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25 **Summary**

- 26 1. Maternal provisioning of offspring in response to environmental conditions (“maternal
27 environmental effects”) has been argued as ‘the missing link’ in plant life histories. Although
28 empirical evidence suggests that maternal responses to abiotic conditions are common, there
29 is little understanding of the prevalence of maternal provisioning in competitive
30 environments.
- 31 2. We tested how competition in two soil moisture environments affects maternal provisioning of
32 offspring seed mass. Specifically, we varied conspecific frequency from 90% (intraspecific
33 competition) to 10% (interspecific competition) for 15 pairs of annual plant species that occur
34 in California.
- 35 3. We found that conspecific frequency affected maternal provisioning (seed mass) in 48% of
36 species, and that these responses included both increased (20%) and decreased (24%) seed
37 mass. In contrast, 68% of species responded to competition through changes in per capita
38 fecundity (seed number), which generally decreased as conspecific frequency increased. The
39 direction and magnitude of frequency-dependent seed mass depended on the identity of the
40 competitor, even among species in which fecundity was not affected by competitor identity.
- 41 4. *Synthesis*. Our research demonstrates how species responses to different competitive
42 environments manifest through maternal provisioning, and that these responses alter previous
43 estimates of environmental maternal effects and reproductive output; future study is needed to
44 understand their combined effects on population and community dynamics.

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49 **Introduction**

50 The amount of resources available to individual offspring at the propagule stage (seeds or
51 eggs) is maternally controlled, and depends on the mother's provisioning strategy and resource
52 environment. Changes in propagule size in response to maternal environmental conditions have
53 been shown to have cascading effects on offspring life histories (Segers & Taborsky 2010; Allen
54 2012) and components of fitness (e.g., germination, dormancy, survival, and reproduction;
55 Westoby *et al.* 1996; Gomez 2004)—a phenomenon known as 'maternal environmental effects'
56 and referred to simply as 'maternal effects' for brevity henceforth, though other forms exist
57 (Roach & Wulff 1987; Galloway *et al.* 2009). Maternal effects that increase propagule size come
58 at the expense of offspring number (offspring size-number tradeoffs, Charnov & Ernest 2006),
59 but in certain environments, mothers that produce few large offspring can have higher fitness
60 than those that produce many small offspring (Allen, Buckley & Marshall 2008). Because of
61 their clear consequences for offspring fitness in many species, maternal effects have been
62 referred to as 'the missing link' between parent and offspring life histories (Donohue 2009), and
63 have remained of interest to evolutionary biologists seeking to understand selection and
64 adaptation for over 50 years (Roach & Wulff 1987; Mousseau & Fox 1998).

65 The diversity of species-specific maternal effects observed in evolutionary studies
66 (Herman & Sultan 2011) implicates the importance of maternal effects for ecological dynamics,
67 such as population persistence and competition. Indeed, the maternal environment can have large
68 effects on trait means and the fitness of whole cohorts of individuals in a population (*i.e.*,
69 population growth rates; Galloway & Etterson 2007) that act additively or interactively with
70 offspring environmental conditions (Uller, Nakagawa & English 2013). Because traits and
71 population growth rates mediate how species interact with each other and their environments,

72 maternal effects might act as temporal dimensions to species' niches that, in addition to
73 responses to current environmental conditions (e.g., Levine & Rees 2004), alter coexistence
74 outcomes; this phenomenon has been demonstrated experimentally in the related field of
75 'carryover effects' of early-life conditions (Van Allen & Rudolf 2015). However, predictions for
76 how maternal effects might influence ecological dynamics cannot be made using existing data
77 from single species experiments because they exclude species interactions, such as competition,
78 that are important to species persistence in multi-species communities (VanAllen & Rudolf
79 2016).

80 In competitive environments, maternal effects on offspring provisioning may manifest in
81 response to the relative frequencies of conspecific to heterospecific competitors, even when total
82 density is maintained (Law & Watkinson 1987). In ecological studies, frequency-dependent
83 demographic rates are used to infer the relative strength of competitive interactions within and
84 among species (Levine & HilleRisLambers 2009). Although seeds have been shown to decrease
85 in size in response to increasing plant density (Larios & Venable 2015), tests of maternal effects
86 in response to impacts of different competitive neighborhoods are lacking. Tests that incorporate
87 frequency-dependent effects are particularly relevant, as parallel tests on fecundity are central to
88 understanding species coexistence (Levine & HilleRisLambers 2009) and may be reinforced or
89 counteracted by maternal effects (Germain & Gilbert 2014). Without knowledge of maternal
90 provisioning responses to different competitive neighborhoods, population and community
91 ecologists cannot build intergenerational effects into a broader understanding of population and
92 community dynamics.

93 Most studies of maternal effects in response to abiotic conditions are conducted in low-
94 competition environments (e.g., Germain & Gilbert 2014) even though organisms rarely occur in

95 the absence of biotic interactors in nature. However, competition might interact with the abiotic
96 environment to affect seed size if competitive interactions alter resource availability or a species'
97 response to abiotic conditions. For example, competitors may exacerbate maternal effects that
98 are driven by a limiting resource (Stratton 1989), such as soil moisture (Fotelli *et al.* 2001). As a
99 result, current estimates of the prevalence of maternal effects are likely conservative. Species
100 responses to the abiotic environment, conspecific competitors, and heterospecific competitors are
101 necessary components of competition models; predicting the influence of maternal effects on
102 ecological dynamics requires an understanding of how the maternal environment modifies each
103 response.

104 We test the effects of competition and soil moisture on maternal seed provisioning using
105 25 annual plant species that occur in the mediterranean-climate regions of the California Floristic
106 Province. The California Floristic Province is characterized by high inter-annual rainfall
107 variability, which determines plant community composition, productivity, and the nature of
108 competitive interactions (Levine, McEachern & Cowan 2011). In variable environments,
109 selection favors plastic responses, such as maternal environmental effects, that offset variability
110 in fitness (Dey, Proulx & Teotónio 2016). The seed stage is important to the life cycle of an
111 annual plant because annual plant populations regenerate entirely each year from the seed bank.
112 Increased seed mass generally provides early growth advantages, allowing individuals to
113 establish prior to the onset of unpredictable hazards, such as drought (Kidson & Westoby 2000),
114 as well as increased competitive ability in productive years (Susko & Cavers 2008).

115 We competed fifteen pairs of species at six relative frequencies and in two soil moisture
116 environments that simulate wet and dry years. We then quantified the mass and number of seeds
117 produced, and used those data to address three questions: (i) How commonly does maternal

118 provisioning respond to conspecific frequency (i.e., changes in interspecific vs. intraspecific
119 frequency) and how does it compare to seed number responses? (ii) Is maternal provisioning in
120 response to abiotic conditions sensitive to the competitive environment? And (iii) does
121 competitor identity alter the strength and direction of frequency-dependent maternal
122 provisioning? In a previous experiment, we found that ~20% of the same species considered here
123 exhibit maternal effects on seed mass in response to soil moisture conditions in the absence of
124 competition (Germain & Gilbert 2014); we use this earlier study to compare maternal effects in
125 non-competitive and competitive environments.

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Materials and methods

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STUDY SPECIES

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To test species responses to competition, we examined maternal effects on seed mass among 15 pairs of annual plant species (25 species total, Table S1) that were competed as part of a previous study (Germain, Weir & Gilbert 2016); species pairs were selected to meet two criteria. First, the 25 species spanned a broad taxonomic range (six angiosperm Orders represented; Table S1), which allowed us to select pairs that represented a range of phylogenetic distances (nine to 170 million years since divergence; phylogeny in Fig. S1). Pairs were selected to represent phylogenetically independent contrasts (i.e., non-overlapping branch lengths), to circumvent phylogenetic pseudoreplication. Second, the selected species overlap in habitat preference (all associate with grassland meadow in mediterranean-type climates) and overlap geographically in California (CalFlora [<http://www.calflora.org>]); as such, they have the potential to compete in the wild. Additional details about species selection are in Supplementary Methods.

141 We initially sought a balanced design with 10 species competed twice to test how
142 strongly maternal effects on seed mass were determined by the identity of the competitor,
143 resulting in a total of 20 species pairs and 30 unique species. However, competition was intense
144 enough among 5 species pairs that seeds were not produced and maternal effects could not be
145 quantified, resulting in the design we present here with 15 species pairs and 25 unique species,
146 with five species competed twice. Seeds were obtained from commercial suppliers and an
147 individual donor, and were sourced from natural populations consisting of relatively few
148 generations (most < 3, all < 20; Table S1) prior to our experiments. It is possible that the genetic
149 diversity of our seed populations is low compared to natural populations, though we suspect that
150 this is not the case given the large numbers of individuals used to establish the commercial
151 populations and the small number of generations that have elapsed.

152 GREENHOUSE EXPERIMENT

153 From January to July 2012, we grew the 15 species pairs in competition in a greenhouse
154 under two soil moisture levels (wet vs. dry); see Supplementary Methods for details on growing
155 conditions. Plants in the wet treatment were watered twice as often as those in the dry treatment,
156 with the total water received designed to mimic rainfall in mesic sites during wet and dry years
157 (Germain & Gilbert 2014). The competitive environment was manipulated using a replacement
158 design (Jolliffe 2000), in which seeds of each species pair were sown at six relative frequency
159 ratios (10:60, 20:50, 30:40, 40:30, 50:20 and 60:10 expected germinants) at a common density of
160 70 individuals. This density is comparable to the seeding density found in annual grasslands
161 (2500 to 5500 plants m⁻² (Bartolome 1979)). To obtain a density of 70 individuals per pot, we
162 tested each species' germination rate prior to the experiment and corrected seeding densities

163 based on these rates (i.e. a pot with 60 individuals of one species would receive 60 seeds of a
164 species with 100% germination, or 120 seeds of a species with 50% germination).

165 For each species pair, we had two replicate pots per combination of soil moisture
166 condition and frequency ratio, for a total of 360 pots of plants that were randomly assigned to a
167 position in the greenhouse. All greenhouse growing conditions were chosen to simulate those
168 typical of annual grassland in mediterranean-climate regions (Germain & Gilbert 2014;
169 Supplementary Methods). We monitored pots daily and collected all seeds produced in each pot
170 as they matured on the parent plants, pooling seed among individuals of the same species in each
171 pot. At the end of the experiment, all seed material produced in each pot was weighed, and a
172 random representative subsample was taken to estimate the average mass per seed and number of
173 seeds produced per plant in a given pot (Supplementary Methods).

174 Concurrent to this experiment, an additional experiment using the same species was
175 conducted to estimate the impact of soil moisture conditions on maternal provisioning (reported
176 in Germain & Gilbert 2014). Key differences between the previous experiment and the
177 experiment we present here are that each species was grown as singles-species monocultures at
178 low densities (~seven individuals per pot, compared to 70 in the current experiment), meaning
179 that competition was greatly relaxed. We include summary results from Germain and Gilbert
180 (2014) in this paper to compare maternal effects on seed mass to soil moisture conditions in the
181 presence and absence of competition.

182 STATISTICAL ANALYSES

183 Prior to analysis, we transformed the data in two ways to meet model assumptions and
184 facilitate comparisons among species. First, we log transformed seed mass, seed number, and
185 conspecific frequency to minimize heteroscedasticity and linearize seed mass and seed number

186 relationships with conspecific frequency. Second, to allow us to compare species that differ
187 markedly in seed production, we standardized the log-transformed seed mass and seed number
188 data for each species to a mean of zero and unit variance. For simplicity, we henceforth refer to
189 the standardized log-transformed data as ‘seed mass’, ‘seed number’, and ‘frequency’, unless
190 stated otherwise.

191 We conducted a cross-species analysis to test if species differed in their seed mass and
192 seed number responses to the competitive and soil moisture environments. For these analyses,
193 we used the ‘lmerTest’ R package to run linear mixed effects (LME) models, with either seed
194 mass or seed number as response variables, and species (30 levels), soil moisture (two levels),
195 conspecific frequency (six levels), and their interactions as fixed factors. Because species
196 competing in a pot are not independent of one another, we included ‘Pot ID’ as a random factor
197 in all models to control for the non-independence of species interacting in a single pot and avoid
198 pseudoreplication (Bolker *et al.* 2009). The identity of the competitive pair (e.g., *Lasthenia*
199 *glabrata* vs. *L. californica*) was also included as a random factor. Following significant species x
200 frequency and species x soil moisture interactions (see Results), we ran species-specific analyses
201 separately to identify species with significant responses to the biotic and abiotic environment. To
202 accomplish this, we used linear models with type II sums of squares to test the effects of
203 conspecific frequency, soil moisture conditions, and their interaction on seed mass and seed
204 number. We used type II sum of squares as opposed to type III sum of squares because the latter
205 prevents interpretation of main effects even in the absence of a significant interaction (Zuur *et al.*
206 2009). In cases where the interaction was significant, we do not interpret the main effects (e.g.,
207 triangle points in Fig. 1). The type of sum of squares used has no effect on the coefficient
208 estimates.

209 We used major axis regression (MAR; R package ‘lmodel2’) to examine the relationships
210 between response variables across species, and tested the significance of these relationships
211 using a Pearson correlation. First, to identify if seed mass and seed number responses are
212 correlated, we performed a MAR with the slopes of species’ seed mass responses and the slopes
213 of species’ seed number responses as variables. Second, we tested whether the presence and
214 absence of competition alters species’ responses to soil moisture conditions. To do this, we first
215 calculated species’ average effect sizes of seed mass responses to contrasting soil conditions (μ_{dry}
216 $- \mu_{\text{wet}}$) in the presence of competition (i.e. when grown at a density of 70 plants per pot) using
217 Cohen’s *d* with pooled variance (Hartung, Knapp & Singha 2008); in cases where a species was
218 used in more than one species pair, a single average effect size was used. We then used MAR to
219 examine the relationship between these effect sizes and previously published, identically
220 calculated effect sizes in the absence of competition (i.e. grow at a density of 7 species per pot;
221 Germain & Gilbert 2014). Because these species are small-statured and occur at high densities in
222 the field, we consider the contrast of 70 vs. 7 plants per plot as representative of a competition
223 vs. no competition contrast.

224 Results

225 Of the 25 species included in this study to produce 15 reciprocal competition trials (see
226 Materials and methods), 16 species showed significant ($P < 0.05$) or marginally-significant ($P <$
227 0.10) maternal effects on seed mass when in competition (Fig. 1a, Fig. S2); we note that 2.5
228 species are expected to show these results by chance alone given a 10% type 1 error rate. Most
229 species responded to conspecific frequency alone (5 species) or in conjunction with the soil
230 moisture environment in an additive (4 species) or multiplicative (3 species) manner; four
231 species responded to the soil moisture environment but not conspecific frequency. The strength

232 and direction of responses varied among species, as indicated by significant species x frequency
233 ($F_{29,464} = 2.84$, $P < 0.001$) and species x soil moisture ($F_{29,410} = 3.19$, $P < 0.001$) interactions in
234 our cross-species statistical model (Table S2). Species were similarly likely to increase (5
235 species) or decrease (6 species) seed mass as conspecific frequency increased (Table S2, Fig.
236 1a). Overall, our results demonstrate that for this plant community, 64% of species are likely to
237 exhibit maternal effects on seed mass when in competition, and that these responses vary by
238 species with biotic or abiotic conditions.

239 In contrast to seed mass, 21 of the 25 species showed significant or marginally significant
240 responses through seed number to conspecific frequency (7 species; Fig. 1b), soil moisture
241 conditions (4 species), both additively (6 species), and both interactively (4 species; Table S2).
242 Analogous to seed mass responses, the effect of conspecific frequency on seed number depended
243 on the focal species (significant species x frequency interaction; Table S3, $F_{29,716} = 6.63$, $P <$
244 0.001). However, in contrast to seed mass responses, frequency-dependent seed number was
245 negative for most species (14 out of 17 species; Table S2), and was sensitive to the soil moisture
246 environment (significant frequency x soil moisture interaction; Table S3, $F_{1,716} = 4.49$, $P =$
247 0.034). These seed number responses were positively correlated with the strength and direction
248 of species' seed mass responses ($r = 0.28$, slope = 0.48, $P = 0.029$; Fig. 2a), even though some
249 species showed opposite seed mass and seed number responses (grey regions of Fig. 2a).

250 The strength and direction of seed mass responses to contrasting soil moisture
251 environments (wet vs. dry) in the presence of competition were positively correlated with those
252 in the absence of competition ($r = 0.50$, $P = 0.010$; Fig. 2b). The slope of this correlation was
253 less than one (major axis regression, slope = 0.67), as many species showed stronger responses to
254 soil moisture when grown in the absence of competition (Fig. 2b). This result was surprising

255 given that, in the current experiment, 44% of species altered seed provisioning in response to soil
256 moisture when in competition, whereas only 21% did so in the absence of competition (Germain
257 & Gilbert 2014). This suggests that the prevalence but not the magnitude of soil moisture-
258 induced maternal effects on seed mass increases in the presence of competition, possibly because
259 the effects of soil moisture are dwarfed by those of conspecific frequency.

260 **Discussion**

261 There is a substantial body of empirical work investigating maternal effects in response
262 to the abiotic environment (see review by Herman & Sultan 2011), yet responses to biotic
263 interactions remain understudied, particularly in plants (Weiner *et al.* 1997; Larios & Venable
264 2015). Our results show that changes to the competitive environment can alter maternal
265 provisioning of seed mass and, much like more commonly measured seed number responses
266 (Law & Watkinson 1987), that the strength and direction of maternal provisioning depend on
267 identities of competing species. Below, we discuss how considering interactions between the
268 biotic and abiotic environment allows us to understand how maternal effects are distributed
269 across species in plant communities. Because species interactions frequently altered provisioning
270 strategies, maternal effects likely have important implications for competitive dynamics, species
271 coexistence and diversity; in this vein, we propose new hypotheses for future study.

272 We detected maternal effects on seed mass in response to the frequency of conspecific
273 competitors in nearly half of the species examined, with negative and positive responses being
274 equally common (Fig. 1a). There are two explanations for the maintenance of species-specific
275 maternal effects that are not mutually exclusive and likely differ in importance among species.
276 First, theory predicts that maternal provisioning strategies should evolve to maximize maternal
277 fitness, either to the benefit or detriment of offspring fitness (Marshall & Uller 2007; Olofsson,

278 Ripa & Jonzen 2009). In that case, the most adaptive strategy will depend on the specific
279 ecologies of focal species (e.g., Sultan, Barton & Wilczek 2009; Germain, Caruso & Maherali
280 2013). Second, even if the same adaptive strategy is shared by two species, genetic or
281 physiological constraints might result in the evolution of an adaptive or maladaptive strategy in
282 one species but not the other (DeWitt, Sih & Wilson 1998). Though the degree to which species-
283 specific maternal effects reflect evolutionary adaptation or constraint cannot be disentangled in
284 our study, the ecological implications for offspring can be – larger seeds are more competitive
285 and tolerant of environmental stress, whereas smaller seeds are more dispersive and likely to
286 persist longer in the seedbank (Larios & Venable 2015; reviewed in Leishman *et al.* 2000). The
287 life-history tradeoff between competitive ability and dispersal ability, as mediated by seed size,
288 has been hypothesized to play a central role in determining coexistence outcomes (Westoby *et al.*
289 1996; Jakobsson & Erikson 2000), and might explain the diversity of responses to conspecific
290 frequency observed in our study.

291 Frequency-dependent seed mass responses were sensitive to the identity of the
292 heterospecific competitor, rather than simply a common response to conspecific frequency. For
293 example, the frequency-dependent seed mass of *Salvia columbariae* was significantly negative
294 when competing with *S. viridis*, but was non-significant in competition with *Collinsia*
295 *heterophylla*. A simple explanation for this result is that seed mass is sensitive to differences
296 among species' competitive abilities, yet this mechanism is unlikely given the lack of frequency-
297 dependent seed number responses to either competitor. The presence of seed mass responses in
298 the absence of seed number responses is intriguing, because the latter would typically lead one to
299 conclude that intraspecific and interspecific competition are equivalent (Harpole & Suding
300 2007). Yet, if competitive interactions were equivalent, we would not expect to see frequency-

301 dependent seed mass responses. Seed mass responses appear to reveal competitive differences
302 among species that are hidden when only seed number responses are considered – as in most
303 ecological studies of plant competition. Previous research in plant monocultures demonstrates
304 that parents produce smaller, more dispersive offspring when neighborhood densities are high
305 (Larios & Venable 2014) – but in multi-species communities, this simple response likely also
306 depends on the relative frequencies of heterospecific competitors.

307 An open question is whether maternal effects (seed mass responses) act to reinforce or
308 counteract frequency-dependent demographic rates (seed number responses). Although our
309 results suggest that seed mass responses to conspecific frequency generally act to reinforce seed
310 number responses (i.e., they are positively correlated, Fig. 2a), some species clearly show
311 opposite seed mass and seed number responses (points in the grey regions of Fig. 2a). In the
312 context of demographic rates, the direction of frequency dependence can indicate whether
313 competition is more likely to result in coexistence (negative frequency dependence) or exclusion
314 (positive frequency dependence). In our experiment, negative frequency-dependent seed number
315 responses were common among species (fig. 1b), but seed size responses were equally positive
316 and negative (Fig. 1a). Previous research suggests that interspecific and intraspecific variation in
317 seed mass alters several important biological parameters, from dormancy to growth and
318 fecundity (Westoby *et al.* 1996; Eriksson 1999; Germain & Gilbert 2014). Thus, commonly-
319 measured seed number responses (Harpole & Suding 2007) may be insufficient to capture the
320 full impact of competitive interactions in the offspring generation (Ginzburg & Taneyhill 1994;
321 Van Allen & Rudolf 2015). An intriguing avenue for future research are experiments that
322 quantify how much variation in population dynamics is being missed without considering lagged
323 responses to conditions of the maternal generation. An effect of the maternal environment on

324 population demography has been demonstrated previously in response to abiotic conditions (e.g.,
325 understory light, Galloway & Etterson 2007), but is not yet understood in competitive
326 environments.

327 We found important differences in the prevalence of maternal effects in response to soil
328 moisture conditions in competitive and non-competitive environments. Specifically, over twice
329 as many species altered seed provisioning in response to soil moisture in the presence of
330 competition (44% of species; this study, Table S2) compared to in the absence of competition
331 (21% of species; Germain & Gilbert 2014). Almost all tests of maternal effects have been
332 conducted in non-competitive environments, with individuals grown alone (e.g., Aarssen &
333 Burton 1990). Because most plants experience competition in their natural environments, current
334 estimates of the prevalence of maternal effects may be conservative, and most relevant to
335 disturbed environments where plant densities are low. Additionally, competition appears to
336 dampen maternal effects in response to soil moisture (Fig. 2b) despite a threefold increase in the
337 number of species that exhibit such an effect. This indicates that, contrary to our initial
338 expectations, competition does not simply exacerbate maternal provisioning of seed mass in
339 response to soil moisture, but instead appears to alter the nature of soil moisture's effects on seed
340 mass in some species. This surprising result is likely due to the shift in maternal provisioning
341 that occurs with a change in the identity of the competitor.

342 An intriguing hypothesis posed by Dyer *et al.* (2010) is that maternal effects might
343 contribute to the invasion success of non-native species. Although our experiment was not
344 specifically designed to test this hypothesis, six of the 25 species used in our trials are not native
345 to California (Table S1), allowing qualitative comparisons. In doing so, we found that frequency-
346 dependent maternal effects are significantly lower among non-native species compared to native

347 species (Fig. 3, Supplementary Methods). Our results suggest that for this system, maternal
348 effects to the competitive environment may be one trait that differentiates native and non-native
349 species and thus could contribute to invasion success. However, we caution that this result is
350 based on limited and unbalanced data (only six non-native species), and could be explored with
351 more species in future studies. For example, we do not have the power to test differences among
352 non-native species that differ in impact, such as naturalized species vs. noxious invaders (Strauss
353 *et al.* 2006; Diez *et al.* 2008), which could explain the considerable overlap in the range of
354 responses among native and non-native species despite significant differences.

355 Although this study advances our understanding of the importance of competition in
356 structuring maternal provisioning, there are two caveats that should be considered in interpreting
357 our findings. First, we were unable to identify how changes in seed mass translate into
358 differences in offspring performance, due to the logistical infeasibility of the full factorial
359 experiment that would be required to test for longer-term impacts of seed mass. It is possible that
360 maternal effects on seed mass may not persist beyond the seed stage, as some studies have found
361 (e.g., Weiner *et al.* 1997). However, many studies demonstrate their effects on some aspect of
362 post-seed performance, such as germination, dormancy, survival, growth, and fecundity (e.g.,
363 Stanton 1984; Gomez 2004; Germain, Caruso & Maherali 2013; see review by Herman & Sultan
364 2011), especially in competitive environments (Stratton 1989). Second, by focusing on seed
365 mass responses, we likely underestimate the overall prevalence of maternal effects that can
366 manifest in other ways, such as through germination or dormancy rates (Germain & Gilbert
367 2014), or through epigenetic effects that can alter the offspring phenotype in more complex ways
368 (Herman & Sultan 2011). As such, this study should be viewed as an important first step in

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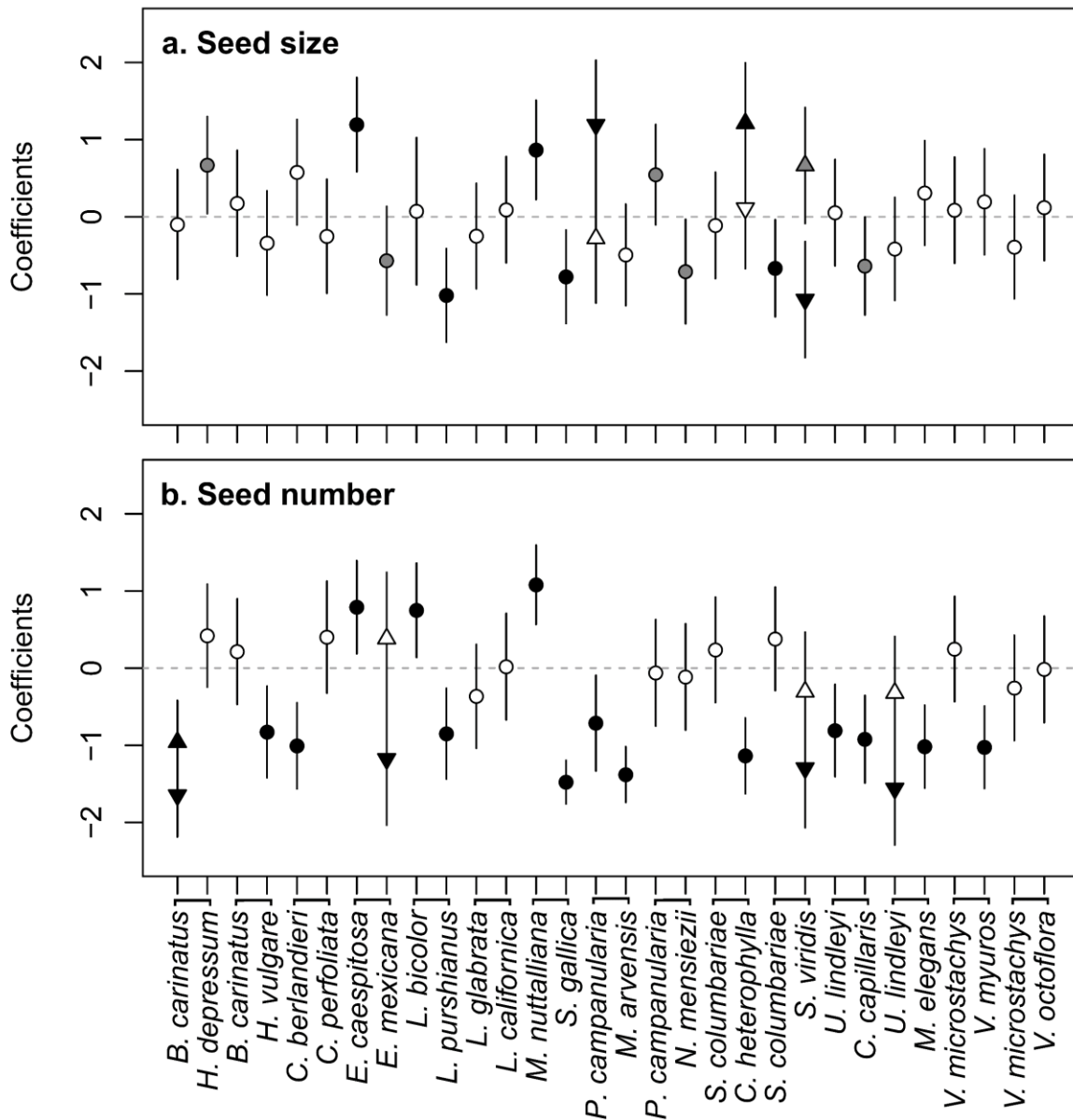
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Figures



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507 **Fig. 1.** Cross-species comparison of frequency-dependent (a) maternal provisioning of seed mass
508 and (b) seed number responses. Points are slope coefficients ($\pm 2 \times$ standard error) of species
509 responses to the frequency of conspecific competitors, and are shaded black, gray, or white to
510 indicate significant ($P < 0.05$), marginally-significant ($P < 0.10$), or non-significant ($P > 0.10$)
511 slopes, respectively. In most cases, frequency \times soil moisture interactions are non-significant,

512 and slopes are averaged across soil moisture environments; when significant, wet (upwards
513 triangle) and dry (downwards triangle) environments are plotted separately. Competitive pairs
514 are delineated by lines connecting species name abbreviations (first letter of genus and species
515 name). See Table S1 for taxonomic and collection information.

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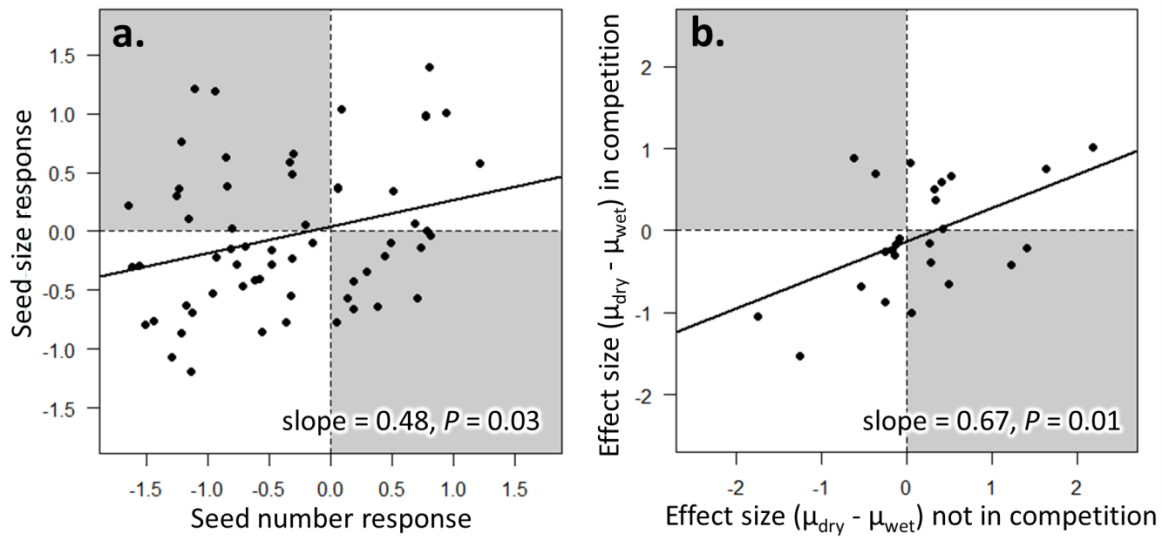
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530 **Fig. 2.** Correlations of (a) seed mass and seed number responses to conspecific frequency ($n = 60$

531 [15 pairs \times two species \times two soil moisture environments]), and (b) seed mass responses to soil

532 moisture conditions in the presence and absence of competition ($n = 25$). Each point is a species,

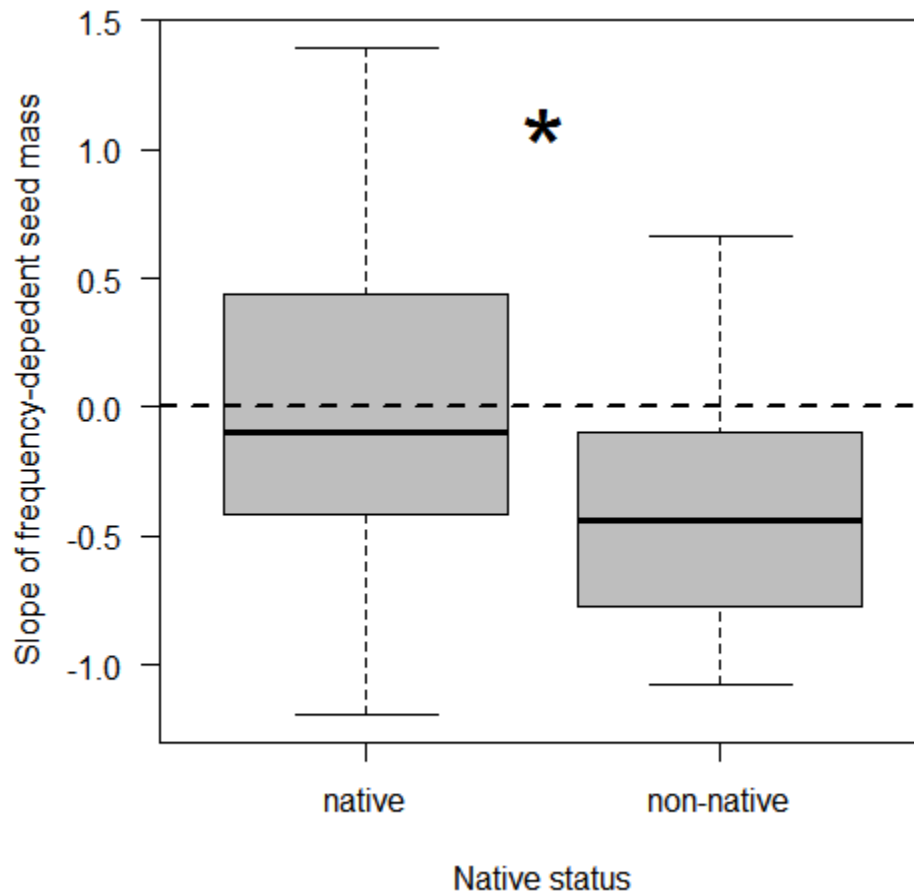
533 and points that fall in the grey zones are species with opposing directions of responses.

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539 **Fig. 3.** A comparison of frequency-dependent seed mass among native ($n = 19$) and non-native
540 ($n = 6$) species. The dashed horizontal line indicates a slope of 0, and the asterisk indicates a
541 significant difference ($P = 0.03$). See Supplementary Methods for details of the analysis.