

Seed predation and climate impacts on reproductive variation in temperate forests of the southeastern USA

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Received: 26 May 2015 / Accepted: 17 December 2015 / Published online: 8 January 2016
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Abstract Climatic effects on tree recruitment will be determined by the interactive effects of fecundity and seed predation. Evaluating how insect and vertebrate seed predators mediate tree reproductive responses to climate depends on long-term studies of seed production, development, and predation. In this study, our objectives were to (1) assess the effects of interannual climate variation on seed abortion rates, (2) assess the impact of seed density on predation rates, and (3) examine the degree to which density-dependent seed predation would amplify or dampen interannual variation in fecundity associated with seed abortion. We used a 19-year study of seed abortion and pre-dispersal predation rates by insects and vertebrates (birds and rodents) for five temperate tree species across forest plots from the North Carolina Piedmont to the Southern Appalachian Mountains in the southeastern USA. We found that rates of seed abortion and predation increased reproductive variation for oaks (*Quercus* species). Probability of seed abortion was greatest during years with cool, dry springs. Responses of seed predation on *Quercus* species to current year's seed density varied by species, but exhibited positive

density-dependence to previous year's seed density consistent with numerical responses of seed predators. Seed abortion and predation rates for two drupe species responded little to variation in climate or seed density, respectively. Given that predation increased interannual variation in seed availability and the negative density-dependence to previous year's seed density, our results indicate that consistent numerical responses of oak seed predators may amplify interannual variation due to climate-mediated processes like seed abortion.

Keywords Masting · Reproductive ecology · Seed abortion · Seed predation · Trees

Introduction

Recruitment is likely one of the most important and poorly understood obstacles for tree populations confronted with climate change (Morin et al. 2007; Clark et al. 2011). While climate-mediated processes, such as flower pollination and seed abortion, contribute to reproductive variation (Sork et al. 1993; Morin et al. 2007; Espelta et al. 2008; Pérez-Ramos et al. 2010; Pearse et al. 2013), seed predators consume essentially the entire reproductive effort from populations of mast-seeding, Northern Hemisphere trees in non-masting years (e.g.; Beal et al. 1952; Koenig et al. 2003; Lombardo and McCarthy 2008); tree recruitment depends upon seed production, development, and escape from predation. Large interannual variation in seed production, known as masting, may be one of the few options for escaping specialist seed predators (Janzen 1971; Sork et al. 1993; Schnurr et al. 2002), but this response may be neutralized by a diverse community of seed predators, including mobile generalist predators supported by a reservoir of

Communicated by Ines Ibanez.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3537-6) contains supplementary material, which is available to authorized users.

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alternative resources (Ostfeld and Keesing 2000). While many studies have examined interannual variation in reproductive effort in tree species (e.g.; Herrera et al. 1998; Koenig and Knops 2000), especially with respect to climate (e.g.; Clark et al. 2011; Kelly et al. 2013; Pearse et al. 2013), understanding the consequences of climate variation in forest communities requires long-term data on the synthetic process: from reproductive variation of multiple host species, to climatically-induced variation in flower pollination and seed development, to density-dependent seed predation. Long-term data offer the opportunity to examine the interacting effects of different processes on reproductive variation. In this study, we take advantage of seed production and damage data spanning 19 years and multiple plots to examine the degree to which seed predation amplifies or dampens the effects of climate-mediated interannual variability in seed development for large-seeded tree species within diverse temperate forests.

Compared to growth and mortality, tree fecundity is more sensitive to climatic cues, but is highly variable among individuals and years (Clark et al. 2011). For species having seed crops that rely on resources stored over several growing seasons, reproductive responses may lag climate variation (Miyazaki 2013). For other species reproductive lags may be minimal (Ichie et al. 2013). Even where climate effects are lagged, those effects may interact with short-term effects. Flower initiation, pollination, and seed development depend on short-term variation in resource availability and environmental cues (Sork et al. 1993; Koenig et al. 1996; Cecich and Sullivan 1999; Houle 1999; Knops et al. 2007; Espelta et al. 2008; Pérez-Ramos et al. 2010; Kelly et al. 2013; Pearse et al. 2013). Studies of individual fecundity over decades have improved our understanding of how climate impacts seed production (Shibata et al. 1998, 2002; Clark et al. 2011; Pearse et al. 2013), but seed production alone poorly predicts tree seedling establishment in large seeded tree species (Clark et al. 1998).

Density-dependent attacks by natural enemies further complicate interpretation of reproductive variation because the influence of seed predators likely differs by tree species and predator type (Kelly 1994; Kelly et al. 2001). Large, infrequent seed crops common in large-seeded species (Koenig and Knops 2000) may saturate specialist predator populations, leading to lower seed predation rates, a phenomenon known as predator satiation (Janzen 1971; Silvertown 1980). In contrast, large seed crops represent a pulsed resource and may attract mobile generalist predators that temporarily concentrate on a specific host species (McShea 2000; Ostfeld and Keesing 2000; Schnurr et al. 2002) (i.e., predator attraction). Under the predator attraction hypothesis, seed predation rates should increase as seed crop sizes of all suitable hosts for mobile seed predators increase, not

just seed density of an individual species. In addition to these functional response, seed predation rates are further complicated by numerical responses, such as small seed crops that depress predator populations and lead to lower predation rates the following year (Ostfeld and Keesing 2000). Observed variation in seed predation rates might characterize density-dependent mechanisms constraining seed escape from natural enemies.

Long-term seed damage patterns provide evidence for how seed predators impact interannual variability in the availability of viable seed. Both insect and vertebrate seed predators in temperate forests rely on tree seeds for all or part of their nutrition (Ostfeld and Keesing 2000; Shibata et al. 2002; Lombardo and McCarthy 2008), potentially reducing seedling recruitment by reducing the availability of viable seed, though germination rates of predated seeds are not necessarily zero (Lombardo and McCarthy 2009). Seed predators may also rely on other plant reproductive tissues, such as the fleshy pericarps (i.e., frugivory). In contrast to seed predation, frugivory can enhance seed dispersal and gene flow (e.g.; Jordano et al. 2007), select for specific genotypes (Sallabanks and Courtney 1992), and improve germination (Traveset 1998; Samuels and Levey 2005). Still, pre-dispersal seed predation is likely to limit tree regeneration, at least when the rates of seed predation are high. Direct examination of seed predation over many years of climate variation could allow us to quantify their interactive effects.

The degree of host specialization varies substantially. Both insect and vertebrate seed predators for large-seeded tree species in eastern deciduous forests often act as generalists. For example, *Curculio* species feed on acorns of closely related species within the genus *Quercus* (Williams 1989; Hughes and Vogler 2004; Govindan et al. 2011). Rodents and birds may rely on seeds opportunistically as they become available in the fall and winter months (Burns and Honkala 1990). Determining the degree of specialization is further complicated by the fact that seed predation cannot be reliably attributed to predator species: damage to the large seeds of some tree species indicate vertebrate predator activity and larval exit wounds indicate insect predator activity, but identification of the species responsible is often impossible. The degree of specialization, along with the mobility of the population, can determine the degree to which seed predator population dynamics, and thus damage rates, are coupled with tree seed production (Kelly 1994; Kelly et al. 2001). Thus, treating insect and vertebrate seed predators separately is necessary to elucidate ecological processes, but the degree that these groups of predators rely on individual species versus multiple species is uncertain.

In this study, we separated climate effects from density-dependent seed predator effects on variation in seed crops

in long-term seed abortion and damage data. We quantified interannual variation in seed abortion, insect seed predation, and vertebrate seed predation rates in a 19-year archive of seeds collected at 12 forests from the North Carolina, USA, piedmont to mountains for five large-seeded tree species: two with drupes, (*Cornus florida* L. and *Nyssa sylvatica* Marshall), and three with nuts, (*Quercus alba* L., *Quercus phellos* L. and *Quercus rubra* L.). We hypothesize that seed abortion rates will depend on climate during the seed maturation process (i.e., spring climate). We expect that the number of seeds damage by seed predators will depend on current and previous year's seed densities (i.e., density-dependent seed predation), but that the direction (positive versus negative density-dependence) and specificity (conspecific vs. multispecies seed densities) of the effects will vary by tree species. As a result, we expect that negative density-dependence will amplify reproductive variation caused by climate effects on seed production and abortion by damaging or destroying nearly all seeds during small reproductive events, while allowing most seeds to escape predation during large reproductive events. Alternatively, positive density-dependent seed predation could dampen reproductive variation.

Materials and methods

Study area

This study was carried out at a network of long-term forest inventory plots in the North Carolina piedmont (Duke Forest; near Durham, NC, 35°58'N, 79°05'W) and mountains (Coweeta LTER; near Otto, NC, 35°04'N, 83°26'W). Some forest plots were transitional between the piedmont and mountains, in terms of elevation, climate and species composition (Mars Hill College; Mars Hill, NC, 35°50'N, 82°33'W) (Table S1). Second-growth hardwood forests dominate these forest plots. This study focused on large-seeded species in the genera *Cornus*, *Nyssa* and *Quercus*, which varied in abundance across the network (Table S1). All species except *C. florida* can become canopy-dominant trees in these forests. All study species disperse fruit in autumn and winter. Seeds of some of the study species matures in a single growing season (*C. florida*, *N. sylvatica*, and *Q. alba*), while the other study species require two seasons for seeds to mature (*Q. phellos* and *Q. rubra*; Burns and Honkala 1990).

Data collection

To quantify pre-dispersal seed predation, we used 13 forest plots ranging in size from 0.34 to 4.11 ha, which represented a variety of climate regimes and included 9–128

seed traps per plot (Table S1). Seed traps 0.16-m² in area were distributed across each plot and located along 2–16 transects in each plot at 5–10 m intervals (Clark et al. 1998). Seed traps were constructed from plastic baskets suspended 1.5 m above the ground on PVC posts and covered with wire mesh to prevent seed removal by vertebrate seed predators. To reduce the likelihood of seed decay prior to collection, drain holes were drilled in the bottom of each trap and 1-mm mosquito netting was hung in the basket to keep seeds elevated. Efficiency trials indicated high trap efficiency across taxa (>86 % of seeds falling on the trap entered successfully; Clark et al. 1998). Because these traps collect seeds in the process of dispersal and protect seeds from further predation, seed removal from traps by post-dispersal seed predators did not affect our observations. Seed collection at each plot began between 1992 and 2004 (Table S1) and continued through March 2011. Seeds were collected three to five times per year at each plot, identified and sorted. All seeds from this 19-year study are archived at Duke University. We limited our analysis to the five species with at least 500 seeds in the archive, each of which had at least 50 seeds collected from each of one (*Q. phellos*) to six (*N. sylvatica*) of the 12 plots (Table S1). The data used in this study have been analyzed extensively to understand spatio-temporal variation in tree reproduction, including the estimation of individual tree fecundity, tree maturation, and interannual variation in fecundity (Clark et al. 1998, 2010, 2011). These studies explore total seed production in great detail, highlighting climatic and competitive controls of tree reproduction. The current study builds on this previous work by examining the fates of these seeds after being produced.

Examination of the data indicated that a few species by plot combinations had no seeds in most years, a handful of years with few observations (generally <10), and sometimes a single large seed year (>100 total seeds). Such a pattern may indicate a number of issues. Tree maturation associated with increasing size and access to light resources (Clark et al. 2010) may explain the pattern. Given that the most extreme example was on *N. sylvatica*, it is also possible that vertebrate seed predators or dispersers were using the seed traps as perches, potentially biasing measurements (Reid et al. 2012). Regardless of the cause, the volatility in the data indicates that those species by plot combinations might bias results. Therefore, we excluded species by plot combinations where no seeds were observed for more than 75 % of years.

Seed abortion and seed predation were quantified for each seed collected for five species over the 19-year history of the study. Total number of seeds n_{jkt} from each forest plot j collected during year t were evaluated for seed abortion and damage for species k (Table S2), which represents flower initiation, at least to some degree. Seeds that

could not be identified to species were not included in the analysis. We recorded the number of mature seeds (m_{jkt}) for each species k at plot j and year t . Seeds were judged to be immature based on seed morphology and size. Because it is often difficult to ascertain pollination of small female reproductive structures (Sork et al. 1993), immature seeds may include both unpollinated and underdeveloped seeds. As a result, our measure of immature seeds includes seeds aborted very early after flower initiation up to relatively late stages of seed development.

Mature seeds were further classified by seed predation. Seed predator damage was common and identified by visual inspection, though only pre-dispersal seed predation could be quantified. Insect damage was characterized by 1- to 2-mm circular exit wounds. Such damage may not necessarily result in the “death” of the seed, but it does reduce germination rates and seedling survival (Lombardo and McCarthy 2009). Vertebrate damage was characterized by damage to the shell and partial or complete consumption of the seed inside. For nuts (*Quercus* species) w_{jkt} was the number of seeds with insect predation, likely associated with acorn weevils (*Curculio* L. species), s_{jkt} was the number of seeds with no insect predation, and f_{jkt} was the number of seeds with both insect and animal damage (Fig. 1). For all species, p_{jkt} was the number of seeds exhibiting only vertebrate seed predation (no insect damage) and o_{jkt} was the number of seeds with unidentified damage. Shell-fragments were classified as vertebrate predation only when the remains of the style or apical portion of the seeds were present. Note that for drupe species (*C. florida* and *N. sylvatica*), removal of the fleshy pericarp by frugivores was common, but because gut passage can actually improve germination rates (Traveset 1998) and there was no observed damage to the seed itself, we counted these seeds as undamaged.

Seed predators at study plots

A diverse suite of seed predators attacks large seeds in temperate forests of eastern North America. Seed predators in these ecosystems include insects, birds, and rodents. For species in the genus *Quercus*, *Curculio* species and rodents cause significant damage to seed crops (Beal et al. 1952; Ostfeld et al. 1996). *Curculio* species often infest acorns during development (Hughes and Vogler 2004), before attacks by vertebrates and many other insects. Many species of *Curculio* attack the seeds of multiple *Quercus* species, such as acorn weevils *Curculio proboscideus* Fabricius and *Curculio sulcatulus* Casey (Govindan et al. 2011). Among vertebrate seed predators, rodents, such as the gray squirrel (*Sciurus carolinensis* Gmelin), are prolific in these temperate forests, either consuming seeds produced by many species in temperate forests while in

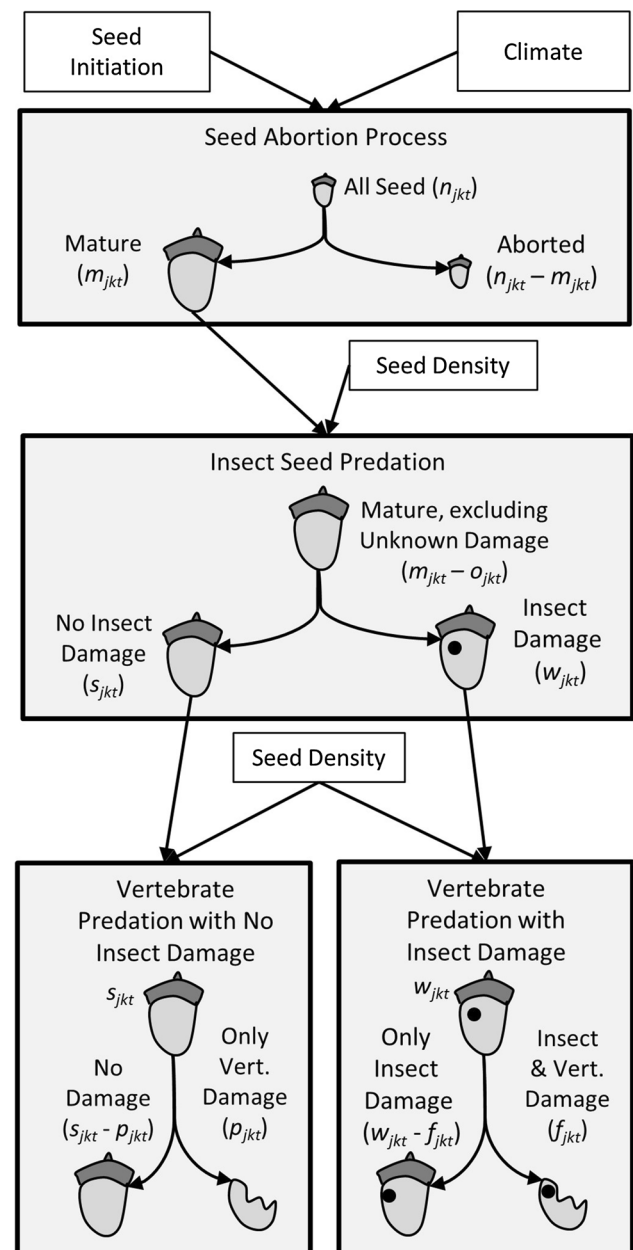


Fig. 1 Conceptual diagram outlining the temporal trajectory of seed mortality from initiation (not modeled here) to maturation (i.e., not aborted in response to different levels of insect and vertebrate seed predator damage). Covariates and statistical models tested here are represented by white and gray boxes, respectively

the canopy or hoarding them for later consumption (Howe 1989; Vander Wall et al. 2005). Of the vertebrate damaged acorns in our seed archive, tooth marks were often noticeable on the acorn remains preserved in the seed archive. For *C. florida* and *N. sylvatica*, birds, such as the American robin (*Turdus migratorius* L.), feed on their fleshy pericarp (i.e., frugivory) whereas other vertebrates attack the seeds (Burns and Honkala 1990). In addition, both birds and

rodents are known to act as seed dispersers for these study species (Herrera et al. 1998; Vander Wall et al. 2005; Jordano et al. 2007), though the effects of animal dispersal are beyond the scope of this paper.

Challenges of quantifying seed predation

Many methods of studying long-term variation in tree reproduction, such as branch observations or stem exclusion (Espelta et al. 2008; Pérez-Ramos et al. 2008; Espelta et al. 2009) or visual inspection of fruiting bodies using binoculars (e.g.; Koenig et al. 1996), are difficult to apply in closed canopy forests and the latter does not generally provide information on seed predation. In comparison, seed traps can be broadly distributed under closed canopy forests to characterize many individuals, can be scaled to area, and have proven successful in estimating both population and individual reproductive processes (Shibata et al. 1998, 2002; Clark et al. 1998, 1999). However, there are challenges for addressing seed predation questions with the seed trap method.

The fate of seeds removed from the canopy, either consumed completely by seed predators or dispersed to another location, is highly uncertain (Vander Wall et al. 2005). Post-dispersal seed predation associated with seed dispersal or scatter-hoarding could account for a large percentage of seeds in non-masting years (e.g.; Marquis et al. 1976), though some of these seeds may still germinate, leading to seedling recruitment. However, high rates of seed removal can be accompanied by high rates of damage on seeds that remain (e.g.; Yi et al. 2010). Although seed predators may consume a seed, evidence of this predation is still recognizable in seed traps, as indicated by frequent incidence of seed fragments. Seed removal directly from seed traps could lead to underestimates of seed predation rates similar to full consumption of seeds. Our own experience over the last 20 years indicates that placing seed traps at 1.5 m above the ground and the use of wire mesh to exclude vertebrates was a sufficient deterrent to seed removal by predators (Clark et al. 1998). While we cannot exclude the possibility that some seeds were removed directly from our seed traps over the course of the study, these removals likely account for a small percentage of total seed crop size observed in the seed traps. Because seeds completely removed by predators could not be accounted for in this study, the pre-dispersal predation rates reported in this paper are taken as an index of seed predation at large.

In addition, the opportunistic use of an existing seed archive to quantify seed predation carries its own challenges. Because seeds in the archive were dispersed years to decades in the past, there is no opportunity to pair the archive with monitoring of seed predator activity. Even with such observations, identifying the predators to an

individual species for each damaged seed would be incredibly difficult. Similar studies have either relied on natural history information (e.g.; Sork et al. 1993) or insect community sampling (e.g.; Shibata et al. 2002) to characterize the community of predators and their likely hosts. Because we could not accurately identify seed damage to species-level agent, quantifying the effects of individual seed predator species is beyond the scope of this project, so we selected broad definitions of predation type: vertebrate and insect.

Model development

To examine the degree to which seed predation might amplify or dampen interannual variation in seed production associated with seed abortion, we needed to quantify the effects of climate and seed density on seed abortion and predation, respectively. This motivated a novel approach that allows integration of combinations of climate data and data on seed damage that can occur from seed predators. Specifically, we required conditional dependence in the discrete categories of seed abortion and damage that is determined by the combination of climate and predators. We developed a hierarchical structure for the causal chain of events from seed abortion to seed predation (Fig. 1). In this section, we describe the hierarchical model for seed abortion and predation, the Bayesian model fitting procedures, and model diagnostics.

To quantify the influence of moisture and temperature on seed abortion rates, we examined the number of seeds aborted ($n_{jkt} - m_{jkt}$) relative to the total number of seeds produced (n_{jkt}) with respect to temporal and spatial variation in temperature and moisture. Following flower initiation, many factors influence the probability of seed abortion, particularly climatic cues occurring during spring months when flowering occurs. For example, spring temperatures were positively correlated with the number of seeds successfully maturing for *Quercus* species in Missouri, USA (Sork et al. 1993). To characterize spring temperature effects, we included mean April and May temperature T_{jt} for plot j in year t , which may impact tree demography (Knops et al. 2007; Mund et al. 2010) and pollination efficiency (Sork et al. 1993; Cecich and Sullivan 1999; Koenig et al. 2015). Previous studies have found that drought increases tree seed abortion rates (Sork et al. 1993; Espelta et al. 2008). We incorporated interannual variation in spring Palmer Drought Severity Index (PDSI) P_{jt} for forest plot j in year t , and spatial variation in mean annual precipitation A_j (cm) for forest plot j . There was no relationship between seed abortion rates and total seed crop size. PDSI is a commonly used measure of interannual deviation from normal moisture conditions with positive values indicating wet conditions and negative values indicating dry

conditions (Keyantash and Dracup 2002). For all climate variables, we used the year seed abortion was observed, assuming that the climate conditions of that year drove seed abortion, not lagged effects for species maturing seeds over multiple years. Given these climate variables, we modeled seed abortion responses to climate as a binomial process with a logit link function similar to a logistic regression model (Appendix S2).

The probability of seed predation was assumed to depend upon density of unaborted, or mature, seeds, excluding those with unidentified damage. For nut-bearing species (i.e., *Q. alba*, *Q. phellos*, and *Q. rubra*), we modeled the number of seeds exhibiting insect seed predation w_{jkt} as a binomial process with a logit link function to represent the influence of seed density on predation rates (Fig. 1). We then modeled vertebrate seed predation for seeds with and without insect damage (p_{jkt} and f_{jkt} , respectively) separately as binomial processes with logit link functions. This assumes that vertebrate seed predation occurs later in the season than the observed insect seed predation (Hughes and Vogler 2004). As a result, vertebrate seed predation for *Quercus* species also depends on the insect seed predation process. For drupe-producing species (*C. florida* and *N. sylvatica*), insect seed predation was not observed. Therefore, vertebrate seed predation in drupes was modeled as a binomial process with a logit link function. Model details can be found in Appendix S2.

To represent seed density effects on seed predation, we calculated seed densities of the focal species (i.e., conspecific) versus other similar species (i.e., intraguild). Conspecific seed densities were calculated for each species k at plot j during year t . For intraguild seed densities, we summed seed counts for all nuts (*Quercus* species), indicated as guild $G = 1$, and for all drupes (*C. florida* and *N. sylvatica*) indicated as guild $G = 2$. Seed densities were obtained for plot j and year t using total trap area ($0.16 \text{ m}^2 \times$ number of traps; Table S1). For modeling, we used the square root of intraguild seed density $M_{jG,t}$ (seeds m^{-2}) and the conspecific seed density $C_{jk,t}$ (seeds m^{-2}). Note that density-dependent effects of intraguild seed density on predation apply to seeds of a given guild: drupe seed density does not affect nut predation rates, and vice versa.

Statistical models were fitted using a metropolis algorithm within a Gibbs sampler (Appendix S2). Model fits were assessed by comparing predicted to observed responses (Appendix S3). To determine which climate variables were important for predicting seed abortion rates and to examine the extent to which seed predation depends on seed densities of the focal species (i.e., conspecific) versus other similar species (i.e., intraguild), we performed model selection by minimizing posterior predictive loss. For the seed abortion model, we fit all eight combinations of the three climate

variables (intercept only, T_{jt} , P_{jt} , A_j , $T_{jt} + P_{jt}$, $T_{jt} + A_j$, $P_{jt} + A_j$ and $T_{jt} + P_{jt} + A_j$). Because *C. florida* and *Q. phellos* only occurred in the Piedmont region, we did not consider models with mean precipitation A_j . For the seed predation models, we fit all seven combinations of the seed density variables, representing effects of current and previous year seed densities as well as conspecific vs. intraguild seed densities (intercept only, $M_{jG,t}$, $M_{jG,t-1}$, $M_{jG,t} + M_{jG,t-1}$, $C_{jk,t}$, $C_{jk,t-1}$, and $C_{jk,t} + C_{jk,t-1}$). After all models were fitted, we calculated posterior predictive loss, which is the sum of a goodness of fit term (sum of squared residuals) and a penalty term for model complexity (sum of predictive variances) (Gelfand and Ghosh 1998). For each process, the model with the minimum predictive loss for each species was chosen as the best model used for further analysis. All statistical analyses were performed in R (<http://www.r-project.org/>).

This statistical approach represents a departure from traditional metrics of reproductive variation, typically a coefficient of variation over years or simple regression techniques. It allows us to draw inference on both the importance and magnitude of ecological drivers of reproductive variation, and it accommodates stand differences in species composition, and thus seed density, as well as length of sampling interval (Table S1). By relating reproductive variation to spatial and temporal variation in climate and seed density, the analysis is less sensitive to differing sample period length than traditional coefficients of variation and provides richer inference. In comparison to traditional regression approaches, our method allows for coherent posterior predictions of species variation in seed abortion and predation. Coefficients of variation provide limited insight on fecundity controls (Koenig et al. 2003; Buonaccorsi et al. 2003; Crone et al. 2011), but they are reported as a metric for comparing populations and species (e.g.; Herrera et al. 1998). We calculated population coefficients of variation (CV; Buonaccorsi et al. 2003), characterizing reproductive variation associated with total seed production as well as changes in variation caused by seed maturation and predation processes. Thus, CV for total seed counts is the baseline reproductive variation while CV for mature and undamaged seeds quantifies variation after maturation and predation processes.

Results

Coefficients of variation for each plot and species combination indicated that seed production, seed abortion, and seed predation all contributed to interannual variation in the temperate forests we examined. While seed abortion resulted in small or no increase in CV, CV nearly doubled

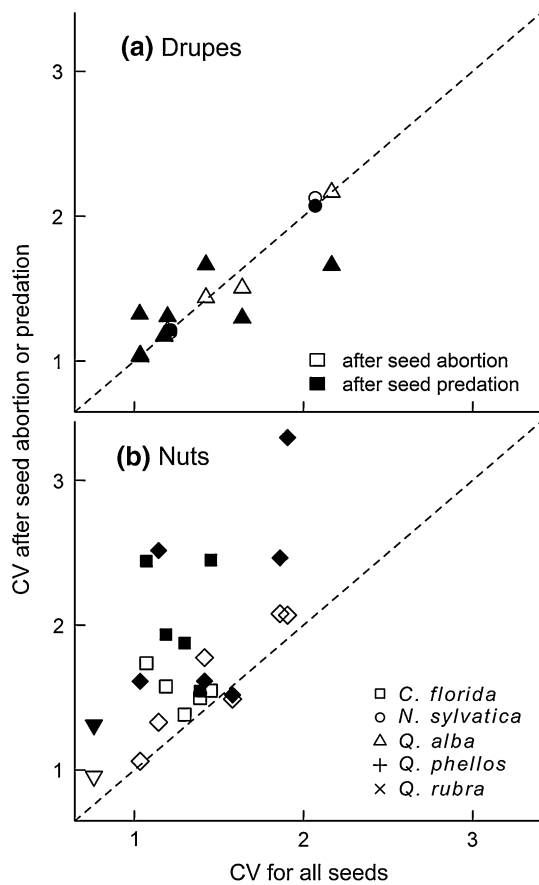


Fig. 2 Comparison of plot-level coefficients of variation (CV) for all seed with seed counts after seed abortion (*open symbols*) and after seed predation (*closed symbols*) for **a** drupes (*C. florida* and *N. sylvatica*), and **b** nuts (*Q. alba*, *Q. phellos*, and *Q. rubra*). Dashed line indicates 1:1 line

after seed predation for some species at some plots (Fig. 2). On average, the seed maturation process did not change CV for *C. florida* or *N. sylvatica* (mean CV change of 0.02 and -0.01 ; Fig. 2a), but increased CV by 0.20 for *Quercus* species (Fig. 2b). Mean changed in CV within a given population jk caused by seed predation were 0.00 for *C. florida*, -0.03 for *N. sylvatica*, 0.70 for *Quercus* species.

The probability of seed abortion decreased with temperature and moisture for many species (Fig. 3). Mean spring temperature effects were negative for three species, with credible intervals not including zero for *Q. alba* and *Q. rubra* (Fig. 3b). The best model for *Q. phellos* did not include temperature effects and only the intercept was included in the best model for *N. sylvatica* (Table S3). Mean spring PDSI effects were negative for four species, with credible intervals not including zero for *Q. alba* and *Q. phellos* (Fig. 3c). Thus, seed abortion rates tended to be higher during dry (low PDSI) and cool (low spring temperature) years. The effects of plot-specific average annual

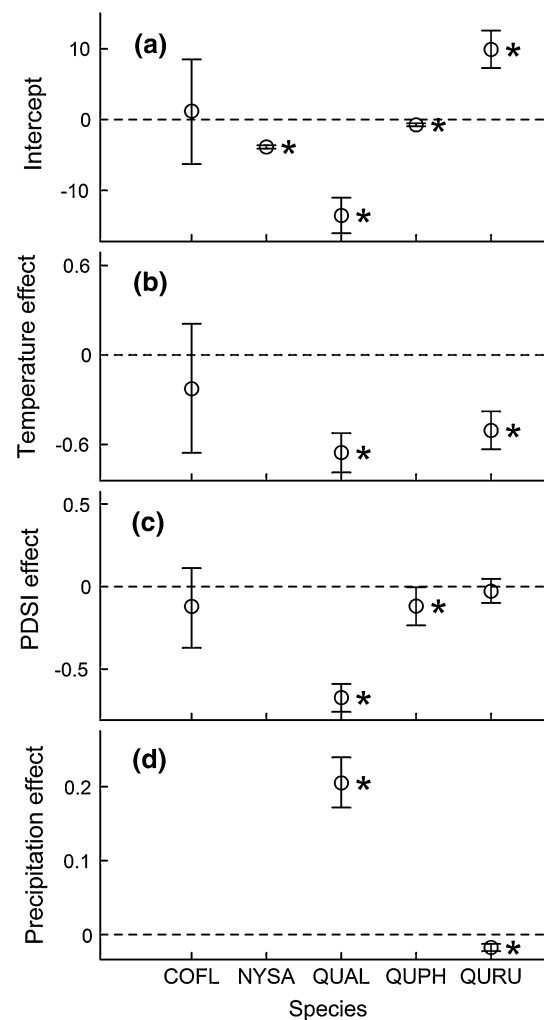
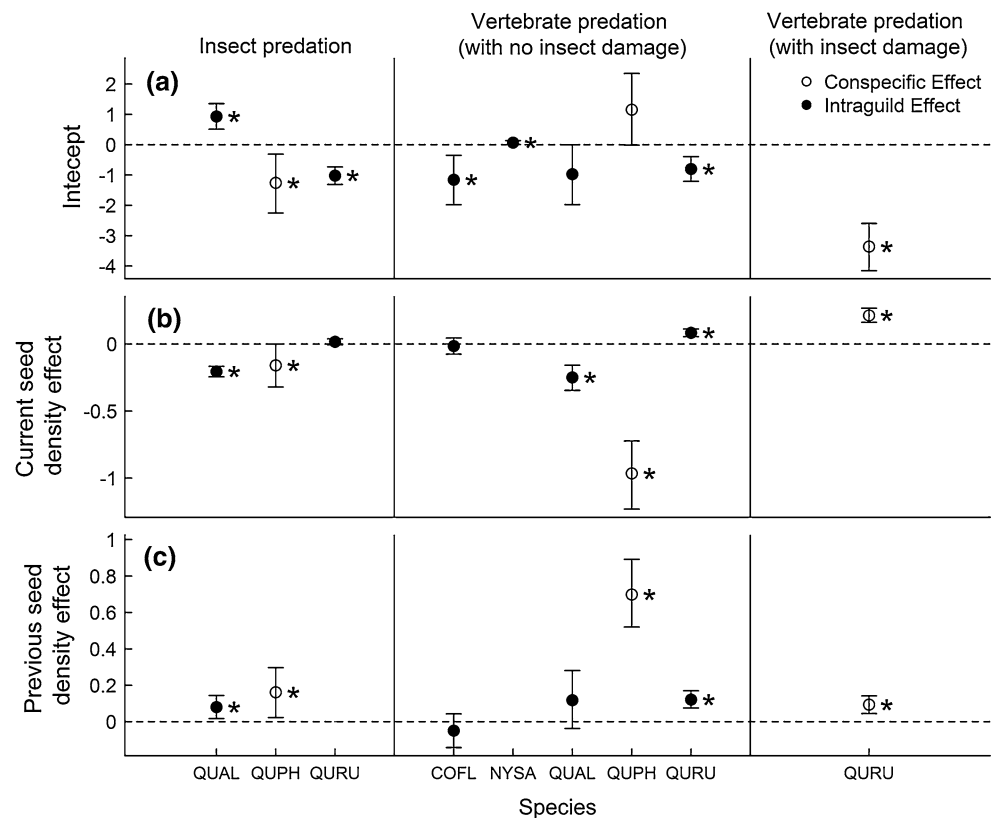


Fig. 3 Parameter estimates (mean \pm 95 % credible intervals) for seed abortion **a** intercepts and responses to **b** spring temperature T_{jt} , **c** spring PDSI P_{jt} , and **d** mean annual precipitation A_j . Credible intervals for parameter estimates marked with an asterisk do not include zero. Species names are abbreviated as: *COFL* *C. florida*, *NYSA* *N. sylvatica*, *QUAL* *Q. alba*, *QUPH* *Q. phellos*, and *QURU* *Q. rubra*

precipitation were included in the best models for *Q. alba* (positive) and *Q. rubra* (negative) (Fig. 3d; Table S3).

Both current and previous year’s intraguild seed densities were often included in the best models of seed predation (Fig. 4, Table S4). Only models of *Q. phellos* (insect seed predation and vertebrate seed predation) and *Q. rubra* (vertebrate seed predation on insect damaged seeds) included conspecific density effects. For insect seed predation, *Q. alba* and *Q. phellos* exhibited negative effects of current year’s seed densities and positive effects of previous year’s seed densities, while *Q. rubra* exhibited a weak positive effect of current year’s seed density. For drupes, current and previous year’s intraguild seed density effects on vertebrate seed predation were either weakly (i.e., effect included in the best model, but credible interval

Fig. 4 Parameter estimates (mean \pm 95 % credible intervals) for seed predation **a** intercepts and responses to **b** current seed densities and **c** previous seed densities. Responses to conspecific seed densities are given as *open symbols* and intraguild seed densities as *closed symbols*. Credible intervals for parameter estimates marked with *asterisk* do not include zero. Species abbreviations are the same as in Fig. 3



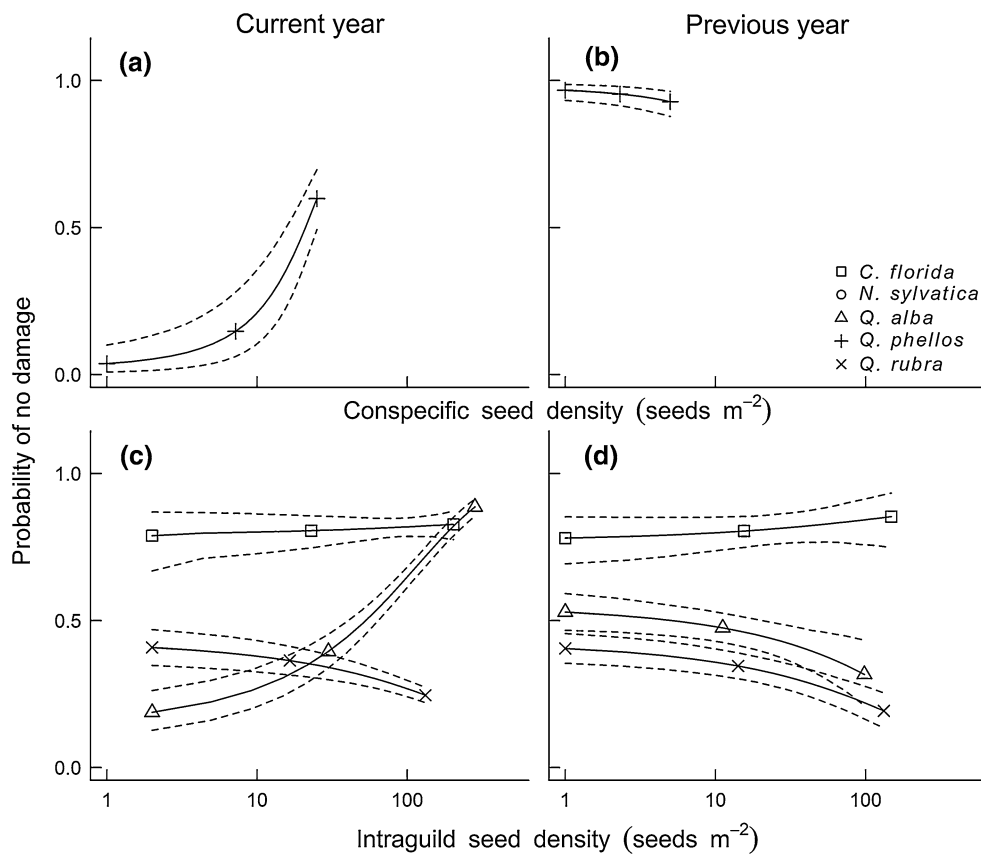
for parameter included zero) negative (*C. florida*) or non-existent (*N. sylvatica*). For vertebrate seed predation when insect damage was absent, *Q. alba* and *Q. phellos* exhibited negative effects of current year's seed densities and positive effects of previous year's seed densities, though, in the latter case, only weakly so for *Q. alba*. In contrast, *Q. rubra* exhibited positive effects of both current and previous year's seed densities on vertebrate seed predation, whether insects had damaged the seed or not. In addition, the estimated intercept for *Q. rubra* vertebrate seed predation for insect damaged seed was less than the estimate in models of vertebrate seed predation on seeds with no insect damage, indicating that insect seed predation depresses the probability of vertebrate seed predation (Fig. 4a).

As a result of the seed predation responses, the probability that seeds were undamaged [$1 - p(\text{insect damage}) \times (1 - p(\text{animal damage} \mid \text{no insect damage}))$] responded to conspecific and intraguild seed densities in different ways for different species (Fig. 5). The probability that seeds were undamaged increased with current year's seed densities for two species (*Q. alba* and *Q. phellos*) and decreased for *Q. rubra* (Fig. 5a, c). The probability that seeds were undamaged decreased for all *Quercus* species with previous year's seed densities, though only weakly so for *Q. phellos* (Fig. 5b, d). For the drupe species, the probability that seeds experienced no damage neither increased nor decreased substantially.

Discussion

Long-term evidence of variation in seed abortion and predation highlights the diverse influences on tree reproductive success (Pearse et al. 2015). As opposed to previous studies of interannual variation in tree fecundity in these forest ecosystems (Clark et al. 1998, 2010, 2011, 2012), the current study partitioned reproductive variation into several components, specifically examining seed abortion and predation (Fig. 1) and the resulting effects on interannual variation in seed availability (Fig. 2). Previous studies in these forests indicated that individual tree reproductive output is sensitive to temperature and moisture variation as well as competitive light environment for some tree species (Clark et al. 2011, 2012). Similarly, we observed that seed abortion rates were lowest during years with warm and wet spring conditions for some of the species (Fig. 3), indicating that total seed production and seed maturation processes may be limited by similar climatic controls. Time between masting events and the length of time required to mature seeds differ among coexisting species (Sork et al. 1993) and species may be responding to different climate variables (Koenig and Knops 2014). If reproduction depends on carbohydrate storage (Satake and Bjørnstad 2007; Mund et al. 2010), species-specific differences in resource allocation may cause interspecific variation in

Fig. 5 Predicted means (solid lines) and 95 % credible intervals (dashed lines) for each species (indicated by different symbols) for the probabilities of seeds experiencing no damage in response to **a** current year’s conspecific seed density, **b** previous year’s conspecific seed density, **c** current year’s intraguild seed density, and **d** previous year’s intraguild seed density. All covariates besides the covariate of interest (on the X-axis) were held constant at their means



seed abortion responses to climate. Because local competitive environment influences tree fecundity directly as well as interactively with climate (Clark et al. 2012), differences in stand characteristics, such as fertility, moisture and age, almost certainly play a role in seed abortion rates. Still, seed abortion contributed less to reproductive variation in comparison interannual variation in total seed production or to changes in viable seeds associated with seed predation, at least for *Quercus* species (Fig. 2).

Compared to seed abortion rates, pre-dispersal seed predation rates exhibited much greater variation among species, reflecting the complexity of the biotic interactions under examination. Density-dependence of seed predation and resulting seed survival in *Quercus* species varied substantially in both magnitude and direction, with *Q. alba* and *Q. phellos* exhibiting negative density-dependence consistent with predator satiation and *Q. rubra* exhibiting positive density-dependence consistent with predator attraction (Figs. 4b, 5a, c). Given that predator satiation is thought to apply to specialist seed predators (Janzen et al. 1971), we did not expect negative density-dependence with respect to intraguild seed densities or vertebrate seed predation exhibiting negative density-dependence as the rodents attacking much of these seeds are most likely generalists. Coupled with the weak to non-existent density-dependent effects on predation rates in drupes, these results imply that neither

mechanism dominates seed predation in these forests. Interestingly, at our study plots *Q. alba* and *Q. phellos* tend to dominate stand structure, making up 71 and 30 % of stand basal area in two particularly extreme plots (DW and DH, respectively) and contributing most of the *Quercus* seeds for those plots. In contrast, *Q. rubra* does not tend to dominate the *Quercus* populations in our stands, often coexisting with other closely related oaks, such as *Q. coccinea*, *Q. falcata*, and *Q. velutina*. Because interannual variation in the seed resource is dominated by a single species, even generalist seed predator populations may be locally suppressed, leading to a greater potential for predator satiation. Local spatial variation in tree community composition and tree reproduction can influence seed predator responses, but has been addressed mostly in theoretical work (Satake and Bjørnstad 2004). While functional groupings, such as “generalist”, may be technically correct, the response of these seed predators may be conditional upon local forest community composition.

All three *Quercus* species exhibited responses to previous year’s seed density consistent with a lagged numerical response in seed predator populations, with increases in seed predation rates following large seed crop years. The representation of previous year’s seed density is necessarily simplistic. Even with the 19-year archive of seed production at the study plots, masting may be rare for some tree

species, making inference on highly complex reproductive and predation processes difficult. When masting cycles are predictable or masting events follow environmental cues (Allen et al. 2011), insect seed predators can match tree reproductive cycles through diapause, making seed predation responses to previous seed densities difficult to identify (e.g.; Maeto and Ozaki 2003). While the degree of reproductive synchrony within and among species can vary substantially (Koenig and Knops 2000; Schaubert et al. 2002), when tree populations are not highly synchronized, the lack of synchrony within and among populations buffers seed predator populations against collapse (Satake and Bjørnstad 2004).

Despite substantial variation between *Quercus* species in seed predation and resulting probability of mature seeds experiencing no damage, all three species exhibited increases in CV due to seed predation, indicating that seed predation generally amplified interannual variation in seed production and abortion processes. Large *Q. alba* and *Q. phellos* seed crops experienced less seed predation than small seed crops (Fig. 4b), and had a lower probability of seed damage during masting events (Fig. 5a, c), but *Q. rubra* experienced the opposite pattern (i.e., increased probability of predation and decreased probability of undamaged seed). Seed predation amplified interannual variation in viable seed availability (Fig. 1), regardless of the direction of density-dependence. Considering that positive density-dependence of seed predation should decrease the interannual variation in viable seed availability, this implies that the numerical responses of seed predators associated with previous year's seed densities can offset the dampening of current year's seed density effects in *Q. rubra*. For example, dry spring conditions resulting in low availability of mature seeds (Fig. 3c, Sork et al. 1993; Clark et al. 2012) could provide increased opportunity for seed escape from predators when density-dependence of seed predation is positive with respect to previous year's seed density (Figs. 4, 5).

The effects of climate-mediated seed production and abortion as well as density-dependent seed predation on viable seed availability could have major consequences for tree regeneration in future forests. Recruitment has been difficult to estimate, in part, due to the potential for extreme variation in seed predation. Recruitment is one of the critical uncertainties in models of climate-mediated migration (Morin et al. 2007; Clark et al. 2011). Therefore, studies examining the presence of both strong biotic and climatic influences on tree reproduction are essential for predicting the effects of climate change on species distributions and forest dynamics. Furthermore, if (1) biotic agents tend to amplify climate-mediated reproductive variation in some species (e.g., Fig. 2) and (2) dry future conditions in southeastern forests (Mearns

et al. 2003) result in fewer large masting events, then mechanisms like predator satiation may become more effective in providing avenues for seeds to escape predation. However, if density-dependent seed predation processes also shift in response to climate change, the stability of interactions between climate and seed predation on viable seed availability may be suspect. For example, tree and migratory bird phenologies can become decoupled under climate change (Sherry et al. 2007). Temporal patterns of masting and insect diapause might respond differently to climate change, altering the sensitivity of seed predation to seed density. Given that pre-dispersal seed predation likely impacts the probability of later attacks (Fig. 4), shifts in seed predation rates are likely to have cascading effects for both hosts and predators (Ostfeld et al. 2006). Our observations of both climate-mediated seed abortion and density-dependent seed predation provided evidence of the synergistic impacts of climate change and natural enemies on tree reproduction.

Acknowledgments We would like to thank Norman Christensen, Fred Hain, Matthew Kwit, Megan Mobley, Ram Oren, Carl Salk, Anne Stein, Denis Valle, Kai Zhu, Ines Ibanez, and three anonymous reviewers for comments on the manuscript. The research was supported by NSF Grants BSR-9444146, DEB 9453498, DEB-9632854, DEB-9981392, IDEA-0308498, DEB 0425465, SEII 0430693 and DDDAS 0540347, as well as the USDA Forest Service Pacific Northwest Research Station. The experiments comply with the current laws of the United States of America in which the experiments were performed.

Author contribution statement DMB and JSC conceived of and designed the study. JSC provided the long-term seed archives and DMB performed measurements. DMB designed and implemented the statistical modeling. DMB and JSC wrote the manuscript.

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