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IDEAS & PERSPECTIVES

The maladaptive significance of maternal effects for plants in anthropogenically modified environments

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Abstract Maternal effects directly and indirectly modify an offspring's phenotype during development, preparing the offspring for an environment similar to an environment experienced by the mother. Evolutionarily, this could be adaptive if organisms did not experience a large amount of environmental variation across generations. We argue increased anthropogenic changes have led maternal effects to be maladaptive in plants. Similar problems in humans have been proposed, where metabolic diseases may be increased by a mismatch between the in utero environment and the adult environment; often referred to as the Barker Hypothesis. Plants may experience similar metabolic and functional disorders, caused by maternal effects generated from unreliable environmental cues. In the last 200 years, human activities have increased habitat fragmentation, changed patterns of nutrient deposition, and increased climatic variation within and among years. In this manuscript, we suggest that ecologists should consider the increased negative influence of maternal effects on plant growth and reproduction in spatially fragmented and temporally stochastic landscapes. Several implications for conservation and research arise from this discussion: (1) researchers should focus on evolutionarily relevant measures of spatial and temporal heterogeneity, (2) the maternal history of seeds used for population restoration should be considered, and (3) contiguous habitats should be constructed to reduce the impact of evolutionary traps.

Keywords Barker hypothesis · Climate change · Environmental cues · Evolutionary trap · Fragmentation · Maternal effects · Nitrification · Plants

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Introduction

Maternal effects are a form of cross-generational phenotypic plasticity, induced by the maternal environment (reviewed by Uller 2008; Wolf and Wade 2009). These non-genetic developmental changes incorporate phenotypic variation that cannot be ascribed to genetic variation (Helenurm and Schaal 1996; Uller 2008). Theoretically, these phenotypic changes should benefit the offspring, given environmental cues the mother experienced are similar to the conditions experienced by the offspring (reviewed by Wolf and Wade 2009). Direct maternal effects physically change phenotypic attributes of the offspring during development offspring (e.g. cytoplasmic influences or seed size), while indirect maternal effects alter the offspring's phenotype later in ontogeny (e.g. growth rate which is correlated with seed size) (Roach and Wulff 1987). Recent evolutionary theory has suggested maternal effects should be an adaptive mechanism allowing organisms to tolerate environmental heterogeneity (Donohue and Schmitt 1998; Mousseau and Fox 1998; Galloway and Etterson 2007; Marshall et al. 2008; Galloway et al. 2009; Dyer et al. 2010). However, some research has shown maternal effects do not increase offspring fitness for plants in natural systems (e.g. Kaplan 1992; Kyneb and Toft 2006; Marshall et al. 2008, 2010), although more research is needed in wild plant populations (see Galloway et al. 2009). For this manuscript we consider maternal effects to be plastic across generations, but irreversible within a generation, e.g., a seed cannot be modified by the maternal plant once separated from the maternal plant. According to recent models addressing phenotypic plasticity (Gabriel 2006), this definition would distinguish maternal effects as maladaptive when environmental heterogeneity increases, and behavioral cues become unreliable (e.g. Marshall et al. 2010). We propose maternal effects were likely adaptive in historically more homogenous environments, but current research may find maternal effects to be maladaptive because environmental cues are unreliable in heterogeneous landscapes, due to climate change, nitrification, and habitat fragmentation.

The idea that increased cross-generational environmental heterogeneity causes reduced fitness of offspring is not new, but has not been considered to be negatively affecting wild plant populations. The Barker Hypothesis (Barker 1997) was proposed to help understand the increased prevalence of human metabolic diseases. Adults whose diets significantly differed from the diet their mother had during pregnancy were proposed to have an increased chance of metabolic disorders. More often, researchers believe this occurs when mothers are food deprived during pregnancy, and then the offspring experience a food-enriched adult environment (Barker 1997; Ravelli et al. 1998; Godfrey and Barker 2000). A commonly cited example of this occurring in humans has been Dutch children born during or just following World War II (although other examples may exist from Polynesian cultures and Americans exposed to the fast-food restaurant boom) (Ravelli et al. 1998; Roseboom et al. 1998). Many Dutch mothers who became pregnant during World War II had very little food, and likely initiated metabolic pathways through direct maternal effects to increase the probability their children survived starvation-like conditions. Following World War II, food resources significantly increased for many families, but many of those children were not metabolically equipped to tolerate "feast" conditions; a probable example of an indirect maternal effect. Interestingly, reduced fitness of these adults should be a single-generation phenomenon (currently unknown for the Barker Hypothesis), but maternal diet effects seem to last for multiple generations in other animals, often referred to as grandmaternal effects (Mech et al. 1991; Kyneb and Toft 2006; Kjaersgaard et al. 2007; Ruager-Martin et al. 2010). Evidence from other animals suggests that humans may experience an increase in metabolic disorders for many generations.

Through maternal effects, plants make morphological and physiological changes to seeds. Experimental studies have shown that maternal effects overwhelmingly affect seed size, germination timing and success, leaf production, and early growth in plants (Roach and Wulff 1987; Helenurm and Schaal 1996), but can also affect later development, such as timing of flowering and reproductive success (Schmid and Dolt 1994; Helenurm and Schaal 1996; but see Bischoff and Muller-Scharer 2010). Changes to seeds by maternal plants are induced by environmental cues, presumably because these environmental cues are reliable predictors of future germinating conditions. Over evolutionary time, the strength of maternal effects should be tempered to match the proportion of offspring that experienced an environment similar to the environment that the maternal plant experienced. Related to this argument, Helenurm and Schaal (1996) discussed that maternal effects should be most evident in large-seeded plants, due to differential provisioning of seeds. Therefore, most seeds modified through maternal effects should experience environments similar to the maternal environment because the majority of large seeds fall near the parent plant, or because animal dispersal vectors frequently deposit seeds in habitats similar to those experienced by maternal plants (Nathan and Muller-Landau 2000). However, in contemporary landscapes, widespread anthropogenic environmental change has altered the composition and connectivity of landscapes. Therefore seeds will more often fall into different habitats, and maternal effects could negatively affect fitness and population growth.

Environmental cues such as precipitation, temperature, light and nutrient availability were historically indicative of ecologically reliable outcomes, such as suitable early-season germination (Khurana and Singh 2001; Donohue et al. 2005; Wolfe and Mazer 2005). These reliable cues perhaps increased offspring fitness when plant phenotypes were modified from environmentally induced maternal effects. Anthropogenic climate change has increased stochasticity in temperature and rainfall, which were historically predictable cues across seasons (see Comstock and Ehleringer 1992; Moron et al. 2006; Garcia et al. 2010). Alterations in precipitation patterns due to climatic change can trigger premature seed germination, which can greatly reduce plant fitness (Rodrigo 2000; Lucas et al. 2008). Spatially, fragmentation has increased edge habitats and altered abiotic cues and biotic interactions (Cordeiro et al. 2009), which would affect the quality of the environmentally induced maternal effects. Edge habitats can reduce plant growth, reproduction, gene flow, and population size (Hooftman et al. 2003). Finally, nitrification and fertilization have created heterogeneous patches of nutrient-rich and nutrient-poor habitats (Strong et al. 1998; Matejek et al. 2010). These rapid environmental changes have decreased the reliability of environmental cues, and seeds have a higher probability of falling in habitats dissimilar from the mother's habitat. Therefore, habitat fragmentation and climate change likely cause unreliable cues for plants, leading to reduced offspring growth and reproduction.

Implications of maternal effects and evolutionary traps in plants

Evolutionary traps occur when organisms make seemingly good decisions, but realize sub-optimal outcomes due to a rapid change in environmental conditions that alters cue reliability and disconnects the cue from its previously adaptive outcome (Schlaepfer et al. 2002; Battin 2004). Historically, the discussion of evolutionary traps has focused almost exclusively on animals; for example, nest-site selection in birds and feeding behaviors in turtles (Schlaepfer et al. 2002; Battin 2004). A literature search using the ISI Web of

Science database revealed only one discussion of potential evolutionary traps in plants (Quintana-Ascencio et al. 2007). In their demographic study of *Hypericum cumulicola*, Quintana-Ascencio et al. (2007) observed reduced average fitness in populations that dispersed seeds to roadside habitats. Seeds could germinate and grow in roadside habitats, but future reproduction was greatly reduced, therefore the species may be experiencing an evolutionary trap (Table 1).

If maternal effects in plants receiving unreliable cues reduce fitness for only one generation, then any reduction in fitness would be expected to be negated in the following generation. However, like animals, plants have been shown to exhibit grandmaternal effects (Wulff et al. 1999; Molinier et al. 2006; Rohde and Junttila 2008). The long-term nature of grandmaternal effects means that any phenotypic changes made by maternal plants within each generation, could leave many generations with unsuitable phenotypes. Additionally, the effects of climate change and fragmentation are not decreasing, so plants will probably experience more environmental variation and unreliable cues in future generations. These combined effects could lead to prevalent evolutionary traps, especially for annual plant species that are rare or endemic.

Evolutionary traps in plants present many of the same challenges as evolutionary traps for animals (Schlaepfer et al. 2002; Battin 2004). Interestingly, few studies proposing evolutionary traps for animals have long-term data sets indicating a population decline (Schlaepfer et al. 2002; Battin 2004). Long-term datasets exist for many plant species, and many plant species are declining, yet the mechanisms responsible for declining plant

Table 1 Maternal effects that may lead to evolutionary traps, when environmental cues become decoupled with photoperiodic cues

Environmentally induced trait	Decoupled cues	Consequence
Seed morphology	Nutrients and temperature	Nutrient deposition and increased temperatures lead to smaller seeds that may disperse far from the maternal plant, and land in habitats that do not match the maternal environment (e.g. Ehrlen and Eriksson 2000). Different soil types will inevitably affect germination and growth.
Germination time	Water and temperature	Early, warm spring rains followed by major frost events kill seedlings because maternal effects change the timing of germination by changing seed size, seed coat and possibly cytoplasmic inheritance (e.g. Rodrigo 2000; Kolesnichenko et al. 2003; Lucas et al. 2008).
Metabolic Pathways	Temperature and nutrients	Temperatures experienced by offspring that differ from the maternal environment reduce growth rates and possibly reduce photosynthetic abilities of seedlings, because maternal plants alter seedling physiologies through cytoplasmic inheritance. (e.g. Major and Davison 1998). Similarly, seeds from plants in low-nitrogen environments may exhibit suboptimal growth or allocation in habitats where nitrogen deposition has occurred due to maternal effects that were fixed in the low-nitrogen maternal environment. This example matches those of the Barker hypothesis (Barker 1997).

These environmental cues were stable across ecological time-scales; due to climate change and fragmentation, they have become unpredictable across habitats. Individuals trapped in an evolutionary behavior of maternal effects experience a detrimental effect, which leads to decreased fitness and reduced population size. The studies cited within the table are examples of when previously adaptive environmental cues are likely decoupled from adaptive fitness outcomes, leading to reduced growth or reproduction in plants populations are often poorly understood (e.g. Ouborg et al. 2006), and the degree to which maternal effects could be generating evolutionary traps is unknown. Fortunately, mechanisms that can help trapped plant populations persist, are similar to those proposed for animals by Battin (2004). For plants, a high potential for evolution and within-generation plasticity are two primary mechanisms that could save plant populations experiencing an evolutionary trap (Thompson 1991).

Maternally derived evolutionary traps have several important implications for conservation and restoration. For plant species that exhibit considerable maternal effects, large contiguous habitats will also help maintain populations above an effective population size, favoring rapid evolution and decreasing the role of genetic drift in affecting changes in allele frequency (e.g. Newman and Pilson 1997). Fortunately, this recommendation is consistent with other conservation goals, such as increased overall population size and increased species diversity.

For animal-dispersed plants, the loss of animal dispersal vectors may exacerbate the effect of evolutionary traps, as seeds are unlikely to be deposited in habitats similar to those experienced by the maternal plant (e.g. Guzman and Stevenson 2008). The loss of dispersal vectors may be particularly detrimental on islands where invasive species have displaced or eliminated vectors (Kueffer et al. 2009). Assisted dispersal (McLachlan et al. 2007) is a popular conservation tool for re-locating plants that may be unable to disperse at a rate sufficient to keep pace with changes in climate (Hoegh-Guldberg et al. 2008; Ricciardi and Simberloff 2009). Successful assisted dispersal and restoration are analogous because both often rely on seed from source populations. If maternal effects are important for successful establishment in new habitats, our work adds further support to the hypothesis that seeds used for assisted migration and restoration will be most successful when collected from nearby source populations in similar habitats, an argument often based on local adaptation (reviewed by Hufford and Mazer 2003; McLachlan et al. 2007). For species with strong maternal effects, maternal plants could be grown under appropriate environmental conditions to promote successful establishment of new populations. For example, if researchers are planning to perform assisted dispersal to habitats where longer day length is indicative of suitable temperatures for growth, maternal plants can be reared under the appropriate light cues so maternal effects are adaptive.

Future directions

We suggest that future research on evolutionary traps caused by maternal effects must grapple explicitly with spatial and temporal scales of heterogeneity. Such heterogeneity should not be defined as a human-measured difference between two conditions in the environment (Kleb and Wilson 1999). Instead, heterogeneity should be examined based on the perceptual range of the maternal plant, the extent of seed dispersal in space and time, and the strength of the maternal effect. More generally, we suggest that evolutionary traps may be common and widespread in plants, and that the possible effects of these evolutionary traps should be considered when planning efforts to conserve and restore plant populations in fragmented landscapes with human-induced climate change.

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