

Context-dependent post-dispersal predation of acorns in a California oak community

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ABSTRACT

Seed dispersal and predation play important roles in plant life history by contributing to recruitment patterns in the landscape. Mast-seeding – extensive synchronized inter-annual variability in seed production – is known to influence the activity of acorn consumers at source trees, but little is known about its effect on post-dispersal predation. We conducted a planting experiment over three years to investigate the relationship between habitat-level post-dispersal predation and landscape-wide acorn production of three sympatric oak species (*Quercus* spp.). We measured post-dispersal predation in three oak-dominated habitats – savanna (under *Q. lobata*), forest edge (under *Q. agrifolia*), and woodland (under *Q. douglasii*) – as well as in chaparral and open fields. Overall, landscape-level predation was similarly high among study years, averaging 61.4%. Neither species nor mass of planted acorns affected predation. Habitat had a significant effect on post-dispersal predation risk with acorns disappearing most rapidly in chaparral and least rapidly in woodlands. However, a significant interaction between year and habitat ($Z = -4.5$, $P < 0.001$) showed that the hierarchy of predation risk among habitats was inconsistent among years. Using annual acorn census data from local populations of each oak species, we found that predation risk in oak-dominated habitats was significantly and positively related to acorn production of the overstory species ($Z = -9.53$, $P = 0.009$). Our findings add to growing evidence that seed dispersal, predation, and regeneration are context-dependent on annual variation in community-level seed production, and we discuss the potential consequences of these dynamics on oak recruitment and animal behavior.

1. Introduction

Seed dispersal plays an important role in the life history of plants, as it drives geographic distributions of species as well as local recruitment patterns (Levine and Murrell, 2003). Successful dispersal does not guarantee survival, however, since recruitment outcomes depend on the habitat to which seeds are dispersed (Schupp and Fuentes, 1995). Abiotic factors including light, moisture, and soil type and biotic conditions such as facilitation and/or competition from established vegetation at the arrival location dictate the probability of germination, seedling establishment, and subsequent survival to reproductive maturity (Schupp, 1993). Consequently, post-dispersal seed predation poses a considerable barrier to recruitment for many taxa, yet its relationship to arrival habitat can be difficult to predict (Christianini and Galetti, 2007; Hulme, 1994; Vaz Ferreira et al., 2011).

In heterogeneous landscapes, the unequal distribution of food

resources among habitats influences the habitat associations of potential predators and their propensity to track seed resources (García et al., 2011). Spatial and temporal variation in seed production are known to drive both short-term effects on feeding behavior as well as delayed effects on consumer populations (Bogdziewicz et al., 2016; Curran and Leighton, 2000). Generalist feeding tendencies of many seed consumers predict that these consumer-resource dynamics are subject to the context of resource production at the community level, rather than being influenced solely by the production and dispersal patterns of a single species (Kuang and Chesson, 2009; Lichti et al., 2014; Xiao and Zhang, 2016). Nevertheless, most studies involving seed predation have adopted a narrow perspective of resource-consumer dynamics in considering seed resources from the scope of a single population. In this three-year study, we investigate how arrival habitat affects post-dispersal predation of acorns in a Mediterranean landscape dominated by multiple sympatric oak species with high annual variation in acorn

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production.

For many plant populations, both pre- and post-dispersal seed predation tend to be density-dependent such that areas with clustered seeds attract more predators and increase the probability that a seed is consumed (Beckman et al., 2012; Janzen, 1970). However, for mast-seeding plants that show high interannual variability and synchrony in reproduction, the intensity and frequency of reproduction may have adaptive value for reducing seed predation (Kelly and Sork, 2002; Koenig and Knops, 2000). According to the *predator satiation hypothesis*, predators are overwhelmed by bumper crops in mast years, thus increasing the proportion of seeds that survive (Silvertown, 1980). The extent to which predators are satiated, however, depends on seed availability at a larger scale than a single tree. A nonexclusive alternative, the *predator dispersal hypothesis*, proposes that some predators that hoard seeds in the ground may respond to high seed production by dispersing larger quantities of seeds to more distant caching sites (Pesendorfer et al., 2016b; Zwolak et al., 2016). In communities of multiple mast-seeding plants, however, the activity of seed predators and dispersers is not only affected by seed production of individual plants or populations, but also by the seed production of other sympatric taxa (Lichti et al., 2014; Pesendorfer and Koenig, 2017; Xiao and Zhang, 2016). Despite this reality, few studies have investigated how community-level seed production affects the spatial patterns of post-dispersal predation.

At our study site in central coastal California, woodlands and savannas are dominated by three oak species – valley oak (*Quercus lobata*), coast live oak (*Q. agrifolia*), and blue oak (*Q. douglasii*) – whose acorns are consumed by corvids (California Scrub-Jay *Aphelocoma californica*, Steller's Jay *Cyanocitta stelleri*, American Crow *Corvus brachyrhynchos*, Yellow-billed Magpie *Pica nuttalli*), woodpeckers (Acorn Woodpecker *Melanerpes formicivorus*), rodents (ground squirrels *Otospermophilus beecheyi*, deer mice *Peromyscus* spp., wood rats *Neotoma* spp., pocket gophers *Thomomys bottae*), and large mammals such as black-tailed deer (*Odocoileus hemionus columbianus*) and introduced pigs (*Sus scrofa*). California Scrub-Jays are the most important seed hoarders in the system, and they frequently transport acorns up to several kilometers away from source trees and cache them in variety of habitats in the landscape (Pesendorfer and Koenig, 2016).

Previous studies in this system have revealed that the rate and distance of acorn scatter-hoarding varies with species- and community-level seed production of the three oak species (Pesendorfer and Koenig, 2017, 2016). To determine whether post-dispersal predation is similarly context-dependent on seed production in cache arrival locations, we conducted a planting experiment for which we distributed acorns to five habitat types most commonly used by scatter-hoarding jays. Our goal was to test the hypothesis that the relative risk of post-dispersal predation among arrival habitats varies with the population-level seed production of the species below which the acorns are cached. We predicted that there should be high inter-annual variability in acorn predation risk in habitats with oak trees and that there should be higher predation in habitats where the dominant oak species produces abundant acorns in any given season.

As an alternative to landscape- and habitat-level factors, we tested the effects of acorn characteristics on predation risk. We predicted that if acorn characteristics determine predation, large seeds should be more prone to removal by predators, since such seeds provide a higher reward relative to handling time, and that *Q. lobata* acorns should be preferred over *Q. agrifolia* acorns given their lower tannin concentration (Koenig and Faeth, 1998).

2. Methods

2.1. Study area

The study was conducted from October through December 2014–2016 at the Hastings Natural History Reservation in central

Table 1

Summary of California Scrub-Jay caching observations by habitat, August–November 2014.

| Habitat Type | Dominant Vegetation Cover | Ground Substrate | Other Features |
|--------------|---|----------------------------|-------------------------|
| QUDO | <i>Quercus douglasii</i> | leaf litter, soil | woodland |
| QUAG | <i>Quercus agrifolia</i> | leaf litter | forest edge |
| QULO | <i>Quercus lobata</i> | grass, soil | isolated tree (savanna) |
| OPEN | non-native perennial grasses | grass, soil | no trees within 25 m |
| CHAP | <i>Adenostoma fasciculatum</i> , <i>Ceanothus</i> sp. | sclerophyllous leaf litter | chaparral edge |

coastal California. The landscape is characterized by a Mediterranean vegetation community with a heterogeneous mosaic of grassland, oak savanna, mixed hardwood woodland, and chaparral scrub (McMahon et al., 2015). We identified five distinguishable habitats in the study area in which California Scrub-Jays are known to cache seeds most frequently (Pesendorfer and Koenig, 2016). Cache sites were characterized primarily by overstory vegetation and ground substrate (Table 1, Schubert et al. unpubl.). Grassland habitats (OPEN) are dominated by non-native Mediterranean grasses, with savannas distinguished by patches of scattered remnant *Q. lobata* (QULO). Mature woodlands in the study region include all three oaks and a number of other hardwood species. Most woodland habitat on site, however, is composed of secondary stands dominated by a canopy of *Q. douglasii* (QUDO). Forest edge and riparian fragments are dominated by large *Q. agrifolia* trees (QUAG). Finally, chaparral habitat (CHAP), found on south-facing slopes, is predominantly composed of chamise (*Adenostoma fasciculatum*) and California lilacs (*Ceanothus* spp.).

2.2. Experimental design

Each year, 200 *Q. lobata* acorns and 200 *Q. agrifolia* acorns were collected from a minimum of 10 individuals per species and stored in a refrigerator for 7–14 days at 2 °C until planting experiments were initiated. Acorns were inspected visually for exit holes produced by weevils (*Curculio* spp.) and mass was determined using a digital balance. Since scatter-hoarding jays are known to avoid parasitized acorns infested with weevils, acorns containing signs of parasitism were excluded from the study (Dixon et al., 1997; Rockwell et al., 2013). Sixteen acorns (8 *Q. lobata* and 8 *Q. agrifolia*) were planted 15 cm apart in five replicate plots of the five habitat types located at least 40 m apart. Acorns were planted to simulate caching by scrub-jays, inserted vertically into a narrow impression in the substrate with the pointed end oriented downward, and the “cache” was covered lightly with the surrounding substrate. In all 3 years of the study, all acorns were planted over a period of 1–2 days in late October.

Survival of individual acorns was determined during weekly plot visits over the subsequent 5 weeks in 2014, 7 weeks in 2015, and 8 weeks in 2016, depending on the onset of winter season rains. Heavy rain obscured acorn planting position for many plots and, thus, was the main factor in deciding when monitoring was discontinued. Both acorn species that we tested for our experiments are known to germinate within the time frame of our monitoring period (Griffin, 1971). However, we did not measure germination, since unnecessary disturbance to the ground near to where other acorns were buried may have influenced predator activity. During each plot visit, we carefully inspected the surface of the ground for tracks, fecal samples, and any removed or damaged acorns. During the first two study years, we rotated a single motion-sensor trail camera among plots to obtain visual confirmation of predators. By combining these two approaches we were able to infer the identity of the predators in many cases; however, data were not consistent enough to permit quantitative analysis of different predator

species.

Annual seed production of the dominant oak species was determined using canopy survey methods that have been conducted annually since 1980 (Koenig et al., 1994a). During the three years of the study period, 196 trees (82 *Q. lobata*, 54 *Q. douglasii*, 60 *Q. agrifolia*) were visited each fall season by two observers who counted all visible acorns during two 15 s count intervals. These counts were then added (N30) and log-transformed ($\ln(N30 + 1)$) to render LN30, a standard measure of relative acorn production.

2.3. Statistical analyses

All analyses were conducted in R 3.4.4 (R Development Core Team, 2018); unless otherwise stated, values presented are means \pm standard deviation. We used parametric survival analyses to test two specific predictions: i) that post-dispersal predation of acorns varies significantly among arrival habitat types, and ii) that it is directly affected by the seed production of the oak species below which they arrive. First, we conducted a random survival forest analysis in the package “RandomForestSRC” 2.6.0 to evaluate the relative importance of variables for inclusion in subsequent analyses (Ishwaran et al., 2017). RandomForestSRC (hereafter RFS) grows a large number of binary decision trees from the data set based on values and levels of different variables, and variable importance can be estimated by measuring the change in prediction error due to randomly permuting each variable (Ishwaran et al., 2008). Variables with large, positive variable importance included “plot”, “habitat”, “year”, while “acorn species”, and “acorn mass”, characteristics reported to influence predation in other studies (Espelta et al., 2009; Pérez-Ramos and Maranon, 2008), were excluded due to low variable importance (Fig. A1).

To determine the drivers of post-dispersal predation, we conducted parametric survival analyses in the package “flexsurv” 1.1 with Weibull error distributions that assume continuous decline of proportional hazard over time (Jackson, 2016). To investigate the context dependence on habitat type and year, our proxy for annual landscape-wide seed production, we modeled seed survival as a function of the two parameters and their interaction. In the second model, we constructed the same type of model for a subset of the acorn survival data from the three oak-dominated habitats to examine seed production (LN30) of the dominant cover species as a fixed effect. All models contained a “cluster ()” function to account for the non-independence between acorns planted within the same plot (Therneau and Lumley, 2015). To visualize the temporal patterns of acorn removal, we plotted Kaplan-Meier curves for each habitat by year combination. Furthermore, to illustrate the relationship between acorn crop and post-dispersal predation independent of the oak species below which it was detected, we simulated a response curve based on the available values of this predictor in our data set using the “simPH” package 1.3.10 (Gandrud, 2015).

3. Results

Acorn production by the three dominant oak species varied considerably among years. *Quercus lobata* produced moderately large acorn crops in all three study years whereas *Q. douglasii* produced similarly large crops in 2015 and 2016 but had low production in 2014. *Q. agrifolia* produced only a moderate crop in 2016, with comparatively smaller crops relative to the other species in the other years (Fig. 1). *Q. lobata* acorns collected for the planting experiment ranged 0.43–19.59 g with an average of 6.59 ± 3.32 g. *Q. agrifolia* acorns ranged 0.67–10.22 g, averaging 3.61 ± 0.98 g.

Over the course of the study, 737 of the 1200 (61.4%) acorns planted were pilfered by seed predators during the censusing periods. The greatest number of acorns was removed from chaparral plots (Fig. 2). Woodland habitats (QUDO) experienced the least predation, and the remaining three habitats experienced intermediate levels of predation. Predation risk was dependent on habitat, plot ID, and year

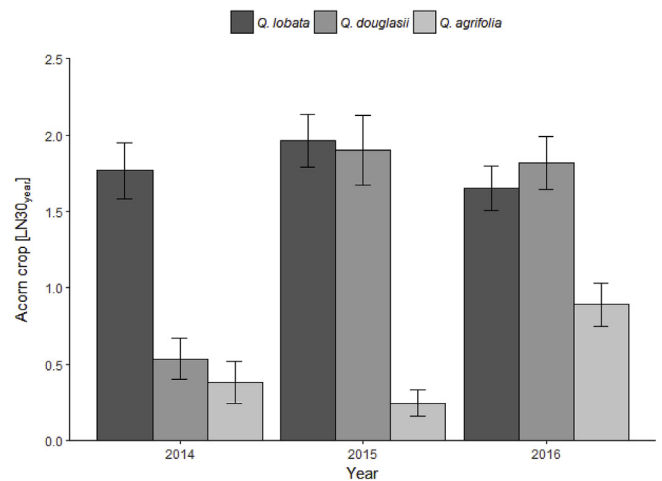


Fig. 1. Landscape-wide acorn production 2014–2016 in the three dominant oak species at Hastings Natural History Reservation with crop size represented as the mean (\pm SE) natural log of standard 30-s acorn counts on 84 *Q. lobata*, 60 *Q. douglasii* and 52 *Q. agrifolia* trees.

with all having comparatively high variable importance in the RSF analysis (Fig. A1). The species and mass of acorns were poor predictors of predation risk and therefore excluded from the final models.

Post-dispersal predation in each habitat type varied among study year, most notably with a significant interaction between habitat and year for QUDO plots (Table 2). Acorns placed in open fields or chaparral were depredated more rapidly in 2014 and 2016 than in 2015. The secondary analysis in which the categorical parameter habitat was replaced with the mean acorn production of the overstory oak species revealed a strong effect on predation risk ($Z = -9.53$, $P = 0.009$) with every unit increase in LN30 corresponding to a 31.3% decrease in survival. Consequently, acorns planted beneath oak canopies with higher acorn density were more likely to be taken by predators (Fig. 3).

4. Discussion

Our findings demonstrate that different arrival habitats vary in the level of post-dispersal predation risk for cached acorns and that these relationships vary across study years with different landscape-wide patterns of acorn production. Among the habitats dominated by oak tree overstory, acorns below *Q. lobata* (QULO) consistently had the highest predation rates, corresponding to the *Q. lobata* population having fairly high acorn productivity in all three study years. Acorn predation was relatively low below *Q. agrifolia* (QUAG) during the first two years of the study when the population had low acorn production but increased in the third year when the crop was highest. The strongest relationship between acorn predation and acorn production was seen in *Q. douglasii* woodlands (QUDO) where acorn predation risk increased significantly between 2014 and the subsequent 2 years as acorn production increased. The overall pattern within the three oak-dominated habitats was a consistent positive relationship between acorn production of the overstory oak species and predation risk.

Based on the interannual variability in acorn production among the three focal species observed during the study period, our results appear to contradict the predator satiation hypothesis which, in this case, predicts a saturating effect on predator activity under conditions of high acorn density and, thus, a higher per capita probability of seed survival. However, when we considered oak fecundity in the study system with respect to previous long-term data sets from the study area (Koenig et al., 1994b), we found that even the largest magnitudes of acorn production observed during our study period did not exceed the median values of annual crop size for these species (i.e. LN30 of approximately 1.5–2.0). Therefore, we did not have the opportunity to evaluate post-

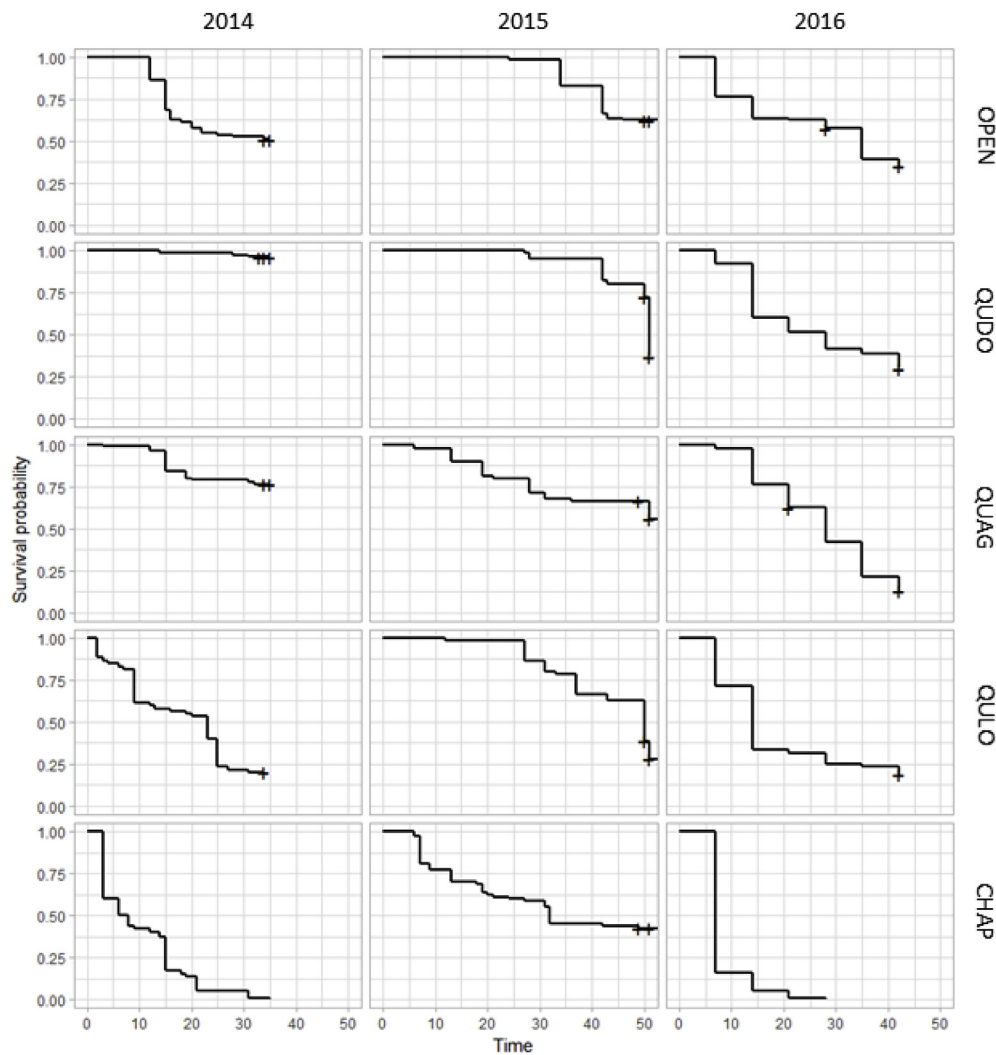


Fig. 2. Kaplan-Meier survival curves for all habitats by year. Predation patterns were highly variable between years and among the habitat types studied. Habitat types: OPEN – grassland; QUDO – below *Quercus douglasii*; QUAG – below *Q. agrifolia*; QULO – below *Q. lobata*; CHAP – Chaparral. See Table 1 for detailed habitat descriptions.

Table 2
Parametric survival model of habitat type and year as predictors of post-dispersal acorn survival.

| Factor | Level | Hazard Ratio | SE | z | p |
|--------------|-----------|-----------------|-------|-------|---------|
| Year | 2014 | Reference level | | | |
| | 2015 | 0.524 | 0.434 | 1.2 | 0.227 |
| | 2016 | -0.044 | 0.315 | -0.3 | 0.890 |
| Habitat | OPEN | Reference level | | | |
| | QUDO | 1.410 | 0.450 | 3.9 | < 0.001 |
| | QUAG | 0.481 | 0.606 | 0.9 | 0.344 |
| | QULO | -0.789 | 0.453 | -1.2 | 0.236 |
| | CHAP | -1.470 | 0.420 | -2.9 | 0.004 |
| Habitat*Year | OPEN*2014 | Reference level | | | |
| | QUDO*2015 | -1.743 | 0.557 | -3.1 | 0.002 |
| | QUDO*2016 | -1.843 | 0.411 | -4.5 | < 0.001 |
| | QUAG*2015 | -0.524 | 0.828 | -0.6 | 0.527 |
| | QUAG*2016 | -0.772 | 0.604 | -1.3 | 0.201 |
| | QULO*2015 | 0.290 | 0.451 | 0.6 | 0.521 |
| | QULO*2016 | 0.123 | 0.407 | 0.3 | 0.762 |
| | CHAP*2015 | 0.912 | 0.560 | 1.6 | 0.103 |
| CHAP*2016 | -0.241 | 0.443 | -0.5 | 0.587 | |

dispersal acorn predation in the context of a true masting event (i.e. LN30 of approximately 3.0–4.0), and we cannot rule out the possibility of localized predator satiation at the habitat level at higher extremes of

acorn density. Importantly, different seed predators perceive and respond acorn production at different spatial scales. For example, while insects and other small animals quickly satiated by high acorn densities, large mammals and birds may recruit to such an area by immigrating from long distances in an aggregational response to short-term resource availability (Pérez-Ramos et al., 2017; Pesendorfer and Koenig, 2016; Sanguinetti and Kitzberger, 2010).

Camera trap footage and other visual clues showed a variety of animals were responsible for pilfering artificial seed caches in our study. The most common of these included California deer mice, dusky-footed wood rats, pocket gophers, and wild pigs. California Scrub-Jays were also observed removing acorns. There was especially notable activity of wood rats in the chaparral plots corresponding to acorns from these plots experiencing the highest rates of predation. Indeed, closer inspection revealed at least one woodrat stick-house nest within 20 m of all 5 plots in chaparral habitat and their droppings were often found near the cached acorns. While this contradicted our expectation that acorn predation should be highest below acorn-producing trees, it is unsurprising given the results of other studies that have shown high foraging activity under shrub cover where concealment from carnivores can facilitate the time spent foraging and transiting through the habitat (Matías et al., 2009; Pons and Pausas, 2007).

We did not find evidence to suggest that predators selected acorns

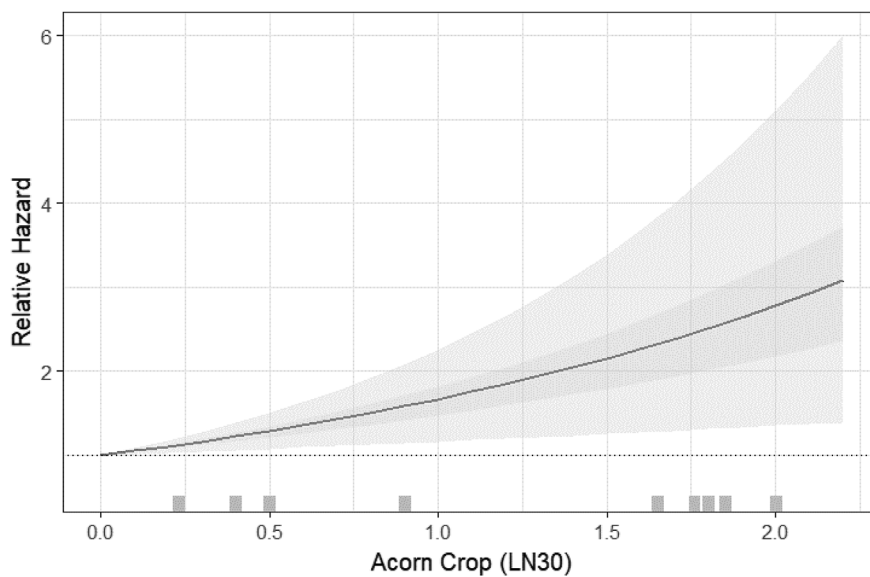


Fig. 3. The simulated relationship between mean annual acorn crop (i.e. natural log of standard 30-s acorn counts) of the overstorey oak species and the relative hazard of post-dispersal acorn predation in the three oak-dominated habitats. Acorns planted in habitats with higher acorn production were at greater risk of predation. 95% and 50% confidence intervals displayed as shaded ribbons. Bars at the bottom of the figure indicate actual acorn crop values from the data set.

based on their species or size, indicating that predators searched for buried seeds opportunistically and did not discriminate among acorns. This was surprising to the extent that intrinsic factors related to seed species and morphology are known to affect selection by seed consumers. However, most studies reporting selectivity based on size or nutritional quality by seed harvesters are based on foraging behavior at sources with clustered and abundant food items where consumer behavior is less constrained by search effort and may result in some taxa foraging optimally (de los Angeles García-Hernández et al., 2016; Rusch et al., 2013; Wang and Yang, 2014).

In a similar study system with sympatric oak species, Yi and Wang (2015) found that initial selection and removal of acorns of each species depended on the availability of acorns of alternative sizes, and that experimental additions of acorns of larger size reduced the probability of dispersal and germination of species with small acorns. In contrast, we did not find any effect of acorn size on post-dispersal predation risk. However, the scope of the present study did not address potential differences in handling and final fates of acorns removed from the plots. Specifically, we were unable to determine whether acorns were consumed immediately upon removal from the plots or carried away for later consumption; that is, we did not track potential secondary dispersal events and absolute survival acorns, but rather used removal from original post-dispersal habitat as a proxy for true predation. We regard this as a reasonable assumption, given that, with the exception of California Scrub-Jays, most potential post-dispersal predators in our study are not considered effective seed dispersers (Griffin, 1976).

High inter-annual variability in seed production of oak populations has long been recognized for its influence in driving resource availability for animal populations, and there is a growing body of research demonstrating how these dynamics can affect the responses of seed predators and potential dispersers (Bogdziewicz et al., 2016). Most previous research has examined masting either from an ecological perspective to determine how predator and/or disperser populations respond to resource abundance at the landscape scale or from an evolutionary perspective to measure plant fitness in populations with high variability in reproduction intensity among individuals (Pesendorfer and Koenig, 2016; Zwolak et al., 2016). One of the principal challenges in modern ecological studies, however, is understanding how community composition and neighboring species indirectly mediate plant-animal interactions (Donoso et al., 2017). Previous studies of sympatric oaks have shown that acorn selection by pre-dispersal predators and potential dispersers is context-dependent based on the presence and abundance of acorns from other oak species (Espelta et al., 2009; Lichti

et al., 2014; Xiao and Zhang, 2016; Yi and Wang, 2015). The significant relationship between acorn production of the three sympatric oaks and predation risk in the habitats to which these corresponded provides support for the context-dependent hypothesis and makes a case for extending this concept from pre-dispersal interactions with animals at the source tree to include seed fate in arrival habitats and recruitment patterns (Schnurr et al., 2004).

Oak populations of many species throughout the world are currently faced with regeneration problems, as aging populations fail to be replenished by a consistent supply of recruits, a pattern also reported in some species of California oaks (Abrams, 2003; Tyler et al., 2006). Numerous environmental factors have been identified as important drivers of oak recruitment, including predation as a barrier to germination and seedling establishment, abiotic factors such as light availability and soil condition post-establishment, and herbivore browsing pressures (Acácio et al., 2007; Griffin, 1971; Thomas et al., 2002). Both pre-dispersal and post-dispersal predation are known to limit recruitment in oak populations with temporal variability in seed production playing a role in these dynamics. In our study, post-dispersal acorn predation depended, at least in part, on the relative acorn production of the three dominant oak species and their distribution in the landscape. In this way, the relative safety of acorn dispersal sites changed among years depending on acorn production among the three sympatric oaks. Spatiotemporal variation in post-dispersal seed predation likely has important effects on community assembly and the demography of plant communities in oak-dominated landscapes. Assuming oak regeneration is at least partially limited by acorn predation, these patterns should have a homogenizing effect on the plant community. Specifically, in years of low acorn production in one population, acorns of other species may be more likely to colonize the understory of these species.

In addition to its implications for oak regeneration dynamics, the magnitude of predation for buried acorns observed in our study and temporal variability in habitat quality may have important consequences for the principal seed disperser of acorns in this study system, the California Scrub-Jay. Jays have highly developed spatial memory that allows them to effectively hoard and recall the placement of hundreds to thousands of independently selected caching sites (Pesendorfer et al., 2016a). Corvids tend to move seeds away from areas of high resource density (e.g. acorn-producing trees), but are also known to respond to potential threats to their cached food supplies by relocating their contents (Emery and Clayton, 2001). In our study system, context-dependent post-dispersal seed predation at the habitat level suggests that safe sites for cached acorns are unpredictable, and

we hypothesize that jays may use environmental cues to inform future caching attempts and re-caching activities. Scatter-hoarding, by definition, implies dispersal of food items by animals from a site with clustered resources to many sites which are presumably characterized by lower resource density. Scatter-hoarding rodents, for example, have been found to cache more energetically valuable seeds at greater distances from source trees and in more open habitat in what is presumed to be a response to higher cache pilfering risk nearer to source trees (Steele et al., 2013). In such instances, the hoarder benefits from a more secure cache site, while the plant benefits from its seed having a greater potential dispersal distance and an overall decreased likelihood of seed predation provided that it is not recovered by the hoarder. However, the extent to which scatter hoarders may adjust their behavior based on cache pilfering in environments where seed predator activity is highly variable and context dependent remains largely unexplored. Future studies of caching behavior by corvids and other scatter hoarders both in the field and the laboratory may shed light onto a novel aspect of oak-hoarder mutualisms.

Conflicts of interest

The authors declare no conflict of interest.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.actao.2018.08.005>.

Appendix A

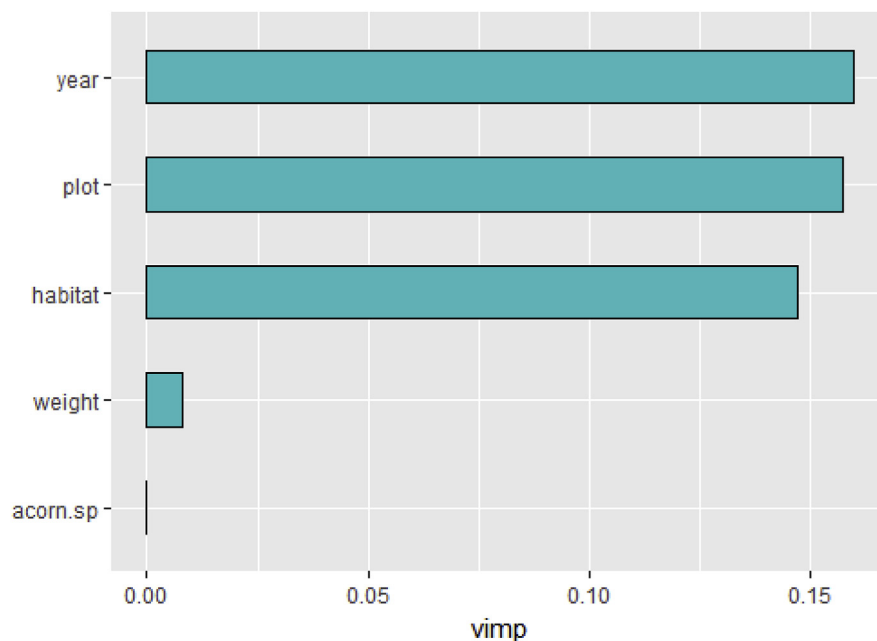


Fig. A1. The results from the random survival forest analysis. Mean variable importance was estimated based on the change in prediction error from the random permutation of each variable from 1000 trees. Large positive variable importance (VIMP) values indicate predictive variables. Since the VIMP for individual acorn characteristics were of much smaller magnitude than the other potential predictors, we excluded these from future analyses.

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