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Research

Maternal provisioning is structured by species' competitive neighborhoods

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Differential maternal provisioning of offspring in response to environmental conditions has been argued as 'the missing link' in plant life histories. Although empirical evidence suggests that maternal provisioning responses to abiotic conditions are common, there is little understanding of how differences in maternal provisioning manifest in response to competition. Frequency manipulations are commonly employed in ecological studies to assess the strength of interspecific competition, relative to intraspecific competition, and we used frequency manipulations to test how competition in two soil moisture environments affects maternal provisioning of seed mass. Specifically, for 15 pairs comprised from 25 annual plant species that occur in California, we varied the relative frequencies of conspecific to heterospecific competitors from 90% (intraspecific competition) to 10% (interspecific competition). We found that conspecific frequency affected maternal provisioning (seed mass) in 12 of the 25 species (eight significantly ($p < 0.05$), four marginally significantly ($p < 0.07$)), and that these responses included both increased (five species) and decreased (six species) seed mass, as well as one species with opposing directions of response to conspecific frequency that depended on the soil moisture environment. Conspecific frequency also affected per capita fecundity (seed number) for 17 of the 25 species (15 significantly ($p < 0.05$), two marginally significantly ($p < 0.09$)), which generally decreased seed number as conspecific frequency increased. The direction and magnitude of frequency-dependent seed mass depended on the identity of the competitor, even among species whose fecundity was not affected by competitor identity; the latter finding reveals competitive differences among species that would otherwise appear to be competitively equivalent. Our research demonstrates how species responses to different competitive environments manifest through maternal provisioning, and that these responses alter previous estimates of environmentally-determined maternal provisioning and reproductive output; future study is needed to understand their combined effects on population and community dynamics.

Keywords: annual plants, competition, maternal effects, seed mass, soil moisture, frequency dependent competition

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Introduction

The amount of resources available to individual offspring at the propagule stage (seeds or eggs) is maternally controlled, and depends on the mother's provisioning strategy and resource environment. Changes in propagule size in response to maternal environmental conditions have been shown to have cascading effects on offspring life histories (Segers and Taborsky 2010, Allen 2012) and components of fitness (e.g. germination, dormancy, survival and reproduction; Westoby et al. 1996, Gomez 2004) – a phenomenon known as 'maternal environmental effects' (Roach and Wulff 1987) and referred to simply as 'maternal effects' for brevity henceforth, though other forms of maternal effects exist (Galloway et al. 2009). Maternal provisioning that acts to increase propagule size necessarily comes at the expense of offspring number (Charnov and Ernest 2006), and the maternal environment may affect the optimal strategy dealing with this tradeoff (Smith and Fretwell 1974). For example, depending on the environment, mothers that produce few large offspring can have higher fitness than those that produce many small offspring, or vice versa (Wilson et al. 2009). Because of their clear consequences for offspring fitness in many species, maternal effects have been referred to as 'the missing link' between parent and offspring life histories (Donohue 2009), and thus maternal provisioning strategies and their consequences for offspring have remained of interest to evolutionary biologists seeking to understand selection and adaptation for over 50 years (Roach and Wulff 1987, Mousseau and Fox 1998).

The diversity of species-specific maternal provisioning strategies observed in evolutionary studies (Herman and Sultan 2011) speaks to their importance to ecological dynamics, such as population persistence and competition. Indeed, the maternal environment can have large effects on trait means and the fitness of whole cohorts of individuals in a population (i.e. population growth rates; Galloway and Etterson 2007) that act additively or interactively with offspring environmental conditions (Uller et al. 2013). Because traits and population growth rates mediate how species interact with each other and their environments, differential provisioning of offspring might introduce lagged responses to temporal environmental variability which, in addition to responses to current environmental conditions (Levine and Rees 2004), determine coexistence outcomes. The influence of lagged environmental responses on coexistence has been demonstrated experimentally in the related field of 'carryover effects' of early-life conditions (Van Allen and Rudolf 2015). Predictions for how maternal provisioning strategies might influence ecological dynamics cannot be made using existing data from single-species experiments because they exclude species interactions, such as competition, that are important to persistence in multi-species communities (Van Allen and Rudolf 2016).

In competitive environments, differential maternal provisioning of offspring may manifest in response to the relative frequencies of conspecific to heterospecific competitors, even when total density is maintained (Law and Watkinson 1987). In ecological studies, frequency-dependent demographic rates are used to infer the relative strength of competitive interactions within and among species (Levine and HilleRisLambers 2009). When the per capita effect of intraspecific competition is stronger than interspecific competition, population growth rates decrease as the relative frequency of conspecific competitors increases. By contrast, when the strengths of intraspecific and interspecific competition are equal, population growth rates do not respond to relative frequencies of conspecific to heterospecific competitors. For brevity, throughout this paper we use "negative frequency-dependence" to refer to decreases in maternal provisioning as the relative frequency of conspecific competitors increases, and "positive frequency-dependence" to refer to the opposite.

Seeds have been shown to decrease in size in response to increasing plant density (Larios and Venable 2015), yet tests of differential maternal provisioning in response to different competitive neighborhoods are lacking. Tests that incorporate frequency-dependent effects are particularly relevant, as parallel tests on fecundity are central to understanding species coexistence (Levine and HilleRisLambers 2009) and may be reinforced or counteracted by differential maternal provisioning of offspring (Germain and Gilbert 2014). Without knowledge of maternal provisioning responses to different competitive neighborhoods, population and community ecologists cannot build intergenerational environmental effects into a broader understanding of population and community dynamics.

Most studies of maternal provisioning in response to abiotic conditions are conducted in low-competition environments (Germain and Gilbert 2014) even though organisms rarely occur in the absence of biotic interactors in nature. Competition might interact with the abiotic environment to affect seed size if competitive interactions alter the effect of seed size on offspring fitness, as may occur through changing resource availability or responses to abiotic conditions (Leishman et al. 2000). For example, competitors may exacerbate differences in seed size provisioning that are driven by a limiting resource (Stratton 1989), such as soil moisture (Fotelli et al. 2001). As a result, current estimates of the prevalence of maternal effects are likely conservative. Species responses to the abiotic environment, conspecific competitors, and heterospecific competitors are necessary components of competition models; predicting the influence of maternal effects on ecological dynamics requires an understanding of how the maternal environment modifies each response.

We tested the effects of competition and soil moisture on maternal seed provisioning using 25 annual plant species that occur in the mediterranean-climate regions of the California Floristic Province. The California Floristic Province is characterized by high inter-annual rainfall variability, which determines plant community composition, productivity, and the nature of competitive interactions (Levine et al. 2011). In variable environments, selection favors plastic responses, such as maternal environmental effects, that offset variability in fitness (Dey et al. 2016). The seed stage is important to the life cycle of an annual plant because annual plant populations regenerate entirely each year from the seed bank. Increased seed mass generally provides early growth advantages, allowing individuals to establish prior to the onset of unpredictable hazards, such as drought (Kidson and Westoby 2000), as well as increased competitive ability in productive years (Susko and Cavers 2008).

We competed fifteen pairs of species drawn from 25 species at six relative frequencies and in two soil moisture environments that simulate wet and dry years. We then quantified the mass and number of seeds produced, and used those data to address three questions: 1) how commonly does maternal provisioning vary in response to changes in the relative frequencies of conspecific to heterospecific competitors, and how do these provisioning responses compare to seed number responses? 2) Is maternal provisioning in response to abiotic conditions sensitive to the competitive environment? And 3) does competitor identity alter the strength and direction of frequency-dependent maternal provisioning? In a previous experiment, we found that ~20% of the same species considered here exhibit differential seed mass in response to soil moisture conditions in the absence of competition (Germain and Gilbert 2014); we use this earlier study to compare maternal provisioning in non-competitive and competitive environments.

Methods

Study species

We examined environmental drivers of variation in maternal seed provisioning and seed number among 15 pairs of annual plant species (25 species total, Supplementary material Appendix 1 Table A1) that were competed as part of a previous study (Germain et al. 2016). We used seed mass as a proxy for seed provisioning rather than a detailed analysis of seed energetic content, following convention from other maternal seed provisioning studies (Sultan 1996). Species pairs were selected to meet two criteria: First, the 25 species spanned a broad taxonomic range (six angiosperm Orders represented; Supplementary material Appendix 1 Table A1), which allowed us to select pairs that represented a range of phylogenetic distances (nine to 170 million years since divergence; phylogeny in Fig. A1). Pairs were selected to represent experimental analogs of phylogenetically independent contrasts (i.e. non-overlapping branch lengths), to circumvent phylogenetic pseudoreplication (Harmon and Glor 2010). Second, the selected species overlap in habitat preference (all associate with grassland meadow in mediterranean-type climates) and overlap geographically in California (CalFlora <www.calflora.org>); as such, they have the potential to compete in the wild. Additional details about species selection are in Supplementary material Appendix 1 Methods.

We initially sought a balanced design with 10 species competed twice to test how strongly seed provisioning was determined by the identity of the interspecific competitor, resulting in a total of 20 species pairs and 30 unique species. However, competition was intense enough among five species pairs that seeds were not produced, resulting in the design we present here with 15 species pairs and 25 unique species, with five species competed twice. Seeds were obtained from commercial suppliers and an individual donor (Supplementary material Appendix 1 Table A1), and were collected from natural populations relatively few generations (most < 3, all < 20; Supplementary material Appendix 1 Table A1) prior to our experiments.

Greenhouse experiment

From January to July 2012, we grew the 15 species pairs in competition in a greenhouse under two soil moisture levels (wet versus dry); see Supplementary material Appendix 1 Methods for details on growing conditions. Plants in the wet treatment were watered twice as often as those in the dry treatment, with the total water received designed to mimic rainfall in mesic sites during wet and dry years (Germain and Gilbert 2014). The competitive environment was manipulated using a replacement design (Jolliffe 2000), in which seeds of each species pair were sown at six relative frequency ratios (10:60, 20:50, 30:40, 40:30, 50:20 and 60:10 expected germinants) at a common density of 70 individuals. This density is comparable to the seedling density found in annual grasslands (2500 to 5500 plants m^{-2}, Bartolome 1979). To obtain a density of 70 individuals per pot, we tested each species' germination rate prior to the experiment and corrected seeding densities based on these rates (i.e. a pot with 60 individuals of one species would receive 60 seeds of a species with 100% germination, or 120 seeds of a species with 50% germination).

For each species pair, we had two replicate pots per combination of soil moisture condition and frequency ratio, for a total of 360 pots of plants that were randomly assigned to a position in the greenhouse. All greenhouse growing conditions were chosen to simulate those typical of annual grassland in mediterranean-climate regions (Germain and Gilbert 2014; Supplementary material Appendix 1 Methods). We monitored pots daily and collected any mature seed, such that all seed produced by the plants was collected by the end of the experiment. At the end of the experiment, all seed material produced in each pot was pooled among individuals of the same species in each pot, weighed, and a random representative subsample was taken to estimate the average mass per seed and number of seeds produced per plant in each pot (Supplementary material Appendix 1 Methods).

Concurrent to this experiment, an additional experiment using the same species was conducted to estimate the impact of soil moisture conditions on maternal provisioning (reported in Germain and Gilbert 2014). Key differences between the previous experiment and the experiment we present here are that each species was grown as single-species monocultures at low densities (~seven individuals per pot, compared to 70 in the current experiment), meaning that competition was greatly relaxed. We include summary results from Germain and Gilbert (2014) in this paper to compare maternal provisioning of seed mass to soil moisture conditions in the presence and absence of competition.

Statistical analyses

Prior to analysis, we transformed the data in two ways to meet model assumptions and facilitate comparisons among species. First, we log transformed seed mass, seed number, and conspecific frequency to minimize heteroscedasticity and linearize seed mass and seed number relationships with conspecific frequency. Second, to facilitate comparisons among species that differ markedly in seed production, we standardized the log-transformed seed mass and seed number data for each species to a mean of zero and unit variance. For simplicity, we henceforth refer to the standardized log-transformed data as 'seed mass', 'seed number', and 'frequency', unless stated otherwise.

We performed a cross-species analysis to test if species differed in their seed mass and seed number responses to the competitive and soil moisture environments. For these analyses, we used the 'lmerTest' R package to run linear mixed effects (LME) models, with either seed mass or seed number as response variables, and species (30 levels), soil moisture (two levels), conspecific frequency (six levels), and their interactions as fixed factors. Because species competing in a pot are not independent of one another, we included 'Pot ID' as a random factor in all models (Bolker et al. 2009). The identity of the competitive pair (e.g. *Lasthenia glabrata* versus *L. californica*) was also included as a random factor. Following significant species × frequency and species × soil moisture interactions, we ran species-specific analyses separately to identify species with significant responses to the biotic and abiotic environment. To accomplish this, we used linear models with type II sums of squares to test the effects of conspecific frequency, soil moisture conditions, and their interaction on seed mass and seed number. We used type II sum of squares as opposed to type III sum of squares because the latter prevents interpretation of main effects even in the absence of a significant interaction (Zuur et al. 2009). In cases where the interaction was significant, we do not interpret the main effects (e.g. triangle points in Fig. 1). The type of sum of squares used had no effect on the coefficient estimates.

We used major axis regression (MAR; R package 'lmodel2') to examine the relationships between response variables across species, and tested the significance of these relationships using a Pearson correlation. First, to identify if seed mass and seed number responses are correlated, we performed a MAR with the slopes of species' seed mass responses and the slopes of species' seed number responses as variables. Second, we tested whether the presence and absence of competition alters species' responses to soil moisture conditions. To do this, we first calculated species' average effect sizes of seed mass responses to contrasting soil conditions ($\mu_{dry} - \mu_{wet}$) in the presence of competition (i.e., when grown at a density of 70 plants per pot) using Cohen's d with pooled variance (Hartung et al. 2008); in cases where a species was used in more than one species pair, a single average effect size was used. We then used MAR to examine the relationship between these effect sizes and previously published, identically calculated effect sizes in the absence of competition (i.e. grow at a density of seven species per pot; Germain and Gilbert 2014). Because these species are small-statured and occur at high densities in the field, we consider the contrast of 70 versus 7 plants per plot as representative of a competition versus no competition contrast.

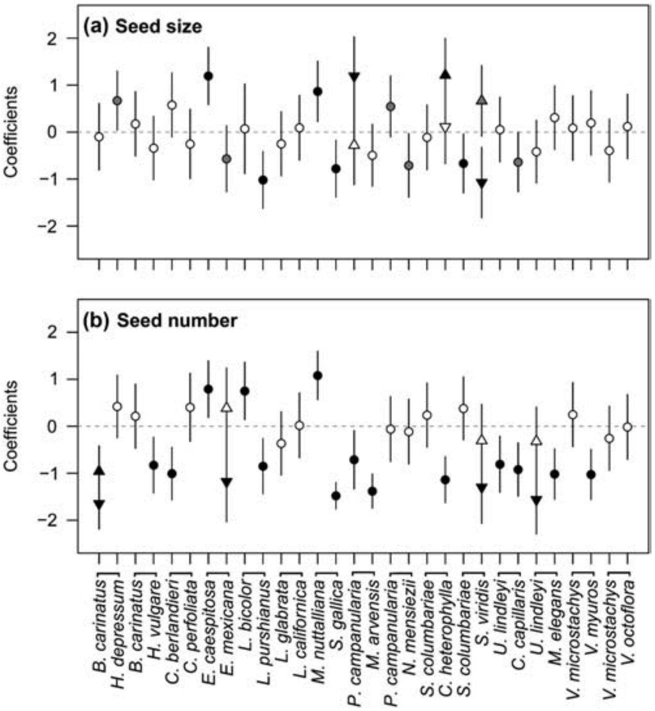

Figure 1. Cross-species comparison of frequency-dependent (a) maternal provisioning of seed mass and (b) seed number responses. Points are slope coefficients (± 2 × SE) of species responses to the frequency of conspecific competitors, and are shaded black, gray, or white to indicate significant ($p < 0.05$), marginally-significant ($p < 0.10$), or non-significant ($p > 0.10$) slopes, respectively. In most cases, frequency × soil moisture interactions are non-significant, and slopes are averaged across soil moisture environments; when significant, wet (upwards triangle) and dry (downwards triangle) environments are plotted separately. Competitive pairs are delineated by lines connecting species name abbreviations (first letter of genus and species name); note that five species were competed twice, but were never double-counted. See Supplementary material Appendix 1 Table A1 for taxonomic and collection information.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.49td812> (Germain et al. 2018).

Results

Seed mass

Of the 25 species included in this study to produce 15 reciprocal competition trials, 12 species showed significant (eight species, $p < 0.05$) or marginally-significant (two species, $p = 0.05–0.07$) differential provisioning of seed mass in response to conspecific frequency, and another four responded to soil moisture when in competition (Fig. 1a, Supplementary material Appendix 1 Fig. A2); we note that 2.5 species are expected to show these results by chance alone given a 10% type 1 error rate. Most species responded to conspecific frequency alone (five species) or in conjunction with the soil moisture environment in an additive (four species) or multiplicative (three species) manner. The strength and direction of responses varied among species, as indicated by significant species × frequency ($F_{29,464} = 2.84$, $p < 0.001$) and species × soil moisture ($F_{29,410} = 3.19$, $p < 0.001$) interactions in our cross-species statistical model (Supplementary material Appendix 1 Table A2). Species were similarly likely to increase (five species) or decrease (six species) seed mass as conspecific frequency increased, and one species, *Salvia viridis*, had a higher average seed mass in a wet environment compared to a dry environment (Fig. 1a, non-significant main effect of frequency, Supplementary material Appendix 1 Table A2). Overall, our results demonstrate that for this plant community, 64% of species are likely to exhibit differential maternal provisioning of seed mass in response to conspecific frequency, soil moisture, or their interaction when in competition (16/25 species), and that these responses vary by species with the biotic or abiotic environment. Note that five species were competed twice but were never double-counted when summing the number of species with significant or marginally-significant responses.

Seed number

Seventeen of the 25 species showed seed number responses to conspecific frequency either alone (seven species; Fig. 1b, Supplementary material Appendix 1 Table A3) or in conjunction with soil moisture conditions (six additively, four interactively; Fig. 1b). All of these responses were statistically significant ($p < 0.05$), except for two of the interactive responses, which were marginally significant ($p = 0.08–0.09$). An additional four species responded to soil moisture alone, for a total of 21 species that responded to biotic or abiotic conditions through seed number. Analogous to seed mass responses, the effect of conspecific frequency on seed number depended on the focal species (significant species x frequency interaction; Supplementary material Appendix 1 Table A3, $F_{29,716} = 6.63$, $p < 0.001$). However, in contrast to seed mass responses, frequency-dependent seed number was negative for most species (14 out of 17 species; Fig. 1b, Supplementary material Appendix 1 Table A3), and was sensitive to the soil moisture environment (significant frequency x soil moisture interaction; Supplementary material Appendix 1 Table A3, $F_{1,716} = 4.49$, $p = 0.034$). These seed number responses were positively correlated with the strength and direction of species' seed mass responses ($r = 0.28$, slope $= 0.48$, $p = 0.029$; Fig. 2a), even though some species showed opposite seed mass and seed number responses (grey regions of Fig. 2a).

Comparison among competitive and non-competitive environments

The strength and direction of seed mass responses to contrasting soil moisture environments (wet versus dry) in the presence of competition were positively correlated with those in the absence of competition ($r = 0.50$, $p = 0.010$; Fig. 2b). The slope of this correlation was less than one (major axis regression, slope $= 0.67$), as many species showed stronger

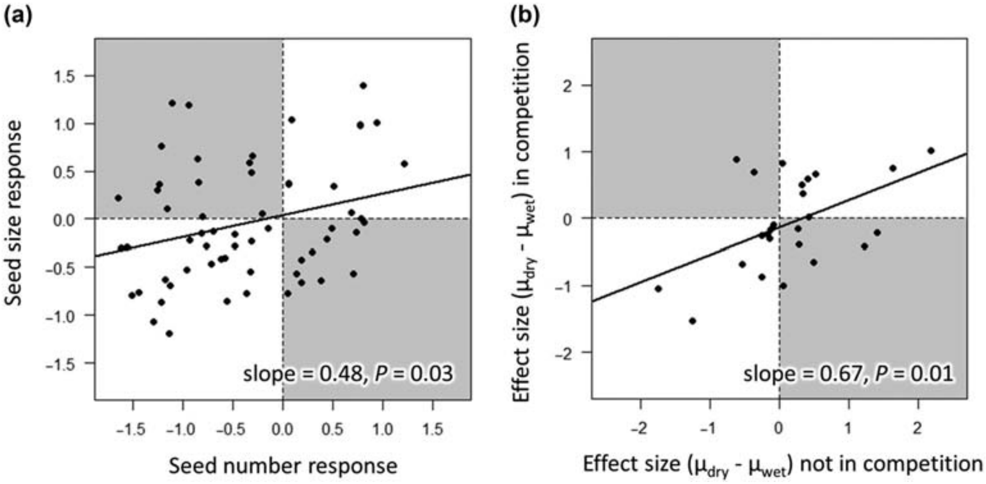

Figure 2. Correlations of (a) seed mass and seed number responses to conspecific frequency (n = 60, 15 pairs × two species × two soil moisture environments), and (b) seed mass responses to soil moisture conditions in the presence and absence of competition (n = 25). Each point is a species, and points that fall in the grey zones are species with opposing directions of responses.

responses to soil moisture when grown in the absence of competition (Fig. 2b). This result was surprising given that, in the current experiment, 44% of species altered seed provisioning in response to soil moisture when in competition, whereas only 21% did so in the absence of competition (Germain and Gilbert 2014). This result suggests that the prevalence but not the magnitude of soil moisture-induced seed mass provisioning increases in the presence of competition, possibly because the effects of soil moisture are dwarfed by those of conspecific frequency.

Discussion

There is a substantial body of empirical work investigating maternal provisioning in response to the abiotic environment (reviewed by Herman and Sultan 2011), yet responses to biotic interactions remain understudied, particularly in plants (Weiner et al. 1997, Larios and Venable 2015). Our results show that changes to the competitive environment can alter maternal provisioning of seed mass and, much like more commonly measured seed number responses (Law and Watkinson 1987), that the strength and direction of maternal provisioning depend on identities of competing species. Below, we discuss how considering interactions between the biotic and abiotic environment allows us to understand how differential maternal provisioning of offspring is distributed across species in plant communities. Because species interactions frequently altered provisioning strategies, maternal effects likely have important implications for competitive dynamics, species coexistence and diversity; in this vein, we propose new hypotheses for future study.

We detected differential maternal provisioning of seed mass in response to the frequency of conspecific competitors in nearly half of the species examined, with negative and positive responses being equally common (Fig. 1a). There are two explanations for the maintenance of species-specific maternal provisioning strategies that are not mutually exclusive and likely differ in importance among species. First, theory predicts that maternal provisioning strategies should evolve to maximize maternal fitness, either to the benefit or detriment of offspring fitness (Smith and Fretwell 1974, Marshall and Uller 2007, Olofsson et al. 2009). Specifically, because increasing offspring size has diminishing fitness returns beyond a critical point, optimal offspring size is one where the fitness benefit of increasing provisioning to individual offspring is matched by the fitness benefit of producing more offspring (Smith and Fretwell 1974). Because the most adaptive provisioning strategy depends on environmental context (Krist and Munclinger 2015), the most adaptive strategy will depend on the specific ecologies of focal species (Sultan et al. 2009, Krist and Munclinger 2015). Second, even if the same adaptive strategy is shared by two species, genetic or physiological constraints might result in the evolution of an adaptive or maladaptive strategy in one species but not the other (DeWitt et al. 1998). Though the degree to which species-specific maternal provisioning strategies reflect evolutionary adaptation or constraint cannot be disentangled in our study, the ecological implications for offspring can be – larger seeds are more competitive and tolerant of environmental stress, whereas smaller seeds are more dispersive and likely to persist longer in the seedbank (Larios and Venable 2015, reviewed by Leishman et al. 2000). The life-history tradeoff between competitive ability and dispersal ability, as mediated by seed size, has been hypothesized to play a central role in determining coexistence outcomes (Westoby et al. 1996, Jakobsson and Eriksson 2000), and might explain the diversity of responses to conspecific frequency observed in our study. We highlight the need for a similar comparative approach specifically designed to disentangle the exact evolutionary mechanisms underlying species-specific maternal provision strategies across species.

Frequency-dependent seed mass responses were sensitive to the identity of the heterospecific competitor, rather than simply a common response to conspecific frequency. For example, seed mass of *Salvia columbariae* decreased significantly as the relative frequency of its competitor, *S. viridis,* decreased, but did not show a significant change in competition with *Collinsia heterophylla*. A simple explanation for this result is that seed mass is sensitive to competitive asymmetries among species; we know from a previous competition experiment that competitive asymmetries differ greatly among these two species pairs (i.e. net competitive differences are ~2× greater among *S. columbariae* and *S. viridis* than among *S. columbariae* and *C. heterophylla*; Germain et al. 2016). What is also interesting, however, is our finding that frequency-dependent seed mass effects emerged in species that did not exhibit frequency-dependent seed number responses. In ecological studies, a lack of frequency-dependent seed production often leads to the conclusion that competing species are competitively equivalent – that replacing an individual of one species with an individual of another would have no impact on the competitive effect experienced by other individuals in the community (Harpole and Suding 2007, Siepielski et al. 2010). Yet, if this conclusion were correct, we would not expect to see frequency-dependent effects on seed mass. As a result, our study suggests that seed mass responses reveal competitive differences among species that are hidden when only seed number responses are examined. Previous research in plant monocultures demonstrates that parents produce smaller, more dispersive offspring when neighborhood densities are high (Larios and Venable 2015), but in multi-species communities, our results suggest this simple response likely also depends on the identities and relative frequencies of heterospecific competitors.

The exact effect of differential maternal provisioning (seed mass responses) on competitive dynamics depends on whether they act to reinforce or counteract demographic responses (seed number responses). Although our results demonstrate that seed mass responses to conspecific frequency generally reinforce seed number responses (i.e. they are positively correlated, Fig. 2a), some species clearly show opposite seed mass and seed number responses (points in the grey regions of Fig. 2a). In the context of demographic rates, the direction of frequency dependence can indicate whether competition is more likely to result in coexistence (negative frequency dependence) or exclusion (positive frequency dependence). In our experiment, negative frequency-dependent seed number responses were common among species (Fig. 1b), but seed size responses were equally positive and negative (Fig. 1a). Previous research suggests that interspecific and intraspecific variation in seed mass alters several important biological parameters, from dormancy to growth and fecundity (Westoby et al. 1996, Eriksson 1999, Germain and Gilbert 2014). Thus, commonly-measured seed number responses (Harpole and Suding 2007) may be insufficient to capture the full impact of competitive interactions in the offspring generation (Ginzburg and Taneyhill 1994, Van Allen and Rudolf 2015). An intriguing avenue for future research are experiments that quantify how much variation in population dynamics is being missed without considering lagged responses to conditions of the maternal generation. An effect of the maternal environment on population demography has been demonstrated previously in response to abiotic conditions (e.g. understory light, Galloway and Etterson 2007), but is not yet understood in competitive environments.

We found important differences in the prevalence of maternal provisioning responses to soil moisture conditions in competitive and non-competitive environments. Specifically, over twice as many species altered seed provisioning in response to soil moisture in the presence of competition (44% of species; this study, Supplementary material Appendix 1 Table A2) compared to in the absence of competition (21% of species; Germain and Gilbert 2014). Almost all tests of maternal effects on seed provisioning have been conducted in non-competitive environments, with individuals grown alone (Aarssen and Burton 1990). Because most plants experience competition in their natural environments, current estimates of the prevalence of maternal provisioning responses may be conservative, and most relevant to disturbed environments where plant densities are low. Additionally, competition appears to dampen maternal provisioning responses to soil moisture (Fig. 2b) despite a threefold increase in the number of species that exhibit such an effect. This indicates that, contrary to our initial expectations, competition does not simply exacerbate maternal provisioning of seed mass in response to soil moisture, but instead appears to alter the nature of soil moisture's effects on seed mass in some species. This surprising result is likely due to the shift in maternal provisioning that occurs with a change in the identity of the competitor.

An intriguing hypothesis posed by Dyer et al. (2010) is that maternal effects, such as those mediated by maternal provisioning strategies, might contribute to the invasion success of non-native species. Although our experiment was not specifically designed to test this hypothesis, six of the 25 species used in our trials are not native to California (Supplementary material Appendix 1 Table A1), allowing qualitative comparisons. In doing so, we found that changes in seed mass were significantly more negative in response to frequency of conspecific competitors among non-native species than native species were (Fig. 3, Supplementary material Appendix 1 Methods). Our results suggest that for this system, differential maternal provisioning in response to the competitive environment may be one trait that differentiates native and non-native species and thus could contribute to invasion success. However, we caution that this result is based on limited and unbalanced data (only six non-native species), and should be explored with more species in future studies. For example, we do not have the power to test differences among non-native species that differ in impact, such as naturalized species versus noxious invaders (Strauss et al. 2006, Diez et al. 2008), which could explain the considerable overlap despite a significant difference in the range of responses among native and non-native species.

Although this study advances our understanding of the importance of competition in structuring environmentally-determined maternal provisioning, there are two caveats that should be considered in interpreting our findings. First, we were unable to identify how changes in seed mass translate into differences in offspring performance, due to the logistical infeasibility of the full factorial experiment that would be required to test for longer-term impacts of seed mass. It is possible that maternal effects on offspring success due to seed mass may not persist beyond the seed stage, as some studies have found (Weiner et al. 1997). However, many other studies demonstrate their effects on some aspect of post-seed performance, such as germination, dormancy, survival, growth, and fecundity (Stanton 1984, Gomez 2004, Germain et al. 2013, reviewed by Herman and Sultan 2011), especially in competitive environments (Stratton 1989). Second, by

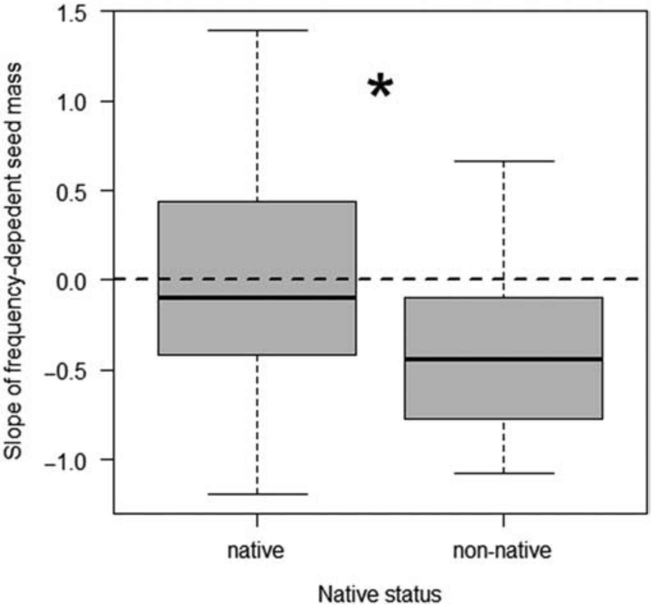

Figure 3. A comparison of frequency-dependent seed mass among native (n = 19) and non-native (n = 6) species. The dashed horizontal line indicates a slope of 0, and the asterisk indicates a significant difference (p = 0.03). See Supplementary material Appendix 1 Methods for details of the analysis.

focusing on seed mass responses, we likely underestimate the overall prevalence of maternal effects that can manifest in other ways, such as through germination or dormancy rates (Germain and Gilbert 2014), or through epigenetic effects that can alter the offspring phenotype in more complex ways (Herman and Sultan 2011). As such, this study should be viewed as an important first step in characterizing maternal effects in competitive environments that can be used to inform future work, such as modelling the dynamics of species which differ in maternal provisioning strategies.

The study of environmentally-directed maternal provisioning has exciting potential to explain population- and community-level responses to heterogeneous environments (Ginzburg and Taneyhill 1994, Van Allen and Rudolf 2013, 2015). Here, we show that current estimates of differential maternal provisioning (i.e. a maternal effect) in non-competitive environments are conservative, that competition can alter maternal provisioning of seed mass, and that maternal provisioning strategies are fine-tuned to competitive differences among species, which in turn are shaped by the abiotic environment. Our research sheds new light on the complex nature of species interactions, and suggests avenues for future research that would further characterize the full range and impact of maternal provisioning (and maternal effects for generally) in ecological communities.

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Supplementary material (available online as Appendix oik-05530 at <www.oikosjournal.org/appendix/oik-05530>). Appendix 1.