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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.

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.

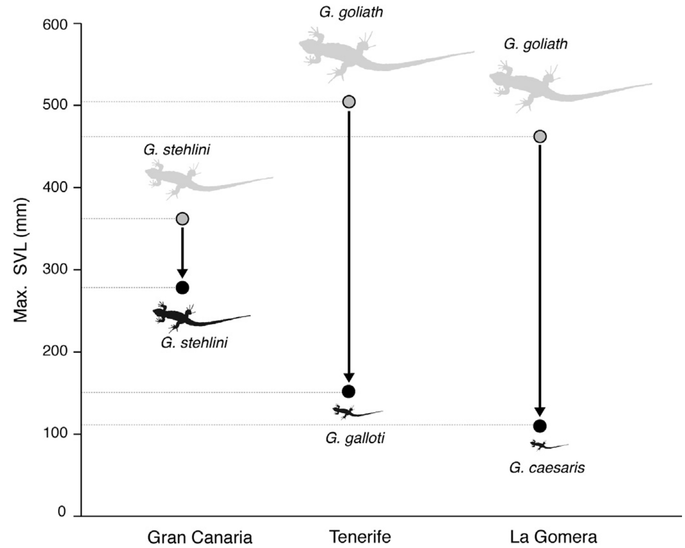

Fig. 1. Schematic representation of the maximum snout-vent length (max SVL) reduction of Canarian giant lizards (g. *Gallotia*, Lacertidae) from the past (light-grey silhouettes) to the present day (black silhouettes). Silhouettes are scaled to the max SVL. Only the islands hosting *Neochamaelea pulverulenta* 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 Canarian 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,