GENETIC CONSEQUENCES OF BIOLOGICALLY ALTERED ENVIRONMENTS

Authors: Michelle D'Aguillo[1,2,3], Caleb Hazelwood[1,2,4], Brandie Quarles[1,2], Kathleen Donohue*[2]

[1] These authors contributed equally to this work and are listed alphabetically

[2] Duke University, Department of Biology, Box 90338, Durham, NC 27708

[3]Wesleyan University, Department of Biological Sciences, 52 Lawn Ave., Middletown, CT 06459

[4]Duke University, Department of Philosophy, Box 90743, Durham, NC 27708

*Author for correspondence: k.donohue@duke.edu

ABSTRACT

Evolvable traits of organisms can alter the environment those organisms experience. While it is well appreciated that those modified environments can influence natural selection to which organisms are exposed, they can also influence the expression of genetic variances and covariances of traits under selection. When genetic variance and covariance change in response to changes in the evolving, modified environment, rates and outcomes of evolution also change. Here we discuss the basic mechanisms whereby organisms modify their environments, review how those modified environments have been shown to alter genetic variance and covariance, and discuss potential evolutionary consequences of such dynamics. With these dynamics, responses to selection can be more rapid and sustained, leading to more extreme phenotypes, or they can be slower and truncated, leading to more conserved phentypes. Patterns of correlated selection can also change, leading to greater or less evolutionary independence of traits, or even causing convergence or divergence of traits, even when selection on them is consistent across environments. Developing evolutionary models that incorporate changes in genetic variances and covariances when environments themselves evolve requires developing methods to predict how genetic parameters respond to environments—frequently multifactorial environments. It also requires a population-level analysis of how traits of collections of individuals modify environments for themselves and/or others in a population, possibly in spatially explicit ways. Despite the challenges of elucidating the mechanisms and nuances of these processes, even qualitative predictions of how environment-modifying traits alter evolutionary potential are likely to improve projections of evolutionary outcomes.

Key words: genotype-environment interaction, GxE, habitat selection, indirect genetic effects, niche construction

Introduction

Organisms alter the environments they experience in many ways: active modification of the environment around them, habitat choice, dispersal, cued developmental timing, or social behaviors. Variously referred to as "habitat selection" (Levins 1968; Holt 1987; Rosenzweig 1987; Brown 1990; Bazzaz 1991; Whitlock 1996; Donohue 2003) "indirect genetic effects" (Moore et al. 1997; Wolfe et al. 1998), and "niche construction" (Odling Smee et al. 1996, 2013; Laland et al. 1999; Saltz and Nuzhdin 2014), the fact that evolvable traits of organisms can determine the environmental factors to which those organisms are exposed has important evolutionary consequences. Much attention has focused on the ability of organisms to modify the environment that exerts natural selection (Day et al. 2003; Donohue 2002 2005; Schwilk 2003, Bolnick and Otto 2013; Snell-Rood 2013). However, environments modify not only the presence and strength of natural selection, but also the expression of genetic variance and covariance of traits under selection. That is, environments modify both of the primary components that determine evolutionary responses to selection: selection and G-matrices. When the environments that modify genetic parameters are the result of biological traits with a genetic basis, genotype-environment correlations will emerge. Because the default assumption in most evolutionary models is that the environment varies randomly with respect to genotype, these correlations have important evolutionary consequences that are frequently neglected. Here we discuss the main evolutionary consequences of the potential of evolvable traits to modify environments in ways that alter genetic variances and covariances.

Evolvable traits modify environments, and environments modify genetic parameters.

Organisms modify the environments they experience in ways that influence the natural selection to which they are exposed, and this outcome of environmental modification has been well acknowledged in the literature on indirect genetics effects and niche construction. How those environments influence the expression of genetic variances and covariances has not been as well appreciated. Here we first discuss the basic mechanisms whereby evolvable traits modify environmental factors to which organisms are exposed, and second review the evidence that those environmental factors in turn modify genetic variance and covariance of traits (Table 1).

Genetically based traits modify the environments that organisms experience

Organisms can modify the environments they experience by adjusting their behavior, morphology, or development (Odling-Smee et al. 1996, 2013). Most intuitively, organisms may actively physically modify aspects of their environment, for instance by constructing shelters from environmental stressors (e.g., nests, burrows, egg sacs, or other provisioning) or structures that improve resource capture (dams, pit traps, cup structures). This sort of direct habitat modification has been referred to as "niche construction" or "ecosystem engineering," with the latter, in particular, referring to cases in which the environments experienced by other members of an ecosystem are also modified, in addition to the environment of the organism that modified the environment.

More passive modifications to the environment include chemical secretions or waste deposition (which may be toxic, act as fertilizer, or some other sort of attractant or inhibitor), and resource depletion, including shading of self or others. For example, bacteria exude metabolic waste products that influence their own population growth as well as that of other bacterial strains, and some plants exude allelopathic chemicals that alter the fertility or toxicity of the soil around them and thereby alter competitive environments (Wardle et al. 2011). The mere depletion of limited resources results in resource-poor environments. For plants, light capture by leaves frequently depletes light beneath a canopy, which can affect the recruitment of progeny, ramets, or even other leaves on the same individual (Enríquez and Pantoja-Reyes 2005; Zimmerman et al. 2010).

Organisms also modify the environments they experience by moving in space, frequently referred to as "environmental tracking." Many organisms actively collect information about their environment, assess that information, and alter their location in response to that information, in a process called "habitat selection." Mobile animals can exhibit this behavior at a local scale, for example by moving from sun to shade for thermoregulation (Muñoz and Losos 2018), or a more regional scale through migration. Even plants can exhibit habitat selection by putting down runners and preferentially establishing roots in locations with high resources, for example (Bazzaz 1991). Other forms of directed dispersal are also known in plants, whereby dispersal structures such as eliasomes (lipid-rich appendages that attract ants) or viscous adherents increase the probability that seeds are deposited in specific favorable locations (e.g., in ant nests, or on tree trunks). Thus, even if the external environment is not itself altered, from the perspective of the organism, the environment it experiences is modified by its behavior.

Organisms can also modify the environment that specific life stages are exposed to by regulating their developmental timing, or phenology, a form of temporal habitat tracking (Donohue 2005). Different life stages frequently have different environmental tolerances or optima; matching each life stage to the environment that permits growth and survival to the next life stage is therefore necessary in environments that vary over time, such as seasonal environments. Developmental transitions in both plants and animals are often cued by environmental factors such as temperature, light, photoperiod, water availability, or crowding. Such regulation of developmental timing by environmental cues is effective at determining the environment that is experienced by the life stages that follow that developmental transition (e.g. Burghardt et al. 2016, D'Aguillo et al. 2019).

Lastly, social behaviors can shape the social environment experienced by others in interacting groups, by modifying density, aggressive environments, acoustic environments, and access to mates or other resources. In *Drosophila melanogaster* for example, the presence of male aggression, which is genotype-specific, affects sex ratios within groups, since aggressive males exclude other males from groups (Saltz and Foley 2011). Parental provisioning, as shown in dung beetles for example (Schwab et al. 2017), is also considered to be a social behavior that affects other group members. The theory on "indirect genetic effects" or "IGEs" was developed to explain these phenomena, whereby evolvable traits of organisms result in social environments that both affect traits that others in the group express and also affect the mode and intensity of natural selection acting on those traits (Moore et al. 1997, Wolf et al. 1998).

In summary, organisms have diverse ways of modifying environments they experience at specific life stages or throughout their lives. Active habitat modification, resource consumption or metabolic exudation, dispersal through space or time, and social behaviors can all regulate the environments that organisms are exposed to. These environments include abiotic (e.g., thermal or moisture) environmental factors, seasonal environmental factors, competitive or pathogen environment, resource environment, or social environment. Many of these factors are indicators of stress or resource quality. All of these classes of traits--behavior, secondary metabolism, dispersal, and phenology--are well known to have a genetic basis. As such, when they evolve in response to natural selection, the environments that result from those traits also evolve.

The environment alters genetic variances and covariances

Dozens of empirical studies have documented that the expression of genetic variance and covariance depends on environmental conditions (reviewed in Hoffmann and Merila 1999, Snell-Rood et al. 2016, Stearns et al. 1991; Table 1, Supplemental Table S1). Such environment-dependent genetic parameters result from genotype by environment interaction (GxE), in which different genotypes respond differently to environmental factors (Fig. 1A). One of the earliest documentations of this phenomenon emphasized that GxE could mask genetic variation in some environments and expose it in others (Via and Lande 1985, 1987), leading to environment-dependent genetic variances. The function whereby environments alter the expression of genetic variation may take many forms (Fig. 2A), but in most cases the precise function is not known. Regarding genetic covariances, when different traits exhibit different patterns of phenotypic plasticity to environments, genetic covariances among traits can be environment-dependent (Donohue 2015; Wood and Brodie 2015). For instance, if one trait does not exhibit plasticity in any genotype, but another trait does exhibit GxE for that trait such that the rank order of genotypes changes, then the direction of correlation between traits can change across environments (Fig. 1B).

Despite some qualitative predictions about how environments are expected to alter genetic parameters, empirical evidence for those trends is mixed (Table 1; Supplemental Table S1). Regarding environment-dependent genetic variance, it has been hypothesized that novel environments, in particular, are likely to reveal genetic variation that has not yet been exposed to natural selection, resulting in higher genetic variance expressed in novel environments. This prediction has sometimes been supported (reviewed in Charmantier and Garant 2005). Similarly, others have speculated that "stressful" environments are also more likely to reveal genetic variation caused by genomic mis-regulation (reviewed in Hoffmann and Merila 1999; Rutherford and Lindquist 1998, Jarosz and Lindquist 2010), including deleterious recessive allelic effects that contribute to inbreeding depression (Armbruster and Reed 2005; Cheptou and Donohue 2011; Fox et al. 2011). This prediction has been supported in cases of stressful temperatures, for instance (Bubily and Loeschcke 2000; Szafraniec et al. 2001). A stressful environment can be considered to be one to which an organism has not yet adapted; as such it reveals genetic variation for the same reason that a novel environment would reveal genetic variation.

Stressful or limiting conditions may magnify the expression of genetic differences in some traits, especially timing traits. When development is slower (takes longer) under poorer conditions, the difference in growth rates may be magnified (as is the distance between horses on a longer racetrack), increasing the expression of genetic variation; conversely, growth may be more synchronous under favorable conditions, leading to lower genetic variances. Both poor food quality (Holloway et al. 1990; Kause and Morin 2001) and lower or sub-optimal temperature, which slows development (De Moed et al. 1997; Guntrip et al. 1997; Snell-Rood et al. 2016; D'Aguillo et al. 2019), have been associated with greater genetic variance. One study in ladybird beetles found that genetic variance for size traits increased over ontogeny as food became more limiting (Dmitriew et al. 2010), illustrating how limiting conditions can magnify genetic differences even over the course of development.

In contrast, stressful environments can also decrease the expression of genetic variance (Table 1, Supplemental Table S1). One reason for this is that limiting conditions may impose boundaries on the expression of extreme phenotypes, whereas favorable conditions may allow a larger range of variation to be attained by genotypes that are endowed with the ability to take advantage of those favorable conditions. Low genetic variation for size, growth, and reproductive traits has been documented under low-resource conditions (Gebhardt-Henrich and Noordwijk 1991; Ebert et al. 1993; Merilä 1997; Lazarević et al. 1998; Bubily and Loeschcke 2000).

Genetic covariances also depend on environmental conditions (Figs. 1 and 3). This has been observed in diverse organisms including insects (Gebhardt and Stearns, 1988; Lazarević et al. 1998; Krebs and Loeschcke 1999; Messina and Fry 2003), birds (Larsson 1993), amphibians (Newman 1988a,b, 1989), and plants (Donohue et al. 2000; Shakhatreh et al. 2001; Stinchcombe 2002). These are sometimes manifest as negative correlations between developmental speed and other traits, such that, for example, slow development occurs with large body size (e.g., Kause and Morin, 2001). Similarly, low temperature, which slows development in many organisms, can induce tradeoffs (Windig 1994; Norry and Loeschcke 2002). Moreover, when limiting conditions alter genetic variances for traits, the corresponding covariances among traits may also be reduced (e.g., Guntrip et al. 1997).

Environment-dependent genetic correlations may also be manifest as resource-dependent allocational tradeoffs, when genetic variation in resource acquisition is expressed only in resource-rich environments (Stearns 1989, 1992; Houle 1991). For example, under conditions in which all individuals are resource-limited, some genotypes may allocate more to immediate reproduction while others allocate more to growth, leading to negative genetic correlations manifest as tradeoffs. In resource-rich environments, in contrast, some genotypes may excel at acquiring resources and have more resources to allocate both to growth and reproduction, leading to positive genetic correlations.

In summary, environments commonly alter genetic variances and covariances. They do so by establishing limits to the expression of phenotypic extremes, by altering developmental rates in ways that magnify or canalize differences among genotypes, by determining resource limitation that influences the expression of allocational tradeoffs, or by reflecting the past history of natural selection (or lack thereof) which may have depleted genetic variance.

Biologically altered environments alter genetic parameters

We have shown that organisms can alter their exposure to diverse environmental factors, and that those environmental factors can alter the expression of genetic variances and covariances (Table 1). In particular, exposure to stressful environments--both abiotic and biotic--and resource abundance or quality are factors that organisms are especially likely to regulate their exposure to. These factors, in turn, are known to alter the expression of genetic variances and covariances. Despite the scarcity of empirical studies that directly document that environment-modifying traits cause changes in the expression of genetic variances and covariances in the same system, the ubiquity with which both steps of that pathway have been documented suggests that such dynamics are likely to be common.

A small number of studies have, in fact, examined both the environmental factors that organisms modify and the effect of those environmental factors on genetic parameters in the same system. For instance, the experimental disruption of provisioning of brood balls by *Onthophagus* dung beetles significantly truncated the range of genetic variation for adult body size that was exposed to natural selection (Snell-Rood et al. 2016). In sand crickets, those with a genetic predisposition toward growing large wings also demonstrate preference for temperatures that produce small wings, and vice versa (Roff and Shannon 1993, Bégin et al. 2004, Saltz and

Nuzhdin 2014). Consequently, the full extent of available genetic variation for wing size is not expressed due to genetically based temperature preferences and GxE for wing size. In another cricket, the acoustic environment, which is socially determined by mating displays, altered the heritability of behavioral "personality" traits, such that genetic variation was lower in the silent acoustic environment than under conditions of vocal displays (Rudin *et al.* 2018).

These studies explicitly connect an organism's capacity to modify its environment and the environment's effect on genetic parameters. Future studies that measure or manipulate an organism's environmental modifications could usefully quantify not only their effects on fitness and natural selection (Matthews *et al*. 2014), but also effects on genetic variances and covariances that determine evolutionary responses to that selection. By modifying environmental factors, organisms can alter the expression of genetic variation of any traits that exhibit GxE to that environmental factor. By influencing the expression of genetic variance and covariance, evolutionary dynamics can be affected independently of effects of the environment on natural selection. Changes in environment-modifying traits, whether plastic or evolutionary, can therefore alter evolutionary dynamics by altering both selection and G-matrices.

Individual to population-level consequences of biological modification of environments

So far, our discussion has concerned how traits of organisms influence the environment that those organisms, themselves, experience. However, genetic variances and covariances are properties of populations. How do the environment-modifying attributes of individuals translate to population-level outcomes? It depends on whether environmental changes are experienced only by the individuals that produced those changes, by groups of interacting individuals in a population, or by the entire population. It also depends on how environmental modifications of collections of individuals combine to influence environments at different spatial scales.

First, if a single individual experiences its modified environment, that individual can have an altered phenotype through phenotypic plasticity, an altered average allelic effect (at one or more loci) through genotype-environment interactions, and altered fitness through altered natural selection on that phenotype. If a collection of individuals in a population all experience the same modified environment simply because they share the trait that modifies that environment for themselves, genetic variation segregating at the loci that determine that trait—and at linked loci elsewhere in the genome—may change in response to the environment caused by the environment-modifying trait.

In this case of organisms determining only their own environment, the population-level genetic variance (and covariance) would depend on the proportion of the population that expresses the allele(s) that result in a specific phenotype of the environmental-modifying trait, and the environment-dependent genetic expression induced by that environment, considered over all environments that the population experiences. Those proportions themselves would depend on the frequency of individuals with specific environment-determining traits. As selection on those traits alters those proportions, genetic variance and covariance itself would change dynamically (Fig. 1C).

In addition, genetic variance and covariances of traits may be determined by other, non-environment determining loci throughout the genome. How these genetic variances and covariances would change in response to allele-frequency changes at the environment-determining loci would depend on the linkage disequilibrium between the environment-determining locus and other segregating loci that determine these other traits.

Traits may modify environments experienced not only by the individual itself, but also environments experienced by other individuals. The extent of environmental change experienced by others would depend on how a trait modifies the environment and how far that modification extends beyond the individual that modified it. Models of IGEs have addressed this issue within the framework of interacting dyads or more extensive networks of interaction among partners of different genetic relatedness and/or within different interaction intensities (Bijma 2011, 2014; Araya-Ajoy *et al*. 2020). Figure 4 illustrates where the dynamics discussed within this paper fit into the IGE framework (with unique components, not currently incorporated within the IGE framework depicted in red). In a simple scenario, if the modification is distributed evenly throughout the population, then the resulting environment experienced by all individuals in the population can be predicted by the frequency of phenotypes in the population (Fig. 4). If environmental modifications have more local effects, however, more spatially explicit models would be necessary to predict which environment is experienced by what proportion of the population. Since environments covary with the traits that determine them, one can expect that certain genotypes would be more likely to be exposed to certain environments than others (Wood and Brodie 2016), but the population-level genotype-environment covariance would also depend on dispersal and population mixing as well, if environmental modifications extend beyond the individual modifying it. As a consequence, the population-level covariance would depend on the degree of spatial population structure, the degree to which environmental modification extends beyond the experience of the modifying individual, and how environments modified by different individuals combine to determine outcomes. For instance, does one environmental modification extend farther than other modifications, is one environment dominant over another, or are they additive?

If the genotype-environment covariance can be estimated for a population, then the resulting environment-dependent genetic variances and covariances of the population may also be estimated. To do so requires knowing a) allele frequencies for environment-determining traits in the population, or the frequency of the environment-determining traits in the population; b) how environmental influences from multiple individuals combine to determine the environment experienced by an individual; c) the frequencies of environments experienced by specific genotypes in that population, which provides information on the covariance between alleles and environments at the population level; d) the function of how average effects of alleles depend on the environment. Clearly, this effort has many challenges, especially considering the multivariate aspects of these dynamics: multiple traits may determine environments, multiple traits may respond to environments, and multiple environmental factors may modify traits and the average effects of alleles that determine those traits. Explicit manipulations of the genetic composition of populations would be required, combined with measurements of the resulting environment, as well as measurement of genotype-specific phenotypes that provide estimates of genetic parameters in the environment that the population inhabits.

Despite the potential complexity of these interactions, rates of evolution and how quickly adaptive plateaus are reached are likely to depend on whether these combined dynamics result in the sustained expression of genetic variance or in the progressive masking of it. Even making such qualitative predictions about whether biologically modified environments release or mask genetic variation could be useful in predicting evolutionary momentum or conversely, evolutionary limits, as discussed next.

Evolutionary consequences of the influence of biologically altered environments on genetic parameters

Environment-dependent genetic variation

When genetic variances change as a consequence of biologically modified environments, evolutionary responses to selection can be more extreme or diminished (Fig. 2C). The magnitude of responses to selection each generation is directly proportional to the magnitude of genetic variance for traits under selection, as defined by the breeder's equation of quantitative genetics, (conditioned by genetic covariances among traits, as discussed in the next section). If traits alter environments in a manner that increases the expression of genetic variation for traits under selection, then populations may evolve more extreme phenotypes per generation of selection. In contrast, if traits result in environments that reduce the expression of genetic variation, smaller per-generation responses to selection would result.

When environment-modifying traits themselves evolve, environments can change directionally over time, affecting how genetic variation is expressed over time (Donohue 2005, 2009; Fig. 2C). Within the framework of IGEs, a new parameter ($E_{a,e}$ in Fig. 4) that describes how genetic variance responds to biologically altered environments ($e_{z'\mathrm{i}}$, in the IGE framework; Fig. 4) can usefully be incorporated. These directional changes in environments can alter how sustained or truncated responses to selection can be. If the environment evolves in a direction that causes genetic variation to be expressed, then adaptation can proceed for longer. For example, Wender et al. (2005) showed that plant traits that influence post-dispersal density have a genetic basis and can evolve, and that the genetic variation and heritability for those traits was of a higher magnitude when those plants were grown at high density (Donohue et al. 2005). If selection favors low post-dispersal density, as it frequently does, then the evolution of traits that produce low density would decrease the expression of genetic variation for those traits, constraining further response to selection. If the opposite happened to be true—that low density revealed rather than masked genetic variation for dispersal traits—then the evolution towards low density would enable even more sustained response to selection for low density (Donohue 2005). A simple model showed that the directional evolution of environments can alter rates and durations of the adaptation of traits whose genetic variance depends on those environments (Donohue 2009). One other theoretical treatment (Marjanovic *et al*. 2018) considered how IGEs could alter phenotypic variation under competitive and non-competitive conditions and found that phenotypic variation (although not genetic variation *per se*) itself can evolve. In this model, the parameter describing the plastic response of a trait to the modified environment (Ψ; Fig. 4) was permitted to evolve; the model did not consider environment-dependent genetic expression *per se*, even though the evolution of plasticity on which the evolution of Ψ depends, requires GxE.

Note that IGEs have previously garnered interest because they can produce “runaway” processes, or positive evolutionary feedbacks. In those prior treatments, one trait determines the environment that elicits plasticity in another trait, and this second trait alters the environment in a manner that exerts selection on the first trait (Wolf et al 1998; Bailey and Moore 2012; Bailey and Kölliker 2019). Here we present another mechanism for positive or negative feedbacks, resulting not from plasticity and selection, but from environment-dependent expression of genetic variation.

Environment-dependent genetic covariances

Environments alter not only the expression of genetic variation for single traits, but genetic covariation among traits, sometimes even altering the direction of the covariance (reviewed above). Because natural selection frequently acts on multiple traits simultaneously or on combinations of traits, changes in genetic covariances can alter patterns of indirect selection, and thereby total selection, on correlated traits (Fig. 3).

Consider a simple case of a correlation between bill length and bill depth in a bird. If those two traits are positively genetically correlated, direct selection for deeper bills would result in the evolution of longer bills as well, via indirect selection. If a change in the environment caused those two traits to become uncorrelated, then natural selection for deeper bills could result in deep bills that remain short: traits may respond more independently to natural selection. The opposite may be true as well. If the environment changes in a manner that causes stronger correlation among traits, indirect selection would be stronger. When correlated traits are being selected in opposing directions, adaptive evolution can be strongly constrained, since indirect selection opposes direct selection. In this manner biological modification of environments has the potential to modify the evolutionary independence of traits or conversely, the strength of evolutionary constraints.

In the extreme, if an environment changes the direction of a correlation, then the direction of indirect selection could change as well. Consider a trait that is not under direct selection, but is correlated to one that is, and the direction of that correlation changes with the environment (Fig. 3D). In one environment it may evolve in a given direction because of direct selection on the correlated trait, yet in another environment, direct selection in the same direction on the correlated trait could cause a response in the opposite direction because of indirect selection. That is, divergence in a trait across environments may result, even when the direction of direct selection is the same in those environments. Biological modifications of the environment can thereby alter trajectories of evolutionary divergence.

Diversification and evolutionary extremes

It has been argued that certain manifestations of biological modifications of environments, such as IGEs (Wolf et al. 1998; Bijma and Wade 2008) or maternal effects in particular (Wolf and Wade 2009, 2016), can contribute to the evolution of extreme phenotypes and ultimately speciation. When environment-modifying traits have a genetic basis and are subject to directional selection, the environment itself can evolve. In these cases, the optimal phenotype can change as a function of the evolving environment-modifying trait, and the population must adapt to a moving target. This alone can lead to the evolution of more extreme phenotypes, since the environment itself may become more extreme.

Adapting to one's own environment, moreover, contributes to diversification and potentially reproductive isolation. Co-adaptation of offspring traits to match the environment created by mothers, for example, results in lineages that are adapted to their own modified environment, but which are potentially less adapted to the environmental modifications of other lineages (Wolf et al. 1998; Wolf and Wade 2009, 2016). Mating across those two lineages produces a mismatch of environments and adaptations, resulting in reduced hybrid offspring fitness: a manifestation of reproductive isolation.

When biologically modified environments influence not only the strength and direction of natural selection but also the expression of genetic variances and covariances, the evolutionary processes of divergence, and possibly diversification as just discussed, are contingent on those changes in genetic parameters. In concert, selection may be in the direction of more extreme phenotypes and divergence, but environmental effects on genetic parameters may limit those trajectories (Fig. 2C). On the other hand, changes in genetic parameters could augment trajectories of divergence, or even change the direction of short-term outcomes. The prevailing scenario will be dependent on how biologically modified environments alter genetic parameters.

Future challenges

Predicting the evolutionary outcomes of biologically modified environments and their ability to modify genetic parameters depends on knowing how genetic variances of traits depend on continuous, multifactorial environments. This review shows abundant evidence that genetic parameters are environment-dependent, and descriptive estimates of functions of how genetic parameters change with environments are certainly possible, as those studies show. However, our mechanistic understanding of how genetic parameters change with environments, especially continuous or multifactorial environments, is very limited. Moreover, descriptive studies in existing environments cannot necessarily project changes in genetic parameters in novel environments.

As of yet, we have little ability to predict values of genetic parameters that would be expressed in novel environments, despite the urgency of doing so under conditions of rapid environmental change. Some process-based models that are calibrated to specific genotypes can predict the phenotypes expressed in novel environments (reviewed in Chuine and Régnière 2017), and the phenotypic differences among genotypes in those environments (i.e., their genetic variance; Burghardt et al. 2015). While we are far from a general framework for making such predictions, these models are an important step forward.

Even assuming such functions of environment-dependent changes in genetic parameters can be obtained, we do not yet have explicit evolutionary models that predict *population* outcomes when environmentally modifying traits evolve in ways that influence the expression of genetic parameters (Fig. 4). Translating the environmental modifications of individuals into spatially explicit models of changes in environments experienced by a population, or subsets of a population, is necessary. Models that include covariances between genotypes and environments are a promising start (Aastveit and Aastveit 1993; Plomin 2014; Wood and Brodie 2015, 2016). More consideration of how environmental changes combine across a landscape is necessary to anticipate how trait evolution alters environments locally or more regionally across the distribution of a population. Future models could project evolutionary trajectories for a single environment-modifying trait in a population, for other traits expressed by individuals in the same population, or even of traits of other organisms in different populations or different species. Coevolutionary models could incorporate how genetic parameters of one species depends on the environmental modifications made by another species.

Working alongside advances in modeling, appropriately designed experiments that can test for changes in genetic parameters due to biological modification of environments are key. Researchers working in systems with niche construction or IGEs should consider violations to the default assumption that genotypes will be randomly distributed across their environments and interpret results in light of these violations. A second step forward will be to add to the growing number of studies that explicitly quantify how individuals with different environment-modifying traits alter the environment (Matthews *et al*. 2014). Experiments that explicitly test for changes in genetic parameters caused by biological modifications of the environment are challenging, but they are possible. For example, "modified” versus “non-modified” environments can be generated as a result of ongoing environmental-modification behaviors within an experiment, or they can be artificially manipulated by manipulating the genetic composition of the population with respect to the environment-modifying traits (as in Matthews et al. 2014); genetic parameters can then be estimated in these "modified" and "non-modified" environments. Lastly, experimental evolution studies can then test if these changes in genetic parameters increase or decrease responses to selection over time by executing selection experiments in modified vs. non-modified environments.

In summary, to incorporate the evolution of environments into models of trait evolution, we need to consider how those environments alter not only selection, but also the expression of genetic parameters. Several challenges remain in that endeavor (Fig. 5). First, abundant evidence exists that phenotypic traits influence the environments that organisms experience, and that those environmental factors can influence the expression of genetic variance and covariance. However, few cases have demonstrated that modified environments alter genetic parameters in the same system. Even descriptive studies of how genetic parameters change in response to changes in evolvable traits would provide valuable information on how common the dynamics discussed here may be in nature. Second, predicting how genetic parameters change in response to environments remains a significant challenge. Process-based models have promise for contributing to this endeavor. Other mechanistic analyses of resource limitation and resource allocation may also offer some predictive ability. Empirically, systems biology may provide insight into how networks of genetic and epigenetic interactions combine to produce phenotypes in environment-specific ways, and experimental evolution in model systems could provide specific estimates of changes in genetic parameters and changes in evolutionary responses to altered environments. Third, developing theoretical models of trait evolution that incorporate environment-dependent genetic parameters, when environments themselves evolve, seems well within range. Doing so requires consideration not only of how G-matrices change with environments, but also how environmental modifications that are determined by individuals in a population combine to determine environments that are experienced by collections of individuals in that population. Finally, extending these approaches to coevolutionary models would enhance our understanding of the evolution of species interactions.

Conclusion

In contemporary environments, with extreme and rapid anthropogenic changes, a pressing question is how quickly populations can adapt to environments that are available to them. It is important to consider not only the effects of those environments on the strength and direction of natural selection, but also their effects on genetic expression, which determines evolutionary potential and the speed of adaptation. Processes of evolutionary rescue—the prevention of extinction via adaptation—are highly dependent on rates of adaptation. Knowing how organisms buffer or expose themselves to environmental change through their own activities is crucial. Considering environmental modifications to genetic parameters is also critical to predicting the plausibility of rescue. Here we show that genetic parameters commonly change in response to environmental change and argue that traits and behaviors of organisms can make similar environmental modifications. Thus, to anticipate evolutionary rates and outcomes including the probability of extinction, it is important to consider how evolvable traits of organisms alter genetic parameters and evolutionary potential.

ACKNOWLEDGEMENTS

We thank the American Genetics Association and the organizers of the symposium on "Genes as Environments," especially Kimberly Hughes. The paper benefitted from input Britany Morgan, Mariano Alvarez, and other members of the Donohue Lab. This work was funded by NSF grant DEB-1556855 to KD.

REFERENCES

Aastveit, A. H., & Aastveit, K. (1993). Effects of genotype-environment interactions on genetic correlations. *Theoretical and Applied Genetics*, *86*(8), 1007-1013.

Araya-Ajoy, Y. G., D. F. Westneat, J. Wright (2020). Pathways to social evolution and their evolutionary feedbacks. Evolution 74-9: 1894–1907.

Armbruster, P., & Reed, D. H. (2005). Inbreeding depression in benign and stressful environments. *Heredity*, *95*(3), 235-242.

Bailey, N. W. and A. J. Moore. 2012. Runaway sexual selection without genetic correlations: social environments and flexible mate choice initiate and enhance the Fisher process. Evolution 66-9: 2674–2684

Bailey, N. W. and M. Kölliker, 2019. Social runaway: Fisherian elaboration (or reduction) of socially selected traits via indirect genetic effects. Evolution 73-8: 1549–1563

Baskin, C. C., & Baskin, J. M. (2014). *Seeds: Ecology, Biogeography, and, Evolution of Dormancy and Germination*. Elsevier.

Bazzaz, F. A. (1991). Habitat selection in plants. *The American Naturalist*, *137*, S116-S130.

Bégin, M., Roff, D. A., & Debat, V. (2004). The effect of temperature and wing morphology on quantitative genetic variation in the cricket *Gryllus firmus*, with an appendix examining the statistical properties of the Jackknife–manova method of matrix comparison. *Journal of Evolutionary Biology, 17*(6), 1255-1267.

Bernier, G., Havelange, A., Houssa, C., Petitjean, A., & Lejeune, P. (1993). Physiological signals that induce flowering. *The Plant Cell*, *5*(10), 1147.

Bijma, P. (2011). A general definition of the heritable variation that determines the potential of a population to respond to selection. Genetics, Vol. 189, 1347–1359.

Bijma, P. (2014). The quantitative genetics of indirect genetic effects: a selective review of modelling issues. Heredity 112, 61–69.

Bijma, P., & Wade, M. J. (2008). The joint effects of kin, multilevel selection and indirect genetic effects on response to genetic selection. *Journal of Evolutionary Biology*, *21*(5), 1175-1188.

Bolnick, D. I., & Otto, S. P. (2013). The magnitude of local adaptation under genotype-dependent dispersal. *Ecology and Evolution*, *3*(14), 4722-4735.

Brown, J. S. (1990). Habitat selection as an evolutionary game. *Evolution*, *44*(3), 732-746.

Bubliy, O. A., & Loeschcke, V. (2000). High stressful temperature and genetic variation of five quantitative traits in *Drosophila melanogaster*. *Genetica*, 110(1), 79.

Burghardt, L. T., Metcalf, C. J. E., & Donohue, K. (2016). A cline in seed dormancy helps conserve the environment experienced during reproduction across the range of *Arabidopsis thaliana. American Journal of Botany*, *103*(1), 47-59.

Burghardt, L. T., Metcalf, C. J. E., Wilczek, A. M., Schmitt, J., & Donohue, K. (2015). Modeling the influence of genetic and environmental variation on the expression of plant life cycles across landscapes. *The American Naturalist*, *185*(2), 212-227.

Charmantier, A., & Garant, D. (2005). Environmental quality and evolutionary potential: Lessons from wild populations. Proceedings of the Royal Society B: Biological Sciences, 272, 1415–1425.

Cheptou, P. O., & Donohue, K. (2011). Environment-dependent inbreeding depression: its ecological and evolutionary significance. *New Phytologist*, *189*(2), 395-407.

Chuine, I., & Régnière, J. (2017). Process-based models of phenology for plants and animals. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 159-182.

D'Aguillo, M. C., Edwards, B. R., & Donohue, K. (2019). Can the environment have a genetic basis? A case study of seedling establishment in *Arabidopsis thaliana*. *Journal of Heredity*, *110*(4), 467-478.

Day, R. L., Laland, K. N., & Odling-Smee, F. J. (2003). Rethinking adaptation: the niche-construction perspective. *Perspectives in Biology and Medicine*, *46*(1), 80-95.

De Moed, G. H., De Jong, G., & Scharloo, W. (1997). Environmental effects on body size variation in *Drosophila melanogaster* and its cellular basis. *Genetics Research*, *70*(1), 35-43.

Dmitriew, C., M. W. Blows, and L. Rowe. (2010) Ontogenetic change in genetic variance in size depends on growth environment. *The American Naturalist, 175*(6), 640-649.

Donohue, K. (2002). Germination timing influences natural selection on life-history characters in *Arabidopsis thaliana. Ecology* 83:1006-1016.

Donohue, K. (2003). Setting the stage: phenotypic plasticity as habitat selection. *International Journal of Plant Sciences*, *164*(S3), S79-S92.

Donohue, K. (2005). Niche construction through phenological plasticity: life history dynamics and ecological consequences. *New Phytologist*, *166*(1), 83-92.

Donohue, K. (2009). Some evolutionary consequences of niche construction with genotype-environment interaction. In: *Adaptation and Fitness in Animal Populations*. J. van der Werf et al. eds. Springer, Dordrecht, *131-149*.

Donohue, K. (2015). Genotype-environment interaction, In: *Encyclopedia of Evolutionary Biology*. J. Wolf ed. Elsevier.

Donohue, K., Polisetty, C. R., & Wender, N. J. (2005). Genetic basis and consequences of niche construction: plasticity-induced genetic constraints on the evolution of seed dispersal in *Arabidopsis thaliana*. *The American Naturalist*, *165*(5), 537-550.

Donohue, K., Pyle, E. H., Messiqua, D., Heschel, M. S., & Schmitt, J. (2000). Density dependence and population differentiation of genetic architecture in *Impatiens capensis* in natural environments. *Evolution, 54*(6), 1969-1981.

Ebert, D., Yampolsky, L., & Stearns, S. C. (1993). Genetics of life history in *Daphnia magna*. I. Heritabilities at two food levels. *Heredity*, 70, 335-343.

Enríquez, S., & Pantoja-Reyes, N. I. (2005). Form-function analysis of the effect of canopy morphology on leaf self-shading in the seagrass *Thalassia testudinum*. *Oecologia*, *145*(2), 234-242.

Fox, C. W., & Reed, D. H. (2011). Inbreeding depression increases with environmental stress: an experimental study and meta-analysis. *Evolution*, *65*(1), 246-258.

Gebhardt, M. D., & Stearns, S. C. (1988). Reaction norms for developmental time and weight at eclosion in *Drosophila mercatorum*. *Journal of Evolutionary Biology*, *1*(4), 335-354.

Gebhardt-Henrich, S. G., & Van Noordwijk, A. J. (1991). Nestling growth in the great tit I. Heritability estimates under different environmental conditions. *Journal of Evolutionary Biology*, *4*(3), 341-362.

Guntrip, J., Sibly, R. M., & Holloway, G. J. (1997). The effect of novel environment and sex on the additive genetic variation and covariation in and between emergence body weight and development period in the cowpea weevil, *Callosobruchus maculatus* (Coleoptera, Bruchidae). *Heredity*, *78*(2), 158-165.

Hoffmann, A. A., & Merilä, J. (1999). Heritable variation and evolution under favourable and unfavourable conditions. *Trends in Ecology and Evolution*, *14*(3), 96-101.

Holloway, G. J., Povey, S. R., & Sibly, R. M. (1990). The effect of new environment on adapted genetic architecture. *Heredity*, *64*(3), 323

Holt, R. D. (1987). Population dynamics and evolutionary processes: the manifold roles of habitat selection. *Evolutionary Ecology*, *1*(4), 331-347.

Houle, D. (1991). Genetic covariance of life history traits: what genetic correlations are made of and why it matters. Evolution 45:630-648

Imasheva, A. G., Loeschcke, V., Zhivotovsky, L. A., & Lazebny, O. E. (1998). Stress temperatures and quantitative variation in *Drosophila melanogaster*. *Heredity*, *81*(3), 246-253.

Jarosz, D. F., & Lindquist, S. (2010). Hsp90 and environmental stress transform the adaptive value of natural genetic variation. *Science*, *330*(6012), 1820-1824.

Kasule, F. K. (1991). Quantitative variation in adult size and fecundity of the cotton stainer bug *Dysdercus fasciatus*. *Heredity*, *66*(2), 273-279.

Kause, A., & Morin, J. P. (2001). Seasonality and genetic architecture of development time and body size of the birch feeding sawfly *Priophorus pallipes. Genetics Research*, *78*(1), 31-40.

Krebs, R. A., & Loeschcke, V. (1999). A genetic analysis of the relationship between life-history variation and heat-shock tolerance in *Drosophila buzzatii*. *Heredity*, *83*(1), 46-53.

Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (1999). Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences*, *96*(18), 10242-10247.

Larsson, K. (1993). Inheritance of body size in the barnacle goose under different environmental conditions. *Journal of Evolutionary Biology*, *6*(2), 195-208.

Lazarević, J., Perić-Mataruga, V., Ivanović, J., & Andjelković, M. (1998). Host plant effects on the genetic variation and correlations in the individual performance of the gypsy moth. *Functional Ecology*, *12*(1), 141-148.

Levins, R. (1968). *Evolution in changing environments: some theoretical explorations*. Princeton University Press.

Marjanovic, J. Mulder, H. A. Rönnegård, L. Bijma, P. (2018) Modelling the co-evolution of indirect genetic effects and inherited variability. Heredity 121:631–647

Matthews, B., De Meester, L., Jones, C. G., Ibelings, B. W., Bouma, T. J., Nuutinen, V., Van De Koppel, J. & Odling-Smee, J. (2014). Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. *Ecological Monographs*, *84*(2), 245-263.

Merilä, J. (1997). Expression of genetic variation in body size of the collared flycatcher under different environmental conditions. *Evolution*, *51*(2), 526-536.

Messina, F. J., & Fry, J. D. (2003). Environment-dependent reversal of a life history trade-off in the seed beetle *Callosobruchus maculatus*. *Journal of Evolutionary Biology*, *16*(3), 501-509.

Moore, A. J., Brodie III, E. D., & Wolf, J. B. (1997). Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution*, *51*(5), 1352-1362.

Muñoz, M. M., & Losos, J. B. (2018). Thermoregulatory behavior simultaneously promotes and forestalls evolution in a tropical lizard. *The American Naturalist*, *191*(1), E15-E26.

Newman, R. A. (1988a). Genetic variation for larval anuran (*Scaphiopus couchii*) development time in an uncertain environment. *Evolution*, *42*(4), 763-773.

Newman, R. A. (1988b). Adaptive plasticity in development of *Scaphiopus couchii* tadpoles in desert ponds. *Evolution*, *42*(4), 774-783.

Newman, R. A. (1989). Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. *Ecology*, *70*(6), 1775-1787.

Norry, F. M., & Loeschcke, V. (2002). Temperature-induced shifts in associations of longevity with body size in *Drosophila melanogaster. Evolution*, *56*(2), 299-306.

Olding-Smee, F. J., Laland, K. N., & Feldman, M. W. (1996). Niche construction. *The American Naturalist*, *147*(4), 641-648.

Odling-Smee, F. J., Laland, K. N., & Feldman, M. W. (2013). *Niche Construction: The Neglected Process in Evolution*. Princeton University Press.

Plomin, R. (2014). Genotype-environment correlation in the era of DNA. *Behavior genetics*, *44*(6), 629-638.

Roff, D. A., & Shannon, P. (1993). Genetic and ontogenetic variation in behaviour: its possible role in the maintenance of genetic variation in the wing dimorphism of *Gryllus firmus*. *Heredity*, *71*(5), 481-487.

Rosenzweig, M. L. (1987). Habitat selection as a source of biological diversity. *Evolutionary Ecology*, *1*(4), 315-330.

Rudin, F. S., L. W. Simmons, J. L. Tomkins. 2018. Social cues affect quantitative genetic variation and covariation in animal personality traits. Evolution 73-3: 540–553.

Rutherford, S. L., & Lindquist, S. (1998). Hsp90 as a capacitor for morphological evolution. *Nature*, *396*(6709), 336-342.

Saltz, J. B., & Foley, B. R. (2011). Natural genetic variation in social niche construction: social effects of aggression drive disruptive sexual selection in *Drosophila melanogaster*. *The American Naturalist*, *177*(5), 645-654.

Saltz, J. B., & Nuzhdin, S. V. (2014). Genetic variation in niche construction: implications for development and evolutionary genetics. *Trends in Ecology and Evolution*, *29*(1), 8-14.

Schwab, D. B., Casasa, S., & Moczek, A. P. (2017). Evidence of developmental niche construction in dung beetles: effects on growth, scaling and reproductive success. *Ecology Letters*, *20*(11), 1353-1363.

Schwilk, D. W. (2003). Flammability is a niche construction trait: canopy architecture affects fire intensity. *The American Naturalist*, *162*(6), 725-733.

Shakhatreh, Y., Kafawin, O., Ceccarelli, S., & Saoub, H. (2001). Selection of barley lines for drought tolerance in low-rainfall areas. *Journal of Agronomy and Crop Science*, *186*(2), 119-127.

Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, *85*(5), 1004-1011.

Snell-Rood, E. C., Burger, M., Hutton, Q., & Moczek, A. P. (2016). Effects of parental care on the accumulation and release of cryptic genetic variation: review of mechanisms and a case study of dung beetles. *Evolutionary Ecology*, *30*(2), 251-265.

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional ecology*, *3*(3), 259-268.

Stearns, S. C. (1992). The Evolution of Life Histories. Oxford University Press.

Stearns, S.C., de Jong, G., & Newman, B. (1991). The effects of phenotypic plasticity on genetic correlations. *Trends in Ecology and Evolution*, *6*(4), 122-126.

Stinchcombe, J. R. (2002). Environmental dependency in the expression of costs of tolerance to deer herbivory. *Evolution*, *56*(5), 1063-1067.

Szafraniec, K., Borts, R. H., & Korona, R. (2001). Environmental stress and mutational load in diploid strains of the yeast *Saccharomyces cerevisiae*. *Proceedings of the National Academy of Sciences*, *98*(3), 1107-1112.

Via, S., & Lande, R. (1985). Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution*, *39*(3), 505-522.

Via, S., & Lande, R. (1987). Evolution of genetic variability in a spatially heterogeneous environment: effects of genotype–environment interaction. *Genetics Research*, *49*(2), 147-156.

Wardle, D. A., Karban, R., & Callaway, R. M. (2011). The ecosystem and evolutionary contexts of allelopathy. *Trends in Ecology and Evolution*, *26*(12), 655-662.

Wender, N. J., Polisetty, C. R., & Donohue, K. (2005). Density-dependent processes influencing the evolutionary dynamics of dispersal: a functional analysis of seed dispersal in Arabidopsis thaliana (Brassicaceae). *American Journal of Botany*, *92*(6), 960-971.

Whitlock, M. C. (1996). The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *The American Naturalist*, *148*, S65-S77.

Windig, J. J. (1994). Genetic correlations and reaction norms in wing pattern of the tropical butterfly *Bicyclus anynana. Heredity*, *73*(5), 459-470.

Wolf, J. B., & Wade, M. J. (2009). What are maternal effects (and what are they not)?. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1520), 1107-1115.

Wolf, J. B., & Wade, M. J. (2016). Evolutionary genetics of maternal effects. *Evolution*, *70*(4), 827-839.

Wolf, J. B., Brodie III, E. D., Cheverud, J. M., Moore, A. J., & Wade, M. J. (1998). Evolutionary consequences of indirect genetic effects. *Trends in Ecology and Evolution*, *13*(2), 64-69.

Wood, C. W., & Brodie III, E. D. (2015). Environmental effects on the structure of the G-matrix. *Evolution*, *69*(11), 2927-2940.

Wood, C. W., & Brodie III, E. D. (2016). Evolutionary response when selection and genetic variation covary across environments. *Ecology Letters*, *19*(10), 1189-1200.

Zimmermann, J., Higgins, S. I., Grimm, V., Hoffmann, J., & Linstädter, A. (2010). Grass mortality in semi-arid savanna: the role of fire, competition and self-shading. *Perspectives in Plant Ecology, Evolution and Systematics*, *12*(1), 1-8.

TABLE CAPTIONS

Table 1: Biologically modified environments can alter genetic parameters. The left-hand column indicates the trait that alters environmental factors to which organisms are exposed, which are indicated in the center column. The last column summarizes general trends whereby environmental conditions can influence genetic variance and covariance.

Table 2: Future challenges

FIGURE CAPTIONS

Figure 1. The environment alters genetic variances and covariances. A) Environment-dependent genetic variance. When different genotypes respond differently to the environment, the differences among genotypes (genetic variance) can change with the environment (left). The rank order of genotypes can also change across environments (right). B) Environment-dependent genetic covariances. When different traits exhibit different patterns of plasticity, genetic covariances among traits can change with the environment. In this example, height is plastic, and genotypes differ in how they respond to height. Width is not plastic, and both genotypes have the same, non-plastic response. The association between height and width is positive in the first environment, but negative in the second environment.

Figure 2: Evolutionary consequences of altered genetic variance. A) The breeder's equation gives the evolutionary response to selection ($\Delta\overline{z}$) as a function of the strength of selection (S), genetic variance (V_g), and total phenotypic variance (V_p). B) Different functions (shown in different colors) may exist for the relationship between traits and the environments they produce (Ψ, in the terminology of IGEs), indicated by axes labeled in black. The simplest function is a linear relationship (black line), but environments may change in response to changes in phenotypes of environment-modifying traits in a threshold (blue), sigmoidal (red), or diminishing (green) manner, or in other functions not shown here. Likewise, those same functions may describe the relationship between environments and how the expression of genetic variation is altered (*E*, in Fig. 4), indicated by axes labeled in red. Those function that are shown exhibit positive relationships between variables on the x- and y-axes, but the mirror image of

those functions (not shown) would show negative associations. C) How genetic variance changes over time (generations) as the environment-modifying trait, z, evolves. The trait, z, (blue line) changes over time; this alters the environment, as in "B". Here we assume a linear relationship between the trait and the environment (black line and black axes in panel B). Genetic variance (black dashed line) changes in response to the environment (as in panel B, red axes). Here again, we assume a linear relationship between the environment and the expression of genetic variation. Depending on whether an increase in the environment-determining trait, z, causes an increase in the expression of genetic variance (positive association; upper panels) or a decrease in the expression of genetic variance (negative association; lower panels), evolutionary responses to selection can be more constrained (left-hand. blue sub-panels) or more sustained (right-hand, green sub-panels). Note that changes in genetic variance may also occur if the environment-altering trait, z, is plastic rather than genetically evolving.

Figure 3: Evolutionary consequences of altered genetic covariances. A) Genetic correlations in three different environments. Environment A (left) produces positive correlations between traits z_1 and z_2; environment B (center) produces no correlation; Environment C (right) produces a negative correlation. If direct selection favors an increase in phenotype z_1, then indirect selection on trait z_2 will be positive, zero, or negative, respectively. By altering environments, niche construction can alter correlations between traits and consequently alter indirect selection. B) Scenario in which direct selection favors an increase in both traits. Adaptation is faster in Environment A than C. Correlations between traits z_1 and z_2 are shown as "+", "∅", or "-". β_1 and β_2 indicate direct selection on traits z_1 and z_2, respectively. C) Scenario in which direct selection favors a decrease (dotted line) in z_1, but an increase (solid line) in z_2. Adaptation is

slower in Environment A than C. D) Scenario in which direct selection favors an increase in z_1, but does not act directly on z_2. Trait z_2 diverges across Environment A and C, despite no direct selection on z_2 and a consistent direction of selection on trait z_1.

Figure 4: Incorporating GxE into models of Indirect Genetic Effects (IGEs). The original formulation of IGE is shown in black type, with the breeder's equation indicating evolutionary responses to selection ($\Delta\overline{z}$) as a function of environment-dependent selection (β) and genetic variances and covariances (**G**). In the original formulation, a phenotype of individual j, z'_j, is determined by additive genetic effects, a'_j, and random environmental effects e'_j. The phenotype of individual j, z'_j, produces an environment, $e_{z'j}$, which then influences the expression of a phenotype in a second individual, z_i, according to the parameter Ψ_{ij}. (See Fig. 2B for potential functions whereby traits may influence environments.) That environment also exerts selection, β, on trait z_i. Red type indicates factors that were not included in the original formulation of IGEs. Also shown (in red) are effects of the trait-dependent environment on genetic parameters, and specifically average allelic effects, "a". How "a" is altered by "e" is described by parameter "E". (See Fig. 2B for potential functions of this parameter). The left-hand panels show different scenarios whereby the combined environment ($e_{combined}$) is determined by all members of the population, including individuals j and i (the grey dotted arrow indicates that the environmental modification by individual i also contributes to the total environmental modification, "e combined"). $e_{combined}$ alters "a" and "β". The upper left panel depicts additive effects of environments, such that the combined environment experienced by all individuals is the mean of the environments produced by individuals in the population. The center left panel shows a scenario in which some environmental modifications have a greater impact on the combined

environment than others (similar to dominance). The bottom left panel shows a scenario in which the environment that is experienced is more strongly determined by individuals that are closer in space (or other metric of interaction). In this example, an individual (near the bottom) is nearer to the red environment than to the blue one, so its environment is nearly red.

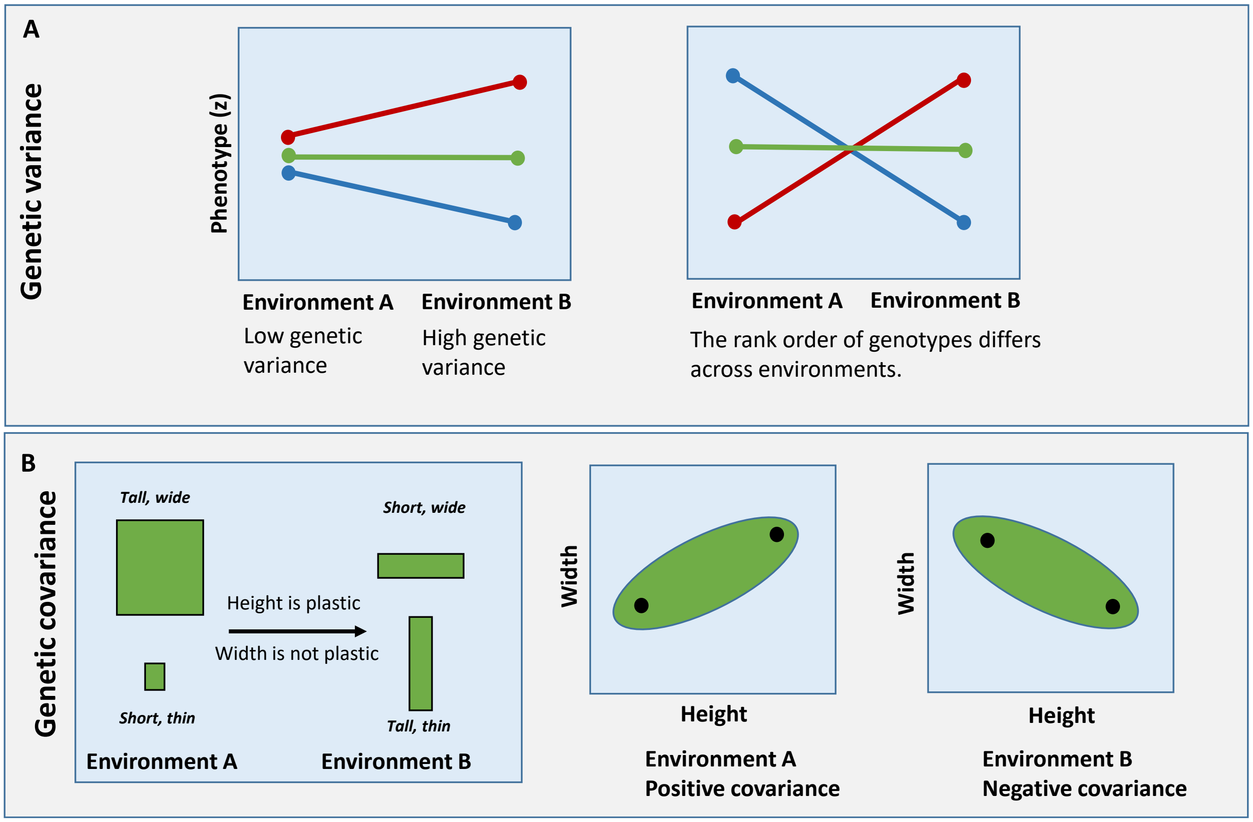
Table 1: Biologically modified environments can alter genetic parameters. The left-hand column indicates the trait that alters environmental factors to which organisms are exposed, which are indicated in the center column. The last column, whose order of items is unrelated to the first two columns, summarizes general trends whereby environmental conditions can influence genetic variance and covariance.

Genetically based traits	➡	**Environments**	➡ **Genetic parameters**
Shelter construction Environmental tracking (spatial and temporal)	➡	Canalized (non-novel) environments Non-stressful environments	Novel environments→ higher genetic variance Stressful environments → higher genetic variance because they are "novel"
Toxicity via secondary metabolites, allelopathy	➡	Reduced competition: Resource abundance (self) or resource quality (recipients of toxins)	Poor resource / stress → slow growth → less synchronized timing, more difference among genotypes, higher genetic variance
Resource-capture constructions Resource consumption Provisioning	➡	Resource abundance	Poor resource / stress → truncated phenotypes, less difference among genotypes, lower genetic variance
Social behaviors	➡	Stressful environments Resource abundance Resource quality	Poor resource → allocational tradeoffs, negative genetic correlations High resources→ genetic variation in resource acquisition is expressed → positive genetic correlations

Table 2: Future challenges.

Future Challenges		
Effects of environment-modifying traits on the environment	***Predicting Vg in different environments***	***Developing population-level evolutionary models of response to selection***
Quantify how individuals with different traits alter specific environmental factors. Determine how those environmental modifications are experienced by the organism itself and/or by other organisms in the population. Quantify how the environment experienced by different individuals within a population changes with different frequencies of environment-modifying phenotypes in a population, using spatially explicit models, if necessary.	Directly measure genetic variances and covariances in experiments that explicitly manipulate or observe biological modification of environments. Develop process-based models based on physiological responses of specific genotypes to specific environments, thereby allowing predictions of how genetic variance will respond. Quantify how altered environments influence genetic parameters of other species, for incorporation into co-evolutionary models.	To model evolutionary dynamics requires considering: a) changes to the population composition with respect to environmentally modifying traits b) consequent changes to the environment experienced by different individuals in the population, c) how those environments alter average effects of alleles and the expression of genetic variance for traits at the population level d) how such environmental effects on multiple traits--estimated as G-matrices in biologically modified environments--combine to influence evolutionary responses to selection.

890 Figure 1



891

892

Figure 2

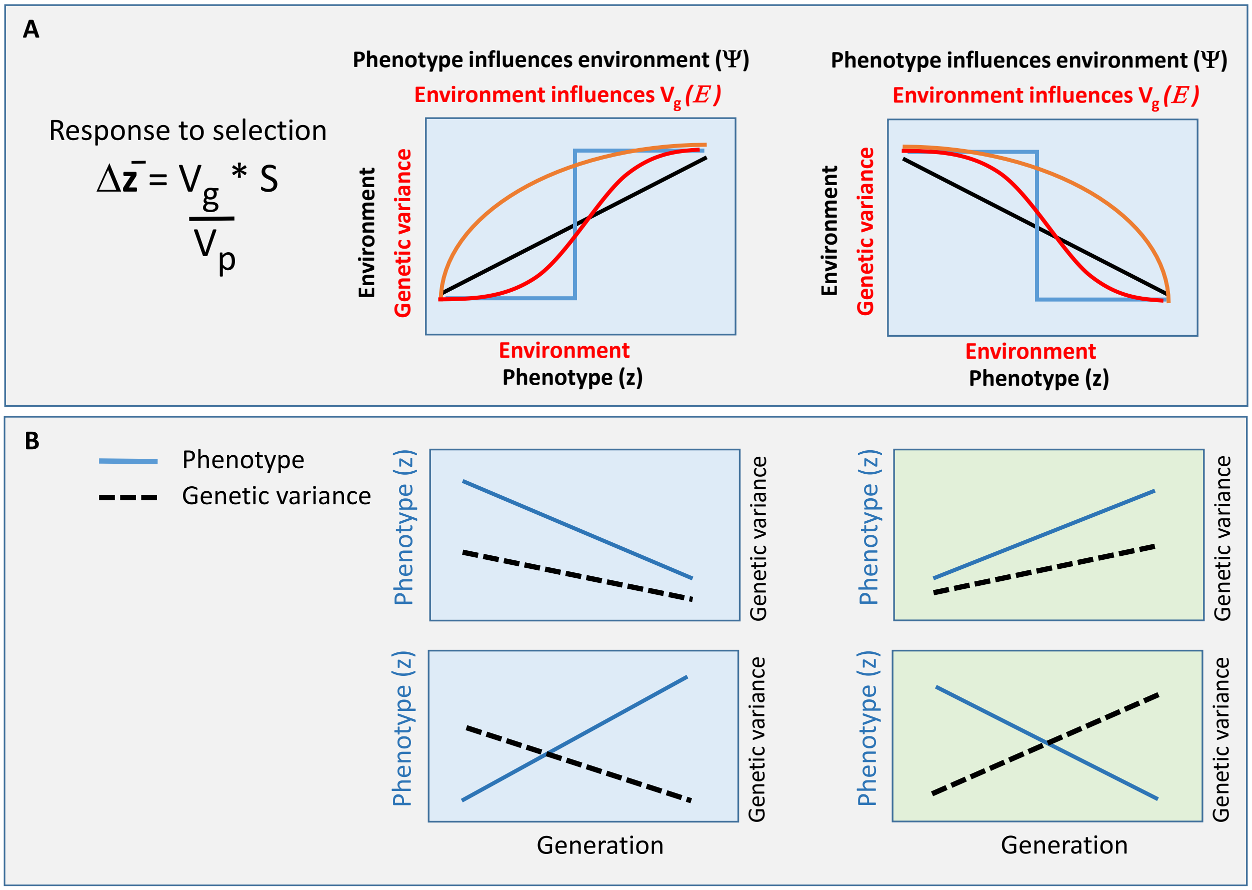
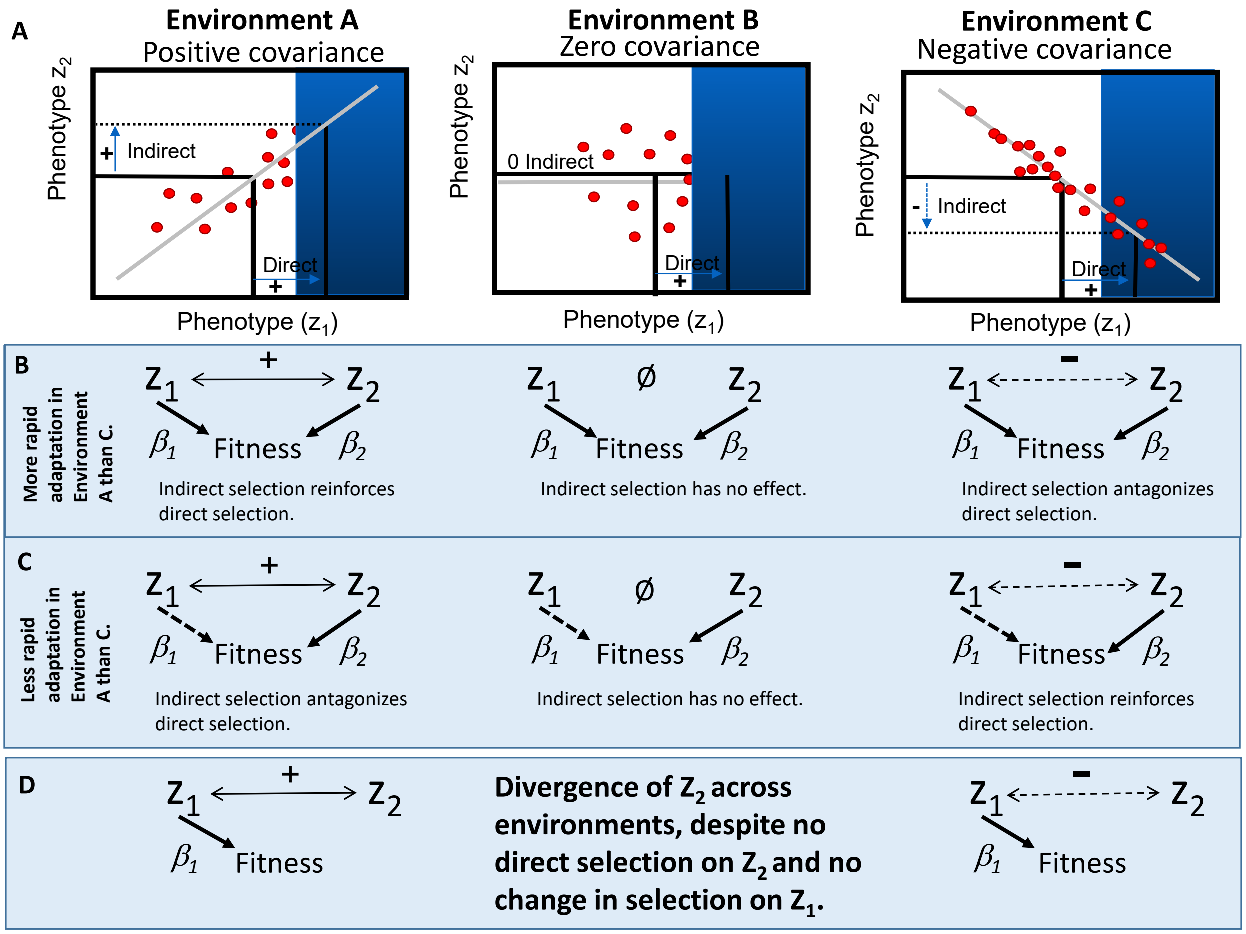
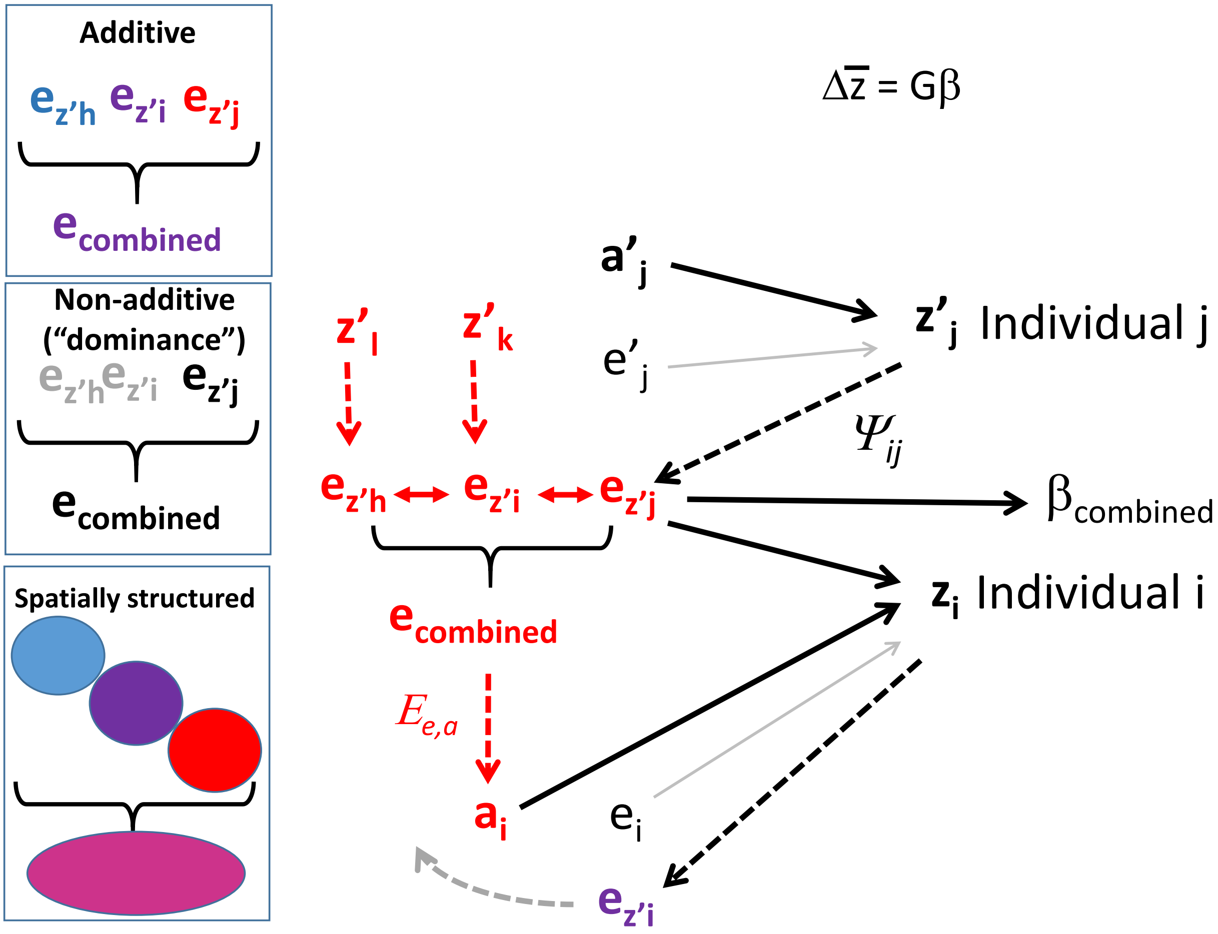

A
Response to selection
$\Delta\bar{z} = \frac{V_g}{V_p} * S$
Phenotype influences environment (Ψ)
Environment influences $V_g(E)$
Environment
Genetic variance
Environment
Phenotype (z)
Phenotype influences environment (Ψ)
Environment influences $V_g(E)$
Environment
Genetic variance
Environment
Phenotype (z)
B
Phenotype
Genetic variance
Phenotype (z)
Genetic variance
Phenotype (z)
Genetic variance
Phenotype (z)
Genetic variance
Phenotype (z)
Genetic variance
Generation
Generation

Figure 3


A
Environment A
Positive covariance
Phenotype z2
+ Indirect
Direct
+
Phenotype (z1)
Environment B
Zero covariance
Phenotype z2
0 Indirect
Direct
+
Phenotype (z1)
Environment C
Negative covariance
Phenotype z2
- Indirect
Direct
+
Phenotype (z1)
B
More rapid adaptation in Environment A than C.
Z1 + Z2
β1 Fitness β2
Indirect selection reinforces direct selection.
Z1 Ø Z2
β1 Fitness β2
Indirect selection has no effect.
Z1 − Z2
β1 Fitness β2
Indirect selection antagonizes direct selection.
C
Less rapid adaptation in Environment A than C.
Z1 + Z2
β1 Fitness β2
Indirect selection antagonizes direct selection.
Z1 Ø Z2
β1 Fitness β2
Indirect selection has no effect.
Z1 − Z2
β1 Fitness β2
Indirect selection reinforces direct selection.
D
Z1 + Z2
β1 Fitness
Divergence of Z2 across environments, despite no direct selection on Z2 and no change in selection on Z1.
Z1 − Z2
β1 Fitness

899 Figure 4



900

901

Figure 5

Future Directions

Effects of niche-constructing traits on the environment

Quantifying how individuals with different niche-constructing traits alter specific environmental factors is necessary. It is also necessary to quantify how the environment changes with different frequencies of niche-constructing phenotypes in a population.

Predicting Vg in different environments

Process-based models based on physiological responses of specific genotypes to specific environments may permit predictions of how specific genotypes respond to environments, and thereby how genetic variance will respond.

Developing population-level evolutionary models of response to selection

The degree to which genetic variance is altered by niche construction depends on the environment experienced by the whole population, which is a function of the frequency of individuals with specific niche-constructing traits and the effect of each individual on the whole environment. To model evolutionary dynamics requires considering changes population composition and consequent changes in the environment.

Supplemental Table S1: How biological modifications of environments alter genetic parameters. "Environmental change" refers to an environmental factor that is altered by organismal traits. If an upward arrow is shown, the table shows the effect of an increase in that environmental factor; if a downward arrow is shown, the table shows the effect of a decrease in that factor. "Change in genetic parameter" indicates the genetic parameter that changes in response to the environmental change indicated in the first column. Arrows show the direction of change in the genetic parameter. "NS" denotes a non-significant change.

Environmental change	Change in genetic parameter	Traits affected	References
Novel environment	↑ genetic variation	Developmental time	Clausen et al. 1940 Holloway et al. 1990 Guntrip et al. 1997
		Morphology	Clausen et al. 1940 Ledón-Rettig et al. 2010
		Size/mass	Guntrip et al. 1997
	Negative to NS correlation	Developmental time, size/mass, fecundity	Simons & Roff 1996 Guntrip et al. 1997
	Negative to more negative correlation	Fecundity, starvation resistance	Service & Rose 1985
↑ food quality	↑ genetic variation	Size/mass	Gebhardt-Henrich & Noordwijk 1991
		Morphology	Ebert et al. 1993 Merilä 1997
	↓ genetic variation	Morphology	De Moed et al. 1997
		Developmental time	Kause & Morin 2001
	Negative (or NS) to positive correlation	Age, size/mass, developmental time	Gebhardt & Stearns 1988 Kause & Morin 2001
		Fecundity, longevity	Messina & Fry 2003
↑ habitat quality	↑ genetic variation	Morphology	Larsson 1993 Garant et al. 2004
		Size/mass	Kasule 1991
		Fecundity, reproductive traits	Kasule 1991 Lazarević et al. 1998
	Negative to positive correlation	Morphology	Larsson 1993
	NS to positive correlation	Developmental time, survival, fecundity	Krebs & Loeschcke 1999
	Decrease in magnitude of positive correlation	Development time, size/mass, fecundity	Lazarević et al. 1998
↑ habitat duration	Negative to positive correlation	Development time, size/mass	Newman 1989
Spring vs. winter dispersal	↑ genetic variation	Development time	Donohue et al. 2005a

	↓ genetic variation	Development time, Morphology	Donohue et al. 2005b
↑ temperature	↑ genetic variation	Developmental time Morphology	Szafraniec et al. 2001 Rutherford & Lindquist 1998
	↓ genetic variation	Morphology Developmental time (2nd generation)	De Moed et al. 1997 D'Aguillo et al. 2019
	Negative to positive correlation	Developmental time, morphology	Windig 1994 Norry & Loeschcke 2002
↑ temperature + stress	↑ genetic variation	Developmental time, viability	Bubliy & Loeschcke 2000
↑ temperature variability	↑ genetic variation	Developmental time	Snell-Rood et al. 2016
↑ light	↑ genetic variation	Plastic response to density	Donohue et al. 2000
	Negative to positive correlation	Fecundity, birth rates	Giesel 1986
↑ light + ↓ density	NS to negative correlation	Morphology, reproduction	Donohue et al. 2000
↑ light + ↓ seed stratification	↑ genetic variation	Developmental time (2nd generation)	Munir et al. 2001
↑ moisture	Negatived to NS correlation	Reproductive traits, developmental time	Shakhatreh et al. 2001
	Negative to positive correlation	Reproductive traits, morphology	Shakhatreh et al. 2001
↑ salinity	↑ genetic variation	Size/mass	McGuigan et al. 2011
↑ competition	↓ genetic variation	Microhabitat use	Emery & Ackerly 2014
↑ density	↑ genetic variation	Post-dispersal density (2nd generation)	Wender et al. 2005 Donohue et al. 2005c
	Positive to NS correlation	Morphology	Donohue & Schmitt 1999
	Negative to positive correlation	Morphology	Donohue & Schmitt 1999
↑ herbivory	NS to negative correlation	Fitness, herbivore tolerance	Stinchcombe 2002
↑ predation cues	↑ genetic variation	Reproductive traits	Auld 2010

References appearing in the Supplemental Information

Auld, J. R. (2010). The effects of predation risk on mating system expression in a freshwater snail. *Evolution*, *64*(12), 3476-3494.

Bubliy, O. A., & Loeschcke, V. (2000). High stressful temperature and genetic variation of five quantitative traits in *Drosophila melanogaster. Genetica, 110*(1), 79.

Clausen, J., Keck, D. D., & Hiesey, W. M. (1940). Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. *Carnegie Institution of Washington Publication no. 520.*

D'Aguillo, M. C., Edwards, B. R., & Donohue, K. (2019). Can the environment have a genetic basis? A case study of seedling establishment in *Arabidopsis thaliana. Journal of Heredity*, *110*(4), 467-478.

De Moed, G. H., De Jong, G., & Scharloo, W. (1997). Environmental effects on body size variation in *Drosophila melanogaster* and its cellular basis. *Genetics research, 70*(1), 35-43.

Donohue, K., Dorn, L., Griffith, C., Kim, E., Aguilera, A., Polisetty, C. R., & Schmitt, J. (2005a). Environmental and genetic influences on the germination of *Arabidopsis thallana* in the field. *Evolution*, *59*(4), 740-757.

Donohue, K., Dorn, L., Griffith, C., Kim, E., Aguilera, A., Polisetty, C. R., & Schmitt, J. (2005b). Niche construction through germination cueing: Life-history responses to timing of germination in *Arabidopsis thaliana*. *Evolution*, *59*(4), 771-785.

Donohue, K., Polisetty, C. R., & Wender, N. J. (2005c). Genetic basis and consequences of niche construction: plasticity-induced genetic constraints on the evolution of seed dispersal in Arabidopsis thaliana. *The American Naturalist*, *165*(5), 537-550.

Donohue, K., & Schmitt, J. (1999). The genetic architecture of plasticity to density in *Impatiens capensis. Evolution, 53*(5), 1377-1386.

Donohue, K., Pyle, E. H., Messiqua, D., Heschel, M. S., & Schmitt, J. (2000). Density dependence and population differentiation of genetic architecture in *Impatiens capensis* in natural environments. *Evolution, 54*(6), 1969-1981.

Ebert, D., Yampolsky, L., & Stearns, S. C. (1993). Genetics of life history in *Daphnia magna*. I. Heritabilities at two food levels. *Heredity*, *70*(4), 335-343.

Emery, N. C., & Ackerly, D. D. (2014). Ecological release exposes genetically based niche variation. *Ecology Letters, 17*(9), 1149-1157.

Garant, D., Sheldon, B. C., & Gustafsson, L. (2004). Climatic and temporal effects on the expression of secondary sexual characters: genetic and environmental components. *Evolution*, *58*(3), 634-644.

Gebhardt, M. D., & Stearns, S. C. (1988). Reaction norms for developmental time and weight at eclosion in *Drosophila mercatorum. Journal of Evolutionary Biology,* 1(4), 335-354.

Gebhardt-Henrich, S. G., & Van Noordwijk, A. J. (1991). Nestling growth in the great tit I. Heritability estimates under different environmental conditions. *Journal of Evolutionary Biology, 4*(3), 341-362.

Giesel, J. T. (1986). Genetic correlation structure of life history variables in outbred, wild *Drosophila melanogaster*: effects of photoperiod regimen. *The American Naturalist, 128*(4), 593-603.

Guntrip, J., Sibly, R. M., & Holloway, G. J. (1997). The effect of novel environment and sex on the additive genetic variation and covariation in and between emergence body weight and development period in the cowpea weevil, *Callosobruchus maculatus* (Coleoptera, Bruchidae). *Heredity, 78*(2), 158-165.

Holloway, G. J., Povey, S. R., & Sibly, R. M. (1990). The effect of new environment on adapted genetic architecture. *Heredity, 64*(3), 323

Kasule, F. K. (1991). Quantitative variation in adult size and fecundity of the cotton stainer bug *Dysdercus fasciatus*. *Heredity*, *66*(2), 273-279.

Kause, A., & Morin, J. P. (2001). Seasonality and genetic architecture of development time and body size of the birch feeding sawfly *Priophorus pallipes. Genetics Research, 78*(1), 31-40.

Krebs, R. A., & Loeschcke, V. (1999). A genetic analysis of the relationship between life-history variation and heat-shock tolerance in *Drosophila buzzatii. Heredity, 83*(1), 46-53.

Larsson, K. (1993). Inheritance of body size in the barnacle goose under different environmental conditions. *Journal of Evolutionary Biology, 6*(2), 195-208.

Lazarević, J., Perić-Mataruga, V., Ivanović, J., & Andjelković, M. (1998). Host plant effects on the genetic variation and correlations in the individual performance of the gypsy moth. *Functional Ecology, 12*(1), 141-148.

Ledón -Rettig, C. C., Pfennig, D. W., & Crespi, E. J. (2010). Diet and hormonal manipulation reveal cryptic genetic variation: implications for the evolution of novel feeding strategies. *Proceedings of the Royal Society B: Biological Sciences, 277*(1700), 3569-3578.

McGuigan, K., Nishimura, N., Currey, M., Hurwit, D., & Cresko, W. A. (2011). Cryptic genetic variation and body size evolution in threespine stickleback. *Evolution, 65*(4), 1203-1211.

Merilä, J. (1997). Expression of genetic variation in body size of the collared flycatcher under different environmental conditions. *Evolution, 51*(2), 526-536.

Messina, F. J., & Fry, J. D. (2003). Environment-dependent reversal of a life history trade-off in the seed beetle *Callosobruchus maculatus*. *Journal of Evolutionary Biology, 16*(3), 501-509.

Munir, J., Dorn, L. A., Donohue, K., & Schmitt, J. (2001). The effect of maternal photoperiod on seasonal dormancy in *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany, 88*(7), 1240-1249.

Newman, R. A. (1989). Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. *Ecology, 70*(6), 1775-1787.

Norry, F. M., & Loeschcke, V. (2002). Temperature-induced shifts in associations of longevity with body size in *Drosophila melanogaster. Evolution, 56*(2), 299-306.

Rutherford, S. L., & Lindquist, S. (1998). Hsp90 as a capacitor for morphological evolution. *Nature, 396*(6709), 336–342.

Service, P. M., & Rose, M. R. (1985). Genetic covariation among life-history components: the effect of novel environments. *Evolution, 39*(4), 943-945.

Shakhatreh, Y., Kafawin, O., Ceccarelli, S., & Saoub, H. (2001). Selection of barley lines for drought tolerance in low-rainfall areas. *Journal of Agronomy and Crop Science, 186*(2), 119-127.

Simons, A. M., & Roff, D. A. (1996). The effect of a variable environment on the genetic correlation structure in a field cricket. *Evolution, 50*(1), 267-275.

Snell-Rood, E. C., Burger, M., Hutton, Q., & Moczek, A. P. (2016). Effects of parental care on the accumulation and release of cryptic genetic variation: review of mechanisms and a case study of dung beetles. *Evolutionary Ecology*, *30*(2), 251-265.

Stinchcombe, J. R. (2002). Environmental dependency in the expression of costs of tolerance to deer herbivory. *Evolution, 56*(5), 1063-1067.

Szafraniec, K., Borts, R. H., & Korona, R. (2001). Environmental stress and mutational load in diploid strains of the yeast *Saccharomyces cerevisiae. Proceedings of the National Academy of Sciences, 98*(3), 1107-1112.

Wender, N. J., Polisetty, C. R., & Donohue, K. (2005). Density-dependent processes influencing the evolutionary dynamics of dispersal: a functional analysis of seed dispersal in *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany, 92*(6), 960-971.

Windig, J. J. (1994). Genetic correlations and reaction norms in wing pattern of the tropical butterfly *Bicyclus anynana. Heredity, 73*(5), 459-470.