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10   **Authors:** Rachel M. Germain[1], Tess N. Grainger[2], Natalie T. Jones[3], and Benjamin Gilbert[2]

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12   **Affiliations:**

13   [1]*Corresponding author:* Rachel M. Germain [email: rgermain@zoology.ubc.ca, phone: 647-884-

14   4312, address: Dept. Botany & Dept. of Zoology, University of British Columbia, Vancouver,

15   BC, CA

16   [2]Dept. Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, CA

17   [3]Dept. Biological Sciences, University of California – San Diego, San Diego, CA, USA

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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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Introduction

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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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127   **Materials and methods**

128   STUDY SPECIES

129   To test species responses to competition, we examined maternal effects on seed mass

130   among 15 pairs of annual plant species (25 species total, Table S1) that were competed as part of

131   a previous study (Germain, Weir & Gilbert 2016); species pairs were selected to meet two

132   criteria. First, the 25 species spanned a broad taxonomic range (six angiosperm Orders

133   represented; Table S1), which allowed us to select pairs that represented a range of phylogenetic

134   distances (nine to 170 million years since divergence; phylogeny in Fig. S1). Pairs were selected

135   to represent phylogenetically independent contrasts (i.e., non-overlapping branch lengths), to

136   circumvent phylogenetic pseudoreplication. Second, the selected species overlap in habitat

137   preference (all associate with grassland meadow in mediterranean-type climates) and overlap

138   geographically in California (CalFlora [http://www.calflora.org]); as such, they have the

139   potential to compete in the wild. Additional details about species selection are in Supplementary

140   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    $- \mu_{wet}$) 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.

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.

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

369   characterizing maternal effects in competitive environments that can be used to inform future

370   work.

371   The study of maternal effects has exciting potential to explain population- and

372   community-level responses to heterogeneous environments (Ginzburg & Taneyhill 1994; Van

373   Allen & Rudolf 2013; Van Allen & Rudolf 2015). Here, we show that current estimates of

374   maternal effects in non-competitive environments are conservative, that competition can alter

375   maternal provisioning of seed mass, and that these maternal effects are fine-tuned to competitive

376   differences among species, which in turn are shaped by the abiotic environment. Our research

377   sheds new light on the complex nature of species interactions, and suggests avenues for future

378   research that would further characterize the full range and impact of maternal effects in

379   ecological communities.

380

381   **Acknowledgements**

385   **Data accessibility**

386   All data will be deposited into the Dryad repository.

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505 **Figures**
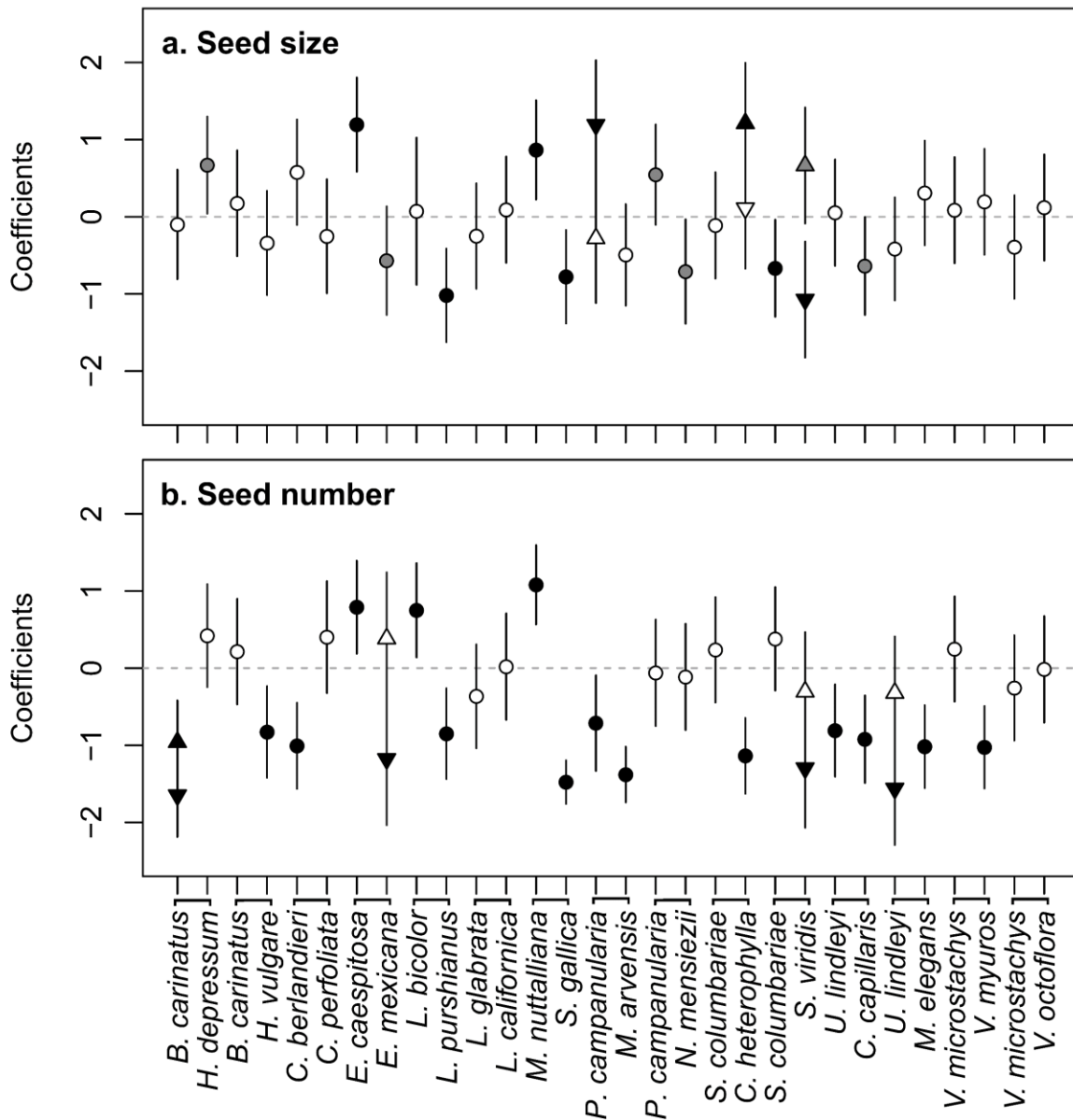
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507 **Fig. 1.** Cross-species comparison of frequency-dependent (a) maternal provisioning of seed mass

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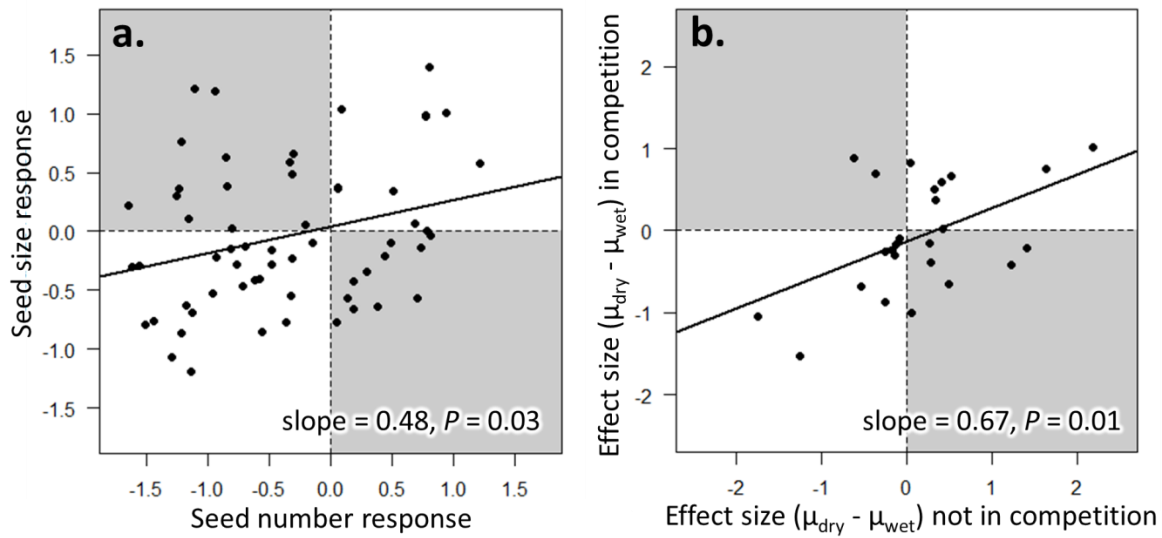
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Fig. 2. Correlations of (a) seed mass and seed number responses to conspecific frequency ($n = 60$ [15 pairs × two species × two soil moisture environments]), and (b) seed mass responses to soil moisture conditions in the presence and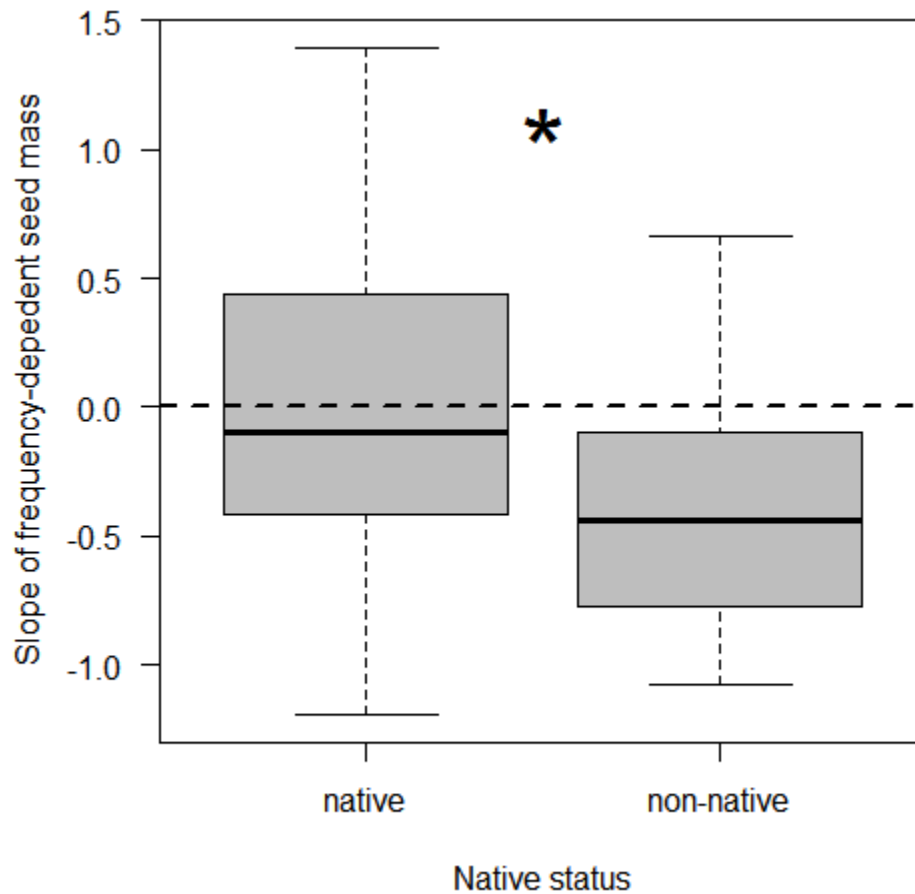 absence of competition ($n = 25$). Each point is a species, and points that fall in the grey zones are species with opposing directions of responses.

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Fig. 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 Methods for details of the analysis.