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1 Rapid aggregative and reproductive responses of weevils to masting of North American oaks
2 counteract predator satiation

3

4 Running head: Masting does not satiate seed predators

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Abstract

The predator satiation hypothesis posits that masting helps plants escape seed predation through starvation of predators in lean years, followed by satiation of predators in mast years. Importantly, successful satiation requires sufficiently delayed, bottom-up effects of seed availability on seed consumers. However, some seed consumers may be capable of quick aggregative and reproductive responses to masting which may jeopardize positive density-dependence of seed survival. We used a 17-year data set on seed production and insect (*Curculio* weevils) infestation of three North American oaks species (northern red *Quercus rubra*, white *Q. alba*, and chestnut oak *Q. montana*) to test predictions of the predation satiation hypothesis. Furthermore, we tested for the unlagged numerical response of *Curculio* to acorn production. We found that masting results in a bottom-up effect on the insect population; both through increased reproductive output and aggregation at seed-rich trees. Consequently, mast seeding in two out of three studied oaks (white and chestnut oak) did not help to escape insect seed predation, whereas in the red oak, the escape depended on the synchronization of mast crops within the population. Bottom-up effects of masting on seed consumer populations are assumed to be delayed, and therefore to have negligible effects on seed survival in mast years. Our research suggests that insect populations may be able to mount rapid reproductive and aggregative responses when seed availability increases, possibly hindering satiation effects of masting. Many insect species are able to quickly benefit from pulsed resources, making mechanisms described here potentially relevant in many other systems.

Key words: bottom-up effects, mast seeding, predator satiation, seed predation, seed survival, top-down effects,

Introduction

In many perennial plant species, seed production fluctuates from year to year and is synchronized among individuals (Kelly 1994, Pearse et al. 2017). This reproductive behavior, called masting, is thought to render a fitness benefit to plants through decreased costs of reproduction per surviving offspring (so called 'economies of scale'; Norton and Kelly 1988, Pearse et al. 2016). Masting may provide economies of scale through enhanced pollination efficiency, increased seed dispersal by animals, and satiation of seed predators in mast years (Kelly et al. 2001, Rapp et al. 2013, Linhart et al. 2014, Zwolak et al. 2016). Among the ultimate factors underlying masting, the predator satiation hypothesis (PSH) has been most frequently tested. It states that seed consumers are controlled by food resources (bottom-up), and therefore years of scarce seed production decrease their abundance (Satake and Bjørnstad 2004). Consequently, consumers are relatively rare in mast years, and therefore easily satiated, which results in a decrease in the proportion of damaged seeds when seed production is high (Kelly et al. 2000, Fletcher et al. 2010, Żywiec et al. 2013, Linhart et al. 2014). Successful satiation requires sufficiently delayed, bottom-up effects of seed availability on seed consumers. Yet, not all consumer responses to masting are delayed (Ostfeld and Keesing 2000, Bogdziewicz et al. 2016). In such cases, predator satiation might be weak or absent.

Immediate bottom-up effects of masting on seed consumers may be driven by behavioral aggregation in resource-rich habitats, rapid reproductive responses, or a combination of both (Yang et al. 2010, Bogdziewicz et al. 2016). Theoretical population models of invertebrate seed predators feeding on masting plants typically assume that insects have limited dispersal abilities and are incapable of aggregative responses to masting (Satake and Bjørnstad 2004, Tachiki and Iwasa 2010). Furthermore, numerical (reproductive) increase in seed consumer populations is a part of these models, but the consequences of increased reproductive output are assumed to be delayed by at least one year and therefore to be

important for the future, but not for seed survival in the current year (Kelly and Sork 2002, Tachiki and Iwasa 2010). Under such assumptions, masting is very likely to result in predator satiation.

However, these conditions might not apply to other tree-seed predator interactions. In many masting systems, the main seed predators are endoparasitic, specialist insects (i.e. adults lay eggs in seeds, and larvae feed on the seed to fuel development, Satake et al. 2004, Bonal et al. 2007, Espelta et al. 2009, Żywiec et al. 2013, Calama et al. 2017). Adult insects are often time-limited due to their short life spans. As a result, increased seed abundance results in an increase in realized fecundity due to lower host-searching costs and lower competition (Desouhant et al. 2000, Debouzie et al. 2002). Such a current-year increase in reproductive output of a consumer population may matter for infestation rates, even if it has not yet translated into higher abundance of adults. From the plant's perspective, this may result in a higher number of seeds infested with larvae, even though potential changes in the abundance of adult seed predators are still delayed to the following year. Furthermore, aggregative responses to masting may be important for seed survival if insects tend to redistribute themselves among trees and target the most productive ones (Pérez-Ramos et al. 2017, Bogdziewicz et al. 2018a).

We analyzed a 17-year data set on seed production, acorn infestation by weevils (*Curculio* sp.), and abundance of weevil larvae in three North American oak species (red oak *Quercus rubra*, white oak *Q. alba*, chestnut oak *Q. montana*). Oaks are classic model organism in masting studies, while weevils are their main pre-dispersal seed consumers (Crawley and Long 1995, Espelta et al. 2008, Koenig et al. 2016). We pursued two main goals. First, we tested the predictions of the PSH. Second, we assessed the ability of weevils to numerically respond to masting. PSH has two components. Thus, we first tested for the satiation of seed predators, i.e. a decreasing proportion of predated seeds with increasing seed

abundance (**prediction 1**). The second component of the PSH involves invertebrate starvation, i.e. lean seed years followed by mast years should favor increased seed survival (Kelly and Sullivan 1997, Żywiec et al. 2013, Espelta et al. 2017). Thus, past acorn production should positively correlate with current predation rates (**prediction 2**). Eventually, if the number of predators is reduced by low seed production in a previous year, the predator population as a whole cannot cope with increased seed production (Kelly and Sullivan 1997, Satake et al. 2004, Espelta et al. 2017). In that case, seed damage rate should be negatively correlated with the change in reproductive effort of plants between subsequent years (**prediction 3**). The underlying assumption of all these predictions is that a higher insect abundance in year T translates into higher insect abundance in year T+1 (**prediction 4**).

Finally, we tested for a numerical response of weevils to acorn production (Yang et al. 2008), i.e. aggregation of insects at seed-rich trees, and increased reproductive output in good seed years. This analysis was based on per tree counts of both larvae and acorns. To test for an aggregative response, we explored whether the relationship between larval abundance and crop size at the tree level differs with the ambient (population) level of acorn production. Lean seed years should result in increased dispersion rates from failure trees and an arrival at relatively productive trees (**prediction 5**). In other words, if aggregation of weevils at highly-productive trees contributes to the positive correlation between weevil larval abundance and the tree-level crop size, the numerical increase at highly-productive trees should be stronger in low-crop years. This is based on weevil life history traits; these insects are expected to disperse only when faced with almost complete seed failure of the host tree (Venner et al. 2011, Pélişson et al. 2012). Moreover, if the increased larval abundance at productive trees is not only an outcome of a re-distribution of weevils in space, but also of increased realized fecundity, we should see a positive correlation between population-level larval abundance and population-level crop size (**prediction 6**).

Materials and methods

Study system

All three oaks (red oak *Quercus rubra* L., white oak *Q. alba* L., chestnut oak *Q. montana*) are widespread hardwood species in Eastern North America that exhibit mast seeding behavior (Lichti et al. 2014) (Fig. 1S). *Curculio* beetles are their main seed predators (Lombardo and McCarthy 2008, Govindan et al. 2012, Bogdziewicz et al. 2017). The insect is univoltine, i.e. has one brood of offspring per year. Adult females perforate a hole in the seed coat with their rostrum and oviposit into the acorns. Infested acorns are dropped and larvae grow inside feeding on the cotyledons. When early stages of development are completed, larvae drill a hole to exit the acorn and bury themselves underground, where they eventually pupate and then develop into adults. Larvae overwinter within earth cells and may experience extended diapause: i.e. most adult weevils emerge after 1 year, but some may go through a longer diapause. After emergence, adults climb the trunk of the oak under which they emerged to the canopy where they mate and females oviposit. Weevils generally show poor dispersal ability, but may be capable of moving between trees if necessary (Pélisson et al. 2012). Laboratory trials show that females may be capable of laying over 40 eggs during their life-time, but realized fecundity is often below 20 eggs/female, likely due to limited time for oviparity (field life span shorter than 10 days) (Debouzie et al. 2002).

Seed production and infestation data

We monitored acorn production over 17 years at three study areas in eastern Pennsylvania, USA: two in Luzerne County (Steele and Venesky) and a third in Schuylkill County (Hawk Mountain). Red and white oaks were monitored at all three sites, while chestnut oaks were not present at one site (the Steele site). Detailed description of the study

sites is given in Moore et al. (2007). We monitored acorn production by individual oak trees by placing two seed traps under each of 15 individuals of each species at each site from 2001 to 2017. The trap dimensions changed over the years from 0.14 m² (2001-2005) to 0.25 m² (2006-2010), and 0.20 m² (2011-2016). Therefore, we corrected seed crop size data accordingly, by multiplying acorn counts to match the 2006-2010 trap size (correction factor for years 2000-2005: 1.71; for years 2011-2017: 1.25). Throughout the analysis, crop size per tree per year is the summed acorn count from the two seed traps. Each year, acorns were collected from seed traps biweekly from late August until seed fall ceased in mid to late November. Collections began in late August to ensure that early-aborted acorns were collected. Acorns were bagged separately according to the tree of origin, then transported to the laboratory and refrigerated (4°C) until further processing.

In the laboratory, we weighed, measured (width and length) and assessed insect infestation for individual acorns from each species (sample sizes: red oak = 2453, white oak = 1687, chestnut oak = 921). We counted all insect larvae found in each acorn. If the acorn had multiple exit holes, we counted one weevil for every exit hole in the acorn.

Statistical analysis

To test whether oak masting results in seed consumer satiation, (prediction 1) we built binomial family, logit link generalized linear mixed models (GLMMs), one for each oak species. Tree ID was included as a random effect while site was a covariate in all GLMM models described below. We used acorn infestation (1 - infested, 0 - not infested) as a response, while the fixed effect included tree-level crop size as an interaction term with the population-level crop size (summed crop per site per year). The interaction term allowed us to test for the effect of background crop production on the infestation rate of each tree. If weevils aggregate at trees producing large crops out of synchrony with the rest of the

population, we should see a negative interaction term, i.e. satiation is only efficient if the whole population masts. We did not include year in these models since it would restrict our analysis to within-year comparisons, while among-year variation in crop production is most important for predator satiation (Fletcher et al. 2010). During initial model fitting, we also included the quadratic term of tree-level crop size, along with the linear one, to distinguish between type II (hyperbolic) and III (sigmoidal, *i.e.* functional responses of weevil predation to crop size, cf. Hooling 1965, Moreira et al. 2017). However, in all cases, the quadratic term was not significant. We therefore dropped it from the final models and do not explore it further.

We tested for the starvation component of the PSH with four models for each oak species. First, we tested whether current year predation rate is related to the previous year crop size or to the summed crop size of the previous two years (prediction 2). We summed the crop size over the past years to account for the ability of delayed diapause by the weevils (see Methods: Study system). We also tested whether the seed damage rate is related to the ratio of the crop in year T to the crop in year T-1, i.e. whether high seed production after lean years helps escape predation (prediction 3). In these tests, we used binomial family, logit link GLMMs with acorn predation (1/0) included as a response. To test for the link in larval abundance between subsequent years (prediction 4) we regressed current year larval abundance per tree to the larval abundance at that tree in the previous year. This was done using the negative binomial GLMMs with log-link.

We tested whether increased acorn production results in higher larval abundance, and whether this numerical response includes aggregation in seed-rich trees (prediction 5). Depending on the species, we used negative binomial or Poisson models and included zero-inflation if necessary (specified by comparing the models with likelihood ratio test). In the tree-level analysis, we included sum of larvae found in all acorns per tree, per year as a

response. The predictors were individual tree crop size, the population-level crop size (summed crop per site per year), and their interaction term.

We also conducted a population level analysis to test whether change in weevil larval abundance is fueled by increased reproduction or, alternatively, an outcome of weevil redistribution among trees (prediction 6). Depending on the species, we used negative binomial or Poisson GLM. The response was summed larval abundance per year, per site, while the fixed effect included the summed crop size per year, per site. Site was included as a covariate.

In all models, crop size was log-transformed before including it in the models. We tested for statistical significance of predictors with likelihood-ratio tests. When the model included more than one predictor, we tested for the collinearity in the models but detected none ($VIF < 1.5$). In each model, we tested for potential temporal autocorrelation of residuals. When we detected one, we extended the model with the temporally autocorrelated random effect of year nested within study site. The statistics were run in R and models were implemented via lme4 and glmmTMB packages (Bates et al. 2014, Brooks et al. 2017).

Results

In all species, the predation rates were relatively low and estimated infestation rates oscillated around 10-30% throughout the 17-year study period (Fig. 1, summary statistics are given in the Table S1 along with comparison of reported predation rates to other studies). In contrast to prediction 1, in white oak ($\chi^2 = 2.67$, $p = 0.10$; Fig. 1c) and chestnut oak ($\chi^2 = 3.01$, $p = 0.08$; Fig. 1d) we detected no decrease in the proportion of acorns infested at the tree level with an increasing tree-level crop size. However, in the red oak, the tree-level predation rate of acorns was negatively related to the tree-level crop size, although this effect was dependent on the population-level seed production ($\chi^2 = 7.89$, $p = 0.004$), i.e. the decrease in proportion

of infested acorns with increasing crop size was only detected if the population-level seed production was high (Fig. 1a, b).

Predictions 2-4 were not supported. We did not detect a relationship between previous year acorn production and current year predation rates (prediction 2; red oak: $\chi^2 = 0.04$, $p = 0.84$; white oak: $\chi^2 = 1.43$, $p = 0.23$), summed crop size over the previous two years (potential diapause effect: red oak: $\chi^2 = 1.15$, $p = 0.28$; white oak: $\chi^2 = 0.87$, $p = 0.42$), or the current to previous-year crop size ratio (prediction 3: red oak: $\chi^2 = 0.34$, $p = 0.56$; white oak: $\chi^2 = 1.87$, $p = 0.39$). Only in the chestnut oak, the current-year predation rate tended to be higher if the previous-year crop size was high ($\chi^2 = 4.28$, $p = 0.04$). Yet, similarly to the other species, summed crop size over the previous two years did not have an effect on the proportion of predated acorns in chestnut oak ($\chi^2 = 0.36$, $p = 0.55$), nor did the current to previous year's crop-size ratio ($\chi^2 = 2.54$, $p = 0.11$). Further, in either species, we did not find a relationship between current- and the previous-year abundance of weevil larvae (prediction 4: red oak: $\chi^2 = 0.007$, $p = 0.93$; white oak: $\chi^2 = 0.014$, $p = 0.71$; chestnut oak: $\chi^2 = 1.19$, $p = 0.27$).

However, in all oak species and in line with predictions 5 and 6, we detected an immediate increase in larval abundance in response to seed production. In red and white oaks, the abundance of larvae per tree was positively related to the current crop size of the tree, and this effect was stronger when the population-level crop size was small (interaction term = tree-level crop size \times population-level crop size, red oak: $\chi^2 = 7.62$, $p = 0.006$; white oak: $\chi^2 = 6.92$, $p = 0.008$; Fig. 2). In chestnut oak, the per-tree larval abundance was also related to the crop of that tree ($\chi^2 = 14.42$, $p < 0.001$; Fig. 2), but not the population-level seed production ($\chi^2 = 0.34$, $p = 0.56$). Finally, population-level larval abundance and crop size at the population level were positively related in all three species (prediction 6: red oak: $\chi^2 = 91.20$, $p < 0.001$; white oak: $\chi^2 = 61.36$, $p < 0.001$; chestnut oak: $\chi^2 = 12.51$, $p < 0.001$; Fig. 3).

Discussion

Bottom-up effects of masting on seed consumer populations are largely assumed to be delayed, and therefore to have negligible effects on seed survival in mast years. Our research instead suggests that insect populations may be able to immediately respond to increased seed availability through a combination of aggregative and reproductive responses, possibly hindering the satiation effect of mast seeding (summarized in Table 1). In line with this reasoning, mast seeding in two out of three studied oaks (white and chestnut oak) did not help to escape insect seed predation, while in the red oak, escape depended on the synchronization of mast crops within the population.

Our results imply that the increase in weevil larval abundance was driven simultaneously by an increase in reproductive output of adult weevils and their aggregation at the seed-rich trees. The increase in larvae number at seed rich trees was particularly strong when acorn crops were low at the population level. At the same time, because weevil population dynamics were not affected by variability in past acorn production (predictions 2-4), this aggregative effect was likely the result of both increased dispersion from seed poor trees (prediction 5) and increased realized fecundity at seed rich trees (prediction 6). The alternative scenario is that the apparently stronger increase at seed rich trees was caused by higher weevil mortality at seed poor trees. Detailed studies of the insect population dynamics should shade more light on this phenomenon.

Many insect species are able to quickly benefit from pulsed resources, making the mechanisms described here potentially important in numerous other systems (Ashton et al. 1988, Crone 2013). The strength of the bottom-up effect, and the importance of aggregative vs. reproductive responses will likely depend on functional traits of focal insects. In the case of univoltine insects, like *Curculio*, the reproductive response should be most important in systems where one female is able to infest multiple seeds, and the effect size will depend on

maximum potential fecundity of females. In turn, an aggregative response will likely depend on mobility of the species, and is likely to be important here, as the *Curculio* are considered limited in their dispersal ability (Menu 1993, Ruiz-Carbayo et al. 2018), yet capable of redistributing among trees in reaction to seed production.

Despite the clear bottom-up response of weevils to current year masting, we found no links between the present infestation rates or insect abundance and past resource availability. We hypothesize that the bottom-up effect of masting on weevil population is followed by an increase in the top-down control. Bottom-up and top-down processes generally operate simultaneously, but resource pulses often create bottom-up and top-down effects that are sequential (Yang et al. 2008). These effects have typically focused on responses by consumers at higher trophic levels (Schmidt and Ostfeld 2003, 2008, Szymkowiak and Kuczyński 2015, Gamelon et al. 2017), but may as well apply to insect seed predators. Thus, at least two non-mutually exclusive mechanisms may drive top-down control on weevils following masting events, preventing weevil populations from capitalizing on their increased realized fecundity. First, aggregation of large mammals and birds in mast-rich habitats is a common consequence of mast years (Yang et al. 2010, Bogdziewicz et al. 2016). Insect larvae exit the seed after the fruit is already dropped, which provides a time window for larger animals to predate both acorns and the larvae inside (Steele et al. 1996, Bonal and Muñoz 2007, Perea et al. 2012, Yang et al. 2018). Second, masting triggers an increase in abundance of small mammals (Wolff 1996, Onodera et al. 2017, Zwolak et al. 2018), but peaks in population density occur after seeds are already depleted, which translates into increased rodent predation pressure on alternative prey, including invertebrates (Jones et al. 1998). Thus, mast-induced fluctuations in rodent predation pressure on over-wintering weevil larvae may be another possible mechanism responsible for patterns found in this study. If true,

masting creates an apparent predation of oaks on weevils that is mediated by seed consumers from higher trophic levels, which suggests an exciting venue for future experimental research.

Two out of three oak species failed to satiate insect seed predators. This result provides a rare example of a lack of density-dependence in insect infestation rates in a masting system (see also Hart 1995, Sperens 1997, Kelly et al. 2000, Maeto and Ozaki 2003). Consequently, masting does not provide ‘economies of scale’ at this stage of the life cycle in these oaks. However, theoretical models of masting indicate that mast seeding may not require satiation of seed predators to evolve, as long as the focal species creates seedling banks with high survivorship, and masting improves pollination efficiency (Tachiki and Iwasa 2010). Both terms are fulfilled in focal oaks; the yearly seedling survival can oscillate around 90% (Lorimer et al. 1994), and pollination efficiency is positively density-dependent (Bogdziewicz et al. 2018b). Nonetheless, we note that lack of insect predator satiation in white and chestnut oak does not preclude satiation of post-dispersal predators (Steele 2008, Lichti et al. 2014). Given that weevils appear to be able to circumvent many of the effects of mast seeding, satiation of post-dispersal seed predators and enhanced dispersal by scatter-hoarders is potentially more important for regeneration of the studied oak species.

Even in red oak, high seed crops only resulted in weevil satiation when the population-level crop size was high enough. Otherwise, trees that produced large crops out of synchrony experienced increased arrival of weevils and no improvement of seed survival. This provides uncommon empirical support for the notion that both variation and synchronization are crucial for predator satiation, even for relatively immobile species such as weevils (Curran and Leighton 2000, Satake and Bjørnstad 2004, Bogdziewicz et al. 2018a).

In closing, insect predators are not always satiated by masting, as demonstrated by our results on the white and chestnut oak. On the other hand, once satiation operates, it might require both variability and among-plant synchrony in seed production to be effective, as was

the case in the red oak. Strong bottom-up effects of masting on the insect population, mediated by a combination of aggregative and reproductive responses, appears responsible for the lack of satiation in two out of three species that we studied. The rapid response of insects is possible because female weevils are ready to lay eggs when masting occurs - in contrast to most vertebrates, which first need to consume the resource and then use the energy to produce offspring (although some exceptions exist: Boutin et al. 2006, Bergeron et al. 2011). The strongest reproductive responses to pulsed resources are in fact expected in short-lived species (Ostfeld and Keesing 2000, Bogdziewicz et al. 2016). Furthermore, dense forests often formed by masting trees may allow dispersal of even poorly mobile species (Govindan and Swihart 2014, Bogdziewicz et al. 2018a, Ruiz-Carbayo et al. 2018). Thus, it appears important to include both reproductive response and behavioral aggregation of insect seed consumers in future models of PSH.

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Authors contributions: All authors conceived the ideas and designed methodology, MAS and SM collected the data, MB analyzed the data, all authors interpreted the results and MB wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility statement: Should the manuscript be accepted, the data supporting the results will be archived in appropriate repository (like Dryad or Open Science Framework), and the data DOI will be included at the end of the article.

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514

515 Table 1. Summary of predictions and results. Predictions 1-4 are based on the predator satiation hypothesis, while 5-6 are based on theoretical
 516 models of the consumer responses to pulsed resources.

Prediction	Result
(1) Proportion of seeds damaged per tree negatively correlates with tree-level seed abundance	Confirmed: red oak. Not confirmed: white oak, chestnut oak.
(2) Proportion of seeds damaged per tree positively correlates with past tree-level crop size (either previous year, or two previous years*)	Not confirmed.
(3) Proportion of seeds damaged per tree negatively correlates with difference in tree-level seed production in subsequent years	Not confirmed.
(4) Tree-level insect abundance correlates positively between subsequent years	Not confirmed.
(5 and 6) Masting results in bottom-up effect on insects, through both aggregation at seed-rich trees and increased reproductive output. Expected relationships between weevil abundance and crop size given the data:	
a) aggregation at seed-rich trees: negative interaction term between tree-level crop size and population-level crop size. Such interaction indicates that increases at seed-rich trees are stronger when other trees fail to produce seeds. One likely mechanism for such an effect is that poor seed production forces weevils to disperse.	Confirmed: red oak, white oak

b) increased reproductive output: positive relationship between population-level weevil abundance and population-level crop size. Confirmed.

Such relationship indicates that the increase in weevil abundance is not simply an outcome of insect re-distribution among trees.

517 * crop was summed over two previous years to account for the diapause abilities of weevils (see Methods for details)

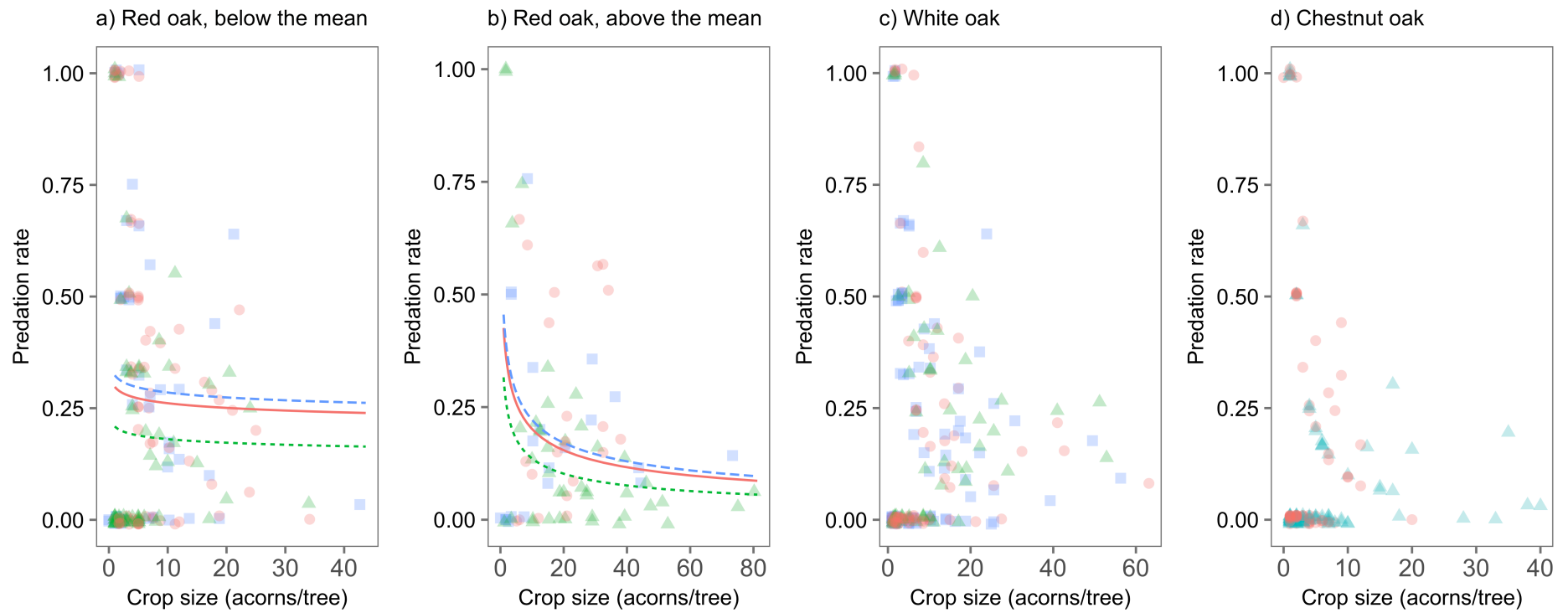
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Figure 1. The proportion of crop size of each tree infested by weevils vs. the acorn production per tree. Different line types and points refer to different study sites. The lines are based on the significant binomial GLMM predictions. In the case of red oaks, the model included the interaction term between tree-level crop size and the population-level crop size; thus, a) shows the prediction from the GLMM model for population-level crop size below the mean, whereas b) shows the prediction for population-level crop above the mean. Points are the per-tree, per-year observations, based on 17-year data set of 15 trees of each species at 3 (red and white oak) or 2 sites (chestnut oak).

Figure 2. Summed larval abundance per-tree, per-year vs. per-year crop size at that tree. The lines are based on the significant negative binomial GLMMs. In red and white oak, the model included the interaction term between tree-level crop size and the population-level crop size; thus, a) and c) show the predictions from GLMM models for population-level crop size below the mean, whereas b) and d) show the predictions for the population-level crop size above the mean. Different line types and points refer to different study sites. Points are the per tree per year observations, based on 17-years of data of 15 trees of each species at 3 (red and white oak) or 2 sites (chestnut oak).

Figure 3. Summed larval abundance per site per year vs. per year crop size at that site. The lines are based on the significant negative binomial GLM predictions. Different line types and points shape refer to different study sites. Points are the per-tree, per-year observations, based on 17-years of monitoring of 15 trees of each species at 3 (red and white oak) or 2 sites (chestnut oak).

544 Figure 1.



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Figure 2.

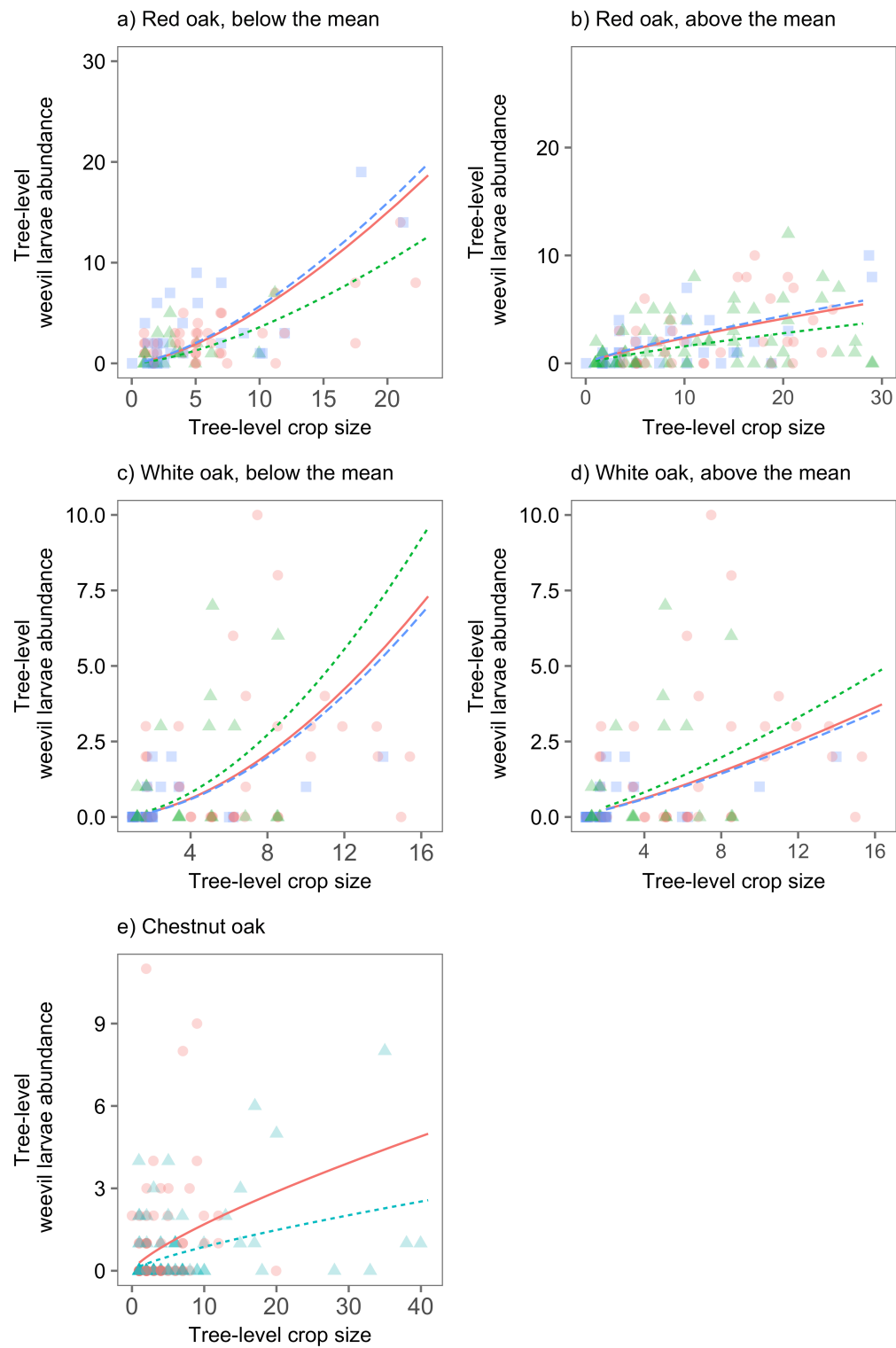


Figure 3.

