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Contrasting responses of insects and vertebrates as seed consumers of two neotropical oak species: The interactive effects of individual crop size and seed mass

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ABSTRACT

Tree species often exhibit considerable variability among individuals in seed crop size and averaged seed mass within the same year. However, very little is known about the consequences for seed consumers' preferences of this potentially large between-individual variability. In this study we quantified seed production and seed manipulation rates by animals over three years in two coexisting oak species of southeast Mexico (*Quercus germana* and *Q. xalapensis*) with the principal aim of evaluating the influence of two relevant plant traits (individual crop size and seed mass) on the responses of two guilds of acorn consumers with contrasting foraging behaviors and dietary breadths (vertebrate versus granivorous insects). We detected interactive effects of these two plant traits on seed consumers' preferences, with important differences between the two groups of acorn-feeding animals. In general, high densities of large-sized acorns triggered a negative density-dependent response (i.e. satiating effect) in granivorous insects and a positive response (i.e. attractive effect) in vertebrates, whereas the opposite occurred when considering the fraction of small-sized acorns. The potential consequences of producing bigger seeds will partly depend on the relative abundance of the two guilds of acorn consumers. Thus, in plant populations with overabundance of vertebrates, the higher attraction of large-sized seeds for these generalist consumers could counteract the satiating effect exercised on granivorous insects through multi-infestation. However, in forest sites with less abundance of vertebrates, the risk of seed predation (mostly by insects) could be reduced in those trees producing huge quantities of large-sized seeds. In summary, we found clear evidences that the direction and magnitude of density-dependent seed removal can differ not only between different groups of seed consumers but also among different fractions of seed size, which highlights the importance of considering this plant trait to better understand the complexity of mechanisms operating in these plant-animal interactions.

1. Introduction

Reproductive investment of perennial plants often varies at two different scales. At a temporal scale, they commonly exhibit a large interannual variability in seed production, a very common reproductive strategy known as masting (Silvertown, 1980; Kelly, 1994) that consists in producing occasional large seed crops followed by years of low seed production. At a spatial scale, populations of many of these plant species also show considerable variability among individuals within a same year (e.g. Sork et al., 1993; Healy et al., 1999; Greenberg, 2000; Carevic et al., 2010), a fact that seems to be driven by differences in local soil conditions (Pérez-Ramos et al., 2014) and/or in some inherent genetically-determined characteristics of the tree (e.g. Linhart and Mitton, 1985).

This spatiotemporal variability in seed production is expected to influence the foraging patterns of seed predators and dispersers and, thereby, plant fitness (Vander Wall, 2010). On the one hand, it is globally assumed that interannual variability in seed production ultimately benefits plant fitness across reduced seed consumption (through predator satiation) in occasional mast events and starvation of seed consumers in more frequent years of low crop size (the "Predator Satiation Hypothesis"; Janzen, 1971; Silvertown, 1980). On the other hand, the potential consequences of between-individual variability (i.e. spatial variability) for plant fitness still remain poorly understood. Previous studies have reported a

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plant-level predator satiation, the most productive trees harboring a larger proportion of seeds escaping from predators (Bonal et al., 2007; Linhart et al., 2014; Pérez-Ramos et al., 2014). Nevertheless, this satiating effect is mainly applied to dietary specialist predators with a limited mobility potential (e.g. weevils and small moths) whose foraging territories are usually restricted to one or a small group of adjacent trees (Bodenham and Stevens, 1981; Keefover-Ring and Linhart, 2010). In the case of highly mobile, dietary generalist consumers such as birds or mammals, this reproductive strategy might not be successful to satiate them. These animals are not usually attracted by low seed densities but they exhibit a positive density-dependent response as resource availability increases (attractive effect; Schauber et al., 2004; Pesendorfer and Koenig, 2016). To our knowledge, how differences in individual seed productivity of a single tree population may trigger differential (even opposite) responses in seed consumers with contrasting traits such as mobility or dietary breadth has been barely explored (see Moreira et al., 2017, but referred to pre-dispersal seed predators).

The nature and strength of plant-seed consumer interactions might be influenced not only by the above-discussed functional attributes of the granivorous species but also by those of the plants involved in these interactions. Thus, consumer's preferences could respond to differences in some seed traits such as size, phenology, coat thickness, content of defensive compounds or nutritional value (e.g. Robbins et al., 1987; Ganeshaiah and Shaanker, 1991; Brewer, 2001; Shimada and Saitoh, 2003; Pérez-Ramos et al., 2007, 2008; Espelta et al., 2009a). Among them, seed size (or seed mass) has been broadly recognized as one of the main plant attributes influencing seed removal rates. Dietary generalist consumers (e.g. birds or rodents) usually prefer larger seeds since larger-sized food items offer more energetic return for foraging effort (Janzen, 1969; Harper, 1977; Brewer, 2001; Gómez, 2004). Larger seeds, however, not only tend to be predated with higher frequency than smaller seeds (i.e. negative effects of seed size) but they also exhibit higher probability of being successfully cached and dispersed further away from the parent tree (i.e. positive effects; Theimer, 2003; Jansen et al., 2004; Gómez et al., 2008). In the case of dietary specialist consumers (e.g. granivorous insects), previous studies have suggested that they do not follow a seed size-based optimal foraging strategy (Desouhant, 1998; Espelta et al., 2009b), but they need a minimum size threshold to infest the seed (Bonal and Muñoz, 2008). Additionally, larger seeds may be exposed to higher insect predation because they require further time to complete their development before being abscised (Moles and Westoby, 2004), and they are more vulnerable to host multiple larvae within the same seed (concept of multi-infestation; Bonal et al., 2007; Muñoz et al., 2014). In contrast, a larger size may confer an advantage to the plant because this reduces the probability of embryo predation after the larva finishes its development inside the seed (seed-level satiation; *sensu* Bonal et al., 2007). The potential existence of conflicting selective pressures on seed size in different guilds of seed consumers indicates the complex interplay between this plant trait and consumer's preferences, and highlights the growing interest in investigating how the outcome of plant-animal interactions can be modulated by the functional traits of the organisms involved (Lavorel, 2013).

In this paper we quantified seed production and seed manipulation rates by animals in two coexisting oak species of southeast Mexico (*Quercus germana* and *Q. xalapensis*) with the principal aim of discerning the potential consequences of individual crop size and seed mass on consumer's preferences. We compared the responses of two guilds of acorn consumers (vertebrate versus granivorous insects) with contrasting foraging behaviors and dietary breadths over three consecutive years, which allowed us to analyze how consumer's preferences were modulated by annual differences in acorn availability on the forest floor. Specifically, we were interested in answering the following questions: (i) How variable is seed production among individuals of two co-occurring oak species?; (ii) Is between-individual variability in crop size and seed mass triggering different responses in seed consumers with contrasting mobility and dietary breadth?; and (iii) Are there opposing selective pressures on seed mass among different guilds of seed consumers? The studied area and species offer an ideal system for such analyses because it encompasses a natural range of trait variation both in plants and seed consumers. First, the two studied oak species exhibit not only large interannual fluctuations in seed production but also considerable variability among individuals within a same year. Second, seed mass is also highly variable at both the within- and between-species levels, with *Q. germana* acorns being up to fourfold larger than those of its congeneric species. Third, seeds of both species are consumed by a large array of different animals with contrasting foraging and dietary habits.

2. Materials and methods

2.1. Study area and species

This study was carried out in a cloud fragmented forest located in the surroundings of the center of Veracruz State, southeast of Mexico, at 1435 m a.s.l. (19°33′22.0″N and 96°56′36.1″W). This region is considered a hot spot for biodiversity conservation (Ellis et al., 2011; Gillespie et al., 2012). Climate is mild and humid with three different seasons: a cold season (from November to March), a dry-warm season (April and May) and a wet-warm season when most precipitation occurs (from June to October) (Williams-Linera, 2007). Annual precipitation ranges from 1500 to 2000 mm (mean = 1517 mm). Mean annual temperature is 18 °C, with a mean maximum of 23 °C and a mean minimum of 14 °C. Soils are mostly derived from volcanic ashes (Williams-Linera, 2007). Vegetation in the study area is mainly dominated by tree species typical from cloud forests, such as the evergreen oaks *Quercus germana* and *Q. xalapensis*. Other abundant species are *Carpinus caroliniana*, *Clethra mexicana*, *Liquidambar styraciflua*, *Platanus mexicana*, *Quercus acutifolia*, *Q. lancifolia* and *Q. sartorii*.

Quercus germana Schltdl. & Cham. is an endemic oak species from Mexico that belongs to the *Quercus* section (white oak). This species commonly grows in cloud forests along an altitudinal range from 800 and 1800 m a.s.l. (González-Espinosa et al., 2011). *Quercus xalapensis* Bonpl. belongs to the Lobatae section (red oak) and inhabits cloud forests located between 1400 and 2300 m a.s.l. (González-Espinosa et al., 2011). Both species typically coexist forming mixed stands in Mexican montane forests but they are critically endangered due to high fragmentation rates of their natural habitat over the last 10 years (González-Espinosa et al., 2011). Both *Q. germana* and *Q. xalapensis* flower in spring and acorn development occurs predominantly during summer (from June to August). Seed fall takes place mainly in autumn (from September to December), with slight inter-specific differences in their phenology (*Q. xalapensis* acorns are dispersed around one month earlier than those of *Q. germana*; Appendix A). *Q. xalapensis* acorns are smaller than those of its conespecific species, with mean values of fresh seed weight of 2.77 ± 0.90 g and 10.60 ± 4.32 g, respectively. Acorns of these species constitute an important part of the diet for many animals. During seed maturation, a variable percentage of acorns are consumed by granivorous insects (basically weevil or moth larvae; Díaz-Fleischer et al., 2010). These acorn consumers can be considered as dietary specialists because they feed upon basically on species of the genus *Quercus*, and their home ranges are mainly restricted to one or various adjacent trees