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LETTER

Hidden responses to environmental variation: maternal effects reveal species niche dimensions

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Abstract

Species responses to fluctuating environments structure population and community dynamics in variable ecosystems. Although offspring number is commonly used to measure these responses, maternal effects on offspring quality may be an important but largely unrecognised determinant of long-term population growth. We selected 29 species across a Mediterranean annual plant phylogeny, and grew populations of each species in wet and dry conditions to determine responses in seed number and maternal effects (seed size, seed dormancy, and seedling growth). Maternal effects were evident in over 40% of species, but only 24% responded through seed number. Despite a strong trade-off between seed size and seed number among species, there was no consistent trade-off within species; we observed correlations that ranged from positive to negative. Overall, species in this plant guild show a complex range of responses to environmental variation that may be underestimated when only seed number responses are considered.

Keywords

Annual grasslands, environmental variability, maternal effects, phylogenetic signal, seed size, seed size–seed number trade-offs, water availability.

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INTRODUCTION

Environmental variability is ubiquitous in nature (Vasseur & Yodzis 2004), and plays a central role in determining the structure and function of many biological communities (Hobbs *et al*. 2007; Elmendorf & Harrison 2009). When species differ in their responses to the environment, this variability can maintain biodiversity by favouring different species in different years (Chesson & Warner 1981; Levine & Rees 2004; Adler *et al*. 2006; Angert *et al*. 2009). As a result, ecologists have devoted significant resources to understanding species-specific responses to varying environments (Angert *et al*. 2010; Gremer *et al*. 2012).

Most research on the impacts of environmental variability has focused on numeric responses, such as the per capita number of offspring produced (Caceres 1997; Levine & Rees 2004; Angert *et al*. 2009). However, there is strong evidence that the environment not only affects offspring quantity but also offspring quality (Mousseau & Fox 1998), in a phenomenon known as ‘maternal effects’ (Roach & Wulff 1987). A maternal effect is ‘any phenotypic variation in offspring that is a consequence of the mother’s phenotype rather than the genetic constitution of the offspring’ (Roff 1998). In plants, for example, increased seed provisioning can alter early survivorship and competitive ability (Jakobsson & Eriksson 2000; Moles & Westoby 2004). These changes in offspring quality have the potential to generate responses to environmental variability that are distinct from changes in offspring quantity, and may therefore play an important but relatively unexplored role in community dynamics (Ginzburg & Taneyhill 1994).

Previous research has revealed several cases where maternal effects can alter the fitness or ecology of individuals (e.g., Galloway 2005; Sultan *et al*. 2009; Dyer *et al*. 2010). However, the general importance of maternal effects for ecological dynamics is unknown for two reasons. First, many studies of maternal effects evaluate their impact on genetically similar individuals, such as closely related genotypes or clones (e.g. Galloway & Etterson 2007). While these tests are relevant to the ecology of asexual organisms, it is not clear whether individual-level trends would be swamped by population-level variation when considered in outcrossing species. In other words, maternal effects need to be studied at the population level to determine if they are comparable to demographic effects. Second, most studies of maternal effects include one or two species that show strong responses (e.g. Galloway 2005). Multispecies tests of maternal effects are currently lacking, and as a result it remains unclear how common they are in natural communities.

In addition to quantifying the prevalence of maternal effects, multispecies tests also allow us to identify key factors that account for variation in maternal effects expression among species. Phylogenetic relationships are a likely candidate, given that they are known to structure plasticity (Kembel & Cahill 2005; Gomez-Mestre *et al*. 2008) and seed size (e.g. Lord *et al*. 1995). Moreover, contemporary hypotheses in the field of phylogenetic community ecology posit that similar environmental responses among closely related species structures species coexistence (e.g. Mayfield & Levine 2010), suggesting that understanding the phylogenetic basis of numeric responses and maternal effects should provide insights into community assembly and diversity.

Annual plants are ideal for contrasting numeric population responses with maternal effects because lifetime reproduction can be entirely captured in a single growing season. As such, the number of offspring produced is estimated by seed number, whereas maternal effects manifest through changes to seed quality, such as seed size. These differences in seed size often confer advantages in early growth, survival and competitive ability among species (Leishman 2001; Moles & Westoby 2002, 2004), and have been shown to change the fitness of individuals (Germain *et al.* 2013). In addition, studies of seed size and seed number across species show a consistent trade-off (e.g., Jakobsson & Eriksson 2000; Levine & Rees 2002). This trade-off can also occur within species (e.g. Germain *et al.* 2013), but the opposite pattern has also emerged (Venable 1992), raising the possibility that maternal effects can counteract or reinforce a species' numeric response to environmental fluctuations depending on whether they are positively or negatively correlated with seed number.

In this study, we use annual plants from Mediterranean-climate regions to test the consequences of variation in water availability on seed production. We chose this system because the high diversity of annual plants in Mediterranean regions is at least partially maintained by species-specific responses to variable rainfall (e.g., Hobbs *et al.* 2007; Elmendorf & Harrison 2009). In addition, several studies have demonstrated the importance of maternal effects in Mediterranean annuals (e.g. Byers *et al.* 1997; Germain *et al.* 2013), but it is unknown how commonly maternal effects occur across a range of species.

To test the general importance of maternal effects relative to numeric responses, we selected 29 species of both closely and distantly related taxa. We grew these species in a greenhouse under wet and dry soil moisture conditions, and estimated the size and number of seeds produced, as well as dormancy and offspring performance. We used these data to address three main questions: (1) How commonly do plants respond to environmental variation with maternal effects, and how does this compare to numeric responses? (2) Is there a consistent relationship between seed size and seed number responses within species, and does this relationship tend to be antagonistic (negative correlation) or reinforcing (positive correlation)? and (3) Does phylogenetic relatedness explain the type and strength of responses to environmental variation?

MATERIALS AND METHODS

Study system

We studied the effect of water availability in the maternal generation on offspring of 29 annual plant species that are native to Mediterranean-climate regions. Mediterranean regions are diversity hotspots, harbouring *c.* 20% of the world's total vascular plant species, many of which are rare or endemic (Cowling *et al.* 1996). These regions are characterised by cool winters and hot summers, where most of the annual precipitation falls in the autumn and winter months (Cowling *et al.* 1996). The timing and total amount of rainfall can vary up to six-fold between years (Hobbs *et al.* 2007), potentially explaining the high turnover in both the density and composition of species over time in these systems (Cowling *et al.* 1996; Levine & Rees 2004; Hobbs *et al.* 2007; Elmendorf & Harrison 2009).

The species were selected to meet three criteria. First, all species have an annual lifecycle to ensure that seed production in a single growing season is representative of that individual's lifetime reproductive success. Second, each species occurred in annual grasslands with similar climatic conditions (Leiva *et al.* 1997) and overlapped geographically with other species in the study as determined by CalFlora (http://www.calflora.org) and Euro+Med (http://www.emplantbase.org) plant databases. These criteria ensured that our species had similar exposure to variation in rainfall over recent evolutionary timescales. Third, species were selected to span seven orders [Asterales, Boraginales, Caryophyllales, Fabales, Lamiales, Poales and Ranunculales; Table S1], to capture the taxonomic diversity of annual species from Mediterranean-climate regions. Seeds were acquired from commercial suppliers and an individual donor, and originated from natural populations relatively few generations (usually < 3, all < 20) before experimentation (Table S1). Although we suspect that our seed sources include levels of genetic variation typical of natural populations, we are unable to test this assumption because of a lack of knowledge of the genetic diversity both in the wild and in our populations. Methods for ensuring genetically representative samples can be found elsewhere (e.g. Project Baseline [http://www.baselineseedbank.org/]), and remain an important goal for future studies. We did not cold stratify seeds prior to planting because doing so is known to induce dormancy in Mediterranean species (Baskin & Baskin 2001).

Maternal generation

We grew the maternal generation in a greenhouse at the University of Toronto from January to July 2012. The greenhouse was initially set to day/night temperatures of 14/7 °C, with supplemental high intensity discharge (HID) lighting provided to maintain a 10-h day length. These conditions gradually increased to a 23/17 °C day/night cycle and 14-h day length to simulate a typical Mediterranean growing season (Fig. S1). For each species, 30 seeds were sown into each of 14 replicate 2.54-L treepots filled with a 3 : 2 mixture of sand and screened topsoil to mimic the sandy loam soils that dominate annual grasslands. Pots were top-watered daily until saturation during a 3-week establishment period.

After establishment, we recorded the number of seedlings and thinned each pot to *c.* eight individuals. Seedlings were selected systematically to maximise their distance from each other in a pot, and were thinned by clipping the base of the stem. This low-density environment allowed us to evaluate the direct effect of soil moisture on a population of individuals, rather than indirect effects of competition. We randomly assigned pots of each species to receive either a wet or dry soil moisture regime through drip irrigation lines. Pots in the wet treatment received 175-mL water twice as often as those in the dry treatment, starting at 1- and 2-day intervals which were extended to 7 and 14 days as the growing season progressed (Fig. S1). These two soil moisture regimes represent realistic among-year differences in precipitation, or equally, the 30-year average differences between mesic [662 mm] and xeric [312 mm] sites across the species ranges in California (http://www.climate-charts.com). We confirmed that the wet

(11.1 ± 0.56%; mean ± SE per cent soil moisture content) and dry (5.8 ± 0.42%) treatments were effective using a volumetric water probe on empty pots. Prior to flowering (*c.* 60 days after planting), each pot was provided with 350 mL of 1500 ppm 20-20-20 NPK fertiliser. Pollination was provided by commercial colonies of *Bombus impatiens*, which were active throughout the flowering period. *Bombus impatiens* are generalist pollinators, and were observed visiting all insect-pollinated species in this experiment.

We monitored pots daily, and collected seeds as they matured on the parent plants. Seed samples were processed in the laboratory by subsampling collected materials to estimate seed size and seed number. Subsampling was conducted using a standardised procedure in which each sample was sequentially divided into equal smaller units until manageable subsample sizes were obtained. A single subsample was then chosen randomly. Seed size was estimated as the mass of all seeds in the subsample divided by number of seeds in the subsample, whereas seed number was calculated as the average number of seeds produced per plant in each pot.

Offspring generation

We performed germination and greenhouse experiments on the offspring generation from January to April 2013. The greenhouse maintained a 15/7 °C day/night temperature regime, with supplemental high intensity discharge (HID) lighting provided to maintain a 10-h day length throughout the experiments.

The germination experiment tested for maternal effects on seed viability and dormancy, with the latter indicating allocation to the seed bank as a bet-hedging strategy for persistence in unfavourable years (Tielbörger & Valleriani 2005). Thirty seeds from each maternal pot were haphazardly selected and placed on moist filter paper in a petri plate, with seven petri plates used per species by maternal environment combination. The plates were placed on a greenhouse bench under a shade cloth and scored for germination every 2 days, and remoistened as needed. After 24 days, once germination plateaued for the majority of species, ungerminated seeds were air dried, transferred to fresh filter paper and moistened with a 500 ppm gibberellic acid solution (GA_3). This naturally occurring plant growth regulator is commonly used to germinate dormant seeds. Because GA_3 application is not always 100% effective for deeply dormant seeds, it provides a conservative estimate of dormancy (Baskin & Baskin 2001). Seed viability was scored as the proportion of seeds that germinated under regular and GA_3 methods; other viability methods, such as tissue staining, could not be used due to the very small seed sizes of some species. Mould growth was spot treated with 0.15% v/v of Previcur® (Bayer CropScience, Lyon, France) fungicide throughout the germination trial.

We also tested for maternal effects on offspring performance at the seedling stage. For each petri plate in the germination trial, two germinants were transplanted into each of two 0.16-L conetainers filled with a peat-based commercial soil (Sunshine Mix 1, Sun Gro Horticulture Canada CM Ltd., Vancouver, British Columbia, Canada). This produced 14 conetainers per species × water level treatment, but low germination in four species led to unbalanced replication among species. After 3 weeks, we measured the height and harvested the aboveground biomass of one randomly selected individual per conetainer. Many individuals had very low dry mass (≤ 1 mg), which increased the relative measurement error; we therefore used the height data to test for offspring performance.

Phylogenetic tree construction

We constructed a phylogenetic tree for 27 of our 29 species using Bayesian methods on nucleotide sequence data. Two species (*Salvia columbariae* and *S. viridis*) were excluded because sequences were unavailable. Sequences from the ITS1/5.8S/ITS2 coding region were retrieved from GenBank, aligned using the MUSCLE algorithm in MEGA (version 4.0; Tamura *et al.* 2007) and combined into a single sequence matrix for analysis. We then generated a Bayesian tree in BEAST (version 1.7; Drummond *et al.* 2002) using a GTR substitution model selected by ModelTest (version 3.7; Posada & Crandall 1998) and an uncorrelated lognormal relaxed molecular clock for branch length estimation. Because this coding region is rapidly evolving, we constrained the tree topology at nodes above the family level based on well-resolved relationships in the angiosperms (Stevens 2001). We ran our MCMC chain for 100 000 000 generations, with a 10 000 000 burn-in and data logging every 10 000 generations.

Our analysis generated 10 000 posterior trees, which were summarised into a single maximum clade credibility tree with median node heights. The resulting tree (Figs. 1 and S2) is fully resolved and consistent with Angiosperm Phylogeny Group III classifications (Stevens 2001).

Data analyses

We used generalised least squares (GLS) analyses to test the effects of our maternal watering treatments on all response variables that were not binomially distributed; those that were binomially distributed (seed dormancy and viability) were tested with generalised linear models (GLMs) using a quasibinomial distribution to account for overdispersion. The GLS allows for heterogeneous variances among treatments, with the varIdent weighting function to account for the different variances among species. In all analyses, we tested for the effect of maternal environment (ME) and a species × ME interaction, with significant results indicating common responses or species-specific responses to the maternal environment respectively.

In all analyses where a significant species × ME interaction occurred, we used *post hoc* tests to determine the species that differed and the direction of effect. The large number of species used in the study made corrections to *post hoc* comparisons impractical. As a result, we restrict our *post hoc* tests to comparisons between environments for each species, and present our data in terms of effect sizes to quantify the magnitude of change relative to the variation. Our effect sizes were measured using Cohen's d with a pooled variance (i.e. $[\mu_{dry} - \mu_{wet}]$/pooled σ; Hartung *et al.* 2011). Because the dormancy tests had higher variances than expected for proportions, we used Cohen's d for these effect sizes as well.

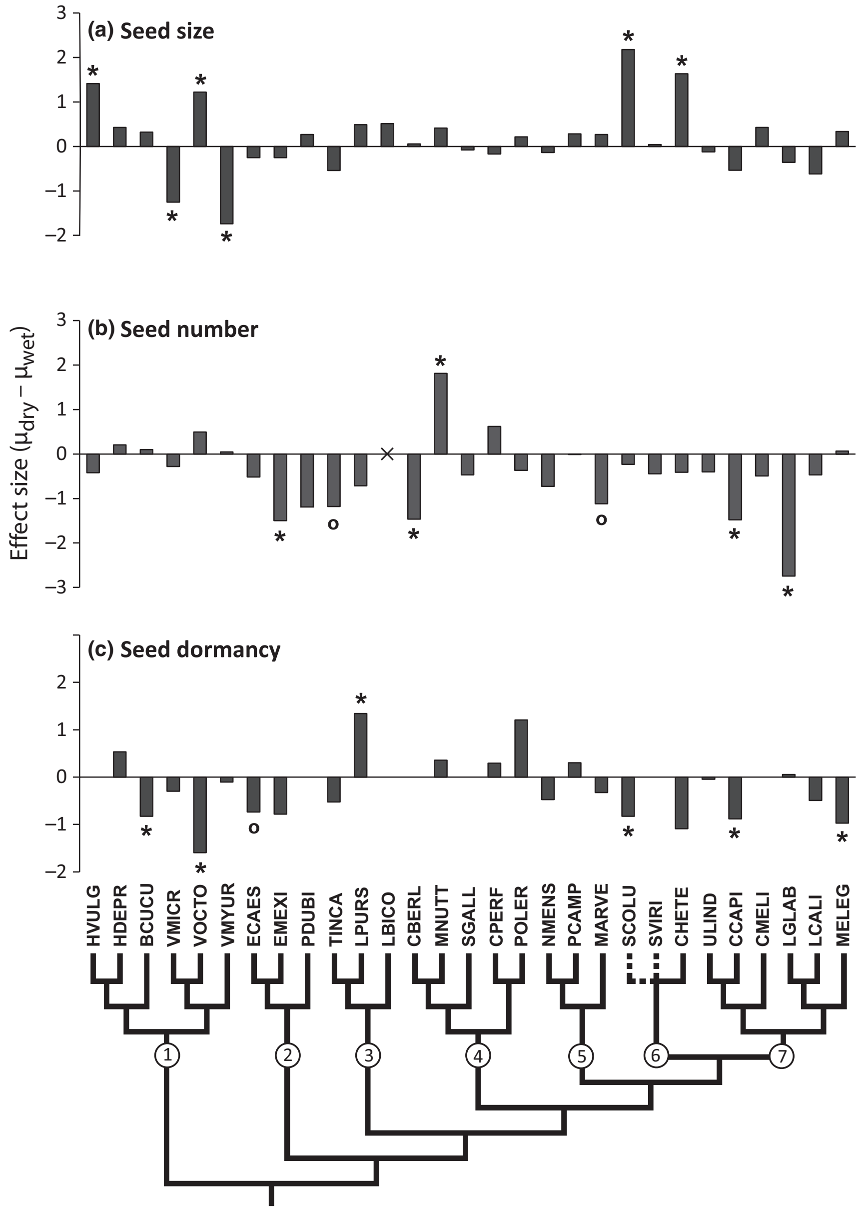

Figure 1 Effect sizes of (a) seed size, (b) seed number and (c) seed dormancy responses to our watering treatments across a phylogeny of 29 species; see Table S1 for species codes. Effect sizes were calculated using Cohen's d (i.e. [$\mu_{dry}-\mu_{wet}$]/pooled σ; Hartung *et al.* 2011). Positive effect sizes indicate that trait values were higher in the dry compared to wet environment, and vice versa. The numbers on the phylogeny correspond to taxonomic orders: (1) Poales, (2) Ranunculales, (3) Fabales, (4) Caryophyllales, (5) Boraginales, (6) Lamiales and (7) Asterales. Dashed branches represent unknown relationships due to missing sequence data [SCOLU and SVIRI], and '×' indicates unavailable trait data rather than a true zero. $*P < 0.05$, $^{o}P < 0.10$.

We tested for maternal effects on seed size, seed number and also seed size–seed number correlations within and among species. All tests with seed size and seed number were performed on log-transformed data. The overall test of the correlation between seed size and seed number within species was done by first standardising seed size and seed number within species and performing a regression that included a species × ME interaction. This standardisation causes the slope of the regression line to be equal to the correlation coefficient, and the test therefore determines if any correlation between seed size and seed number is the same (or different) for our species (Quinn & Keough 2002). The *post hoc* test on seed size–seed number correlations was performed using Pearson correlations for each species, and the effect size presented is the correlation coefficient. The correlation among species was calculated using mean values by species for both seed size and seed number.

Maternal effects were measured in the following generation by measuring seed dormancy, viability and seedling height. For seedling height, we first tested for differences in height using GLS, and subsequently tested for whether populations that produced larger seeds tended to produce taller plants. For this second analysis, we first standardised data within each species, using mean seed size per pot and mean height of offspring from a given pot. We then performed a regression that included a species × ME interaction. As with the correlation test above, this test determines if species differ in the correlation between mean seed size and the height of seedlings.

We tested for a phylogenetic signal in species responses to the maternal environment using the ‘phylosignal’ function in the *picante* package of R (Kembel *et al.* 2010), to determine if closely related species are responding more or less similar to environmental variation. First, when the species × ME terms were significant, we calculated effect sizes for each species, except the seed size–seed number correlation, for which we used the correlation coefficients. Second, we contrasted observed phylogenetic independent contrasts (PICs) to those generated by randomising the tips of the tree (10 000 randomisations). The rank of the observed contrasts relative to the randomised contrasts was used to generate p-values, with p-values approaching one or zero indicating that responses were convergent or conserved, respectively, with a null expectation of a Brownian motion model of evolution. Because we used the randomisations for two-tailed tests, the p-values reported are 2 × rank observed/10 000 for conserved responses, and 2 × (1 − rank observed/10 000) for convergent responses.

RESULTS

Seed size, seed number and their correlation

Close to half of species (45%) responded to environmental variation by altering seed size or seed number, with these two responses being equally common (Fig. 1a,b). We detected a significant maternal environment × species interaction for both responses (seed size: $F_{28,331} = 2.20$, $P < 0.001$, seed number: $F_{27,320} = 2.39$, $P < 0.001$), with seed size responses significant in six of 29 species and seed number responses significant to marginally significant in seven of 28 species ($P = 0.05$–0.08 in two of those species). Interestingly, there was no overlap in the species that responded through seed size and those that responded through seed number. Despite a significant interaction, we found that seed number decreased by 85% on average in the dry environment ($F_{1,320} = 20.44$, $P < 0.001$), and only one species significantly increased seed number in this treatment (Fig. 1b). In contrast, seed size showed no mean effect of watering treatment ($F_{1,331} = 2.20$, $P = 0.136$; Fig. 1a), meaning that species were equally likely to increase or decrease seed size in response to moisture.

There were significant seed size–seed number correlations, but their direction depended on whether our focus was among or within species (Fig. 2). At the among-species level, seed size and seed number were negatively correlated ($r = -0.67$, $P < 0.001$; Fig. 2a), and the slope of this relationship was not statistically different from −1 ($P > 0.05$), meaning that the relationship can be considered linear and is therefore consistent with hypothesised energetic trade-offs (Levine & Rees 2002). Within species, however, we observed both positive and negative correlations ranging from $r = 0.76$ to $r = -0.65$ (Fig. 2b). Overall, there were a similar number of significant positive (three of 28 species) and negative (two of 28 species) correlations, with most species having smaller correlation coefficients ($-0.5 < r < 0.5$) that were not statistically significant.

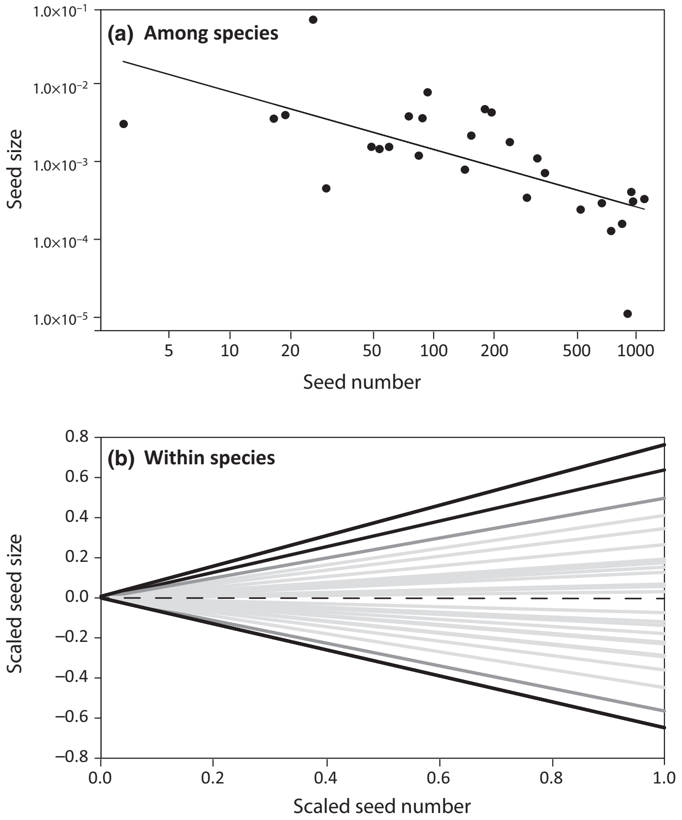

Figure 2 Seed size–seed number correlations. (a) Correlation among species, with values representing the species-level means with a best-fit line indicating a significant correlation ($R^2 = 0.45$, $P < 0.001$). (b) Correlations within species; seed size and seed number were standardised by species and a constant added to visualise the correlation coefficients for each species. Black and dark grey lines represent significant ($P < 0.05$) and marginally significant ($P < 0.10$) correlations, respectively; light grey lines are non-significant. The dashed line represents no correlation ($r = 0$). All data were log transformed (a) prior to standardisation (b).

We found some support of convergent evolution in the response of seed size, with closely related species responding less similarly than expected by chance (Blomberg’s $K = 0.09$, $P = 0.057$). This was particularly evident with *Vulpia*, where one species was less similar to its congeners than to the other grasses (Fig. 1a), but similar patterns were seen in other closely related taxa (e.g., Fabaceae and Boraginaceae). There was no phylogenetic signal in species responses through seed number (Blomberg’s $K = 0.22$, $P = 0.86$) or seed size–seed number correlations (Blomberg’s $K = 0.33$, $P = 0.14$).

Offspring performance

The maternal environment had significant effects on seedling height after 3 weeks of growth ($F_{1,575} = 15.92$, $P < 0.0001$), with a significant maternal environment × species interaction ($F_{25,575} = 2.03$, $P = 0.003$; Fig. S2). The height responses were only partially consistent with the seed size effects – one species that had significantly larger seeds in the dry environment

(*Hordeum vulgare*) also had taller offspring when grown from those seeds in the dry environment. However, this was not the case for many species that showed seed size effects; only 3 of 26 species showed significant or marginally significant ($P = 0.06$ for one species) responses. Nonetheless, a subsequent analysis revealed a positive correlation between seed size and mean plant height ($r = 0.11$, $P = 0.047$, Fig. S3), which was consistent across species (non-significant seed size × species interaction; $P = 0.52$).

We detected maternal effects on seed dormancy that varied by species (significant maternal environment × species interaction; $F_{26,282} = 1.96$, $P = 0.004$), with changes to dormancy being equally frequent as changes to seed size or seed number (Fig. 1c). Although seeds tended to have higher dormancy when the maternal plant was raised in wet environments (six of seven significant responses; $F_{1,334} = 7.1$, $P = 0.008$), there was one species that showed a significant, opposite trend. The maternal environment caused large changes to dormancy for some of these species (from 20 to 48% for *Vulpia octoflora* and from 3 to 9% for *Lotus purshianus*), whereas other species shifted from no detectable dormancy to some dormancy (1–9%). Maternal environment had no detectable effect on seed viability ($P = 0.73$). There was no phylogenetic signal for maternal effects on dormancy (Blomberg's $K = 0.194$, $P = 0.998$) or seedling height (Blomberg's $K = 0.154$, $P = 0.650$).

DISCUSSION

We have shown that the effects of environmental variation on the ecological responses of species are greatly underestimated when maternal effects are not considered. Ecologically important maternal effects, such as changes in seed size and dormancy rates, are not only common, but occur at similar frequencies as changes in seed number (Fig. 1). Because these maternal effects produce responses at the population level, they likely influence long-term growth rates and stability of populations in ways that cannot be predicted by measuring population growth rates based on seed number alone. This study represents the first comprehensive investigation of maternal effects that spans a guild of ecologically similar species, and demonstrates that ecologists should consider these effects on population dynamics, species coexistence and phylogenetic patterns on the landscape.

We detected maternal effects on seed size directly, as well as associated differences in performance. Seed size is known to influence the realised niches of species, with larger seeds conferring competitive advantages and also contributing to survival in stressful conditions such as light or nutrient limitation (reviewed in Westoby *et al.* 1996). We found supporting evidence that within-species variation in seed size confers a weak but significant advantage to early growth even when seedlings are grown in benign, non-competitive environments (Fig. S3), as has been demonstrated in cross-species comparisons (Jurado & Westoby 1992). Previous work on interspecific differences in seed size suggest that the advantages associated with larger seeds may be less than an equal investment in seed number, with every x-fold increase in seed size producing roughly $x^{0.6}$-fold increase in per capita success in the following generation (Freckleton & Watkinson 2001; Levine & Rees 2002). However, the authors of these studies highlight that this estimate provides a guideline at best; further research on the nature of seed size advantages and their importance in different offspring environments is needed both within and among species (Leishman 2001; Moles & Westoby 2004; Germain *et al.* 2013).

Increased investment in seed size may come at the cost of decreased seed number, a trade-off that is commonly observed in plants. We only found strong supporting evidence for this trade-off among species (Fig. 2a), which is consistent with previous studies (e.g. Jakobsson & Eriksson 2000). Within species, however, seed size–seed number correlations ranged from positive to negative (Fig. 2b), suggesting that different constraints may be operating at different levels of ecological organisation. For example, Venable (1992) predicted that positive correlations can arise if variation exists in the resource environment or the size of individual genotypes in a population. Because changes in soil moisture conditions could induce changes to both seed size and number, our experimental setup was well suited to producing a range of correlations. The small sizes of our experimental populations (*c.* eight individuals) likely also increased the likelihood of high-yielding genotypes having large impacts on population-level responses. As such, the variety of correlations between seed size and seed number likely reflects the combined effects of species' allocation strategies across environments as well as individual-level variation within species.

The clearest signal of the maternal environment on offspring performance was through changes in dormancy rates. Dormancy is known to have a large impact on population dynamics, but is often thought to be highest with appropriate environmental signals (e.g. Angert *et al.* 2009) or to be relatively constant when growing conditions vary unpredictably (Cohen 1966). The finding that dormancy tended to decreased in response to a dry maternal environment was surprising, as dormancy is generally thought to increase in response to resource limitation, such as water availability (Tielbörger & Valleriani 2005). One potential explanation is that other reproductive responses may influence dormancy. For example, a negative correlation between seed size and dormancy is predicted by models of bet hedging when large seeds help ensure seedling success in poor years (Venable 2007). We found limited support for this hypothesis, with approximately one-third of species that responded by changing dormancy rates also responded by altering seed size (Fig. 1a,c). For these species, parents in dry soils produced larger seeds with lower dormancy rates.

The maternal effects observed in our study have important implications for species coexistence that are distinct from population-level implications. In particular, coexistence of annual plants in temporally variable environments requires that (1) species respond differently to environmental conditions, (2) they have storage dynamics via seed dormancy and (3) species experience a positive covariance between reproductive potential and intraspecific competition, which allows a rare species to have high reproductive rates in good years (Chesson 1994; Abrams *et al.* 2013). The maternal effects that we observed influence each of these conditions. For example, changes to seed size doubled the number of species showing significant responses to soil moisture and generated almost all of the positive responses to drought, meeting condition (i). Similarly, the effect of the maternal environment on dormancy rates differentially alters both storage (condition (ii)) and germination of species, with the latter contributing to coexistence by altering condition (iii; e.g. Angert *et al.* 2009). Finally, condition (iii) can be met even in species with constant germination rates so long as the per capita competitive effect and reproductive potential of each species respond similar to environmental conditions (Chesson 1994; Chesson *et al.* 2004; Abrams *et al.* 2013). Seed size may generate this covariance, as large seeds have been shown to produce plants that have a greater competitive effect and higher fecundity (Freckleton & Watkinson 2001; Levine & Rees 2002).

The phylogenetic signature of maternal effects also offers new insights into the processes that alter patterns of local species coexistence. Theoretical work predicts that phylogenetic convergence in competitive traits, such as seed size, should deter local coexistence between closely related species (Mayfield & Levine 2010). In temporally fluctuating environments, however, the phylogenetic convergence that we observed in seed size responses to soil moisture may actually promote coexistence between close relatives by favouring different species in different years, as has been predicted by theory (Abrams *et al.* 2013). This intricate matching of competitive ability and environmental conditions leads to contrasting predictions for phylogenetic effects on coexistence depending on the timescale considered (i.e. single vs. multiple years). Moreover, the phylogenetic signal observed was only apparent in seed size responses, suggesting that this maternal effect likely contributes to phylogenetic patterns that emerge from species interactions in this guild.

Although we have shown that maternal effects are common in this annual guild, there are four important caveats to our conclusions. First, our study only measured a subset of maternal effects by quantifying three responses to environmental variation: seed size, seed dormancy and seedling growth. Other studies have found that the maternal environment can also alter seed composition, seed coat characteristics and epigenetics (Roach & Wulff 1987; Donohue 2009). As a result, our results likely underestimate the prevalence of maternal effects. Second, we examine only two environmental conditions. Previous research has shown diverse responses of annual plants to the timing and patterns of variation in precipitation, for example, and quantifying the overall importance of maternal effects requires tests across a broader range of environmental variation (e.g. Hobbs *et al.* 2007). Third, because we obtained seed from commercial suppliers (Table S1), it remains unclear how representative our seeds are of the genetic diversity found in natural populations. Future work on the ecological importance of maternal effects should use a standardised seed collection procedure that provides a representative sample of genetic diversity in populations. Finally, the long-term impacts of maternal effects on population and community dynamics are speculative in our study, which highlights the need for long-term studies that quantify these impacts.

In sum, the diversity of responses that we observed suggests that maternal effects can alter species niches through several pathways, including seed size, dormancy and offspring performance. In evolutionary ecology, it is well recognised that maternal effects can affect the fitness of individuals, often strongly enough to generate artificial signals of natural selection (Roach & Wulff 1987; Donohue 2009). In ecology, however, maternal effects have yet to be incorporated into most models of population growth and species interactions. Our study demonstrates that this failure to incorporate maternal effects effectively eliminates over half of the ways in which species respond to the environment. The varied responses that we observed suggest that testing the range of maternal effects that function in any guild of species may be necessary for understanding the complexity of interactions that promote diversity.

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AUTHORSHIP

RMG and BG designed the experiment, RMG collected the data, RMG performed the phylogenetic analysis, BG analysed the data and RMG/BG wrote the manuscript.

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