Functional responses of contrasting seed predator guilds to masting in two Mediterranean oak species

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The predator satiation hypothesis poses that synchronous and variable seed production during masting events increases seed escape through seed predator satiation. The success of this strategy depends upon the type of consumer functional response, in this case defined as the change in seed consumption rate by a predator as a function of change in seed density. Type II (where the proportion of seed consumed is highest at low levels of seed availability) and type III (where the proportion of seed consumed is highest at some intermediate level of seed availability and then declines towards zero) functional responses describe negative density-dependence and indicate predator satiation. The type of function response should be contingent upon herbivore traits: type II responses are predicted for dietary specialist predators with low mobility, and type III responses are predicted for highly mobile, dietary generalist predators. Surprisingly, most studies have not evaluated whether functional responses vary among seed predator guilds. Here we describe the functional responses at population and individual tree level of highly mobile generalist (birds and rodents) and less mobile specialist (insects) pre-dispersal seed predators attacking acorns of two sympatric oaks (*Quercus suber* and *Q. canariensis*) over a 10-year period. Our results showed that in most cases specialist seed predators exhibited the predicted type II functional response at both the individual tree and population level for both oak species. However, generalist seed predators did not exhibit the predicted type III response; instead, they also exhibited a type II response at the individual tree and population level for both oak species. By independently assessing the effects of multiple seed predators associated with the same host tree species, our work highlights the influence of herbivore traits on the outcome of plant–seed predator interactions in masting species, and thus furthers our understanding of the ecological and evolutionary mechanisms underlying masting behaviour.

Mast seeding, a reproductive strategy exhibited by many species of perennial plants, is defined as an annually variable and synchronous production of large seed crops by a population of plants (Silvertown 1980, Kelly 1994, Moreira et al. 2015, Pearse et al. 2016). From an evolutionary standpoint, the fitness advantages of masting to individual plants originate from economies of scale associated with population-level reproductive synchrony such as increased pollination efficiency through synchronized flowering effort (Kelly et al. 2001, Koenig et al. 2012, Rapp et al. 2013, Moreira et al. 2014), increased seed dispersal through greater attraction of animal seed dispersers (Norton and Kelly 1988, Kelly 1994), and reduced seed consumption through predator satiation (Janzen 1971, Fletcher et al. 2010, Archibald et al. 2012, Linhart et al. 2014).

According to the predator satiation hypothesis (PSH), superabundant, synchronous and variable production of seeds maximizes seed escape through starvation of predators in most years, followed by satiation of depressed seed predators populations in occasional mast years (Janzen 1976, Silvertown 1980). However, the success of this strategy

depends upon the type of functional response exhibited by a seed predator, defined as the change in resource (e.g. seed) consumption rate by a predator as a function of a change in resource density (Koenig et al. 2003, Fletcher et al. 2010, Linhart et al. 2014, Moreira et al. 2016). In his seminal work, Holling (1959) reported three types of predator functional responses: 1) type I responses, where the proportion of seeds consumed by seed predators remains constant, independently of the level of seed availability; 2) type II responses, where the proportion of seed consumed by seed predators is highest at low levels of seed availability; and 3) type III responses, where the proportion of seed consumed by seed predators is highest at some intermediate level of seed availability and then declines towards zero (Fig. 1). Type II and type III functional responses (Holling 1965), are indicative of seed predator satiation (i.e. negative density-dependence; Fig. 1), whereas type I responses do not support the PSH as the proportion of consumed seeds remains unchanged across levels of seed density (i.e. density-independence; Fig. 1). Overall, the presence of negative density-dependence described by type II and III functional responses (relative to
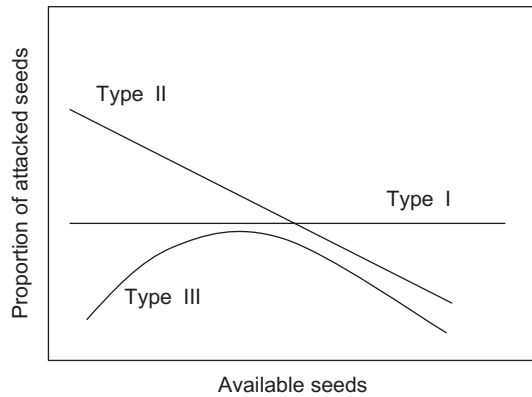
Figure 1. Predicted types of functional responses of seed predators to seed availability. Type I responses describe relationships where the proportion of consumed seeds remains unchanged across levels of seed density (i.e. lack of density-dependence). Type II functional response describe relationships where the proportion of consumed seeds decreases steadily with increasing seed density. Type III functional responses describe an increasing proportion of consumed seeds at low densities (i.e. positive density dependence) followed by a decreasing proportion of attacked seeds at high densities (negative density dependence).

type I responses) is of key relevance for predicting effects on plant fitness; they both describe scenarios where seed escape (lower attack rates and thus increased fitness) occurs at high seed densities because predator consumption ceases to keep pace with increasing resource abundance.

The functional responses of seed predators are expected to be highly contingent upon herbivore traits, such as size, mobility and diet breadth, which determine their foraging behaviour and responses to resource abundance (Koenig et al. 2003, Liebhold et al. 2004, Klinger and Rejmánek 2009, Linhart et al. 2014, Mezquida et al. 2016). For example, relatively immobile dietary specialist predators (e.g. some insect species or guilds) frequently exhibit a type II response (Holling 1965) as they commonly specialize on one or a few resources. In contrast, type III functional responses are predicted for highly mobile, dietary generalist predators (e.g. birds and rodents) with large foraging territories. Resources at low abundance may go undetected initially by these generalist herbivores, but as resource availability increases, these species exhibit an accelerating (positively density-dependent; Fig. 1) response and are able to fully exploit a resource (to then switch to another locally abundant resource). Although it is generally agreed that type II and type III functional responses result in an important fitness advantage of masting for plants (Fletcher et al. 2010, Linhart et al. 2014), variation in functional responses among different guilds of seed predators, particularly in masting tree species, has been poorly examined (but see Ruscoe et al. 2005, Fletcher et al. 2010, Linhart et al. 2014). Further, to date no study has evaluated within a single plant population or compared among coexisting/sympatric host plant species whether the functional responses vary among different guilds of seed predators differing in traits such as mobility and diet breadth.

Using a 10-year data set for two sympatric masting oaks (*Quercus suber* and *Q. canariensis*) found at a single site, and based on patterns of pre-dispersal acorn attack, we offer a novel test of the PSH by documenting and comparing the

functional responses of two guilds of seed predators recruiting to these tree species. Specifically, we evaluate the functional responses of highly mobile generalist (birds and rodents) and less mobile specialist (moth and beetle larvae) pre-dispersal seed predators to acorn availability at both the population and individual tree level. We predicted type II and type III functional responses (i.e. predator satiation) for immobile specialist and mobile generalist seed predators, respectively (Fletcher et al. 2010, Linhart et al. 2014). The plant–seed predator dynamics reported here are of key ecological relevance since that these two oaks are dominant species in many forested areas of southern Europe and jointly account for a substantial portion of plant biomass and resources to seed predators in such regions. These two oak species are sympatric throughout most of their distribution range but they differ in key life-history traits such as leaf habit and seed phenology as well as in the frequency and magnitude of reproductive (including masting) events that may influence seed predators. Based on the above, this study provides a unique assessment of the generality of the PSH across seed predators and tree species with contrasting life histories. This study therefore furthers our understanding of the ecological and evolutionary mechanisms underlying masting behaviour under a realistic setting where multiple coexisting herbivores feed on the same sympatric host plants.

Material and methods

Natural history

We conducted this study in a mixed-oak forest in Aljibe Mountains, near the Strait of Gibraltar, in southern Spain. Climate is sub-humid Mediterranean-type, with cool and wet winters, alternating with warm and dry summers. At this site, vegetation is dominated by forests of two sympatric oak species with contrasting leaf habit: the evergreen cork oak *Quercus suber* (Fagaceae) and the winter-deciduous oak *Quercus canariensis* (Urbieta et al. 2008). These two oak species flower in spring (April–May) and fruits ('acorns' hereafter) develop predominantly during summer (from June to September). Fruitfall takes place in autumn (Pérez-Ramos et al. 2014). They exhibit phenological differences in their endogenous dynamics of acorn development at the study area, with *Q. suber* requiring a single year to mature acorns and *Q. canariensis* predominantly requiring two years (Pérez-Ramos et al. 2014). Acorn production within a given year is quite variable in both species, ranging from 0 to more than 25 000 acorns per tree (Pons and Pausas 2012, Pérez-Ramos et al. 2014). Acorns of both oak species are attacked by mobile generalist pre-dispersal predators ('generalist acorn predators' hereafter) such as birds (at the study site principally *Sitta europaea*, *Garrulus glandarius* and *Parus major*) and arboreal rodents such as *Apodemus sylvaticus*, as well as less mobile, specialist pre-dispersal seed predators that feed mostly upon on species of the genus *Quercus* ('specialist acorn predators' hereafter) such as larvae of weevils *Curculio* spp. and moths *Cydia* spp. Both of these groups of acorn predators consume high amounts of acorns during the period of seed maturation (Pulido and Díaz 2005, Espelta et al. 2008, 2009, Perea et al. 2011, Pérez-Ramos et al. 2014).

Estimation of acorn output and pre-dispersal acorn predation

In summer 2002, we randomly selected 20 individuals of *Q. canariensis* and 30 of *Q. suber* within the study area. All selected trees had a diameter ≥ 20 cm at the beginning of the study and occupied dominant or co-dominant crown positions in the forest canopy. To estimate annual acorn density and pre-dispersal attack, we randomly placed four circular traps (0.50 m diameter) under the crown of each tree, avoiding overlap with crowns of neighbouring trees. Each trap consisted of a plastic mesh attached around an iron ring, which was soldered to an iron rod of 1.5 m in height to avoid acorn removal by rodents (the main post-dispersal predators at the study area; Pérez-Ramos et al. 2013) after acorn drop. Each year we collected trap content at the end of the acorn-drop period (February–March) for ten consecutive years (from 2002 to 2012). We estimated acorn density (number $\times$ m^{-2}) by counting the total number of mature acorns (acorns attaining complete size) falling in the traps (and converted to per m^2). We classified these mature acorns into three categories: 1) acorns with no signs of predation (i.e. undamaged), 2) acorns attacked by specialist predators (i.e. insects) which were identified by typical oviposition marks, and 3) acorns attacked by generalist predators (i.e. birds and arboreal rodents) which were identified by signs of rodent gnawing or bird pecking (Pérez-Ramos et al. 2014). We estimated the total number of acorns produced per tree (damaged and undamaged) by multiplying acorn density by the area (m^2) of the underlying ground resulting from a downward projection of the tree canopy (hereafter canopy area) at the initiation of the study. Tree canopy area was estimated by measuring two orthogonal diameters of the projected crown and calculating the area of the resultant ellipse as $\pi \times D1 \times D2 / 4$, where D1 was the plant's largest diameter (from tip to tip of the largest pair of leaves) and D2 was the smaller diameter, perpendicular to the former. Given that virtually all acorns with signs of predation were non-viable, classifying acorns as attacked translates into actual seed predation. We note that our sampling design may underestimate attack by generalist seed predators to the extent that birds and rodents remove acorns from the tree, as these were not recorded. However, we assumed that this underestimation did not lead to a bias in the estimation of generalist functional responses (i.e. the degree of underestimation of actual levels of acorn attack was unrelated with acorn production). In addition, we also note that in most cases individual acorns were not simultaneously attacked by both acorn predator groups ($< 5\%$, Pérez-Ramos unpubl.).

Descriptive statistics

We calculated the following population-level metrics separately for each oak species: 1) acorn production per year, calculated as the mean number of acorns produced each year across all trees (i.e. the sum of predator-damaged and intact acorns) (n = 10 years), and 2) the proportion of acorns attacked during each sampling year, calculated as the mean proportion of attacked acorn across all trees for each year (n = 10 years). In both cases, we performed calculations separately for specialist and generalist acorn predators. In addition, we also calculated two statistics at the individual tree level for each oak species: 1) total acorn production per tree, calculated as the mean number of acorns collected across all years for each individual tree (n = 20 for *Q. canariensis* and 30 for *Q. suber*), and 2) proportion of acorns attacked per tree calculated as the mean proportion of attacked acorns across all years for each individual tree (n = 20 for *Q. canariensis* and 30 for *Q. suber*). Again, we performed these individual-level calculations separately for specialist and generalist acorn predators.

Assessment of functional responses of pre-dispersal acorn predators

To analyse seed predator functional responses we followed the approach of Trexler et al. (1988). Specifically, we performed generalized linear regressions with a binomial error distribution and logit link function, modelling the proportion of attacked acorns as dependent upon acorn density (PROC GENMOD in SAS 9.4, SAS Inst.) (Littell et al. 2006). Although the dependent variable in this analysis is a proportion, and thus continuous, this approach is analogous to a logistic regression (i.e. each acorn being attacked versus unattacked) but produces the most accurate estimates of the true regions (Trexler et al. 1988). First, for each oak species we calculated population-level functional responses by modelling the proportion of attacked acorns for the population onto the linear and quadratic terms of acorn density, separately for specialist and generalist acorn predators and we did this for each year such that the years were the replicates for this analysis (n = 10 years) (Linhart et al. 2014). Second, for each oak species we calculated individual-level functional responses by modelling the proportion of attacked acorns onto the linear and quadratic terms of acorn density for each tree (using sums of values across years per tree; n = 20 or 30 trees depending on the oak species), and we did this separately for specialist and generalist acorn predators (Fletcher et al. 2010, Linhart et al. 2014). Evaluating individual and population functional responses provides an assessment the ecological (probability of escape for each plant) and evolutionary (from synchrony at the population level) benefits of masting, respectively (Fletcher et al. 2010, Linhart et al. 2014, Moreira et al. 2016). A type I functional response is described by non-significant linear and quadratic coefficients of acorn density, whereas a type II response is indicated by a significant negative linear coefficient and a type III response is indicated by a significant positive linear coefficient and a negative quadratic coefficient (Trexler et al. 1988, Juliano 2001, Fletcher et al. 2010). Type II and III functional responses support the PSH because the proportion of seeds consumed by predators decreases at some point with increasing seed availability (Holling 1959). For each analysis, we initially ran quadratic models, but where the quadratic coefficient was not significant ($p > 0.05$), we removed it and present results only for the linear coefficient.

Results

Patterns of acorn production and overall levels of pre-dispersal seed predator attack

For *Quercus canariensis,* we estimated a total of 1 143 790 acorns across all trees and years, with a population (n = 20 trees) average of 114 379 ± 56 015 acorns year⁻¹. Acorn production per tree varied substantially among years, ranging from 200 to 27 899 acorns tree⁻¹ (Fig. 2a). Across all trees and years a total of 457 061 acorns (proportion = 0.47) were attacked by specialist (insect) pre-dispersal acorn predators, with the proportion of attacked acorns at the population level ranging from 0.21 to 0.68 among years (Fig. 2a). Across all trees and years a total of 204 847 acorns (proportion = 0.20) were attacked by generalist (birds and rodents) pre-dispersal acorn predators, with the proportion

of attacked acorns at the population level ranging from 0 to 0.71 among years (Fig. 2a).

For *Quercus suber*, we estimated a total of 367 512 acorns across all trees and years, with a population (n = 30 trees) average of 36 751 ± 6510 acorns year⁻¹. Acorn production per tree varied substantially among years, ranging from 365 acorns to 2179 acorns tree⁻¹ (Fig. 2b). Across all trees and years a total of 114 128 acorns (proportion = 0.32) were attacked by specialist pre-dispersal acorn predators over the 10-year period, with the proportion of attacked acorns ranging from 0.08 to 0.51 across years (Fig. 2b). Across all trees and years a total of 64 097 acorns (proportion = 0.22) were attacked by generalist pre-dispersal acorn predators over the 10 years of study, with the proportion of attacked acorns ranging from 0.03 to 0.78 among years (Fig. 2b).

Assessment of functional responses of pre-dispersal acorn predators

In accordance with predictions by the PSH, for *Q. canariensis* we found a type II functional response for specialist acorn predators at the individual tree-level (n = 20 trees), as demonstrated by a significant negative linear coefficient (Table 1a, Fig. 3c). Although a type II functional response is indicated by a significant positive linear coefficient alone, we also found a significant positive quadratic coefficient, indicating a non-linear decrease in the proportion of attacked acorns with increasing acorn number (Fig. 3c). Against expectations, at the population-level we found a type III functional response for these specialists predators, as demonstrated by a positive significant linear and a negative significant quadratic coefficient (Table 1a, Fig. 3a). On the other hand, for generalist acorn predators we found a type II response (rather than the predicted type III response) at both the individual- and population-level, as demonstrated by a significant negative linear coefficient (Table 1b, Fig. 3b, d). The quadratic coefficient was positively significant in both of these models, indicating non-linear decreases in the proportion of attacked acorns with increasing acorn number (Table 1b, Fig. 3b, d).

Consistent with the PSH, for *Q. suber* we found a type II functional response for specialist acorn predators at both the population- and individual-level, as demonstrated by a significant negative linear coefficient (Table 2a, Fig. 4a, c). The quadratic coefficient was positively significant in the population-level model, indicating a non-linear decrease in the proportion of attacked acorns with increasing acorn number (Fig. 4a). However, counter to expectations, for generalist acorn predators we also found a type II functional response at both the individual- and population-level, as demonstrated by a significant negative linear coefficient (Table 2b, Fig. 4b, d). As for specialist acorn predators, the quadratic coefficient was positively significant in the individual-level model, indicating a non-linear decrease in the proportion of attacked acorns with increasing acorn number (Table 2b, Fig. 4d).
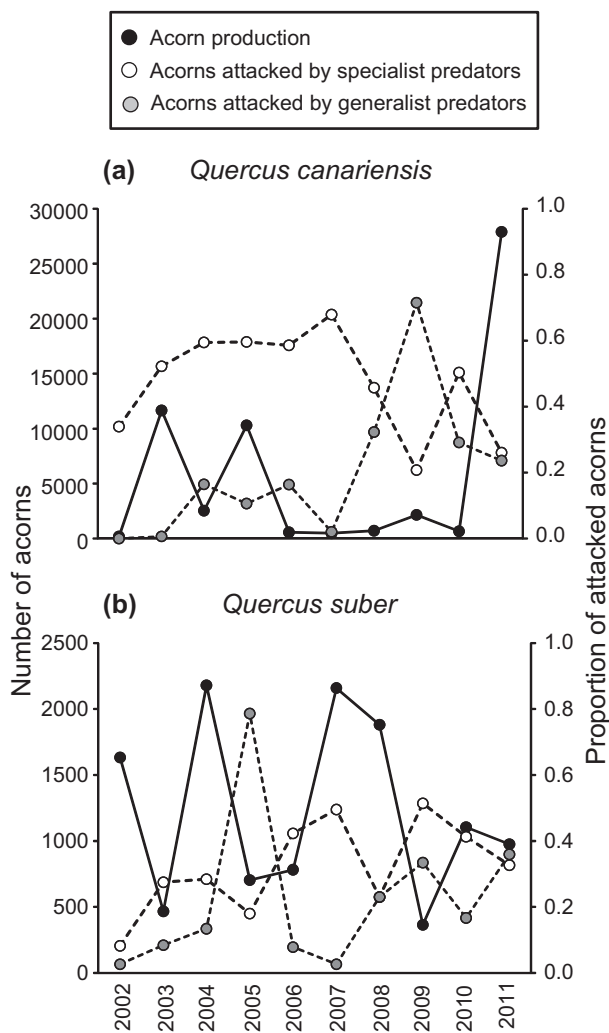

Figure 2. Mean annual (2002 to 2011) acorn production (black dots, solid line and left axis) (measured as the number of acorns per tree) and proportion of them attacked by specialist (white dots, dashed line and right axis) and generalist (grey dots, dashed line and right axis) pre-dispersal acorn predators recruiting to (a) *Quercus canariensis* and (b) *Q. suber*. Each point represents the average of (a) 20 *Q. canariensis* trees and (b) 30 *Q. suber* trees.

Discussion

Our results indicated negative density-dependent attack by pre-dispersal seed predators recruiting to both oak species,

Table 1. Type of functional response of (a) specialist and (b) generalist pre-dispersal acorn predators to acorn production at the population level (n = 10 years) and individual level (n = 20 trees) for *Quercus canariensis*. Logistic regressions were used to examine the linear and quadratic effects of total acorn production on the proportion of attacked acorns. Significant p-values are shown in bold. As the statistical model did not converge we log-transformed acorn production for individual level analyses.

Effects	DF	Parameter	SE	χ^2	p
(a) Specialist acorn predators					
Population level					
acorn production	1,7	9.11×10^{-5}	4.48×10^{-6}	413.31	**<0.001**
acorn production^2	1,7	-4.26×10^{-9}	1.31×10^{-10}	1056.10	**<0.001**
Individual level					
acorn production	1,17	-143.54	16.19	78.57	**<0.001**
acorn production^2	1,17	71.66	8.09	78.40	**<0.001**
(b) Generalist acorn predators					
Population level					
acorn production	1,7	-3.73×10^{-4}	6.54×10^{-6}	3255.81	**<0.001**
acorn production^2	1,7	10^{-8}	2.06×10^{-10}	3396.09	**<0.001**
Individual level					
acorn production	1,17	-155.83	20.14	59.87	**<0.001**
acorn production^2	1,17	77.75	10.06	59.66	**<0.001**

thus supporting predictions by the PSH. However, we found mixed support for the type of functional responses exhibited by each group of seed predators; findings for specialists were consistent in most cases with predictions (i.e. type II functional response), whereas for generalists results did not support our initial hypotheses (i.e. type III response) in any case. Specifically, we found that, except in one case, specialist acorn predators exhibited the predicted type II functional
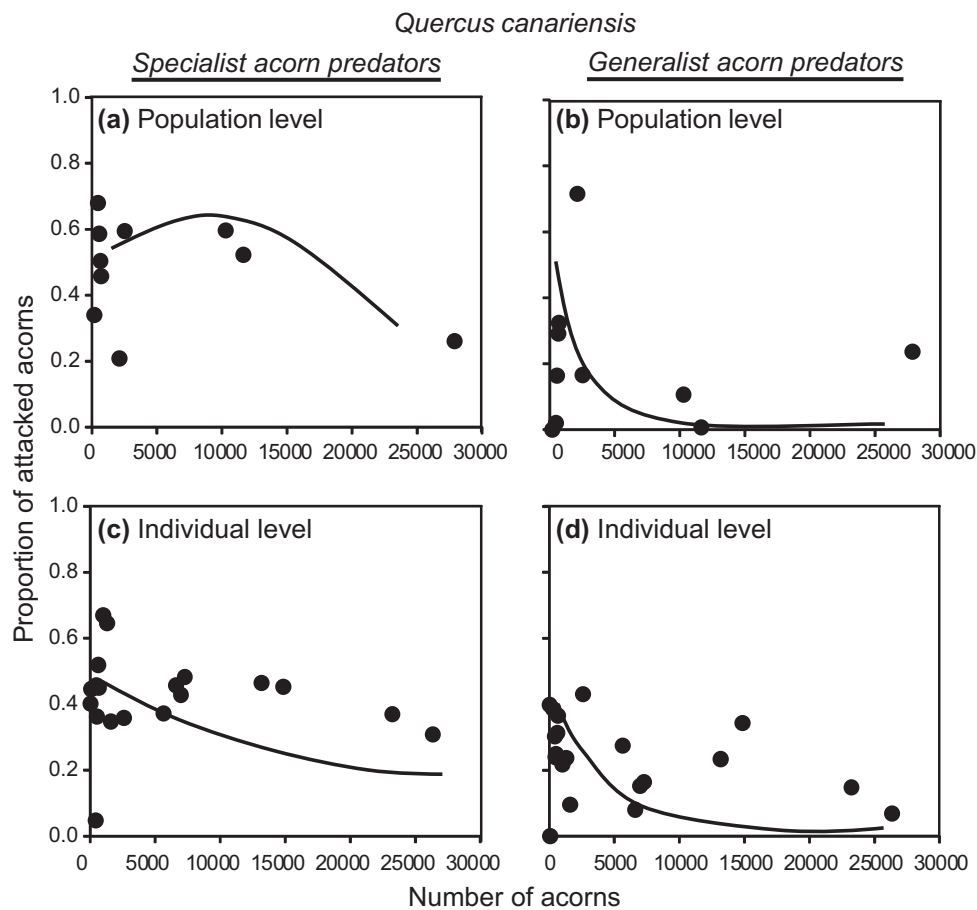

Figure 3. Types of functional responses of predators to total acorn production at population and individual level in *Quercus canariensis*. Relationship between total acorn production and the proportion of attacked acorns by (a) specialist and (b) generalist pre-dispersal acorn predators at the population level. Each point represents the mean value for a year (n = 10 years) over 20 individual trees. Relationship between total acorn production and the proportion of attacked acorns by (c) specialist and (d) generalist pre-dispersal acorn predators at the individual level. Each point represents the mean value for an individual tree (n = 20 trees) over 10 years. Regression lines are predicted relationships based upon binomial models plotted onto the original data.

Table 2. Form of the functional response of (a) specialist and (b) generalist pre-dispersal acorn predators to acorn production at population level (n = 10 years) and individual level (n = 30 trees) for *Quercus suber*. Logistic regressions were used to examine the linear and quadratic effects of total acorn production on the proportion of attacked acorns. Significant p-values are shown in bold. We initially ran quadratic models and if the quadratic coefficient was not significant, we removed it and presented results only for the linear coefficient.

Effects	DF	Parameter	SE	χ^2	p
(a) Specialist acorn predators					
Population level					
acorn production	1,7	-3.22×10^{-3}	2.13×10^{-4}	228.92	**<0.001**
acorn production^2	1,7	1.15×10^{-6}	7.51×10^{-8}	233.89	**<0.001**
Individual level					
acorn production	1,28	-3.37×10^{-5}	2.91×10^{-6}	134.19	**<0.001**
(b) Generalist acorn predators					
Population level					
acorn production	1,8	-10^{-3}	3.95×10^{-5}	645.27	**<0.001**
Individual level					
acorn production	1,27	-4.07×10^{-4}	2.15×10^{-5}	356.42	**<0.001**
acorn production^2	1,27	1.45×10^{-8}	2.01×10^{-9}	51.91	**<0.001**

response across both oak species. However, for generalist acorn predators we did not find the hypothesized type III response, but rather a type II response in all cases.

Type II responses are density-dependent responses which are typical of relatively immobile specialist predators (Holling 1959, 1965, Van Leeuwen et al.

2007). Accordingly, we found that larvae of weevils and moths specialized on *Quercus* spp. followed a type II functional response where attack rates decreased steadily with increasing acorn availability. The few studies that have evaluated the functional responses of specialist seed predators have agreed with patterns observed here (Tachiki
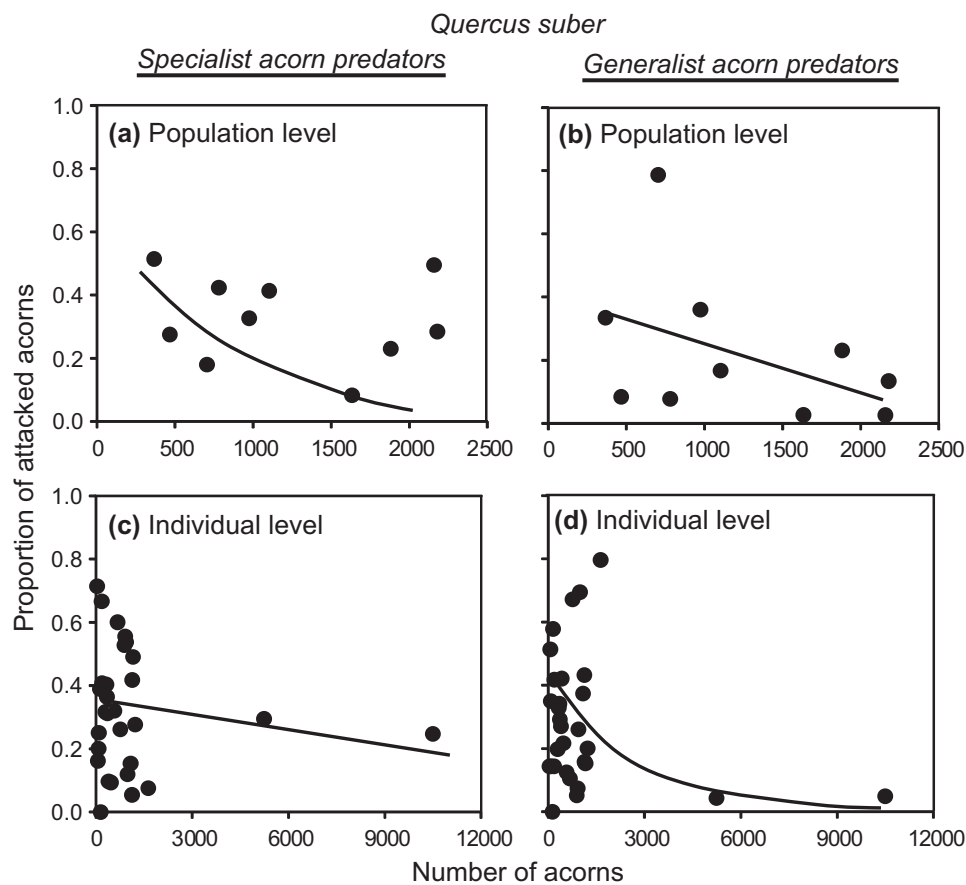

Figure 4. Types of functional responses of predators to total acorn production at population and individual level in *Quercus suber*. Relationship between total acorn production and the proportion of attacked acorns by (a) specialist and (b) generalist pre-dispersal acorn predators at population level. Each point represents the mean value for a year (n = 10 years) over 30 individual trees. Relationship between total acorn production and the proportion of attacked acorns by (c) specialist and (d) generalist pre-dispersal acorn predators at individual level. Each point represents the mean value for an individual tree (n = 30 trees) over 10 years. Regression lines are predicted relationships based upon binomial models plotted onto the original data.

and Iwasa 2010, Zywiec et al. 2013, Linhart et al. 2014, Moreira et al. 2016). For example, Linhart et al. (2014) found a type II functional response at both the population- and individual-tree level for specialist moths and weevils to available cones in ponderosa pine *Pinus ponderosa*. Similarly, Tachiki and Iwasa (2010) found that specialist seed predators generally attack seeds of trees in mature forests according to type II functional responses.

Type III functional responses are predicted for dietary generalist predators for two reasons. First, generalist predators may switch among alternative resource or prey types, selectively foraging in patches of high prey density and, in this way, may progress from positive to negative density-dependence as resource abundance increases (Akre and Johnson 1979, Schauber et al. 2004). Second, generalist predators typically reduce prey handling time through experience, also leading to density-independence or even positive density-dependence at low to moderate resource densities (Ruscoe et al. 2005, Fletcher et al. 2010). Nonetheless, contrary to expectations we instead found that the proportion of attacked acorns by generalist birds and arboreal rodents followed a type II functional response. In line with our finding, a meta-analysis by Oksanen et al. (2001) reported that the occurrence of type III functional responses for generalist predators under field conditions is less common than previously thought. To date, most evidence of type III functional responses is from experiments performed under controlled conditions (frequently under a laboratory setting; but see Fletcher et al. 2010), and these studies may yield different results relative to studies conducted under field conditions. Laboratory studies typically investigate functional responses of generalist predators by manipulating resource density (Holling 1959, Akre and Johnson 1979), but do not account for prey or predator aggregation (Nachman 2006), temporal changes in predator abundances (e.g. seasonal variation; Erlinge et al. 1983), or long-term dynamics leading to feedbacks between predatory–prey populations (van Baalen et al. 2001, Van Leeuwen et al. 2007). All of these factors may influence predator functional responses and predatory–prey interactions and lead to unexpected outcomes. For example, it is possible that under controlled conditions highly mobile predators exhibit positive density-dependence at intermediate prey abundance, thus following a type III functional response. However, under natural conditions, and despite their high mobility, mobile predators might not be able to cover large areas and exhaust all the available resources within individual patches and this could lead to a type II response. Having said this, we should note that our 10-year study represents a relatively short time interval relative to the entire lifespan of oak trees, and this could have led to a narrower range of inter-annual variation in acorn output and thus influence our ability to detect a type III functional response.

Our results also showed that in most cases the functional responses exhibited by each group of acorn predators were consistent at the individual tree and population level. In one of the few available studies, Linhart et al. (2014) also observed similar (type II) functional responses at both spatial scales for specialist (insect) seed cone predators attacking ponderosa pine. In addition, at the same site Moreira et al.

(2014) also reported that synchronous male and female reproduction at both the individual tree and population level boosted reproductive success in this pine species. Together, those findings and the present study demonstrate the population-level fitness benefits of masting and also highlight the evolutionary implications of these seed predation dynamics at the individual tree level.

This study also shows that the nature and strength of plant–seed predator interactions may be contingent upon not only seed predator functional traits but also depend on tree species variation in traits or abundance influencing consumers. For instance, plant life-history strategies associated with resource acquisition and allocation are considered fundamental drivers of reproductive investment and phenology, including masting behaviour in long-lived plants (Pérez-Ramos et al. 2015). In this sense, the two oak species under study exhibit differences in life-history traits such as leaf habit and differences in duration of acorn development, which could influence the frequency and magnitude of reproductive events (Pérez-Ramos et al. 2015). For instance, *Q. suber* is an evergreen species and requires a single year to mature acorns, whereas *Q. canariensis* is deciduous and requires two years to mature acorns (Pérez-Ramos et al. 2014). Despite these differences, our results nonetheless showed that the functional responses of both groups of seed predators were similar across oak species (consistently type II, except for specialists on *Q. canariensis*), suggesting that the function of plant–seed predator interactions are relatively insensitive to plant inter-specific variation (e.g. reproductive phenology of seed crop size, frequency and magnitude of masting events, etc.), at least for the studied site. Determining which traits influence the outcome of plant–animal interactions is of central importance for ecological research (Lavorel 2013), and in this case furthers our understanding of the ecological mechanisms that shape consumer responses to masting in long-lived tree species.

Future directions

Plant–seed predator interactions represent a key and ecologically pervasive interaction in temperate or Mediterranean-type forests. We therefore consider that a fruitful avenue of future research will be to determine the degree to which the shape (i.e. functional response) and overall strength of these interactions remain consistent (or not) across sites within particular regions as well as across ecosystem types. Studies incorporating multiple sites across broader spatial scales will help us understand how spatial variation in plant seed-predator dynamics is associated with and potentially influences masting in long-lived plant species. In addition, we consider that further efforts to include species replication across two or more guilds of seed predators or tree species would be highly valuable in order to test for the effect of species traits on the shape of functional responses. This would ultimately allow us to predict under which plant and predator trait combinations and in which systems (based on the identity of plant and consumer species) we would expect stronger (or weaker) ecological benefits of predator satiation and thus selection for increased and synchronous reproductive output, particularly in masting species.

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