Some authors consider the presence of other extinct taxa in these islands (see text for details).

				
	Lizard species	max SVL	References	
 El Hierro (H)	  	† <i>G. goliath</i> 434 mm * <i>G. simonyi</i> 226 mm <i>G. caesaris</i> 110 mm	[1,2] [3] [4]	
 La Palma (P)	 	† <i>G. goliath</i> / † <i>G. auaritae</i> 444 mm <i>G. galloti</i> 121 mm	[1,5,6] [4]	
 La Gomera (G)	  	† <i>G. goliath</i> 466 mm * <i>G. bravoana</i> 212 mm <i>G. caesaris</i> 111 mm	[1,7] [8] [9]	
 Tenerife (T)	  	† <i>G. goliath</i> 502 mm * <i>G. intermedia</i> 174 mm <i>G. galloti</i> 145 mm	[1,10] [11] [12]	
 Gran Canaria (GC)	 	† <i>G. stehlini</i> 367 mm <i>G. stehlini</i> 280 mm	[1,13] [13]	
 Fuerteventura/Lanzarote (F/L)	 	† <i>G. atlantica</i> NA <i>G. atlantica</i> 104 mm	[14,15] [16]	

[1] Barahona et al., 2000; [2] Izquierdo et al., 1989; [3] Rodríguez-Domínguez et al., 1998; [4] Valido, A. (*personal observation*); [5] Bravo, 1953; [6] Mateo et al., 2001; [7] Hutterer et al., 1985; [8] Hernández-Divers et al., 2003; [9] Molina-Borja and Rodríguez-Domínguez, 2004; [10] Mertens, 1942; [11] Martín, A. (*personal communication*); [12] Martín, 1985; [13] Mateo and López Jurado, 1992; [14] Michaux et al., 1991; [15] López-Jurado and Mateo, 1995; [16] Márquez et al., 1997



**Figure S2.** Map showing *N. pulverulenta* populations sampled in this study from Gran Canaria, Tenerife, and La Gomera. Population codes are ordered from the easternmost to the westernmost island, and clockwise ordered within island. The codes correspond to those shown in the Table S1. The potential geographic distribution of *N. pulverulenta* (dotted lines) was modified from Atlantis 3.1 (Gobierno de Canarias. Banco de Datos de Biodiversidad de Canarias; [http://: www.biodiversidadcanarias.es/atlantis/](http://www.biodiversidadcanarias.es/atlantis/)).



**Table S1.** Information about the 42 sampled populations of *Neochamaelea pulverulenta* from the Canary Islands. The population codes match with those indicated in the Figure S2. Populations with letter codes were sampled only for age structure but not for the other demographic variables. Populations with asterisk (\*) in Tenerife indicate the presence of *G. galloti* but also *G. intermedia* in the vicinity. The Emberger index is log-transformed ( $-\ln Q$ ). The number of individuals of each age class sampled in the populations, and the number of seedlings growing outside the canopy (within brackets) are shown. (d) indicates populations where at least 6 seedlings were measured (stem diameter).

Code	Population	Island	Lizard species	Latitude (N)	Longitude (W)	-lnQ	Adults	Juveniles	Saplings	Seedlings
1	Montaña de Tabaiba	Gran Canaria	<i>G. stehlini</i>	27°48'08"	15°31'04"	-5.9	88	10	2	1 (0)
2	Barranco de Ayagaures	Gran Canaria	<i>G. stehlini</i>	27°48'36"	15°37'09"	-5.6	55	17	30	67 (4) d
3	Barranco de La Verga	Gran Canaria	<i>G. stehlini</i>	27°46'50"	15°41'42"	-5.9	61	11	35	6 (1) d
4	Barranco de Tauro	Gran Canaria	<i>G. stehlini</i>	27°49'07"	15°43'08"	-5.8	64	3	34	11 (0) d
5	Barranco de Tiritaña	Gran Canaria	<i>G. stehlini</i>	27°48'58"	15°44'36"	-5.7	79	5	16	33 (22) d
6	Barranco de Tasarte	Gran Canaria	<i>G. stehlini</i>	27°56'06"	15°45'12"	-6.1	47	8	54	121 (0)
7	Barranco de Güigüi	Gran Canaria	<i>G. stehlini</i>	27°56'01"	15°49'14"	-5.8	23	18	65	108 (0) d
8	Tirma	Gran Canaria	<i>G. stehlini</i>	28°02'05"	15°45'23"	-6.5	73	4	32	33 (5) d
9	La Laja del Risco	Gran Canaria	<i>G. stehlini</i>	28°03'33"	15°43'44"	-6.5	65	31	25	100 (10) d
A	Barranco de Tamaraccite	Gran Canaria	<i>G. stehlini</i>	28°07'31"	15°27'36"	-6.4	98	20	16	1
B	Barranco de Veneguera	Gran Canaria	<i>G. stehlini</i>	27°51'43"	15°46'21"	-5.7	516	96	175	NA
10	Punta de Juan Centella	Tenerife	<i>G. galloti</i>	28°23'32"	16°41'38"	-6.9	112	23	19	4 (0)
11	Charco de la Arena	Tenerife	<i>G. galloti</i>	28°23'58"	16°40'08"	-6.9	228	113	75	8 (2)
12	Tabaiba Alta	Tenerife	<i>G. galloti</i>	28°24'14"	16°20'21"	-6.9	56	11	41	76 (0) d
13	La Hidalga	Tenerife	<i>G. galloti</i>	28°19'53"	16°23'34"	-6.7	72	8	28	106 (0)
14	Abades	Tenerife	<i>G. galloti</i>	28°08'23"	16°27'24"	-6.4	73	12	10	47 (11) d
15	Arico	Tenerife	<i>G. galloti</i>	28°09'04"	16°28'17"	-6.4	35	5	42	131 (0) d
16	Malpaís Punta de Rasca	Tenerife	<i>G. galloti</i>	28°00'42"	16°41'54"	-6.0	54	2	3	272 (13) d
17	El Palm-Mar	Tenerife	<i>G. galloti</i>	28°01'23"	16°41'30"	-6.0	96	24	17	5 (1)
18	Montaña de Guaza I*	Tenerife	<i>G. galloti</i>	28°01'59"	16°42'26"	-5.9	31	5	24	511 (87) d

**Table S1.** (Continuation)

19	Montaña de Guaza II*	Tenerife	<i>G. galloti</i>	28°02'08"	16°42'29"	-5.9	29	13	13	45 (3)
20	Montaña de Guaza III*	Tenerife	<i>G. galloti</i>	28°02'54"	16°42'03"	-5.9	106	12	26	25 (11)
21	Los Menores	Tenerife	<i>G. galloti</i>	28°08'42"	16°45'26"	-6.5	23	14	109	247 (15) d
22	Barranco Guía de Isora	Tenerife	<i>G. galloti</i>	28°11'34"	16°46'22"	-6.5	67	15	44	90 (75) d
C	Teno Bajo I	Tenerife	<i>G. galloti</i>	28°21'08"	16°54'43"	-6.6	98	15	7	0
D	Teno Bajo II	Tenerife	<i>G. galloti</i>	28°21'13"	16°54'33"	-6.6	50	22	61	90
E	Cueva del Rey	Tenerife	<i>G. galloti</i>	28°22'59"	16°42'42"	-6.9	67	36	78	17
F	Malpaís de Güímar	Tenerife	<i>G. galloti</i>	28°18'37"	16°22'22"	-6.2	54	5	8	50
G	Barranco de Masca*	Tenerife	<i>G. galloti</i>	28°17'35"	16°50'56"	NA	83	37	33	28
H	Barranco Los Carrizales*	Tenerife	<i>G. galloti</i>	28°19'12"	16°52'17"	NA	97	17	12	24
23	Barranco de La Sabina	La Gomera	<i>G. caesaris</i>	28°07'54"	17°07'28"	-6.6	36	44	25	22 (1) d
24	Punta Llana	La Gomera	<i>G. caesaris</i>	28°07'41"	17°06'17"	-6.6	438	75	25	12 (0)
25	Roque de la Roja	La Gomera	<i>G. caesaris</i>	28°03'59"	17°09'11"	-6.4	20	10	72	125 (0) d
26	Barranco de Chinguarime	La Gomera	<i>G. caesaris</i>	28°02'31"	17°10'47"	-6.2	10	29	74	80 (0) d
27	Barranco Biguillo	La Gomera	<i>G. caesaris</i>	28°02'37"	17°11'03"	-6.2	82	21	7	30 (0)
28	Juan Barba	La Gomera	<i>G. caesaris</i>	28°02'11"	17°13'47"	-6.7	29	33	48	59 (1) d
29	La Caldera	La Gomera	<i>G. caesaris</i>	28°02'06"	17°16'00"	-6.6	26	11	64	88 (0) d
30	Barranco de la Negra	La Gomera	<i>G. caesaris</i>	28°03'04"	17°16'51"	-6.4	7	1	225	527 (0) d
31	Lomo Gerián	La Gomera	<i>G. caesaris</i>	28°04'28"	17°18'48"	-6.2	39	4	57	14 (3) d
32	Lomo del Balo	La Gomera	<i>G. caesaris</i>	28°09'21"	17°18'43"	-7.1	25	36	50	18 (0) d
I	Barranco de La Era Nueva	La Gomera	<i>G. caesaris</i>	28°11'01"	17°16'36"	-7.3	82	14	4	0
J	Cerro del Cepo	La Gomera	<i>G. caesaris</i>	28°11'51"	17°12'11"	-7.2	85	4	11	0

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

Several sampled populations of *N. pulverulenta* were geographically close, thus being subjected to similar biotic/abiotic conditions. This may result in similar values of the demographic variables, violating the required independence of data to properly apply generalized linear models. Thus, and as a complement of the performed analyses, we also tested for spatial autocorrelation among the residuals of the models used (the age structure patterns, the proportion of seedlings outside the canopy and the effective recruitment rate). Given that we did not record the geographic position of each sampled seedling (sample unit) we could not perform this analysis for the “seedling stem diameter” model (LMM). As an alternative, we pooled the individual data at the population level (population mean), performed a linear regression (LM) with “island” as a fixed factor and Emberger index as a covariate and we tested for spatial autocorrelation.

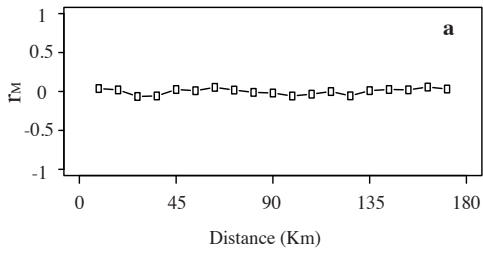
Spatial autocorrelation was assessed by computing multivariate Mantel correlograms following Matesanz et al. (2011). We tested at different distance classes including all pairs of populations located at a certain distance from each other (9 km distance classes). This distance interval was selected in order to include a sufficient number of populations in the first distance class. We did not detect spatial autocorrelation for any of the fitted models ( $p$ -values > 0.05 after a progressive Bonferroni correction), thus geographic information of plant populations was not included as covariates. The results of these analyses are shown in Figure S3.

All analyses were carried out with R (R Development Core Team, 2010). Specifically we used nlme (for GLM and LMM models; Pinheiro et al., 2014),

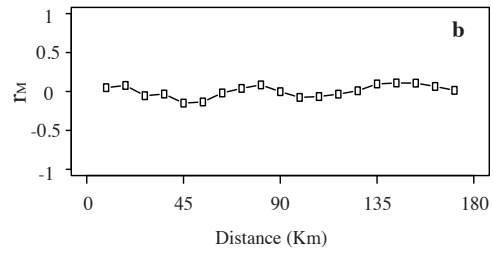
multcomp (post-hoc Tukey tests; Hothorn et al., 2008) and mpmcorrelogram packages (Mantel correlograms; Matesanz et al., 2011).

**Figure S3.** Results of the multivariate Mantel correlograms using the Mantel statistic ( $r_M$ ; Matesanz et al., 2011). Empty squares indicate non-significant spatial autocorrelation at each distance class (9 km) for the dependent variables examined (see text for details): a) the proportion of seedlings relative to the other age classes, b) the proportion of pooled subadults (seedlings, saplings and juveniles) relative to the proportion of adults, c) the proportion of seedlings outside the canopy relative to the proportion of seedlings beneath the canopy, d) the effective recruitment rate of seedlings (i.e. the number of seedlings outside the canopy relative to the number of adults sampled), e) the averaged stem diameter at the population level.

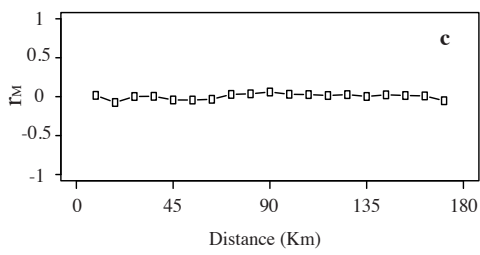
Age structure pattern (Subadult ages)



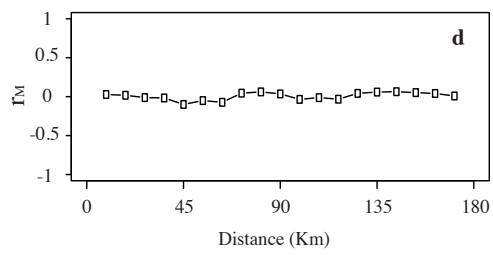
Age structure pattern (Seedlings)



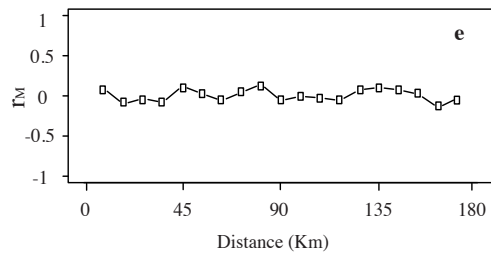
Proportion of seedlings outside adult plants



Effective recruitment rate of seedlings



Seedling stem diameter (mm)



**Figure S4.** Photo-collage illustrating the studied system. A) *Gallotia stehlini* (Ad male), the extant largest species of lizards from Gran Canaria (photo: P. Jordano). B) Medium-sized lizard *G. galloti* (Ad male) from Tenerife (photo: C. Camacho). C) Lowland xerophytic scrubland (Teno Bajo, Tenerife, photo: P. Jordano). D) *Neochamaelea pulverulenta* from Punta de Juan Centella, Tenerife (photo: A. Valido). E) Ripe fruits of *N. pulverulenta* from Tenerife (photo: A. Valido). F) Depulped seeds accumulating beneath the canopy of *N. pulverulenta* from La Gomera (photo: N. Pérez-Méndez). G) *G. galloti* droppings with dispersed seeds of *N. pulverulenta* from Tenerife (photo: N. Pérez-Méndez).





## Supplementary references

Alberto, V., 1999. Los otros animales. Consumo de *Gallotia goliath* y *Canariomys bravori* en la prehistoria de Tenerife. El Museo Canario 53, 59–86.

Arechavaleta, M., Rodríguez, S., Zurita, N., García, C., 2010. Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. Gobierno de Canarias, S/C Tenerife.

Arnay-de-la-Rosa, M., González-Reimers, E., Yanes, Y., Velasco-Vázquez, J., Romanek, C.S., Noakes, J.E., 2010. Paleodietary analysis of the prehistoric population of the Canary Islands inferred from stable isotopes (carbon, nitrogen and hydrogen) in bone collagen. J. Archaeol. Sci. 37, 1490–1501.

Arnay-de-la-Rosa, M., González-Reimers, E., Yanes, Y., Romanek, C.S., Noakes, J.E., Galindo-Martín, L., 2011. Paleonutritional and paleodietary survey on prehistoric humans from Las Cañadas del Teide (Tenerife, Canary Islands) based on chemical and histological analysis of bone. J. Archaeol. Sci. 37, 884–895.

Arnold, E.N., 1973. Relationships of the Palaeartic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia: Lacertidae). Bull. Br. Mus. Nat. Hist. 25, 289–366.

Barahona, F., Evans, S.E., Mateo, J.A., García-Márquez, M., López-Jurado, L.F., 2000. Endemism, gigantism and extinction in island lizards: the genus *Gallotia* on the Canary Islands. J. Zool. 250, 373–388.

- Barquín-Díez, E., Wildpret, W., 1975. Diseminación de plantas canarias. Datos iniciales. *Vieraea* 5, 38–60.
- Barquín-Díez, E., Nogales, M., Wildpret, W., 1986. Intervención de vertebrados en la diseminación de plantas vasculares en Inaga, Gran Canaria (Islas Canarias). *Vieraea* 16, 263-272.
- Bischoff, W., 1998. Bemerkungen zu den “fossilen” Rieseneidechsen der Kanarischen Inseln, in: Bischoff, W. (Ed.), *Handbuch der reptilien und amphibien Europas*. Bd. 6 Die reptilien der Kanarischen Inseln, der Selvagens-Inseln und des Madeira archipels. Aula-Verlag, Wiesbaden, pp. 387–407.
- Bocherens, H., Michaux, J., Billiou, D., Castanet, J., García-Talavera, F., 2003. Contribution of collagen stable isotope biogeochemistry to the paleobiology of extinct endemic vertebrates from Tenerife (Canary Islands, Spain). *Isot. Environ. Health. S.* 39, 197–210.
- Böhme, W., Bings, W., 1975. Zur frage des überlebens von *Lacerta s. simonyi* Steindachner (Sauria. Lacertidae). *Salamandra* 11, 39–46.
- Bravo, T., 1953. *Lacerta maxima* n.sp. de la fauna continental extinguida en el Pleistoceno de las Islas Canarias. *Estudios Geológicos (Instituto Lucas Mallada)* 17, 7–34.
- Carretero, M., Roca, V., Martín, J., Llorente, G.A., Montori, A., Santos, X., Mateos, J., 2006. Diet and helminth parasites in the Gran Canaria giant lizard *Gallotia stehlini*. *Rev. Esp. Herpetol.* 20, 105–117.

- Carretero, M., Jorge, F., Llorente, G.A., Roca, V., 2014. Relationships between helminth communities and diet in Canarian lizards: the evidence from *Gallotia atlantica* (Squamata: Lacertidae). *J. Nat. Hist.* 48, 1199–1216.
- Castillo, C., Rando, J., Zamora, J., 1994. Discovery of mummified extinct giant lizards (*Gallotia goliath*, Lacertidae) in Tenerife, Canary Islands. *Bonn. Zool. Beitr.* 45, 129–136.
- Castillo, C., Coello, J., Martín González, E., 2001. Distribución geográfica del Lagarto Gigante de El Hierro (*Gallotia simonyi*) en el Cuaternario: aplicación de los datos paleontológicos para la conservación de las especies. *Rev. Esp. Paleontol.* n° extraordinario, 15–20.
- Cox, S.C., Carranza, S., Brown, R.P., 2010. Divergence times and colonization of the Canary Islands by *Gallotia* lizards. *Mol. Phylogenet. Evol.* 56, 747–757.
- Del Arco, M.C., 1976. El enterramiento canario prehistórico. *Anuario de Estudios Atlánticos* 22, 13-124.
- Del Arco, M.C., 1993. Recursos vegetales en la Prehistoria de Canarias. Museo Arqueológico. Cabildo Insular de Tenerife.
- García-Cruz, C.M., Marrero-Rodríguez, A., 1978. Sobre la distribución geográfica de los yacimientos de vertebrados fósiles de las Islas Canarias. *Vieraea* 8, 95–106.
- González, E., Cerón-Souza, I., Mateo, J.A., Zardoya, R., 2014. Island survivors: population genetic structure and demography of the critically endangered giant lizard of La Gomera, *Gallotia bravoana*. *BMC Genetics* 15, 121.

- González-Castro, A., Calviño-Cancela, M., Nogales, M., 2014. Comparing seed dispersal effectiveness at the community level. *Ecology*, In press.
- Hernández, E., Bischoff, W., Bannert, B., Siverio, M., 1997. Rieseneidechsen auf Teneriffa. *Herpetofauna* 19, 19–24.
- Hernández, E., Nogales, M., Martín, A., 2000. Discovery of a new lizard in the Canary Islands, with a multivariate analysis of *Gallotia* (Reptilia: Lacertidae). *Herpetologica* 56, 63–76.
- Hernández-Divers, S.J., Lafortune, M., Martínez-Silvestre, A., Pether, J., 2003. Assessment and conservation of the Giant Gomeran Lizard (*Gallotia bravoana*). *Vet. Rec.* 152, 395–399.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biometrical J.* 30, 346–363.
- Hutterer, R., 1985. Neue funde von Rieseneidechsen (Lacertidae) auf der Insel Gomera. *Bonn. Zool. Beitr.* 36, 365–394.
- Izquierdo, I., Medina, A., Hernández, J., 1989. Bones of giant lacertids from a new site on El Hierro (Canary Islands). *Amphibia-Reptilia* 10, 63–69.
- Lomolino, M.V., 2005. Body size evolution in insular vertebrates: generality of the island rule. *J. Biogeogr.* 32, 1683–1699.
- López-Jurado, L.F., 1985. Los reptiles fósiles de la Isla de Gran Canaria (Islas Canarias). *Bonn. Zool. Beitr.* 36, 355–364.

- López-Jurado, L.F., Mateo, J.A., 1995. Origin, colonization, adaptive radiation, intransular evolution and species substitution processes in the fossil and living lizards of the Canary Islands, in: Llorente, G.A., Montori, A., Santos, X., Carretero, M. (Eds.) *Scientia Herpetologica*. Asociación Herpetológica Española, Barcelona, pp. 81–91.
- López-Jurado, L.F., Mateo, J.A., 1999. El Lagarto Gigante de El Hierro: Bases para su conservación. *Monografías de Herpetología Vol. 4*. Asociación Herpetológica Española, Las Palmas de Gran Canaria.
- Maca-Meyer, N., Carranza, S., Rando, J.C., Arnold, E.N., Cabrera, V.M., 2003. Status and relationships of the extinct giant Canary Island lizard *Gallotia goliath* (Reptilia: Lacertidae), assessed using ancient mtDNA from its mummified remains. *Biol. J. Linn. Soc.* 80, 659–670.
- Machado, A., 1985a. Hypothesis on the reasons for the decline of the large lizards in the Canary Islands. *Bonn. Zool. Beitr.* 36, 563–575.
- Machado, A., 1985b. New data concerning the Hierro Giant lizard and the Lizard of Salmor (Canary Islands). *Bonn. Zool. Beitr.* 36, 429–470.
- Machado, M.C., 2007. Una visión de las *islas afortunadas*, a partir de los restos arqueológicos. *Tabona* 15, 71-90.
- Márquez, R., Cejudo, D., Pérez-Mellado, V., 1997. Selected body temperatures of four lacertid lizards from the Canary Islands. *Herpetol. J.* 7, 122–124.

- Martín, A., 1985. Los lagartos de los roques del norte de Tenerife. *Bonn. Zool. Beitr.* 36, 517–528.
- Martín, J., Llorente, G.A., Roca, V., Carretero, M., Montori, A., Santos, X., Romeu, R., 2005. Relationship between diet and helminths in *Gallotia caesaris* (Sauria: Lacertidae). *Zoology* 108, 121–130.
- Mateo, J.A., López-Jurado, L.F., 1992. Study of dentition in lizards from Gran Canaria Island (Canary Islands) and its ecological and evolutionary significance. *Biol. J. Linn. Soc.* 46, 39–48.
- Mateo, J.A., García-Márquez, M., López-Jurado, L.F., Barahona, F., 2001. Descripción del lagarto gigante de La Palma (Islas Canarias) a partir de restos subfósiles. *Rev. Esp. Herpetol.* 15, 53–59.
- Mateo, J.A., 2007. *El Lagarto Gigante de La Gomera*. Editorial Turquesa, S/C Tenerife.
- Mateo, J.A., Crochet, P., Afonso, O.M., 2011. The species diversity of the genus *Gallotia* (Sauria: Lacertidae) during the Holocene on La Gomera (Canary Islands) and the latin names of Gomeran giant lizards. *Zootaxa* 68, 66–68.
- Matesanz, S., Gimeno, T.E., de la Cruz, M., Escudero, A., Valladares, F., 2011. Competition may explain the fine-scale spatial patterns and genetic structure of two co-occurring plant congeners. *J. Ecol.* 99, 838–848.
- Meiri, S., 2008. Evolution and ecology of lizard body sizes. *Global Ecol. Biogeogr.* 17, 724–734.

- Mertens, R., 1942. *Lacerta goliath* n. sp., eine ausgestorbene Rienseneidechse von den Kanaren. *Senckenbergiana* 25, 330–339.
- Michaux, J., Hutterer, R., Lopéz-Martínez, N., 1991. New fossil faunas from Fuerteventura, Canary Islands: Evidence for a Pleistocene age of endemic rodents and shrews. *Comptes Rendus l'Academie des Sciences* 312, 801–806.
- Molina-Borja, M., Rodríguez-Domínguez, M.A., 2004. Evolution of biometric and life-history traits in lizards (*Gallotia*) from the Canary Islands. *J. Zool. Syst. Evol. Res.* 42, 44–53.
- Morales, J., 2010. El uso de las plantas en la prehistoria de Gran Canaria: alimentación, agricultura y ecología. Cabildo Insular de Gran Canaria, Gran Canaria.
- Morales, J., Gil, J., 2014. Gathering in a new environment: the use of wild food plants during the first colonisation of the Canary Islands, Spain (2<sup>nd</sup>-3<sup>rd</sup> century bce to 15<sup>th</sup> century ce), in: Chevalier, A., Marinova, E., Peña-Chocarro, L. (Eds.), *An offprint from plants and people: choices and diversity through time*. Oxbow books, Oxford.
- Naranjo, J.J., Nogales, M., Quillis, V., 1991. Sobre la presencia de *Gallotia stehlini* en la Isla de Fuerteventura (Canarias) y datos preliminares de su alimentación. *Rev. Esp. Herpetol.* 6, 45–48.
- Nogales, M., Rando, J.C., Valido, A., Martín, A., 2001. Discovery of a living giant lizard, genus *Gallotia* (Reptilia: Lacertidae), from La Gomera, Canary Islands. *Herpetologica* 57, 169–179.



Nogales, M., Padilla, D.P., Nieves, C., Illera, J.C., Traveset, A., 2007. Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands. *J. Ecol.* 95, 1394–1403.

Padilla, D.P., González-Castro, A., Nieves, C., Nogales, M., 2009. Trophic ecology of the Southern Grey Shrike (*Lanius meridionalis*) in insular environments: the influence of altitude and seasonality. *J. Ornithol.* 150, 557–568.

Padilla, D.P., González-Castro, A., Nogales, M., 2012. Significance and extent of secondary seed dispersal by predatory birds on oceanic islands: the case of the Canary archipelago. *J. Ecol.* 100, 416–427.

Pérez-Mellado, V., Romero-Beviá, M., Ortega, F., Martín-García, S., Perera, A., López-Vivente, M., Galache, C., 1999. El uso de los recursos tróficos en *Gallotia simonyi* (Sauria, Lacertidae) de la isla de El Hierro (Islas Canarias), in: López-Jurado, L.F., Mateo, J.A. (Eds.), *El Lagarto Gigante de El Hierro: Bases para su conservación*, Monografías de Herpetología Vol. 4. Asociación Herpetológica Española, Las Palmas de Gran Canaria.

Pinheiro, J., Bates, D., Debroy, S., Sarkar, D., R Core Team, 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1-117, <http://CRAN.R-project.org/package=nlme>.

Pregill, G., 1986. Body size of insular lizards: a pattern of Holocene dwarfism. *Evolution* 40, 997–1008.

- R Development Core Team., 2010. R: A Language and Environment for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
- Rando, J.C., Hernández, E., López, M., Gonzales, A.M., 1997. Phylogenetic relationships of the Canary islands endemic lizard genus *Gallotia* (Sauria: Lacertidae), inferred from mitochondrial DNA sequences incorporation of a new subspecies. *Mol. Phylogenet. Evol.* 8, 114–116.
- Rodríguez, A., Nogales, M., Rumeu, B., Rodríguez, B., 2008. Temporal and spatial variation in the diet of the endemic lizard *Gallotia galloti* in an insular mediterranean scrubland. *J. Herpetol.* 42, 213–222.
- Rodríguez-Domínguez, M.A., Castillo, C., Coello, J., Molina-Borja, M., 1998. Morphological variation in the lacertid *Gallotia simonyi machadoi* and a comparison with the extinct *Gallotia simonyi simonyi* from El Hierro (Canary Islands). *Herpetol. J.* 8, 85–91.
- Valido, A., Nogales, M., 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* 70, 403–411.
- Valido A., 1999. Ecología de la dispersión de semillas por los lagartos endémicos canarios (g. *Gallotia*, Lacertidae). Ph.D., Tenerife: Univ. La Laguna
- Valido, A., Rando, J.C., Nogales, M., Martín, A., 2000. “ Fossil ” lizard found alive in the Canary Islands. *Oryx* 34, 75–76.

Valido, A., Nogales, M., 2003. Digestive ecology of two omnivorous Canarian lizard species (*Gallotia*, Lacertidae). *Amphibia-Reptilia* 24, 331–344.

Valido, A., Nogales, M., Medina, F.M., 2003. Fleshy fruits in the diet of Canarian lizards *Gallotia galloti* (Lacertidae) in a xeric habitat of the island of Tenerife. *J. Herpetol.* 37, 741–747.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford University Press, Oxford.