SYMPOSIUM

Natural Selection, Larval Dispersal, and the Geography of Phenotype in the Sea

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Synopsis Populations evolve generalist, specialist, and plastic strategies in response to environmental heterogeneity. Describing such within-species variation in phenotype and how it arises is central to understanding a variety of ecological and evolutionary topics. The literature on phenotypic differences among populations is highly biased; for every one article published on a marine species, at least 10 articles are published on a terrestrial species and eight focus on terrestrial plants. Here, I outline what we know from the marine literature about geographic variation in phenotype in the sea, with a principal focus on local adaptation. The theory of environmental "grain" predicts that the most likely evolutionary response (e.g., local adaptation, phenotypic plasticity, generalism, and balanced polymorphism) depends on the spatial scale of environmental variation relative to the distance that an organism disperses. Consistent with these predictions, phenotypic plasticity is stronger among invertebrates with geographically broad dispersal versus restricted dispersal (i.e., planktonic-dispersers versus direct-developers). However, contrary to predictions, the relative frequency, and spatial scale of local adaptation is not consistently greater among direct-developers relative to planktonic disperers. This indicates that the likelihood of local adaptation depends on other organismal or environmental traits. Two of the most vexing issues that remain include (1) predicting the extent to which barriers to dispersal are a cause versus consequence of phenotypic differentiation and (2) delineating the relative importance of evolutionary forces that favor or impede local adaptation. Understanding the mechanistic basis of the geography of phenotypic differences, or phenogeography, has gained recent momentum because of a need to predict impacts of global climatic change, anthropogenic disturbances, and dispersal of organisms to non-native habitats.

Introduction

Marine populations exist in heterogeneous environments, where salinity, temperature, risk of predation, food availability, wave energy, and other forces vary across temporal (seconds to decades) and spatial (meters to latitudes) scales. In response, individuals, and populations display a remarkable variation in behavioral, life-history, and morphological traits. This variation arises because traits are plastic and respond to local environmental cues (via acclimation, developmental plasticity, or maternal effects), traits have a strong genetic basis and these genotypes differ in frequency across environments, or traits are determined by both phenotypic and genetic processes.

Describing intra-specific variation in phenotype and how it arises is important for several reasons. As recognized initially by Darwin, phenotypic variation within and among populations is the grist for speciation (Endler 1986). Moreover, phenotypic variation within species can drive extant patterns in the distribution, abundance, and ecological roles of organisms (Fox and Morrow 1981; Zandt and Mopper 1998; Bolnick et al. 2011), including responses of populations to natural or anthropogenic disturbance and climatic change (Frankham and Kingsolver 2004; Davis et al. 2005; Helmuth et al. 2005; Visser 2008). Finally, management strategies that preserve phenotypic variation ensure the

long-term sustainability of ecosystems and their function (e.g., Hauser and Carvalho 2008; Hughes et al. 2008).

Phenotypic variation across space can be generated via local adaptation, in which local genotypes are more fit than foreign genotypes on local habitats (Kawecki and Ebert 2004). The study of local adaptation is robust, in large part because of conservation concerns over invasive species, restoration ecology, and climatic change. However, there is a profound bias in the literature on local adaptation. I surveyed recent studies of local adaptation from 280 publications and found that 80% of studies explored local adaptation on land, and 64% of studies were on terrestrial plants (Fig. 1). For every one article published on a marine species, at least 10 articles are published on a terrestrial species and eight focus on terrestrial plants. The remaining studies are divided relatively evenly among vertebrates and invertebrates from terrestrial, marine, and freshwater systems. A similar percentage of 10% (marine to terrestrial studies) was seen in the meta-analysis of Hereford (2009); from 74 studies of local adaptation, six are marine species (one plant, four snails, and one amphipod). This bias toward terrestrial organisms (and in particular, plants) may simply reflect the fact that seeds are easy to transplant and transport, which facilitates reciprocal-transplant and common-garden experiments. By this reasoning, local adaptation is equally as likely in the sea and we simply have not looked for it (Sotka 2005).

Another possible explanation for the dearth of marine examples of local adaptation is that it reflects
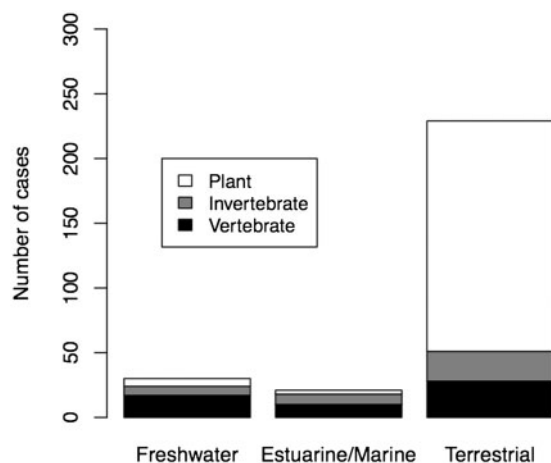
Fig. 1 The study of local adaptation is biased by type of biome and organism. I searched ISI's Web-of-Science using the following search terms ("reciprocal-transplant experiment or common-garden experiment" and "geographic variation or local adaptation") across the years 1980–2012. Each "case" is a published study, even when two or more species were examined.

reality. Most marine organisms spawn their larvae into the water column, where they must feed and float for days, weeks, or months before becoming competent to settle. During this time, the marine larvae could potentially be entrained within currents for 10 s to 100 s of kilometers before returning to the shoreline (Shanks 2009). The evolutionary consequences of dispersal over broad spatial scales are clear; dispersal homogenizes genetic differences that may have been generated by local selection and instead favors the evolution of generalism and plasticity (Sultan and Spencer 2002). Contrast this scenario with the situation for terrestrial plants, in which seed dispersal is "long" when it exceeds 100 m (e.g., Cain et al. 2000). Moreover, there may be more geographic barriers to dispersal on land than in the sea (e.g., mountain ranges and rivers) and greater environmental heterogeneity (soil, light, and water all vary across relatively fine spatial scales) (Vermeij and Grosberg 2010). There are clear exceptions to these generalities (e.g., rocky intertidal shores have high environmental heterogeneity, fruigivores can disperse seeds many kilometers, and some marine invertebrates can disperse only a few meters). But, it remains likely that plants dominate this literature because marine populations disperse more broadly and such gene flow minimizes genetic differentiation of populations.

Whatever the cause of the literature bias toward terrestrial plants, it appears to skew our broader view of local adaptation in nature. As an example, I present the meta-review by Hereford (2009), who surveyed reciprocal transplant experiments without regard to biome. Maladaptation was documented in 37% of these field studies, whereby native populations had lower fitness than did foreign populations in native habitats. A variety of evolutionary forces may yield maladaptation, including broad gene flow, co-evolution, genetic drift, maternal effects, genetic architecture, and adaptive tradeoffs in alternative environments (see "Discussion" section in Hereford 2009). Among these, Hereford dismissed gene flow as an important driver of maladaptation and focused instead on the primacy of genetic drift. However, it is not all that surprising that drift plays a more profound role in plants, whose populations are often smaller and rarer relative to populations of marine invertebrates and fishes (Vermeij and Grosberg 2010; Hare et al. 2011). Other reviews that have cited maladaptation in the sea indicate it is primarily a consequence of broad gene flow rather than of strong genetic drift (Hedgecock 1986; Marshall et al. 2010).

Here, I focus on the geography of phenotype in the sea, with a principal focus on local adaptation of marine populations. This is not intended to be an exhaustive review (see Sotka 2005; Conover et al.

2006; Marshall et al. 2010; Sanford and Kelly 2011) but instead a broad overview of the state of the field. First, I outline a useful framework (Levins 1968) for predicting conditions under which local adaptation (e.g., specialization onto local habitats) versus phenotypic plasticity should be favored. Second, I review evidence that tests several model predictions. Finally, I outline my view of the primary gaps in the study of geography of phenotype, including areas in which marine systems may be uniquely able to provide important insight.

A modified Levins model for predicting local adaptation

The seminal book by Richard Levins in 1968 summarized a body of developing theory focused on environmental heterogeneity and its role in maintaining genetic diversity. Here, my treatment of this model is highly simplified, and I refer the reader to the fantastic amount of literature on the relationships between dispersal, selection, heterogeneity, local adaptation, and plasticity (Kawecki and Ebert 2004; Thompson 2005; Crispo 2008; Chevin et al. 2010). The principal contribution of this book was to popularize the concept of environmental grain and how it may predict evolutionary responses. In broad terms, the grain of the environment (or habitat) is its scale of variability relative to that of the dispersing population experiencing those habitats. Fine-grained environments are those in which the organism disperses (and thus experiences) all habitat variability, while coarse-grained environments are those in which the organism tends to experience a single habitat (Fig. 2) (Brown and Pavlovic 1992). In other words, is the spatial scale of dispersal greater or less than spatial scale of environmental shift (i.e., is it fine-grained or coarse-grained)?
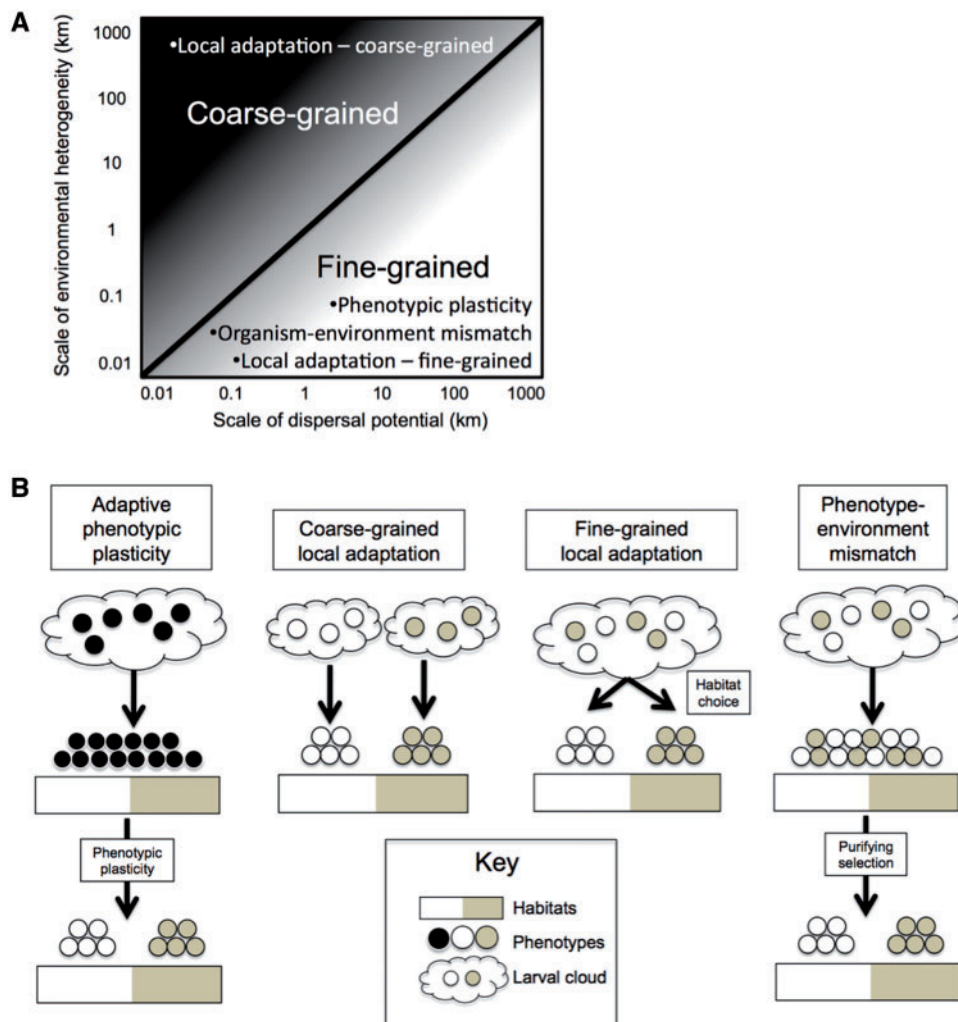

Fig. 2 The evolutionarily responses of populations that are most likely depend on environmental grain. This is represented as (A) a graph of the relative spatial scale of environmental change and dispersal distance and (B) a cartoon model.

The principal reason for focusing on dispersal is because of the powerful effect that gene flow may have on the favored evolutionary response. Generally, migration has to be far less than 10% of the population per generation in order to favor the evolution of local adaptation (Brown and Pavlovic 1992; Holt and Gaines 1992; Sultan and Spencer 2002). Thus, when dispersal is narrower than the spatial scale of environmental shift, then coarse-grained local adaptation may arise (Kawecki and Ebert 2004) in which both adults and newly settled individuals contain locally-favorable genotypes (Fig. 2).

When dispersal is more broad than the spatial shift in environmental conditions (i.e., fine-grained environment), theory predicts that generalist traits (e.g., Dawes et al. 1988) and phenotypically plastic traits (Hollander 2008) will be more likely (Fig. 2). However, these are not the only outcomes. Local adaptation in these fine-grained scales may arise when animals can choose habitats in which they perform best (Rosenzweig 1987; Brown 1990) or simply when habitat choice itself is adaptive (Jaenike and Holt 1991). I term these outcomes "fine-grained local adaptation," and the net effect is to minimize gene flow to alternative habitats mediated simply by choice. Examples in the marine environment can be seen among small invertebrates on larger host plants and animals (e.g., Giesel 1970; Mackay and Doyle 1978; Stanhope et al. 1992; see review by Sotka 2005).

A final possibility is that passive dispersal (i.e., no active habitat choice) occurs across spatially-segregated habitats and strong post-settlement selection yields genetic differentiation (Fig. 2). Marshall et al. (2010) labeled this dynamic "phenotype-organism mismatch" although, historically, this was termed a balanced polymorphism. Detecting such mismatches require an estimate of purifying selection across life stages, as has been seen in the Mpi enzyme from a barnacle (Schmidt and Rand 2001) and Lap enzyme in a mussel (Koehn et al. 1980).

Delineating among these evolutionary responses requires a specific set of empirical data (Table 1). Once a phenotypic pattern has been documented across populations, one has to ensure that some portion of this variation has a genetic component, or wholly reflects developmental plasticity or acclimation. This requires a common-garden experiment or reciprocal-transplant experiment. These experiments also address whether counter-gradient selection occurs (Conover et al. 2006), in which environmental shifts oppose genetic shifts in phenotype. Estimates of dispersal help to understand whether the populations are differentiated in a coarse-grained versus fine-grained environment. The problems of estimating dispersal in marine organisms are varied (Levin 2006), but in broad strokes, either direct observations (tracking, otolith chemistry, or genetic fingerprints) or indirect estimates from population genetics can be used to give a first-order estimate of dispersal distance. The caveat is that it is sometimes difficult to assess whether patterns of dispersal are a cause or a consequence of genetic differentiation (see below). When there are strong habitat preferences then the situation should be considered as a fine-grained local adaptation. If, on the other hand, strong purifying selection acts across life-stage, then a phenotype–environment mismatch dominates the system.

Testing outcomes from the modified Levins 1968 model

Given the modified Levins 1968 model (Fig. 2), we predict at least three patterns to emerge from the literature. First, planktonic dispersers should have

Table 1 Empirical tests to distinguish evolutionary processes when a single species occurs in two or more habitats

Empirical test	Coarse L.A.	Fine L.A.	P.E.M.	Plasticity	Generalism
Adult phenotype differs across habitats	Yes	Yes	Yes	Yes	No
Phenotypic difference has genetic component[a]	Yes	Yes	Yes	No	No
The potential dispersal distance is shorter than spatial shift in environment (i.e., coarse-grained)[b]	Yes	No	No	Yes or No	Yes or No
Link between preference and performance: Larvae, settlers or post-settlers choose habitats in which they perform best	Yes or No	Yes	No	No	No
Purifying selection across life stages (e.g., juvenile to adult)	Yes or No	No	Yes	No	No

L.A. = local adaptation; P.E.M. = Phenotype–environment mismatch.
[a]Tests: Rearing juveniles to maturity in alternative habitats (field or common garden).
[b]Tests: Dispersal is several orders of magnitude shorter than shift in environment.

a greater magnitude of phenotypic plasticity than do direct developers. While inferring dispersal distances from life-history traits (e.g., duration of the pelagic larval stage) has been fraught with discouraging results, among the most consistent finding is that direct-developers tend to have relatively narrow dispersal distances (generally <1 km on average) while planktonic-dispersers move greater distances (between 10 s to 100 s of kilometers on average) (Bradbury et al. 2008; Shanks 2009; Kelly and Palumbi 2010; Selkoe and Toonen 2011). Thus, given the Levins 1968 model, planktonically-dispersed species are exposed to finer-grained environments, and should have greater levels of plasticity in their phenotype. Hollander (2008) gathered examples of phenotypic plasticity among 258 experiments from 57 studies. Across phyla, direct-developers routinely displayed plastic responses, but the average magnitude of this plasticity was stronger in planktonic-dispersers (Fig. 3A). Thus, the result of Hollander 2008 is consistent with the modified Levins 1968 model.

Second, direct-developers should have greater frequency of local adaptation than do planktonic dispersers. This stems from the assumption that direct-developers evolve within coarse-grained environments more favorable to local adaptation. I compared the frequency of local adaptation among direct-developers and planktonic dispersers. I combed through previous reviews of local adaptation of marine invertebrates (Sanford and Kelly 2011) and fish (Conover et al. 2006) for a composite list of 62 unique species for which geographic variation in a trait was inferred (Fig. 3B). Among these, 27 and 35

of the species were direct-developers and planktonic-dispersers, respectively. My test unfortunately suffers mightily from publication bias, in that I cannot generate a proper and neutral expectation for how many studies of local adaptation have been pursued and not published among published studies. At a minimum, however, the frequency of local adaptation does not appear to be biased by life history. This result is also consistent with previous reviews of marine (Sotka 2005; Sanford and Kelly 2011) and terrestrial (Zandt and Mopper 1998) animals.

Third, planktonic disperers should have a spatial scale of adaptive differentiation that is greater than that for direct-developers. For this, I re-analyzed the spatial scale of local adaptation among only marine invertebrates (i.e., Table 1 of Sanford and Kelly 2011), given that all the fishes studied by Conover et al. (2006) are planktonic-dispersers. The spatial scale across which planktonic dispersers showed local adaptation was on average greater than the spatial scale for direct-developers (scale of divergence [mean, SD, n] for direct-developers is 166 km, 363 km, 13 and for planktonic dispersers is 396 km, 513 km, 26), but the variance was large and accounts for the barely non-significant difference (Wilcoxan rank sums test: W = 105; P = 0.058). Note that these values are the minimum distance across which local adaptation was detected, and depend greatly on the spatial scale across which a researcher tested for local adaptation. For any given example, the spatial scale across which local adaptation occurs is likely lower than reported.
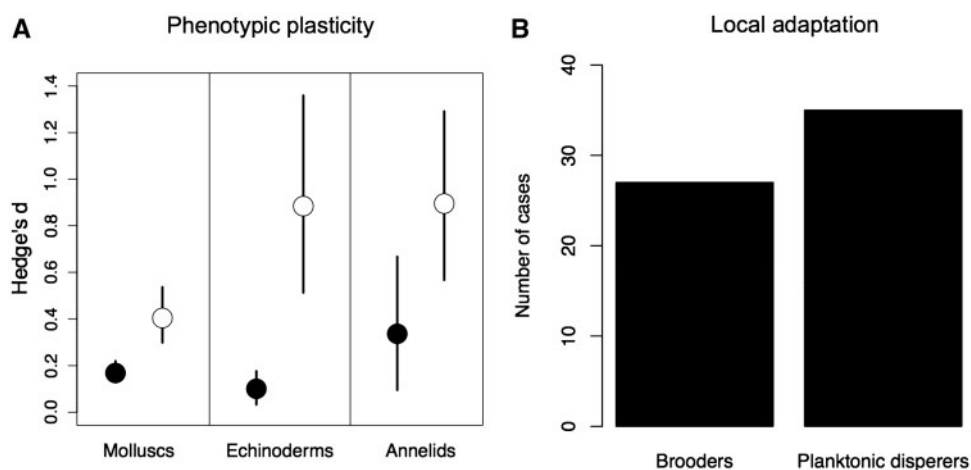
Fig. 3 Empirical tests of a modified version of Levins' (1968) model. (A) Planktonically dispersed invertebrates (white circles) are phenotypically more plastic than are direct-developers (black circles) (reprinted from Hollander 2008). The strength of plasticity (i.e., the mean effect size or Hedges'd) and its 95% bias-corrected confidence interval are shown. (B) Local adaptation has been documented within 62 marine species, 27 and 35 of which are direct-developers and planktonic disperers, respectively.

Overall, then, Levins' (1968) environmental "grain" predicted patterns of phenotypic plasticity (Fig. 3A) and was a poor predictor of the relative frequency of published examples of adaptive differentiation (Fig. 3B). Consistent with the model, there was a tendency for direct-developers to differentiate across much finer geographic scales than was the case for planktonic-dispersers. The caveat is that publication bias may strongly impact these conclusions, which means that we require more studies of the topic. Ideally, we would systematically test for local adaptation in a phylogenetically-corrected set of species with different dispersal capabilities but across the same environmental gradient (Parsons 1997); however, a systematic analysis across more than a few species has yet to be published. Another interesting approach is to experimentally compare the strength of local adaptation across populations varying in the degree of local connectivity (see an outstanding example published by Tack and Roslin [2010]).

Future directions

I would now like to address two vexing questions that remain concerning the geography of phenotype, and in particular, of local adaptation.

When are barriers to dispersal a cause versus a consequence of phenotypic differentiation?

The spatial connectivity of patches of adults remains one of the most important and vexing problems of marine biology (Cowen and Sponaugle 2009). Barriers to dispersal between patches arise because the geographic distances are too great, or because physical or oceanographic features limit organismal movement. As a consequence of isolation (i.e., in a coarse-grained environment) (Fig. 2A), populations and their phenotypes will be more likely to diverge by natural selection (Endler 1986) or by genetic drift when effective sizes of isolated populations are small (Lande 1985). In this case, the barrier to dispersal causes phenotypic differentiation. In contrast, when adult patches occur across fine-grained environments, it is possible that fine-grained local adaptation or phenotype-environment mismatches can arise and consequently, that phenotypic differentiation causes barriers to dispersal. This is a chicken-and-egg problem, and discerning which came first (phenotypic differentiation versus physical or oceanographic barriers to dispersal) requires the intensive, multi-disciplinary approach (outlined in Table 1) that quantifies the strength of selection, habitat choice, and dispersal distances. Complicating matters is the fact that dispersal itself is a trait that is subject to strong selective pressures (e.g., Baskett et al. 2007), that may,

in turn, interact with phenotypic differentiation in surprising ways.

What forces favor or impede local adaptation in the sea?

In general, there is a need for studies on the mechanisms that favor or impede local adaptation (Kawecki and Ebert 2004; Hereford 2009; Sanford and Kelly 2011). This is particularly true in marine systems for which studies lag behind those of terrestrial systems both in the number of species studied, and in experiments that test the underlying mechanisms (Fig. 1). We need more information on the roles of habitat choice, the environmental forces that sculpt locally-adapted populations, the traits that are under selection and their genetic architecture, genetic drift, and "processes affecting immigrants (such as heterosis or out-breeding depression)." (Kawecki and Ebert 2004, 1233). Clearly, gene flow will continue to be important to quantify as it likely impedes local adaptation among marine populations more frequently than among other systems (e.g., terrestrial plants) where dispersal is restricted. Yet, the notion that gene flow impedes local adaptation has dominated the marine literature for at least 40 years (Scheltema 1971; Gooch 1975; Ament 1979; Hedgecock 1986) and arguably, to the neglect of studies that explicitly test for these other, potentially important, forces. Ultimately, my hope is that we can predict the likelihood of local adaptation (or its absence) starting from traits of the organism (e.g., life-history or dispersal strategies, metabolic rate, trophic level) population (age, demography, isolation, and habitat quality), and environmental conditions (temperature, salinity, and risk of predation).

Conclusions

Understanding the mechanistic basis of the geography of phenotypic differences, or phenogeography (coined by Conover et al. 2006) has clear implications for speciation and ecological dynamics. These studies have also gained recent momentum because of global changes in climate, disturbance, and movement of organisms to non-native habitats, and our desire to understand the impacts of these processes on local populations. For example, it is abundantly clear that we have little ability to predict whether marine (and for that matter, terrestrial) populations will move, adapt, or acclimate to shifts in temperature due to climatic change (Davis et al. 2005; Helmuth et al. 2005; Somero 2012). It is hoped that by generating predictive models on how spatial patterns in phenotype arise, we can extend these

lessons to understand the consequences of decadal shifts in environmental forces.

Finally, my view is that studies of the geography of phenotype will benefit from the genomic revolution, as unprecedented insight into the genetic architecture of quantitative traits is becoming cheaper and more readily available for non-model species. However, I recommend that we maintain an emphasis on phenotype, rather than amassing (sometimes uninterpretable) genomic data (Barrett and Hoekstra 2011). I worry that a growing gap in knowledge is emerging in the genomic revolution because of bottlenecks in the translation of genes to phenotype (and thereby fitness) (Clarke 1975). We have vastly increased our capacity to describe genes using ''-omic'' tools, but tools to describe phenotype and its impact on fitness have not similarly exploded in number. This includes studies on the transcriptome (i.e., gene expression patterns), which can be considered a phenotype, but remain difficult to link to fitness consequences in the field. Understanding the impact of phenotype on fitness requires time, logistically difficult experiments, and a great deal of understanding of the natural history of organisms. Yet, because the environment largely affects phenotype directly, we ignore phenotype at the peril of missing the true effects of selection.

Acknowledgments

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