

IDEA AND PERSPECTIVE

Evolutionary response when selection and genetic variation covary across environments

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Abstract

Although models of evolution usually assume that the strength of selection on a trait and the expression of genetic variation in that trait are independent, whenever the same ecological factor impacts both parameters, a correlation between the two may arise that accelerates trait evolution in some environments and slows it in others. Here, we address the evolutionary consequences and ecological causes of a correlation between selection and expressed genetic variation. Using a simple analytical model, we show that the correlation has a modest effect on the mean evolutionary response and a large effect on its variance, increasing among-population or among-generation variation in the response when positive, and diminishing variation when negative. We performed a literature review to identify the ecological factors that influence selection and expressed genetic variation across traits. We found that some factors – temperature and competition – are unlikely to generate the correlation because they affected one parameter more than the other, and identified others – most notably, environmental novelty – that merit further investigation because little is known about their impact on one of the two parameters. We argue that the correlation between selection and genetic variation deserves attention alongside other factors that promote or constrain evolution in heterogeneous landscapes.

Keywords

Anthropogenic change, breeder's equation, cryptic genetic variation, environmental heterogeneity, heritability, novel environments, response to selection.

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INTRODUCTION

The environment is a major source of variation in the strength and mode of natural selection and the expression of heritable genetic variation, the two primary determinants of adaptive evolutionary change (Wade & Kalisz 1990; Ledón-Rettig *et al.* 2014). Although environmental effects on selection and expressed genetic variation are usually thought to occur independently, concurrent environmental effects on both parameters could induce a correlation between selection and genetic variation that influences the rate of phenotypic evolution. The only two studies that have investigated this possibility to date found significant environmentally induced correlations between the strength of selection and the expression of genetic variation (Wilson *et al.* 2006; Husby *et al.* 2011), suggesting that the causes and consequences of the correlation deserve investigation. Here, we explore the evolutionary consequences and ecological causes of non-independence between the strength of selection acting on a trait and the expression of genetic variance in that trait in spatially and temporally variable environments.

Differences in the strength, direction and form of selection acting on a trait across environments are common (Grant & Grant 1995; Kingsolver *et al.* 2001; Brodie *et al.* 2002; Gosden & Svensson 2008; Kasumovic *et al.* 2008; Siepielski *et al.* 2009). In perhaps the best-known example, Grant & Grant (1995) demonstrated that the direction of selection on beak depth in the Galapagos finch *Geospiza fortis* varied among

years as a function of seed availability. More recently, Calsbeek and Cox used an experimental manipulation of population density to show that intraspecific competition increases the strength of selection on body size in *Anolis* lizards (Calsbeek & Cox 2010). Studies such as these isolate the ecological agents responsible for generating phenotypic selection, and thereby provide a direct link between the environment and variation in selection (Cain & Sheppard 1954; Boughman 2001; Vignieri *et al.* 2010; MacColl 2011; Siepielski *et al.* 2013).

The environment likewise influences expressed genetic variation in a trait (Queitsch *et al.* 2002; Gibson & Dworkin 2004; Barrett & Schluter 2008; Barrett *et al.* 2009). In marine sticklebacks, for example, significantly more genetic variation for body size is expressed when fish from a single genetic source population are reared in freshwater rather than in their native marine environment (McGuigan *et al.* 2011). Such environmental effects on expressed genetic variation are a form of genotype × environment interaction, occurring whenever the interaction results in a difference in variation among genotypes in the alternative environments (Fig. 1). Contrary to evolved changes in genetic architecture, which take place over long timescales (Arnold *et al.* 2008), environmental effects on expressed genetic variation occur in a single generation because they are due to environment-specific allelic effects rather than evolved changes in allele frequencies or allelic effects (Wood & Brodie 2015). Environmental effects on genetic variance are reported in the literature as differences between environments in additive genetic variance (V_A), total

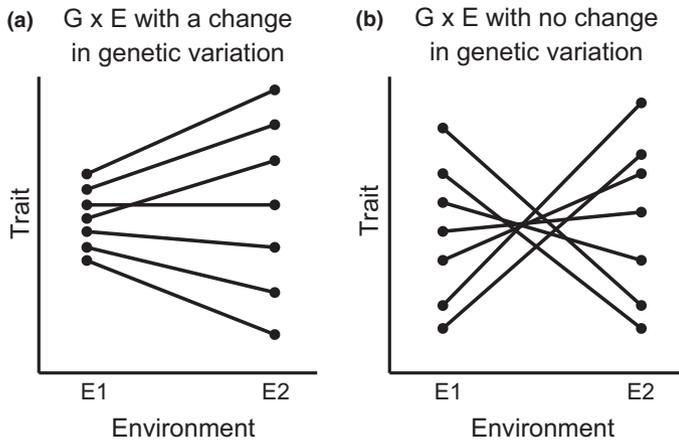


Figure 1 Environmentally induced changes in genetic variation are due to genotype \times environment interactions ($G \times E$), but not all $G \times E$ result in changes in genetic variation. Lines connect hypothetical genotype means for a given trait in two hypothetical environments. (a) $G \times E$ results in a change in genetic variation when among-genotype variation differs between environments. (b) $G \times E$ does not change genetic variation when the among-genotype variation is similar between environments.

genetic variance (V_G) or heritability, although it is important to distinguish differences in heritabilities due to genetic effects from those due to changes in non-genetic components (i.e. residual environmental variance) (Houle 1992; Hansen *et al.* 2011).

In the decades since Waddington documented that exposure to a novel environment uncovered previously unobserved genetic variation in thorax number in *Drosophila* (Waddington

1956), many studies have documented environmentally induced change in genetic variances or heritabilities (Hoffmann & Merila 1999; Weigand *et al.* 2003; Le Rouzic & Carlborg 2008; Schlichting 2008; Barrett *et al.* 2009). The release of this ‘cryptic genetic variation’ is hypothesised to fuel adaptation to novel environments (McGuigan & Sgrò 2009; Ledón-Rettig *et al.* 2014). In a recent meta-analysis, we found that short-term environmental effects on expressed genetic variation can be as large as the differences that accumulate between populations over much longer timescales (Wood & Brodie 2015), suggesting that environmentally induced change in expressed genetic variation is large enough to play an important role in adaptive evolution.

Because environmental change or differences can alter selection acting on a trait and expressed genetic variation in that trait, a correlation between these two components of evolutionary change could arise whenever the same ecological factor jointly influences both (Fig. 2) (Wilson *et al.* 2006; McGuigan & Sgrò 2009; Pemberton 2010). Either spatially or temporally variable environments could generate this correlation. In the former, selection and genetic variation would covary among *populations* inhabiting different environments, while in the latter, the two parameters would covary among *generations*. When genetic variation is abundant in the same environmental conditions that generate strong selection, the correlation is positive; when there is little genetic variation expressed in the environments that generate strong selection (or *vice versa*), the correlation is negative.

The correlation between the strength of selection acting on a trait and expressed genetic variation in that trait could impact the rate of evolutionary change in quantitative traits. A positive correlation should increase the microevolutionary response

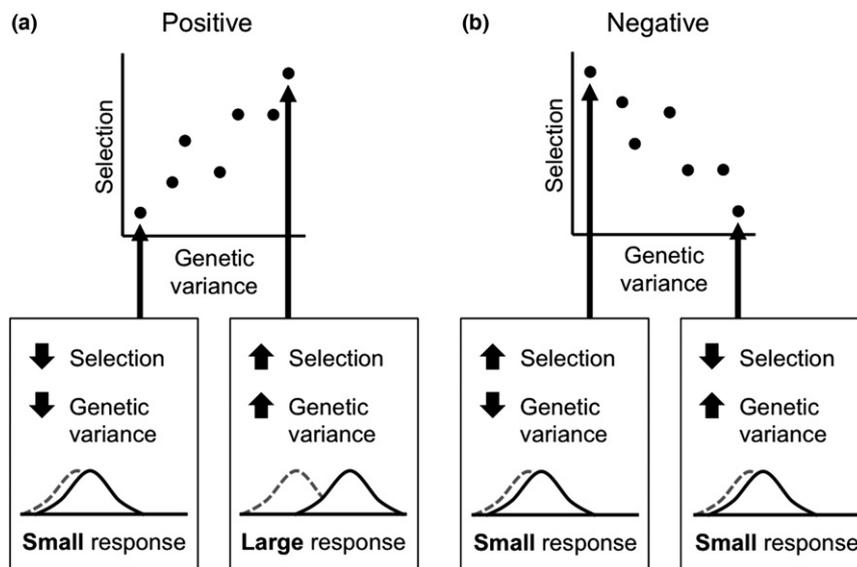


Figure 2 The effect of an environmentally driven correlation between selection and heritable genetic variation on the evolutionary response to selection. Each point in the scatterplots represents a single population (in a spatially varying environment) or generation (in a temporally varying environment). (a) Positive correlation: the same environments that generate strong selection are characterised by abundant genetic variation and exhibit a large evolutionary response, and the environments that generate weak selection have little genetic variation and exhibit a small response. (b) Negative correlation: the environments that generate strong selection have little genetic variation, and the environments that generate weak selection have abundant genetic variation. When the correlation is negative, the evolutionary response is always small.

to selection (the change in the trait mean in from one generation to the next) because it pairs strong selection with abundant genetic variation in at least some populations or generations (Fig. 2). A negative correlation, on the other hand, should decrease the response to selection because it couples abundant genetic variation with weak selection in some populations or generations and scarce genetic variation with strong selection in others (Fig. 2). Disregarding the correlation between selection and genetic variation may therefore lead the evolutionary ecologists to consistently under- or overestimate the rate of evolution in natural metapopulations (Wilson *et al.* 2006; Husby *et al.* 2011) or the rate of evolutionary response to changing environments. In fact, pervasive negative correlations could partially account for the frequent observation of microevolutionary stasis in natural populations in the face of strong selection (Merilä *et al.* 2001; Pemberton 2010).

In spite of the potentially broad ramifications of a correlation between the strength of selection and expressed genetic variation, most models of trait evolution in variable environments implicitly assume that the two are independent (Ronce & Kirkpatrick 2001; Hanski *et al.* 2011). Similarly, empirical biologists rarely estimate both parameters in multiple populations or generations, thereby making the simplifying assumption that one of the two is constant (McAdam & Boutin 2003; Gosden & Svensson 2008; Weese *et al.* 2010). To the best of our knowledge, only two studies have measured the correlation, both using long-term pedigree data in natural populations of vertebrates (Fig. 3). Wilson *et al.* (2006) found a negative correlation between selection and genetic variation for lamb birth weight in Soay sheep (Fig. 3a,b). Harsh years, characterised by poor climatic conditions, generated strong selection on birth weight but were associated with low heritable variation for the trait, while benign years generated weak selection and uncovered substantial heritable variation. Husby *et al.* (2011) found the opposite correlation in great tits. Elevated spring temperatures were associated with strong selection and high heritability for the timing of breeding, while low spring temperatures were associated with weak selection and low heritability (Fig. 3d). The fact that both studies found evidence for a correlation between selection and expressed genetic variation suggests that it merits theoretical and empirical investigation.

Here, we address the evolutionary consequences and potential ecological causes of a correlation between the strength of selection on a trait and expressed genetic variance in that trait in metapopulations inhabiting spatially or temporally heterogeneous environments. We focused on the strength rather than the direction of selection because we were primarily interested in the consequences of the correlation for the *rate* of evolution, and because differences in the direction of evolution are less meaningful when compared across trait types. Using a simple analytical model, we demonstrate that a correlation between selection and genetic variance impacts both the mean and variance in the responses to selection in a hypothetical metapopulation. We then synthesise the literature on the biotic and abiotic aspects of the environment that separately affect selection and genetic variance to identify the conditions likely to generate the correlation in natural populations, and suggest directions of future research.

EVOLUTIONARY CONSEQUENCES OF A CORRELATION BETWEEN SELECTION AND GENETIC VARIATION

To assess the evolutionary consequences of a correlation between the strength of selection and expressed genetic variation, we examine how the correlation affects the mean and the variance in the change in the mean of a single trait in a single generation (hereafter, ‘responses to selection’ or ‘evolutionary responses’) in a hypothetical metapopulation. This hypothetical metapopulation inhabits a spatially variable environment that generates variation among populations in the strength of selection and expressed genetic variation in the focal trait. Although we describe the model below in the context of *spatial* covariation between selection and genetic variation, the inferences that we draw translate to *temporal* covariation in the two parameters as well. We initially make the simplifying assumption that there is no migration between local populations in the spatially variable environment, but we relax this assumption later on (see ‘Incorporating migration’ below).

A simple analytical model

The response to selection in a single population i in the focal metapopulation is given by the breeder’s equation,

$$\Delta \bar{z}_i = G_i \beta_i \quad (1)$$

where $\Delta \bar{z}_i$ is the change in the trait mean, G_i is the additive genetic variance in the trait (hereafter, ‘genetic variation’) and β_i is a selection gradient that describes the strength of directional selection acting on the trait (i.e. the absolute value of the selection gradient) (Lande & Arnold 1983). For notational simplicity, we use β_i throughout to refer to the absolute value of the selection gradient, $|\beta_i|$.

The mean evolutionary response describes the average rate of evolution across all populations in the metapopulation. The mean response to selection in a focal metapopulation consisting of n populations is given by

$$\overline{\Delta \bar{z}} = \frac{\sum_{i=1}^n G_i \beta_i}{n} \quad (2)$$

Equation 2 can be re-written in expectation notation as

$$\begin{aligned} E(\overline{\Delta \bar{z}}) &= E(G\beta) \\ &= E(G)E(\beta) + cov(G, \beta) \end{aligned} \quad (3)$$

where E is the expected value (i.e. mean), and $cov(G, \beta)$ is the covariance between selection and genetic variation, equivalent to the correlation between the two parameters when both are standardised to a variance of one. This expression demonstrates that the covariance between selection and genetic variation linearly changes the mean evolutionary response: a positive correlation increases the mean response and a negative covariance decreases it. The effect is directly proportional to the strength of the correlation.

The variance in the evolutionary response captures the degree to which the rate of evolution differs among constituent populations. The variance among populations in the evolutionary response is

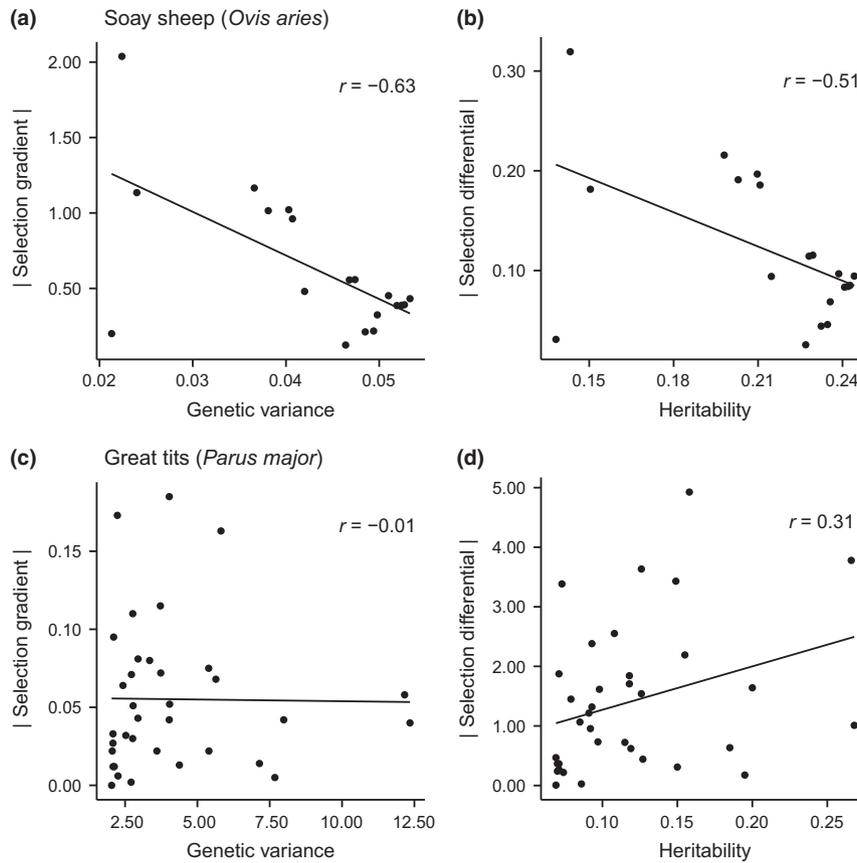


Figure 3 The two existing estimates of the correlation between the strength of selection and genetic variation. (a, b) Lamb birth weight in Soay sheep (Wilson *et al.* 2006). (c, d) Egg-laying date in great tits (Husby *et al.* 2011). Each point corresponds to a single year. Both studies estimated the correlation in two ways: using genetic variation and selection gradients (a, c) and using heritability and selection differentials (b, d). Selection differentials are the covariance between a trait and fitness; selection gradients are differentials standardised by the phenotypic variance (Brodie *et al.* 1995; Lande & Arnold 1983). In great tits, the correlation was non-zero only when heritability and selection differentials were used, which Husby *et al.* (2011) attribute to the fact that both of these parameters depend on phenotypic variance, resulting in a stronger relationship between the two. The data to reproduce panels (a) and (b) were provided by Alastair Wilson; panels (c) and (d) were reproduced using Table S2 in Husby *et al.* (2011).

$$\text{var}(\Delta\bar{z}) = \frac{\sum_{i=1}^n (\Delta\bar{z}_i - \overline{\Delta\bar{z}})^2}{n} \quad (4)$$

or, in expectation notation,

$$\begin{aligned} \text{var}(\Delta\bar{z}) &= \text{var}(G\beta) \\ &= E(\beta)^2 \text{var}(G) + E(G)^2 \text{var}(\beta) \\ &\quad + 2E(G)E(\beta)\text{cov}(G, \beta) + \text{var}(G)\text{var}(\beta) \\ &\quad + \text{cov}(G, \beta)^2 \end{aligned} \quad (5)$$

assuming that selection and genetic variance are bivariate normally distributed (Bohrnstedt & Goldberger 1969). This equation demonstrates that a correlation between selection and genetic variation increases the differences in the rate of evolution among populations when the correlation is positive, and homogenises evolutionary rates when it is negative. A positive correlation inflates the between-population or -generation variance in the response because populations in which selection is strong and genetic variation is abundant exhibit an extremely large evolutionary response, while the response in populations with weak selection and little genetic variation is near zero. A negative correlation reduces the variance in the

response among populations because strong selection is tempered by low genetic variation, and abundant genetic variation by weak selection, in all populations.

Because the assumption of bivariate normality of selection gradients and expressed genetic variance may be violated in natural metapopulations, we visualised the evolutionary consequences of the correlation relaxing this assumption. We modelled empirically reasonable distributions of selection and genetic variance, in which weak selection and low genetic variation are common (Kingsolver *et al.* 2001; Geber & Griffen 2003; Hansen *et al.* 2011). For nine values of the correlation between selection and genetic variance ranging from -0.95 to 0.95 , we randomly generated 100 000 pairs of selection gradients and genetic variances and calculated a response to selection from each pair using the breeder's equation. We plotted the distribution of the resulting responses for each value of the correlation (Fig. 4). To generate paired selection gradients and genetic variances with the desired correlation, we used the inverse transform method (Law & Kelton 2000), which applies the inverse cumulative distribution functions of the desired marginal distributions to two uniform variables with a specified correlation. Selection gradients were drawn from a half-normal

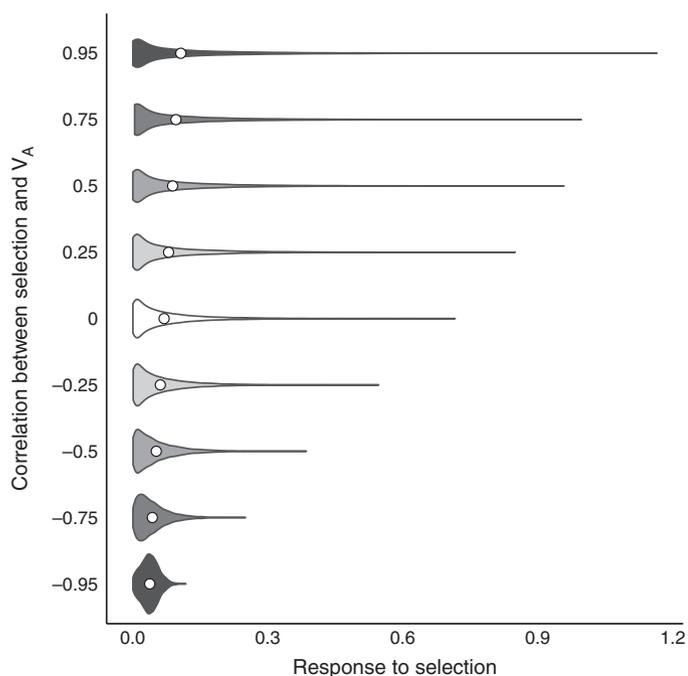


Figure 4 Violin plots (smoothed histograms) of the effect of a correlation between selection and genetic variance (V_A) on the evolutionary response. The distribution of the response when selection and V_A are uncorrelated is shown at $r = 0$ on the vertical axis; above, the correlation becomes increasingly positive, and below, increasingly negative. The mean response is indicated by the white circle on each distribution.

distribution (scale parameter $\theta = 4.75$), which approximates the distribution of the absolute value of directional selection gradients reported in Kingsolver *et al.* (2001) (mean = 0.21, median = 0.16, variance = 0.025). Genetic variances were drawn from a beta distribution ($\alpha = 0.95$, $\beta = 1.90$). To estimate the shape parameters of this distribution, we fitted a beta distribution to the heritabilities reported in Supplemental Table 1 from Hansen *et al.* (2011) using the function *fitdistr* in package *fitdistrplus* (Delignette-Muller & Dutang 2015) in R, excluding cases where $h^2 < 0$ and $h^2 > 1$ ($n = 20$ out of 1460).

Our visualisation shows that correlation between selection and expressed genetic variation has a larger impact on the variance in the evolutionary response than it does on the mean response (Fig. 4). While the mean evolutionary response was not quite threefold larger for a correlation of 0.95 than it was for a correlation of -0.95 , the standard deviation of the evolutionary response was nearly sevenfold larger (mean response [SD] _{$r = -0.95$} : 0.04 [0.02]; mean response [SD] _{$r = 0.95$} : 0.11 [0.14]). The differences in evolutionary outcomes among populations (or generations, in the case of temporal covariation between selection and genetic variation) are greater when the correlation is strongly positive and nearly eliminated when it is negative. The strong effect of the correlation on the variance has been largely overlooked in the few existing studies that have explored the evolutionary consequences of the correlation, which have focused on its consequences for the mean evolutionary response across years in a temporally variable environment (Wilson *et al.* 2006; Pemberton 2010; Husby *et al.* 2011).

Evolutionary implications

Although we outlined our analytical model in the context of spatial environmental variation (i.e. covariance between selection and expressed genetic variance among populations in a metapopulation), the results can be applied to temporally variable environments that generate covariation between the two parameters among years as well. Temporally fluctuating environmental conditions may not have a lasting impact on the evolutionary response, but progressive change in the environment – such as that driven by global climate change and anthropogenic habitat modification – could slow or increase the rate of evolutionary change if it induces a correlation between selection and genetic variation.

The degree to which adaptive evolution can keep pace with rapidly changing ecological conditions remains a major outstanding question in evolutionary conservation biology (Shaw & Etterson 2012). Our simple model suggests that the evolutionary consequences of temporal environmental change may depend on the sign of the correlation. The release of cryptic genetic variation under novel conditions is often invoked as a mechanism by which threatened populations may rapidly adapt to changing environments (Reed *et al.* 2011). However, the evolutionary fate of cryptic genetic variation released in novel environments depends on the selection regime it experiences. Cryptic genetic variation will only contribute substantially to evolutionary change if it is released for traits that experience strong selection, a condition that is only satisfied if positive correlations between selection and genetic variation predominate. Negative correlations would shield cryptic genetic variation from strong selection, preventing it from contributing to adaptation. In fact, negative correlations between the strength of selection and genetic variance could contribute to microevolutionary stasis (i.e. a lack of a response to selection) that is often documented in natural populations (Merilä *et al.* 2001; Pemberton 2010).

The strong effect of the correlation on the variance in the response to selection implies that the evolutionary response could differ by an order of magnitude in neighbouring populations or subsequent generations when the correlation is positive, or could remain nearly identical across populations or generations when the correlation is negative. In a heterogeneous landscape, positive correlations have the potential to create a mosaic of evolutionary hotspots (*sensu* Brodie *et al.* 2002; Thompson 2005), with the potential to exert strong influence on metapopulation-level evolution. If the few populations with the capacity to respond to selection export migrants to other populations, they could drive a change in the trait mean even in populations that do not experience strong selection or harbour the genetic variation to respond to it (Vuilleumier *et al.* 2008). This change may not always be adaptive, though, especially if the direction of selection differs among populations (Thompson 2005).

On a pragmatic note, the effect of the correlation between selection and expressed genetic variation on the among-population or among-generation variance in the evolutionary response influences our ability to extrapolate evolutionary predictions beyond the population or generation in which

selection and genetic variation were originally measured, potentially confounding assessments of adaptive potential in rapidly changing environments (Gienapp *et al.* 2008). When selection and genetic variance are positively correlated, the response to selection measured in one population or year cannot be generalised to others because evolutionary outcomes differ substantially. However, the evolutionary response in a single population or generation is a reasonably accurate estimate of the response in other populations or generations when the correlation is negative, because variance in the response is minimal even in the face of large differences in selection or genetic variation.

Incorporating migration

Because populations in a metapopulation are often connected by migration in spatially variable environments, we briefly considered how migration influences the inferences drawn from our model. Below, we modify our analytical model to show that migration between environments decreases the effect of the correlation between selection and genetic variance on the mean evolutionary response by decoupling the environment in which selection occurs and the environment in which genetic variation is expressed. We present an extended model for the mean evolutionary response. Incorporating the effect of migration on the variance in the evolutionary response would require the model to be expanded beyond the scope of this paper. In the model below, we assumed a migrant pool and equal population sizes, and further assumed that selection acts before migration and reproduction occurs after migration.

We take advantage of the fact that a single trait expressed in two environments can be treated as separate traits that are genetically correlated (Via & Lande 1985). Individuals in environment i carry an 'expressed' value z_{ii} for the trait in environment i and 'unexpressed' values z_{ij}, \dots, z_{in} for the trait in environments j through n . We denote the value of the expressed trait in environment i after selection \bar{z}_{ii}^s , the value of the trait in the migrant pool \bar{z}_i^m and the value of the expressed trait in environment i after selection and migration \bar{z}_{ii}^{sm} . G_{ii} is the genetic variance for the expressed trait in environment i and G_{ji}, \dots, G_{ni} are the genetic covariances between the expressed and unexpressed traits in environments j through n . β_i, \dots, β_n are the direct selection gradients on the expressed traits in environments i through n . Unexpressed traits cannot experience direct selection, and only experience indirect selection through genetic correlations with the expressed trait.

The response to selection on the expressed trait in each environment can be partitioned into the change due to selection in that environment and the change due to migration from other environments. After selection in environment i , the mean expressed trait value in environment i , \bar{z}_{ii}^s , is

$$\bar{z}_{ii}^s = \bar{z}_{ii} + G_{ii}\beta_i \quad (6)$$

The mean trait value in the migrant pool, \bar{z}_i^m , is the mean unexpressed trait value for environment i in all other environments after selection,

$$\bar{z}_i^m = E(\bar{z}_{ji}) + E(G_{ji})E(\beta_j) \quad (7)$$

assuming that the strength of selection is independent of the genetic correlation between the expressed and unexpressed traits.

After selection and migration, the mean expressed trait value in environment i , \bar{z}_{ii}^{sm} , is the mean expressed trait value after selection in environment i , weighted by the proportion of individuals that are non-migrants ($1 - m$), plus the mean expressed trait value in the migrant pool, weighted by the proportion of migrants (m),

$$\bar{z}_{ii}^{sm} = (1 - m)\bar{z}_{ii}^s + m\bar{z}_i^m \quad (8)$$

The mean response to selection in the expressed trait, $E(\Delta\bar{z}_{ii})$, is the mean difference between the expressed trait before and after selection across all environments,

$$\begin{aligned} E(\Delta\bar{z}_{ii}) &= E(\bar{z}_{ii}^{sm} - \bar{z}_{ii}) \\ &= (1 - m)[E(\bar{z}_{ii}) + E(G_{ii})E(\beta_i) + cov(G_{ii}, \beta_i)] \\ &\quad + m[E(\bar{z}_{ji}) + E(G_{ji})E(\beta_j)] - E(\bar{z}_{ii}) \end{aligned} \quad (9)$$

Equation 9 shows that the correlation between selection and genetic variation, $cov(G_{ii}, \beta_i)$, only contributes to the response to selection in the non-migrants, because these are the only individuals that experience selection and express genetic variation in the same environment. Migration decreases the effect of the correlation on the mean evolutionary response by increasing the proportion of the population for which the correlation does not contribute to the evolutionary response. Therefore, the correlation between genetic variation and selection will have the strongest effect in 'coarse-grained' environments (*sensu* Levins 1968), in which migration among environments is rare.

ECOLOGICAL CAUSES OF A CORRELATION BETWEEN SELECTION AND GENETIC VARIATION

The main impediment to evaluating the evolutionary implications of a correlation between the strength of selection and expressed genetic variation is a logistical one: few researchers measure environmental effects on both selection and genetic variance in the same system, such that those measurements could be synthesised into estimates of a correlation between the two parameters. However, many aspects of the environment – such as environmental novelty and quality – have been independently linked to changes in both selection and genetic variance (Bennington & McGraw 1996; Hoffmann & Merila 1999; Stanton *et al.* 2000; Charmantier & Garant 2005; Plough 2012). We reviewed the literature to identify the biotic and abiotic ecological factors that influence selection and genetic variation in order to begin to predict the environmental conditions likely to generate the correlation.

Literature review methods

We searched for studies that found a difference in selection or genetic variation between environments, and compared the resulting datasets to identify the common abiotic and biotic variables that influence both parameters. We performed our search in Web of Science in October–November 2015, and searched for papers from all available years in the database

using the keywords ‘environment*’, ‘selection’, ‘genetic varia*’, ‘heritability’ and ‘cryptic genetic variation’, and supplemented the results with studies cited by the papers we found. We excluded studies that measured environmental effects on the direction, rather than the magnitude, of selection, and any studies that did not statistically test the putative environmental cause underlying differences in selection or genetic variation. Where possible, we also excluded studies in which differences in heritabilities between environments were due to changes in environmental variance rather than genetic variance because we were interested in changes that resulted from genotype \times environment interactions. Because the studies in our dataset varied in their original sample sizes, and therefore in their power to detect environmental effects on selection and genetic variation, we included studies regardless of whether they found significant differences in selection or expressed genetic variation between environments.

For studies that reported selection gradients, genetic variances, heritabilities and their associated standard errors and sample sizes for each environment, we also calculated effect size as the difference between the two most extreme environments, divided by their pooled standard error (Hedge’s *G*) (Nakagawa & Cuthill 2007). The sample sizes for selection gradients were the number of individuals; for genetic variances and heritabilities, the sample sizes were the number of families or genotypes (Lynch & Walsh 1998). A few studies reported a correlation between an ecological factor and selection or genetic variation, and we included the value of the correlation in lieu of Hedge’s *G* in these cases. For each trait, we recorded whether the original study detected a significant difference in the strength of selection or expressed genetic variation between environments. Finally, because it was not possible to calculate effect sizes for all traits in all studies, we recorded whether the original study found a positive or negative effect of the environment on genetic variation or selection for each trait, regardless of whether the difference was significant.

Literature review results

We identified 28 studies that measured environmental effects on genetic variation and 23 studies that measured environmental effects on selection (two studies, Wilson *et al.* 2006 and Husby *et al.* 2011; measured both) (Table S1, Appendix S1). These studies measured genetic variation on a mean of 2.96 traits (median = 2, range = 1–12) and selection on a mean of 2.9 traits (median = 2, range = 1–10). Our resulting dataset consists of 83 estimates of environmental

effects on genetic variation and 68 estimates of environmental effects on selection across all traits reported in all studies. Similar to other literature reviews (Kingsolver *et al.* 2001; Siepielski *et al.* 2009), most estimates were for morphological (61%) or phenological (23%) traits. Our dataset included vertebrates (mammals, reptiles, amphibians, birds), invertebrates (insects, crustaceans, molluscs, annelid worms) and flowering plants. Although similar number of studies estimated selection and genetic variation in vertebrates, invertebrates were under-represented for estimates of selection, and plants were under-represented for estimates of genetic variation.

A key methodological difference between studies that measured environmental effects on genetic variation and selection is the type of experimental population and environmental conditions that each considered (Table 1). The vast majority of estimates of selection were obtained in wild populations, using both experimental and natural environmental variation. In contrast, most studies of environmental effects on genetic variation were conducted in artificially manipulated environments in laboratory populations. Estimates of genetic variation in different natural environments were very rare; existing estimates were primarily derived from temporally variable natural environments (Garant *et al.* 2004; Wilson *et al.* 2006; Husby *et al.* 2011).

Due to the limitations inherent in our dataset and its relatively small size, we chose not to perform a formal quantitative meta-analysis. It is important to note that the qualitative conclusions presented below are subject to two caveats. First, our results do not account for the sampling process in each individual study (Morrissey & Hadfield 2012). Second, the individual data points presented in Figs 5 and 6 are not statistically independent because many studies measured multiple traits. Therefore, the results of our literature review should be viewed as a preliminary attempt to illuminate the ecological factors with the potential to generate a correlation between selection and expressed genetic variation, as well as to identify factors less likely to do so.

Across trait types, a broad range of abiotic (e.g. temperature, precipitation) and biotic (e.g. competition, predation, herbivory and diet) conditions influenced the strength of selection and expressed genetic variation. All environmental factors influenced selection and genetic variation in at least some traits and taxa, which suggests that a broad array of abiotic and biotic conditions could potentially generate a correlation between the two. However, some environmental factors seem to influence one parameter more than the other, and are thereby less likely to produce a correlation (Fig. 5). For

Table 1 The number of studies identified in our literature review, broken down by taxon, type of environmental replication, experimental population and unit of replication

	Taxon			Environmental variation		Population		Replication	
	Vert.	Invert.	Plant	Natural	Exper.	Wild	Lab	Spat.	Temp.
Genetic variation	12	14	2	4	24	7	21	2	5
Selection	14	4	10	11	12	16	6	8	8

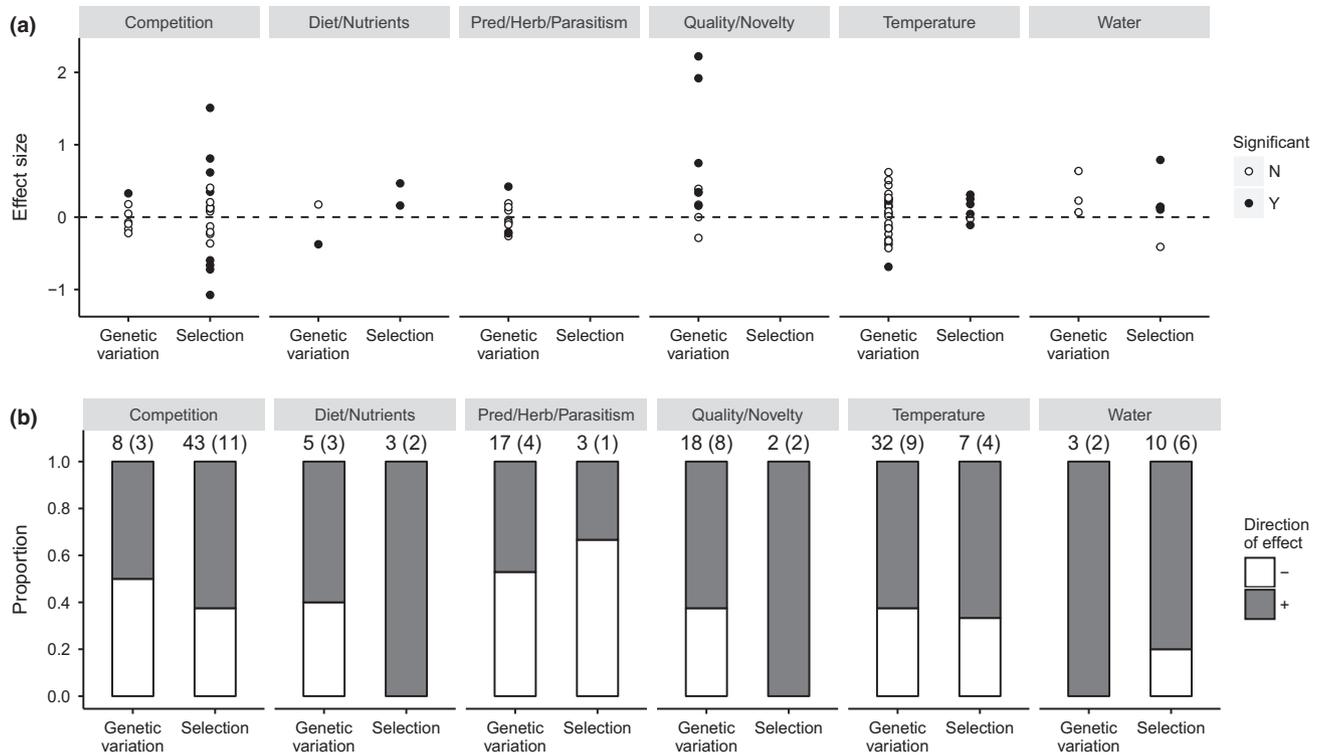


Figure 5 The change in genetic variation or in the magnitude of selection for different environmental manipulations. (a) The effect size, with the points colour-coded according to whether the difference was significant in the original study. For any points above the dashed line ($y = 0$), an increase in the environmental variable (competition, diet/nutrients, etc.) led to an increase in genetic variation or the magnitude of selection; for points below the dashed line, an increase in the environmental variable decreased genetic variation or the magnitude of selection. (b) Because we could not calculate the effect size for all studies, we also tabulated the number of increases and decreases in genetic variation and selection (regardless of whether they were significant). This panel includes all measured traits, regardless of significance in the original study. Sample sizes – the number of traits and the number of studies (in parentheses) – are above each bar.

example, competition appeared to strongly impact selection but have little effect on expressed genetic variation. Conversely, temperature generated differences in genetic variation but had little effect on the strength of selection. Environmental effects on both selection and genetic variation occurred across trait types as well as across environments. Significant differences in the strength of selection and expressed genetic variation between environments were detected in morphological, phenological and fitness traits (Fig. 6), indicating that the evolutionary consequences of environmental variation extend to many aspects of the multivariate phenotype.

Overall, our results suggest that the effect of the environment on selection and genetic variation may be quite broad, encompassing many environmental factors and trait types. However, because all ecological factors had both positive and negative effects on selection and genetic variation across all trait types, we are unable to make clear predictions about the direction of the correlation between selection and genetic variation that might predominate in natural populations. This result illustrates how crucial it is to estimate both parameters in the same populations to address this fundamental question.

Intriguingly, our survey suggests that anthropogenic ecological change may induce major changes in selection and genetic variation, potentially influencing the prevalence and/or magnitude of the correlation between the two parameters in natural populations. Biological invasions, habitat modification and

global climate change are expected to affect at least some of the biotic and abiotic factors with effects on selection and genetic variation in our literature review (Fig. 5) (Adams *et al.* 1990; Jump & Peñuelas 2005; Howden *et al.* 2007; Tylanakis *et al.* 2008; Tomiolo *et al.* 2015). The principal abiotic environmental changes anticipated under climate change – temperature and precipitation – have been linked to changes in both selection and genetic variation in some species, although we note above that the impact of temperature on the two parameters appears asymmetric (Fig. 5) (Franks & Weis 2009; Berger *et al.* 2011; Logan *et al.* 2014). Anthropogenic changes in the biotic environment may also generate a correlation between selection and genetic variation (Fig. 5). Biological invasions and anthropogenic habitat modification alter the frequency and nature of species interactions, influencing intra- and interspecific competition (Beans & Roach 2015a,b), food sources (Carroll *et al.* 2005) and predatory and parasitic interactions, which are linked to changes in selection (Losos *et al.* 2004; Carroll *et al.* 2005; Rose *et al.* 2005; Behm *et al.* 2010) and genetic variation (Ledón-Rettig *et al.* 2010; Heath & McGhee 2012) (Fig. 5).

Finally, there are some critical asymmetries of information for selection and genetic variance. For example, existing data suggest that environmental quality and/or novelty influences genetic variation, but very few studies have measured its impact on selection (Fig. 5). The absence of data on selection

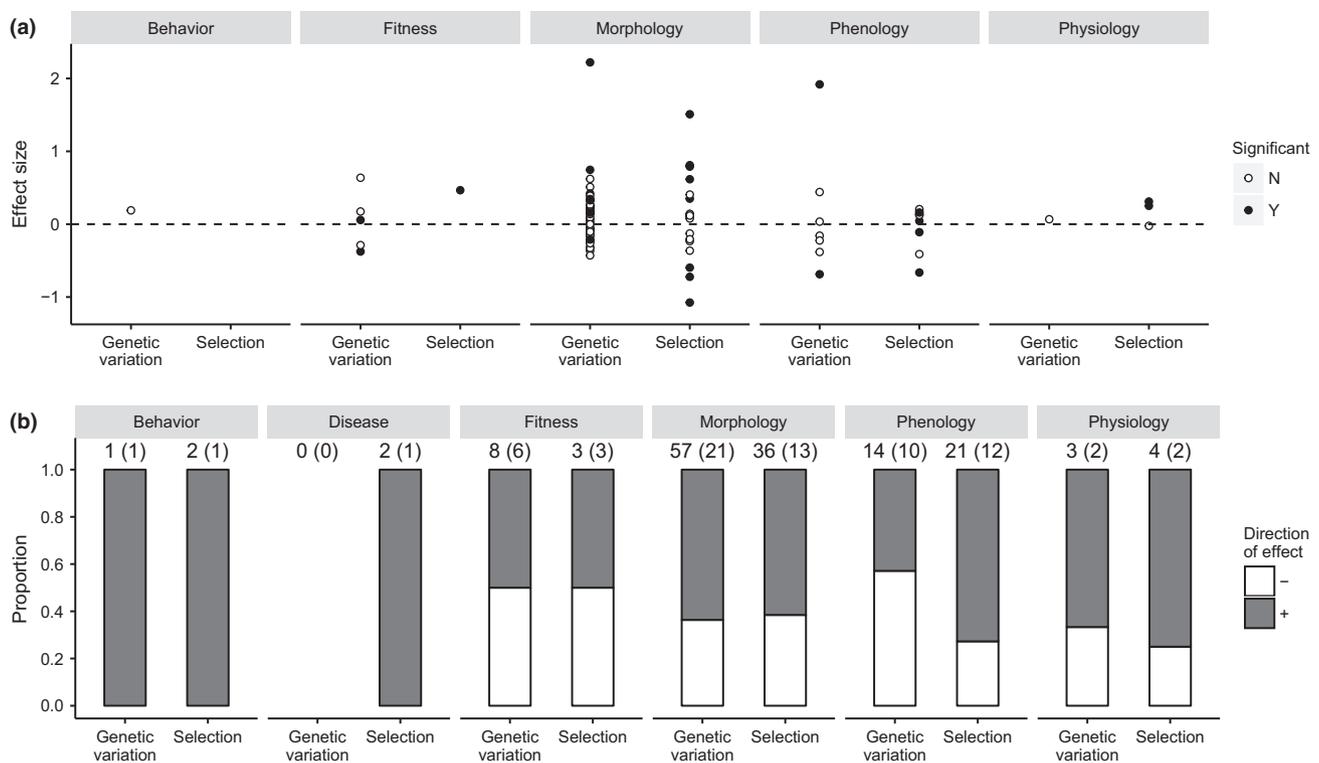


Figure 6 The change in genetic variation or in the magnitude of selection for different traits. (a) The effect size, with the points colour-coded according to whether the difference was significant in the original study. For any points above the dashed line at $y = 0$, an increase in the environmental variable (competition, diet/nutrients, etc.) led to an increase in genetic variation or the magnitude of selection; for points below the dashed line, an increase in the environmental variable decreased genetic variation or the magnitude of selection. (b) Because we could not calculate the effect size for all studies, we also tabulated the number of increases and decreases in genetic variation and selection (regardless of whether they were significant). This panel includes all measured traits, regardless of significance in the original study. Sample sizes – the number of traits and the number of studies (in parentheses) – are above each bar.

may stem from limitations inherent in literature reviews like ours: there may be many more studies in our dataset that measured selection under conditions the focal population had not experienced before, but we relied on author-designated novelty, so we did not categorise an environmental treatment as novel unless the original study did. Nevertheless, the discrepancy between these datasets is noteworthy because novel biotic and abiotic conditions are expected to become increasingly common in the face of rapid anthropogenic environmental change (Strauss *et al.* 2006; Carroll 2007; Gienapp *et al.* 2008; Hoffmann & Sgrò 2011). Our results are consistent with the growing consensus that novel or stressful environments influence evolutionary potential by uncovering previously unexpressed genetic variation (Hoffmann & Merila 1999; Gibson & Dworkin 2004; McGuigan & Sgrò 2009; Ledón-Rettig *et al.* 2014; Paaby & Rockman 2014). Ultimately, the evolutionary consequences of these changes depend on concurrent changes in the strength of selection.

FUTURE DIRECTIONS

In spite of the potentially broad evolutionary consequences of a correlation between the strength of selection acting on a trait and expressed genetic variance in that trait, its net effect is difficult to predict due to the almost complete lack of empirical estimates. Specifically, we know little about the

relative frequency of positive and negative correlations in the wild, which have strikingly different evolutionary implications (Fig. 4). In the light of this empirical gap, we envision several productive avenues for future research.

Evolutionary ecologists should prioritise the joint estimation of selection and genetic variation in natural populations. Many researchers may already have long-term datasets consisting of phenotype and fitness measurements on the same individuals from multiple populations or generations, combined with a pedigree, that could be used to estimate the correlation between selection and genetic variance. Although studies of genetic variance in natural populations have historically been limited to species with observation-based pedigrees (e.g. birds and mammals) (Grant & Grant 1995; Wilson *et al.* 2006; Husby *et al.* 2011), the increasing availability of genetic tools in non-model organisms relaxes this constraint. Future work should focus on spatial covariation between selection and genetic variation (estimating the two parameters in multiple populations of a single cohort), or on temporal covariation between selection and genetic variation in annual species. The two existing studies of the correlation measured temporal variation in selection and genetic variation in long-lived vertebrates, in which inferring the response to selection on an annual basis requires caution due to overlapping generations (Merilä *et al.* 2001).

Species that occur along ecological gradients or in multiple habitats are excellent natural systems in which to study the correlation in ecologically relevant phenotypes. Many model systems in evolutionary ecology are found along altitudinal clines (e.g. *Mimulus*) (Kooyers *et al.* 2014) and temperature gradients (e.g. *Drosophila* or Glanville fritillary butterflies) (Hanski & Singer 2001; Frentiu & Chenoweth 2010; Kvist *et al.* 2012), and their responses to ecologically relevant biotic and abiotic stressors are extensively characterised (e.g. *Arabidopsis*) (Assmann 2013). Well-studied species that inhabit multiple discrete environments include insects that feed on alternative host plants (e.g. pea aphids) (Brisson & Stern 2006), and plants growing in different soils (e.g. serpentine communities) (Baythavong 2011) or with different symbionts (e.g. *Medicago* and its mutualistic rhizobia) (Heath *et al.* 2012). To gauge the consequences of anthropogenic environmental change for the correlation between selection and genetic variation, empirical work should include species and traits that are affected by climate change (e.g. thermal performance in lizards) (Logan *et al.* 2014) or biological invasions (e.g. the colonisation of introduced hosts in soapberry bugs and apple maggot flies) (Strauss *et al.* 2006).

Identifying the ecological causes of a correlation between the strength of selection and expressed genetic variation would be substantially advanced by a quantitative measure of environmental harshness or novelty that can be applied across taxa (Wood & Brodie 2015). Most studies rely on author-designated novelty, a subjective metric that limits our ability to reconcile conflicting results from different study systems (Gebhardt-Henrich & van Noordwijk 1991; Charmantier & Garant 2005; Tibbetts 2010). Ideally, environmental variation would be quantified with a metric that reflects how much the focal environment deviates from familiar or benign conditions. For example, environmental conditions could be described in terms of the difference between the focal environment and the average environment, and standardised by the variance in the relevant ecological factor. However, the challenges inherent in deploying this metric are at least twofold: first, it requires a great deal of information about typical environmental conditions in the focal population, and second, it would be difficult to translate to discrete environmental variation.

Experimental environmental manipulations should be used to complement these studies in natural populations (Kawecki *et al.* 2012). Mesocosm studies with small-bodied species (e.g. fish, insects or plants) in semi-natural settings could allow researchers to manipulate single environmental factors and concurrently estimate selection gradients and genetic variances (relying on marker-based pedigrees for the latter) across multiple replicates. Finally, experimental evolution with microorganisms offers a direct test of the central prediction of our model – that a correlation between selection and genetic variance affects both the mean and variance in the rate of evolution – in replicated experimental metapopulations. Genera like *Daphnia*, which experience well-characterised environmental stresses and exhibit easily measured phenotypes in response to those stresses (Orsini *et al.* 2013), are especially good candidates for this avenue of investigation. Testing the effect of migration on the evolutionary consequences of the correlation

would also be empirically tractable in an experimental evolution context, in which the migration rate can be easily manipulated.

Although we restrict this study to the univariate case, the consequences of an environmentally driven correlation between selection and genetic variance could extend to multivariate evolution as well. There is mounting evidence that the environment changes genetic correlations between traits as well as genetic variances (Sikkink *et al.* 2015; Wood & Brodie 2015). Genetic correlations constrain evolution when they oppose the direction of selection, and facilitate evolution when aligned with selection (Conner 2012), so if the environments that generate strong selection consistently weaken opposing genetic correlations, the evolutionary response of each trait should be less constrained by indirect selection on correlated traits. The opposite association would increase the role of genetic constraint.

CONCLUSION

While the pervasive effects of environmental heterogeneity on both selection expressed genetic variance imply that the correlation may be common, it remains difficult to predict whether a positive or negative correlation – and their concomitant alternate evolutionary consequences – is more likely in the absence of empirical data. Our results underscore the complex nature of the consequences of environmental heterogeneity for adaptive evolution, and highlight the need for future empirical work to address the frequency, ecological causes and evolutionary consequences of non-independence between the strength of selection and the expression of genetic variation in natural populations.

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AUTHORSHIP

CWW and EDB III developed the conceptual basis for the manuscript, developed the analytical model and wrote the manuscript. CWW performed the literature survey.

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SUPPORTING INFORMATION

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