

REVIEW AND SYNTHESIS

The spatial patterns of directional phenotypic selection

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Abstract

Local adaptation, adaptive population divergence and speciation are often expected to result from populations evolving in response to spatial variation in selection. Yet, we lack a comprehensive understanding of the major features that characterise the spatial patterns of selection, namely the extent of variation among populations in the strength and direction of selection. Here, we analyse a data set of spatially replicated studies of directional phenotypic selection from natural populations. The data set includes 60 studies, consisting of 3937 estimates of selection across an average of five populations. We performed meta-analyses to explore features characterising spatial variation in directional selection. We found that selection tends to vary mainly in strength and less in direction among populations. Although differences in the direction of selection occur among populations they do so where selection is often weakest, which may limit the potential for ongoing adaptive population divergence. Overall, we also found that spatial variation in selection appears comparable to temporal (annual) variation in selection within populations; however, several deficiencies in available data currently complicate this comparison. We discuss future research needs to further advance our understanding of spatial variation in selection.

Keywords

Adaptation, environmental variation, evolution, local adaptation, natural selection, selection mosaic, sexual selection, spatial variation.

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INTRODUCTION

Selection is a key process shaping the phenotypic diversity we observe among contemporary populations (e.g. Darwin 1859; Rieseberg *et al.* 2002) and in the fossil record (e.g. Simpson 1944, 1953; Eldredge 2005; Hunt *et al.* 2008). Different populations will often experience differences in abiotic and biotic environments (Pigliucci 2001; Bell 2008), and these local conditions may ultimately shape the selective landscape (Wade & Kalisz 1990; MacColl 2011) because different environments will often favour different phenotypes (Schluter 2000; Thompson 2005). Determining the patterns of selection in space therefore has broad implications for understanding the processes giving rise to phenotypic diversity.

Spatial variation in selection is an important underlying component of many theorised and observed evolutionary patterns and processes including adaptive geographical variation in traits (Endler 1980; Arnqvist 1992), speciation (Endler 1977), coevolution (Thompson 2005) and the maintenance of heritable variation in traits (Felsenstein 1976; Grant & Price 1981). Numerous studies have shown that variation in environments across space can impose differential selection leading to phenotypic divergence, including those on snails (Cain & Sheppard 1952), guppies (Endler 1980), sticklebacks (McKinnon & Rundle 2002), conifers (Benkman *et al.*

2010), among many others (e.g. Thompson 2005; Urban 2011; Sotka 2012). Likewise, the finding that environments vary and local adaptation is common (e.g. Hereford 2009) suggests that spatial variation in selection must also be common (but see counter-examples in Thompson 2005).

Thus, evidence for the evolutionary consequences of spatial variation in selection is abundant, and this is one important form of data with which to compliment existing theory on the topic (Levins 1968; Thompson 2005). Currently, we lack a comprehensive synthesis of another abundant form of relevant data: selection gradients (and differentials) as formalised by evolutionary quantitative genetic theory (Lande 1979; Lande & Arnold 1983). Evolutionary quantitative genetic approaches (following Lande & Arnold 1983; hereafter the ‘L–A approach’) have been especially useful for estimating selection empirically because the strength, direction, and form of selection can be compared among populations for different organisms, traits, and components of fitness. As hundreds of studies of selection in the wild using the L–A approach have now accumulated (Kingsolver *et al.* 2012), syntheses of this work have considered some of the major patterns of phenotypic selection in the wild. These reviews have focused on understanding the strength and direction of selection in nature and how these patterns may vary among trait types or fitness components (Endler

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1986; Hoekstra 2001; Kingsolver 2001; Hereford *et al.* 2004; Siepielski *et al.* 2011; Kingsolver *et al.* 2012), the extent to which selection may vary through time within populations (Hoekstra 2001; Siepielski *et al.* 2009, 2011; Morrissey & Hadfield 2012), and what factors may act to limit directional selection (Kingsolver & Diamond 2011).

Here, we aim to quantify the major features (namely variation in strength and direction among populations) that characterise spatial variation in patterns of selection. Numerous spatially replicated studies of selection (e.g. estimates of selection on the same trait and fitness component from two or more populations) from wild populations now exist. This provides an excellent opportunity to address outstanding questions about the spatial structure of selection in the wild. We first present meta-analyses of selection to provide a general understanding of the extent to which selection varies spatially. We then address a number of outstanding questions regarding the underlying spatial patterns of selection. We also highlight the additional information that authors should report, beyond selection coefficients as strictly defined in the quantitative genetic sense that would facilitate future primary and synthetic studies to more comprehensively address ecological hypotheses about variation in contemporary selection, and also to address associated consequences for adaptive evolution in wild populations.

METHODS

Database assembly

We reviewed the published literature from 1983 to December 2011 using the Web of Science indexing database system with the goal of identifying all studies estimating selection on multiple populations using the L–A method. Using the ‘times cited’ feature within the Web of Science, we searched the subset of articles citing Lande & Arnold’s (1983) article that additionally included one or more of the following phrases: spatial variation, population divergence, spatio-temporal, fluctuating selection, geographical variation, spatial variation in selection, selection variation in space, interpopulation variation in selection, selection mosaic, spatial variation natural selection and spatial variation sexual selection. The resulting database builds on earlier databases assembled by Kingsolver (2001) and Siepielski *et al.* (2009), and includes data reported in those databases if they met our inclusion criteria. When articles reported that they had measured selection on different populations but data from multiple populations were combined for analyses, we contacted the authors to ask for population-specific selection coefficients.

Our requirements included criteria used in previous database compilations (Kingsolver 2001; Siepielski *et al.* 2009). Specifically, we included only those studies that: (1) focused on wild, unmanipulated populations, (2) estimated selection on quantitative traits that showed continuous variation and (3) presented variance standardised selection differentials and/or gradients (*sensu* Lande & Arnold 1983) to facilitate comparisons across studies. Finally, we included studies that (4) estimated selection in at least two populations, and the populations were either noted by the authors as geographically distinct (no within-population replication) or were reported in the article to be genetically distinct. We suspect some level of dispersal might occur between some populations, but most studies lacked information (e.g. analysis of neutral genetic markers) to evaluate this possibility.

Each article was entered by one author and error checked by a different author. For some of the studies (8 of 60), careful review of the methods revealed the misclassification of selection differentials (generated from univariate linear regressions) as selection gradients (generated from multiple linear regressions). Such studies were checked by at least two authors, and the misclassified selection gradients were reclassified as selection differentials in the database.

In many studies, multiple data sets existed *within* studies. These within-study data sets represent selection estimated on different subsets of data defined by species, trait, fitness component, sex, age, year or season. For clarity, we use the term ‘data set’ to refer to each unique combination of the above within studies. We use the term ‘metapopulation’ to refer to study-specific groups of populations for a given species.

ANALYSES AND RESULTS

Overview of the database

We reviewed a total of 1402 studies identified through our Web of Science search. Of these, 60 studies met the above criteria and were included in the spatial database. The database includes 3937 estimates of selection (Table 1). The number of spatial replicates ranged between 2 and 41 populations, with a mode of 2, a median of 3 and a mean of 5 populations. The number of data sets, as described above, is 708. The database is biased in favour of linear coefficients, invertebrates, studies using fecundity as a fitness component and morphological traits (Table 1). Geographically, the database contains many estimates of selection from temperate, mid-latitude regions centred at 40° N (Fig. 1). It is illuminating to see how few spatially replicated estimates of selection exist in tropical and extreme latitude areas, despite considerable interest in the ecological and evolutionary dynamics in these regions. We have included the database in Appendix S1 of the Supporting Information and have posted it to the DRYAD data repository (<http://www.datadryad.org/repo/>). Although we provide the quadratic components in the database for completeness, we focus our analyses only on linear (directional) components of selection because their interpretation is much more straightforward, and without estimates of population means of traits inferences on quadratic components are tenuous. In addition, quantification of quadratic components is often done incorrectly (Stinchcombe *et al.* 2008). Ideally, we would like to be able to quantify the extent of adaptive peaks across the landscape and how fitness surfaces vary among populations, but methods are currently lacking for quantifying this in a meta-analytic context (e.g. Siepielski *et al.* 2009).

A meta-analytic framework for detecting a spatial signal in directional phenotypic selection

We used random effects meta-analysis to model spatial variation in selection after taking into account sampling error. We used a random effects generalised linear mixed model of the same type presented by Morrissey & Hadfield (2012) of the form:

$$\beta_{ij} = \mu + u_j + m_{j,i} + e_{j,i} \quad (1)$$

where $\beta_{j,i}$ is the i th selection coefficient (linear gradient or differential) estimate for the j th trait/study combination (i.e. a given combination of phenotypic traits and/or fitness components for a given study;

Table 1 Summary of studies with spatial replication in the database

	Number of items in the database
Studies	60
Journals	22
Records	2384
Selection coefficients	3937
Linear differentials	1325
Linear gradients	1483
Quadratic differentials	758
Quadratic gradients	371
Species	47
Taxon type	
Invertebrates	1062
Plants	781
Vertebrates	541
Trait type	
Behavioural	12
Other	119
Morphological	1913
Life History	241
Principal Components	99
Fitness Component	
Fecundity/Fertility	993
Mating Success	712
Other	215
Survival	406
Survival and Fecundity	16
Total Fitness	39

hereafter 'trait'), μ is the mean selection coefficient averaged across the entire database, u_j is the deviation of the mean selection gradient for trait j from the grand mean, e_{ji} is the residual (the deviation of the selection coefficient for population i from the trait mean), m_{ji} is the deviation of the mean selection coefficient for the j th trait/study com-

ination between the estimate and the true value due to sampling error. Note that unlike most applications of mixed models, e_{ji} is not simply random noise, but is the variation in selection within studies. The variances of the trait effects (σ_u^2) as well as the variance of the residuals (σ_e^2) are estimated; the variance of the sampling errors ($\sigma_{mj,i}^2$) was taken to be the measurement error variance (the $SE_{j,i}^2$). As in Morrissey & Hadfield (2012), we present variance components for those fractions that represent the between-trait variation and the within-trait variation after taking into account sampling error. The total variation in selection can be estimated as the sum of the between and within-trait variation. Thus, that fraction of the variation that can be attributed to the variation among populations (i.e. spatial variation in selection) across the database can be quantified as:

$$\frac{\sigma_u^2}{\sigma_u^2 + \sigma_e^2} \quad (2)$$

We were necessarily limited to those records that included standard errors (SE) for the selection coefficient estimates of β ($n = 534$ data sets; 36% of the total number of estimates of β) and S ($n = 405$ data sets; 31% of the total number of estimates of S). The model was fit in a Bayesian framework using the R package MCMCglmm (Hadfield 2010) with flat improper priors on both variances (σ_u^2 and σ_e^2). We obtained 1000 quasi-independent samples of the posterior distributions from the posterior distributions of the fitted models.

Overall patterns of spatial variation in directional selection

For both linear gradients and differentials, the meta-analytic model revealed a clear signal of spatial variation in selection across the database. The overall standard deviation (SD) of within-study directional selection coefficients is 0.049 (95% CI: 0.045–0.058) for gra-

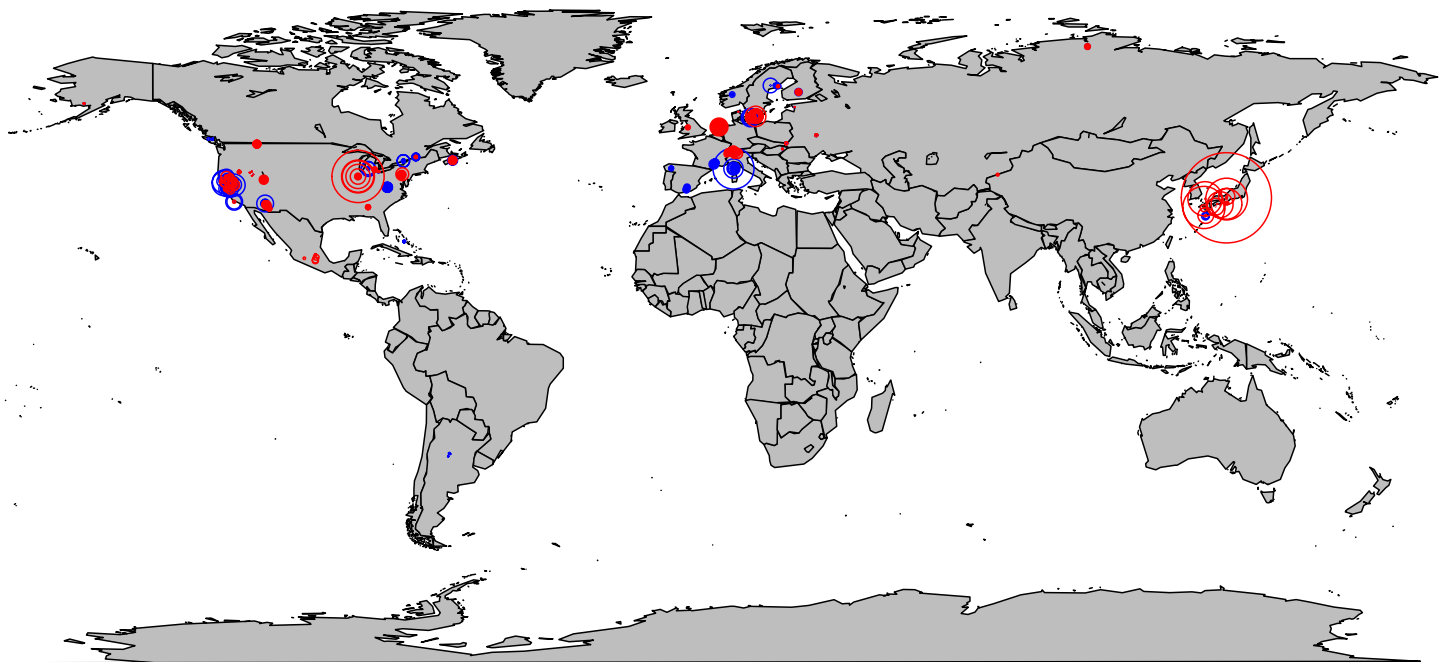


Figure 1 Most estimates of spatially replicated selection in the wild come from mid-latitudes in the northern hemisphere. The map shows the geographical location and magnitude of selection for linear selection gradients (blue) and differentials (red). The size of the circle is proportional to the magnitude of selection. Plotted are individual, trait-level linear coefficients because they represent the bulk of the database.

dients and 0.126 (95% CI: 0.109–0.151) for differentials. The variances in gradients and differentials represent 12.5% (95% CI: 9.4–23.1%) and 31.7% (95% CI: 17.6–40.0%) of the total variation in selection coefficients, respectively, after accounting for sampling error. It is unclear why spatial variation in selection captured with linear differentials is greater than variation through selection gradients. In general, linear gradients tend to correlate strongly with linear differentials (Kingsolver 2001); however, in the database some studies reported only one or the other, and the data set does contain some large values of differentials that do not have corresponding selection gradient estimates. In addition, means and also potentially variances of differentials could generally be larger than those for gradients if phenotypic correlations among traits are frequently the same sign as the product of associated selection gradients. This will often be the case for morphological traits, which tend to be positively selected and often covary positively, as they are often components of overall size (Kingsolver & Pfennig 2004). In addition, selection differentials may vary more than selection gradients if and when phenotypic correlations among traits vary substantially among populations.

Spatial variation in the direction of selection

Here, we quantify spatial variation in the direction of linear selection among populations and use a metric to infer the potential importance of such spatial variation in selection across the metapopulation for local adaptive evolution. We first estimate the probability that any two selection coefficients at different populations differ in direction across the metapopulation. This metric can range between 0, when selection is uniform in direction among populations, to a maximum value of 0.5, when selection coefficients are equally positive or negative among all populations [the full method is described in Morrissey & Hadfield (2012)]. Briefly, we modelled the probability that selection differs in direction among any two sub-populations as the extent of overlap with zero of the distribution of study level selection coefficients given u_j and $\sigma^2(e_{ij})$. The expectation of the metric was calculated across the entire database. We use the estimates σ^2_u and σ^2_e from the above meta-analytical model to calculate the expected values for this statistic after accounting for sampling error.

The probability that the sign of a selection coefficient differs in direction in between two locations, averaged over populations and factoring out statistical noise due to sampling error, is 0.16 (95% CI: 0.13–0.21) for directional selection gradients (this metric has a maximum value of 0.5). This aspect of variation is somewhat greater for directional differentials, 0.23 (95% CI: 0.17–0.27). Thus, overall the direction of selection differs among populations at non-trivial frequencies.

The above analysis provides a measure of the extent to which the direction of selection varies across space. A key question to understand is to what extent does spatial variation in the direction of selection generate differences in selection relative to a scenario in which selection varies in strength but not direction among populations (e.g. Bell 2010; Kingsolver & Diamond 2011)? Answering this question helps reveal the potential for spatial variation in selection to be an important driver of adaptive population divergence. To address this question, we used a metric developed by Kingsolver & Diamond (2011); see also Morrissey & Hadfield 2012). The metrics $|\text{mean}(\beta_i)|/\text{mean}|\beta_i|$ and $|\text{mean}(S_i)|/\text{mean}|S_i|$, where the selection coefficients are averaged across each population i for each data set,

reveal the extent to which spatial variation in the direction of selection affects selection among populations relative to the expectation of selection varying in strength but not direction. That is, this metric can be interpreted as the extent to which spatial variation in the direction of selection reduces the total selection experienced across the metapopulation relative to sub-populations. If selection was uniform in direction and varied only in magnitude this ratio would be 1.0; values increasingly less than one indicate a greater potential for variation in the direction of selection to affect overall spatial variation in selection. To interpret this metric, we plot the above ratio relative to the mean selection coefficients across all populations for each data set as this allows us to intuit the possible evolutionary significance of spatial variation in selection. We graphically present all values of this metric across the entire database (e.g. not just those estimates with SE's). We also used the results of the above meta-analytical model to estimate the expected value of this metric after taking into account the effects of sampling error [using an approach described in the Appendix of Morrissey & Hadfield (2012)].

Overall, this analysis, combined with the above results, revealed that although differences in the direction of selection occur fairly frequently, the ultimate effect on the average selection experienced among populations is relatively modest (Fig. 2). The ratio of $|\text{mean}(\beta_i)|/\text{mean}|\beta_i|$ is 0.82 (95% CI: 0.79–0.87) and the ratio of $|\text{mean}(S_i)|/\text{mean}|S_i|$ is 0.76 (95% CI: 0.71–0.82). Most values of this metric are generally below 1.0. In general, at locations where selection is of an opposite sign to its overall spatial average, it is small in magnitude, resulting in a muted effect on the overall selection experienced across the metapopulation (Fig. 2). Thus, differences in the direction of selection might have little consequence for overall selection in a metapopulation context, limiting the potential for spatial variation in selection to affect adaptive population divergence. However, there are clearly cases where changes in the direction of selection among populations are considerable and these are often accompanied by strong selection as well (Fig. 2). Variation in the extent of spatial replication does not appear to affect our interpretation (Fig. 2). Both of these metrics are subject to the caveats necessary for the interpretation of spatial consistency of selection (above). In addition, it should be noted that any spatial effects capture only a snapshot of the dynamics of selection, as any spatial variation occurs against a background of temporal variation in selection as well (Siepielski *et al.* 2009; Morrissey & Hadfield 2012).

The random effects meta-analysis is also useful for characterising not only patterns across the entire database but also the average within-study spatial variation in selection and provides an additional way to quantify the variation in selection due to differences in strength and direction. To better resolve variation among studies in the extent of spatial variation in selection, we extended the model in eqn (1) to a three-level meta-analytical model. We modelled the within-study spatial variation in selection as:

$$\beta_{ij} = \mu + u_j + m_{j,i} + e_{j,i} \quad (3)$$

$$e_{i,j} \sim N(0, \sigma_{e,j}^2) \quad (4)$$

$$\sigma_{e,j}^2 \sim \exp(N(\mu_a + \alpha|\mu_j|, \sigma_a^2)) \quad (5)$$

Equation 3 is thus the same as eqn 1, but we expand on the model of $e_{j,i}$. Specifically, we allow within-data set spatial differences in selection to be drawn from data set-specific distributions with variances $\sigma_{e,j}^2$ (eqn 4). We model the distribution of $\sigma_{e,j}^2$ as normal on the log scale and as a function of an overall mean (μ_a), an effect of the mean absolute value of selection in each data set

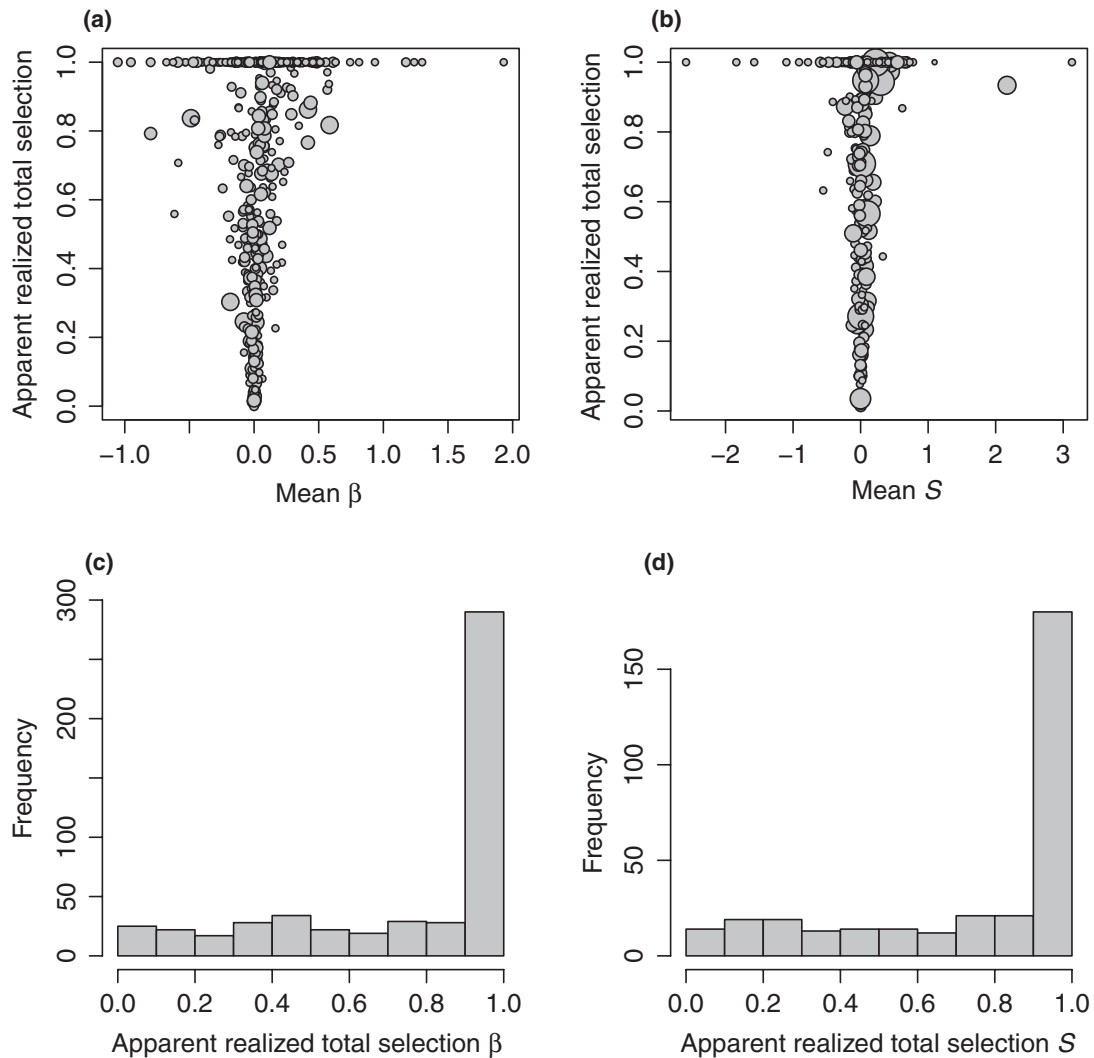


Figure 2 Distributions of metrics for spatial consistency in selection suggest that spatial variation in the direction of selection may only occasionally have important implications for adaptive evolution. Apparent realised total selection (y-axes in panels ‘a’ and ‘b’; x-axes in panels ‘c’ and ‘d’) refers to the metrics (a, c) $|\text{mean}(\beta_i)|/\text{mean}|\beta_i|$ and (b, d) $|\text{mean}(S_i)|/\text{mean}|S_i|$, where the selection coefficients are averaged across each population i for each data set. Values of the realised total selection metric increasingly less than one indicate a greater potential for variation in the direction of selection to affect overall spatial variation in selection. The x-axes in panels ‘a’ and ‘b’ are the mean selection coefficients averaged across each population for each data set. Sizes of the symbols are proportional to the number of populations.

($\mu_j = \mu + u_j$), mediated by regression parameter α and with (log scale) normal residuals with estimated variance σ_a^2 (eqn 5). As such, we allow the spatial variance in selection to vary among studies, partially as a function of the mean study-specific magnitude of selection.

The individual parameter estimates of the model in eqn (1), as extended using eqn (3–5) to model among-study variation in the variance of selection coefficients, are difficult to interpret in isolation. We therefore summarised the resulting fitted models by posterior predictive simulation (as in Morrissey & Hadfield 2012). We simulated predictions for 10^5 hypothetical studies, and summarised these in terms of the associated SD of selection and SD of the absolute values of selection. We also include the SD and the SD of the absolute values of the estimated selection coefficients across the entire database. The SD is ideal because it describes the distribution of selection coefficients and is reported in the same units as the original measures. The SD measure describes spatial variation in selection due to changes in both the strength *and* direction of selection on

traits among population, whereas the absolute values provide a measure of spatial variation attributable to strength only. Thus, by comparing both of these we can gain some insight into the contributions of strength and direction for overall spatial variation in selection.

The analysis of the model-based inferences of the distribution of spatial SD of selection and the SD of the estimated selection coefficients reveal similar patterns: most variation in selection is likely due to variation in the strength of selection as opposed to variation in the direction of selection among populations (Fig. 3). In all cases, the distributions of the SD and the SD of the absolute values of selection coefficients were nearly coincident. While the overall patterns might be similar, note the importance of the meta-analytic approach, where the apparent within-study variation in selection is inflated by sampling error in individual estimates of selection when inferences are made based on distributions of summary statistics.

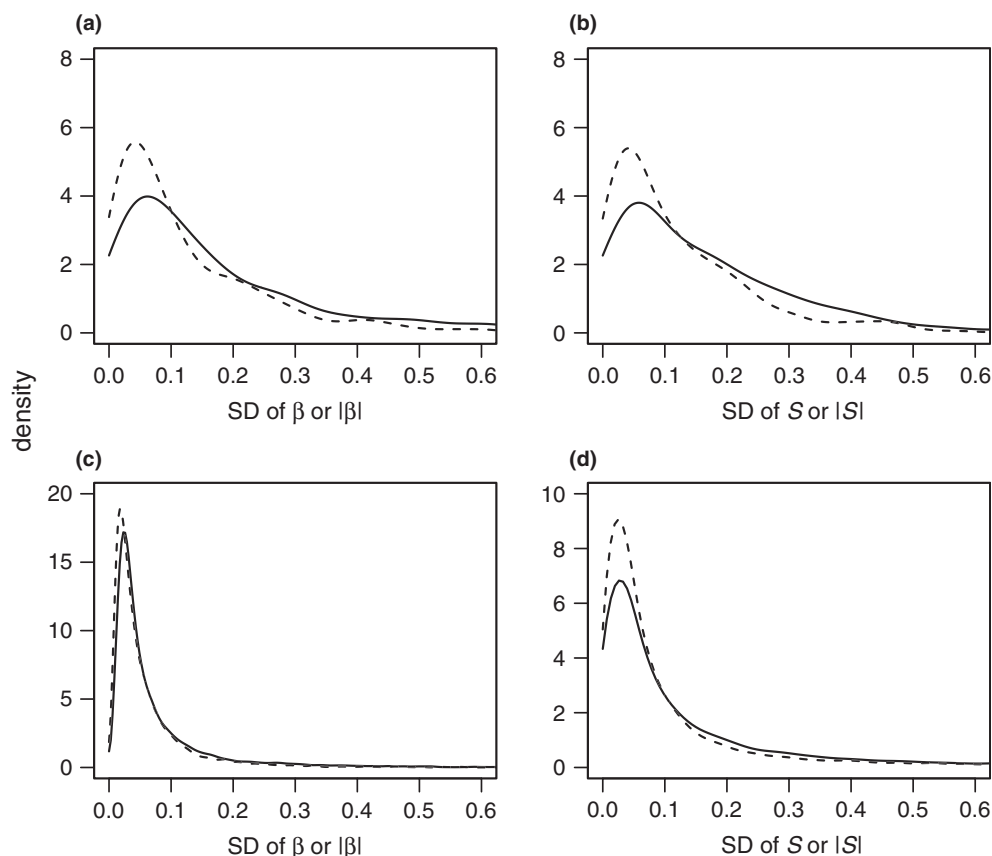


Figure 3 Distributions of the standard deviation (SD) of linear selection coefficients (solid line) and absolute values of linear selection coefficients (dashed line). Panels 'a' and 'b' show the distributions of SDs for the estimated values of the selection coefficients for gradients, and differentials respectively. Panels 'c' and 'd' show the distributions of the three-level meta-analytic model-based inferences of the distribution of spatial SDs, which control for the effects of SE to upwardly bias estimates of variation.

Potential sources of bias in understanding spatial variation in selection

Many of the potential sources of bias in conducting synthetic meta-analyses of selection coefficients have been previously discussed in detail in the context of temporal variation (Siepielski *et al.* 2009; Morrissey & Hadfield 2012), and highlighted in other reviews and syntheses (Kingsolver 2001; Hereford *et al.* 2004; Hersch & Phillips 2004; Knapczyk & Conner 2007). These possible sources of bias include the following: a bias against publishing studies with small sample sizes or weak estimates of selection, against failures to replicate patterns of selection and/or failure to demonstrate differences in selection, the effects of small sample size and few population replicates, sampling error and the potential for environmental correlation between traits and fitness components to generate apparent selection. We present a full discussion of these issues in Appendix S2 where we report analyses to investigate several of these potential biases in the context of spatial variation, beyond those explicitly controlled for by formal meta-analysis. Overall, we find that while some biases almost certainly exist in the data set, they should not strongly affect our results (Appendix S2).

DISCUSSION

Because environments are heterogeneous, spatial variation in selection is widely anticipated (Schluter 2000; Wade & Kalisz 1990;

Thompson 2005; MacColl 2011). In support of this, our formal meta-analysis indicates a clear signature of spatial variation in selection. Additional analyses revealed several features characterising the spatial patterns of selection in the wild: (1) selection tends to vary mainly in strength among populations, (2) differences in the direction of selection among populations occur fairly regularly, but (3), such spatial differences in the direction of selection tend to occur where selection is weakest, which may limit the potential for ongoing adaptive population divergence. Below, we discuss the implications of these results, compare differences between temporal and spatial variation in selection and highlight future research needs.

The strength of selection varies among populations

Variation in the strength, as opposed to direction, of selection among populations is the dominant feature of spatial variation in selection on phenotypes among populations. That is, in most cases, some populations will experience strong selection and others weak selection. The basis for this argument is that comparisons of the SD between selection coefficients and the SD based on the absolute values (which quantify only the strength and are necessarily equal to or larger than SD of the coefficients) are very similar (Fig. 3). Differences in the direction of selection contribute to the $SD(|\beta| \text{ or } |S|)$ being less than $SD(\beta \text{ or } S)$; close concordance between the distributions of these metrics indicates that the majority of variation in selection is manifested in differences in magnitude. Note that

$SD(|\beta \text{ or } S|)$ takes a maximum value of $SD(\beta \text{ or } S)$ when there is no variation in the direction of selection.

Variation in the strength of selection could act to accentuate adaptive population divergence. If levels of quantitative genetic parameters for traits experiencing selection are comparable among populations, populations under stronger selection should adapt more quickly. Alternatively, populations which are already better adapted may experience weaker directional selection. As a result, variation in the strength of selection among populations could also be interpreted as representative of either different degrees of adaptation, with populations experiencing less contemporary selection being currently closer to selective optima, or could represent different patterns of genetic constraints, either in a quantitative- or population-genetic sense (e.g. Chevin 2013). At present, we do not have a good sense of which of these alternatives is most likely and this remains an important question deserving future investigation. One approach for investigating the former possibility would be to conduct reciprocal transplant experiments and simultaneously quantify the strength of selection as well as the extent of local adaptation. In addition, gene flow into populations experiencing stronger directional or stabilising selection would be less likely to swamp the potential for local adaptation because of stronger selection against immigrants or hybrids (Slatkin 1985). Variation in the strength of selection among populations could also be an important mechanism during adaptive radiation, allowing populations to move across fitness valleys (Schluter 2000).

A number of possibilities might explain why most systems tend to experience predominately spatial variation in the strength (as opposed to direction) of selection. One possibility is that different populations are experiencing selection in response to spatial variation in shared environmental factors. A useful, although surprisingly little used, approach for investigating this is to examine the correlation between selection coefficients and putative environmental factors that are thought to be the ecological agents of selection (Wade & Kalisz 1990; MacColl 2011). For example, spatial variation in selection has been attributed to variation in climate (Toju & Sota 2006), the intensity of species interactions (Vanhoenacker *et al.* 2013) and conspecific density (MacArthur 1962; Roughgarden 1971; Clarke 1972).

Second, spatial variation in selection can be generated in the absence of any difference in the functional basis of trait-fitness relationships. For example, different populations with the same fitness function (unstandardised trait-absolute fitness relationship) can experience quantitatively different selection if they differ in the mean and/or variance of phenotype (e.g. Steele *et al.* 2011). Populations adapting to common ecological conditions, but established with different mean phenotypes resulting in different distances to an optimal phenotype, could result in differences in the strength of selection if the strength of selection increases further from an optima (e.g. Steele *et al.* 2011). Similarly, variation in the strength of selection may represent differences among populations in mean absolute fitness, but not necessarily any fundamental differences in fundamental relationships between traits and fitness. We note that while variation in selection gradients is typically interpreted as evidence for variation in the functional relationship between traits and fitness, the correct application of the Lande & Arnold (1983) method – conversion of fitness to the relative scale and standardisation of phenotype – precludes the exclusion of the two alternatives presented here. More consistent reporting of basic summary statis-

tics (e.g. phenotypic means, variances, mean absolute fitness, opportunity for selection) would be very useful in this regard. Also, consideration of the full complexity of fitness functions in conjunction with strictly defined selection gradients would further facilitate the interpretation of information about selection in a more ecologically informed way (Morrissey & Sakrejda 2013) and are important for understanding the position of adaptive peaks.

Third, gene flow could also have an important role in determining spatial variation in the strength of selection. Gene flow from populations experiencing different selection regimes can impede adaptive divergence and local adaptation, whereas gene flow from populations experiencing similar local selection regimes can facilitate local adaptation by increasing genetic variation (see Gillespie 1974; Slatkin 1987; Hendry *et al.* 2001; Lenormand 2002; Garant *et al.* 2007). Thus, if one population is experiencing greater maladaptive gene flow (e.g. gene flow is coming from a population adapted to different ecological conditions) than another population, this could generate stronger selection on the population experiencing greater gene flow because it is hampered from ascending their local adaptive peak. We cannot ascertain the role of gene flow in the observed patterns of spatial variation. However, Urban's (2011) meta-analysis found that gene flow tends to play only a minor role relative to spatial variation in selection in explaining patterns of adaptive trait variation across the landscape.

Variation in the direction of selection is a modest component of variation in selection

Although our analysis indicates that differences in the strength of selection among populations are likely the dominant feature of overall variation in selection among populations, our analysis also indicates that changes in the direction of selection do occur fairly often. However, most changes in the sign of selection involve selection coefficients of only modest magnitude, limiting the influence of changes in direction. Indeed, by comparing the extent to which spatial variation in the direction of selection affects the overall selection experienced at the metapopulation level, we find that such spatial variation is likely to have little effect on the average selection experienced among populations. This implies that among those studies present in the database, spatial variation in selection may be limited in its evolutionary consequences for ongoing adaptive divergence among populations. However, as we note in the discussion of spatial and temporal variation in selection, this inference necessarily represents only a snapshot of selection as populations exhibit some degree of temporal variation in selection as well (e.g. Siepielski *et al.* 2009; Morrissey & Hadfield 2012). Moreover, it is important to note that this pattern does not imply that populations are not locally adapted in response to spatial variation in selection, which appears common as revealed by previous metaanalyses (e.g. Hereford 2009). Indeed, the limited spatially variable selection, combined with patterns of temporally varying selection (e.g. Siepielski *et al.* 2009; Morrissey & Hadfield 2012), is completely consistent with populations being well adapted.

Differences in the direction of selection among populations have the potential to create rugged fitness landscapes and are required for divergent selection (Schluter 2000). Moreover, differences in the direction of linear selection would imply that the populations are being pushed to different optima (divergent selection), but differences in the direction of selection among populations could simply be driving population convergence on a similar mean. For example,

one population could currently be at a value above the optima (favouring a reduction in a trait value) and the second below the optima (favouring an increase in a trait value). Our analysis therefore only indicates that the potential for divergent selection across the landscape may be common, but given the weak effect of spatial variation in the direction of selection experienced by most populations such spatial variation may have limited immediate consequences.

A useful approach for more explicitly estimating divergent selection would be an analysis based on whether differences in selection among populations are correlated with differences in mean trait values among those populations. For example, Nosil & Crespi (2006) showed that differences in the direction and magnitude of selection among populations were strongly positively correlated with differences in the direction and magnitude of trait means among populations. Moreover, they were able to link this with a causal agent because the populations differed in relation to a known environmental factor, the presence or absence of a visual predator (Nosil & Crespi 2006). Quantifying these kinds of patterns would be an informative way to understand the strength of divergent selection in an ecological context.

We note that many of the reasons listed above for explaining spatial variation in the strength of selection are also possible explanations for spatial variation in the direction and form of selection. Consequently, determining if there are consistent differences in the factors driving spatial variation in strength vs. direction would be informative.

A critical point emerging from our analysis of spatial variation in direction and strength is that variation in selection coefficients is very difficult to interpret beyond the strict implications for the evolutionary trajectory in any given population. Essentially, there is information loss inherent to the calculation of population-specific selection gradients and differentials. Consequently, the existence of variation in the sign and/or magnitude of selection coefficients among populations is consistent with: (1) different functional effects of traits on fitness, i.e. different 'selective pressures' in different populations, and (2) different degrees and patterns of adaptation (i.e. it is difficult to interpret weaker selection as necessarily indicative of a population being closer to a fitness optimum) among populations in which traits have a common mechanistic relationship with fitness. The finding of variation in the form or strength of selection is typically interpreted in terms of the former (e.g. Siepielski *et al.* 2009; MacColl 2011), but the latter is equally plausible. While no formalised framework exists for characterising variation in fitness functions, e.g. nothing comparable to methods for evaluating selection coefficients (Lande & Arnold 1983), general and generalised linear mixed modelling approaches relating (absolute) fitness to (non-standardised) phenotype could be useful. A combined analysis including trait and fitness data from multiple populations (or temporal replicates) could in principle allow a formal test for variation among populations in intercepts and in slopes, using fixed interaction terms, and/or random regression approaches (see Chevin 2013).

The spatial structure of selection remains poorly understood

The spatial structure of selection can be broadly categorised as selection being patchy, varying along gradients or varying randomly through space. Determining whether selection is patchy or varies along clines has important implications for patterns of adaptive evolution. For example, the spatial distribution of selection will also determine the extent to which gene flow may influence the potential

for adaptive evolution (Bulmer 1972; Gillespie 1974; Urban 2011). If selection varies in a spatially auto-correlated fashion, then populations closer together might experience more similar selection regimes, and as consequence the effects of gene flow could be less deleterious for local adaptation (e.g. Bulmer 1974; Gillespie 1974; Thompson 2005; Urban 2011). In contrast, if selection exhibits more of a patchy pattern, then the effects of gene flow on local adaptation are less predictable. If selection varies greatly among neighbouring populations, then the effects of gene flow would likely be deleterious for adaptive evolution because immigrants would presumably be less likely to invade a population matching their home environment (Kawecki & Stearns 1993; Thompson *et al.* 2002; Hendry & Gonzalez 2008; Urban 2011).

Several metrics exist that in principle could be used to quantify the spatial structure of selection. For example, Mantel tests can be used to quantify the strength of the association between selection and geographical distance and Moran's *I* can be used to quantify whether selection tends to be dispersed or clustered spatially. However, application of these methods to our database is limited by low levels of spatial replication (the mean number of population replicates is two) and sampling error, both of which would undoubtedly affect the distribution and moments of these metrics. Indeed, we conducted simple simulations of Mantel and Moran statistics, which showed that estimates of these spatial statistics are likely strongly affected by the magnitude of sampling error and the low levels of population replication present in the database. For example, Mantel *r* will tend towards extremes (Mantel $r = 1$ or -1) because of low-replication and tend towards zero because of sampling error.

An even more serious impediment to analysis of spatial patterns in the database is non-random (or exhaustive or even haphazard) spatial sampling. The criteria for population inclusion in a given study likely biases detecting the true spatial pattern. Most researchers do not randomly choose populations. Instead, populations are often chosen because they reflect different environmental conditions. For example, populations could be selected at opposing ends of environmental gradients (e.g. high vs. low population density) or in contrasting environments (e.g. with vs. without predators). In 46 of the 60 studies in this database, we could unambiguously determine why particular populations were chosen: 37 studies selected populations in contrasting environmental conditions and 9 studies selected populations along gradients. Using this information, it is interesting to note that the SD at lower levels of replication (e.g. the bulk of which are in contrasting environmental conditions) are typically greater (Fig. S3), which suggests that different environmental conditions do indeed shape the patterns of selection among populations.

To more fully investigate this possibility, we took advantage of additional information present in the studies. Of the studies in the spatial database, 69% of the papers report that their studies were intended to elucidate differences in selection by studying populations in contrasting environments. Among studies that report SE and are thus amenable to meta-analysis, 63% of selection estimates come from the studies that report estimates from contrasting environments. Restricting the analysis in eqn (1) to this subset does reveal marginally greater spatial variation in selection, as expected, especially for selection differentials. The proportion of the total variation in selection that is attributable to space in the contrasting subset for linear gradients is 17.6% (95% CI: 10.03–34.33%), and the SD of spatial variation in selection is 0.05 (95% CI: 0.043–0.068). For linear differentials, the proportion of the total variation is 58.88% (95%

CI: 27.3–80.29%), and the SD of spatial variation in selection is 0.20 (95% CI: 0.144–0.247). We cannot rule out random sampling of populations for studies that do not specifically articulate how populations were selected. Moreover, studies that consider contrasting environments in the interpretation of their data did not necessarily sample populations non-randomly with respect to space. Thus, the extent of spatial variation in selection in the meta-data set is inflated to some extent by non-random sampling of populations, but it is very difficult to determine the magnitude of this effect.

Selecting study locations that differ in environmental features is, however, desirable as it has the potential to maximise differences in selection and affords an opportunity to understand the ecological causes of selection (MacColl 2011). We therefore stress that non-random sampling is not a deficiency of existing studies. Most studies are designed to test particular hypotheses about different environments, however, sensible designs for this purpose are likely to be misleading if used for inferences about underlying spatial patterns in a general way. However, without random sampling of populations, it will be difficult to address the overall 'true' spatial structure of selection. Of course, this spatial structure is likely to vary among organisms and among regions and as a result is going to be idiosyncratic. In addition, we note that the bulk of the studies in the data set included few populations. As a result, detecting weak, clinal patterns in selection could be more difficult when the underlying gradient has a broad spatial distribution and populations chosen for investigation are close together.

Although the sampling bias noted above provides one explanation for the observed patterns, there are clearly examples where the spatial structure of selection has been well documented. In many of these cases, selection tends to vary in a mosaic-like fashion and the underlying causes of this mosaic spatial variation in selection have been determined. For example, geographical variation in the presence or absence of competitors (Benkman *et al.* 2001; Siepielski & Benkman 2007), alternative hosts (Zangerl & Berenbaum 2003), densities and colour morphs of potential mates (Gosden & Svensson 2008) and co-pollinators (Thompson & Cunningham 2002) has been shown to alter selection across the landscape. Likewise, while a mosaic-like pattern might be common, especially for biotic interactions (Thompson 2005), there are nevertheless numerous cases where selection varies in a clinal pattern (see the discussion on spatial variation in the strength of selection). Understanding the environmental factors that cause selection to vary may be the key to understanding the spatial structure of selection.

Urban (2011) assessed the spatial structure of selection and gene flow by examining how population means of traits mediating biotic interactions varied across the landscape as a function of spatial variation in inferred biotic agents of selection and spatial proximity among populations. This analysis suggested that spatially autocorrelated selection was a dominant feature characterising selection on traits mediating species interactions and that gene flow had a negligible role. Importantly, Urban's (2011) analysis focused only on traits mediating biotic interactions. Selection generated through biotic interactions could have a different underlying spatial distribution than selection generated through abiotic conditions. Indeed, the feedback generated by biotic interactions (e.g. coevolution; Thompson 1999; Schemske *et al.* 2009) necessarily makes the patterns potentially different from that of selection imposed by an abiotic factor. Consequently, understanding how and if the spatial structure of selection varies differently among abiotic and biotic factors would be informative.

Comparison of spatial and temporal patterns of variation in selection

The dynamics of selection can vary along two main axes: space and time. Determining the relative importance of each has important implications for understanding the patterns and process of adaptive evolution (Levins 1968). Namely, stronger spatial variation in selection should lead to adaptive population divergence, whereas stronger temporal variation within populations can limit the potential for such divergence. A previous set of analyses comparable to those performed here sought to determine major features of the temporal dynamics of selection in the wild (Siepielski *et al.* 2009, 2011; Morrissey & Hadfield 2012). Thus, combined with the results from this study, we can compare the patterns of selection along these two axes.

Quantitative comparison of variation in selection in time and space is therefore potentially very interesting, and common methods between this study and previous analyses of temporal variation in selection (for selection gradients) allow some comparisons to be made. As a proportion of the total amount of selection, after accounting for sampling error, selection appears to vary similarly in space and time: 12.5% of the total variation in selection gradients in the spatial data set is attributable to variation in space, compared to 12.4% of the total variation in the temporal data set being attributable to time (Morrissey & Hadfield 2012). Analyses based on selection differentials in this study do reveal that 31.7% of the total variation can be attributed to space. However, while the proportional metric is a useful within-meta-data set description of variation in selection, the absolute variation in selection is more directly comparable between the data sets. The absolute spatial SD of selection (σ_e^2 in 1) is 0.049 (95% CI: 0.040–0.058), compared to 0.074 (95% CI: 0.057–0.086) in the temporal data set. Overall, we find that spatial and temporal variation in selection is of similar magnitude.

It is important to note, however, that comparisons of variation in space and time is complicated by sampling schemes noted above where many estimates of spatial variation in selection are chosen in contrasting environmental conditions. In contrast, inference of temporal variation in selection is less directly influenced by non-random sampling. Given the decision to conduct a temporally replicated study, the choice of contrasting temporal environments is under much less control of the investigator. However, there may be a broader source of bias, in that temporal variation in selection can only be studied in populations in habitats that are sufficiently temporally stable for long-term studies to be conducted. Consequently, the degree of temporal variation in selection is probably downwardly biased in the available meta-data set, and the degree of spatial variation is probably upwardly biased, but the extent of each of these biases is very difficult to determine.

Finally, it is worth noting that spatial data sets represent snapshots of variation in space at particular times, and this further complicates the comparison of variation in selection in space and time. Consider a large number of populations, each in different locations, and each experiencing identical regimes of temporal variation in selection. At any given time, each hypothetical population's selection gradient is drawn at random from a distribution with a common mean and variance across populations. In such a scenario, the temporal variation in selection would appear as spatial variation to a degree depending on the degree of spatial synchrony of temporal variation in selection through time. We do not know how synchronous selection may be, and there is insufficient data simultaneously

considering spatial and temporal variation in selection to begin to study the extent to which asynchrony in selection may influence apparent patterns of spatial variation in selection. Taken together, potential opposite biases in inferences of variation in selection in space and time, due to study design, combined with a paucity of information on synchrony in selection limits even general conclusions at this time about the relative importance of spatial and temporal variation in selection. Finally, these inferences on space vs. time are, however, only considering selection across the entire database. Necessary for developing a greater understanding of differences in the spatial and temporal dynamic of selection are studies that consider both, but few studies have done so.

CONCLUSION

Knowledge of the spatial structure of selection among populations informs us of the underlying mechanisms driving adaptive evolution. Our analysis shows that selection frequently varies among populations in both the magnitude and direction, which can have implications for adaptive divergence among populations. We have also identified gaps in our understanding of the spatial structure of selection such as the strong bias of estimates of selection in temperate regions and the non-random selection of populations. Studies conducted over broad spatial (and temporal) scales will continue to provide important information on the spatial structure of selection. Although our focus here was on developing an understanding of the major features characterising the spatial patterns of directional selection, determining the causes of this spatial variation will provide us with a more complete understanding of adaptive evolution and how phenotypic diversity arises. Understanding the mechanism of selection, i.e. how an individual's traits influence its ability to complete its life cycle in any given set of environmental conditions, would improve our understanding of how variation in those environmental conditions feeds back to influence patterns of selection. Broadening the evolutionary quantitative genetics framework beyond the traditional selection gradient framework to better accommodate 'functional ecology' in general is therefore an important and major challenge.

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STATEMENT OF AUTHORSHIP

All authors contributed to designing the study; AMS, KMG, SMC, and JDD assembled the database; AMS, KMG, MBM and SED performed analyses; AMS led the writing, with all authors contributing to the writing.

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