

Predicting Responses to Contemporary Environmental Change Using Evolutionary Response Architectures

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ABSTRACT: Rapid environmental change currently presents a major threat to global biodiversity and ecosystem functions, and understanding impacts on individual populations is critical to creating reliable predictions and mitigation plans. One emerging tool for this goal is high-throughput sequencing technology, which can now be used to scan the genome for signs of environmental selection in any species and any system. This explosion of data provides a powerful new window into the molecular mechanisms of adaptation, and although there has been some success in using genomic data to predict responses to selection in fields such as agriculture, thus far genomic data are rarely integrated into predictive frameworks of future adaptation in natural populations. Here, we review both theoretical and empirical studies of adaptation to rapid environmental change, focusing on areas where genomic data are poised to contribute to our ability to estimate species and population persistence and adaptation. We advocate for the need to study and model evolutionary response architectures, which integrate spatial information, fitness estimates, and plasticity with genetic architecture. Understanding how these factors contribute to adaptive responses is essential in efforts to predict the responses of species and ecosystems to future environmental change.

Keywords: population genomics, environmental change, adaptation, plasticity, evolutionary prediction.

Introduction

As contemporary environments change at an unprecedented rate, species persistence will increasingly depend on the ability to respond and adapt to novel environmental conditions. Models used currently to predict species responses to environmental change often involve a climate envelope approach, assuming static environmental tolerance over time, such that organisms will track current preferred environmental conditions in the future (Fernandes et al. 2013; Pinsky et al. 2013). However, decades of empirical research contradict this assumption, as evolutionary and physiological studies have revealed that tolerance to rapid environmental change varies among individuals, among populations, and across species (Somero 2010; Hoffmann and Sgrò 2011) and has the potential to rapidly evolve (Hendry and Kinnison 1999; Reznick and Ghalambor 2001). The question of whether the rate of adaptation can keep up with unprecedented rates of human-induced environmental change—and whether this ability varies among species, populations, and ecosystems—remains an essential and unresolved question in evolutionary biology (Merilä and Hendry 2014).

Two major lines of inquiry have developed in response to this question. First, theoretical models of population genetic responses to environmental change have been created to explore the conditions under which populations can

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evolve quickly enough to avoid extinction (Gomulkiewicz and Holt 1995; Hermisson and Pennings 2005; Chevin et al. 2010; Orr and Unckless 2014; Uecker et al. 2014). These models have clarified the parameter space in which rapid adaptation is expected to play an important role in population persistence and have demonstrated that these processes are expected to contribute significantly to future ecosystem function. Second, empirical studies have repeatedly identified a genetic basis for variation in environmental tolerance within populations, clarifying the architecture of local adaptation between populations and providing evidence of recent rapid adaptation and speciation across environmental gradients. These include common garden and experimental evolution studies examining local adaptation and evolution of environmental tolerance (Bradshaw and Holzapfel 2001; Collins and Bell 2004; Van Doorslaer et al. 2007; Paul et al. 2011), genetic monitoring (e.g., Umina et al. 2005; Balanyá et al. 2006), and more recently, analysis based on genome-wide sequence variation and transcriptomic profiling (Hancock et al. 2011; Pespenti et al. 2013; Bay and Palumbi 2014; Dixon et al. 2015; Ghalambor et al. 2015). These experiments show that contemporary adaptation and acclimation are playing a major role in the persistence of real-world populations.

These theoretical and empirical studies highlight the information we need to understand and predict future response to environmental change, which we call the evolutionary response architecture (fig. 1). This outlines types of data needed to answer outstanding questions related to predicting evolutionary response to environmental change such as the following: How can the direction, rate, magnitude, and limits of potential evolutionary change be inferred using genomic data from natural populations, and do estimates match observed outcomes? How do parameters like the amount of standing sequence variation, gene flow, population size, and genomic architecture vary among populations? Under what conditions will populations re-

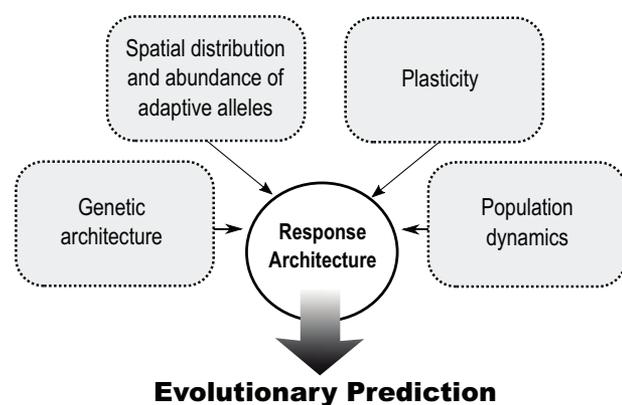


Figure 1: Conceptual map of response architecture for predicting evolution in response to environmental change.

spond to environmental change through phenotypic plasticity, evolution, or both? In this synthesis, we review the key theoretical determinants of evolutionary responses to rapid environmental change and outline current methods that use genomic data to estimate these factors. Finally, we examine major challenges and knowledge gaps and discuss strategies for filling these gaps.

Determinants of Population Responses to Environmental Change

A growing body of theoretical work examines conditions under which rapid environmental change is expected to drive rapid evolutionary change. These conditions include that there must be sufficient standing genetic variation in the relevant trait(s) and that adaptation must proceed quickly enough to avoid extinction (Orr et al. 2008; Messer and Petrov 2013; Carlson et al. 2014; Orr and Unckless 2014). This evolutionary response is further modified by several attributes of the system of interest. Standing genetic variation in environmental response may be highly polygenic or dependent on only a few loci (Lynch and Lande 1993; Burger and Lynch 1995; Gomulkiewicz and Holt 1995). This variation may be present within populations or stratified across populations or parts of a species' range (Ralph and Coop 2010; Uecker et al. 2014). Selection may vary due to spatio-temporal environmental gradients or frequency-dependent selection (Holt et al. 2004; Ralph and Coop 2015). Finally, plasticity may either promote or inhibit selection on environmental tolerance traits (Chevin et al. 2010). Theoretical studies have covered many portions of this range of possibilities, and a key step in applying theory will be to determine which sorts of models to use.

Genetic Architecture and Population Dynamics

Most studies have investigated the fixation dynamics of a trait determined by a single locus that is sufficient to rescue an isolated population exposed to an instantaneous environmental shift. The most fundamental insight from these studies is that, given an environmental tolerance allele with large benefit and high frequency in the starting population, fixation is likely and extinction can be averted (Hermisson and Pennings 2005; Orr and Unckless 2014). By contrast, if the selective advantage of the environmental tolerance allele is too low or if it is present in too few copies, it is very likely to be lost due to random genetic drift before it can contribute to adaptation (Hermisson and Pennings 2005; Barrett and Schluter 2008). Because reduced absolute fitness caused by rapid environmental change will in many cases reduce population sizes, populations may go extinct before adaptation can restore a positive population growth rate (Lynch and Lande 1993; Orr and Unckless 2014). The special case

in which environmental change reduces population mean absolute fitness to below replacement but extinction is averted by rapid evolutionary change is referred to as evolutionary rescue. However, these effects are strongly dependent on the maximum population growth rate, because a sufficient reproductive excess may be able to accommodate high levels of mortality without a decrease in adult population size if growth rate is not reduced to below replacement (Crow 1970).

Orr and Unckless (2008), for instance, combined these contributions to find the probability of adaptation from mutations or rare standing variation in a randomly mating population. If the population is declining at rate r (absolute fitness $1 - r$), then the total number of individuals that will ever live, if adaptation does not occur, is N_0/r , where N_0 is the initial population size; and if u is the per-generation mutation rate of the rescuing allele, there are expected to be uN_0/r such mutants, added to the initial number N_0p_0 present as standing variation. Each new mutant has probability $2s/v$ of establishing, so the expected number to escape drift is $2N_0s(u/r + p_0)/v$, and by Poisson approximation the probability that at least one new mutant establishes is

$$P_{\text{rescue}} = e^{-2N_0s(u/r+p_0)/v} \quad (1)$$

(Orr and Unckless 2008). Note that in this equation, $1 + s$ is the population growth rate of the new allele when rare (this is $s - r$ in Orr and Unckless 2008) and that N_0/v is the effective population size. Studies of standing variation for traits promoting environmental tolerance should therefore give strong insight into the likely evolutionary dynamics of a focal population in response to contemporary environmental change by providing estimates of starting allele frequencies (p_0) and selective coefficients (s) of environmental tolerance loci. However, understanding which genotype combinations yield positive population growth rates, especially if these effects are nonadditive, will be a critical component of an effective model.

Although rapid environmental change often involves selection on complex quantitative traits—for example, those involved in climate adaptation—the above theory has largely focused on fixation of small numbers of alleles affecting simple traits. In a brief review of recent studies examining climate-associated genomic variation (table A1), we show that climate adaptation is likely to be highly polygenic; genome-wide association study and genotype-environment association analyses found between 5 and 14,287 single nucleotide polymorphisms (SNPs) with signals for environmental selection, comprising 0.002%–4.6% of tested markers. For example, Bay and Palumbi (2014) scanned transcriptome-derived SNPs from reef-building corals in warmer and cooler habitats and identified 114 loci potentially under selection, show-

ing allele frequency differences between habitats. In nearly half of the studies surveyed that did not examine quantitative trait loci (9/20), signals for selection covered more than 1% of markers, though only a single analysis estimated that greater than 3% of markers were under selection. Although we realize that these studies are not directly comparable—they vary in spatial scale, experimental and analytical methods, and significance cutoff—each study does represent a parameter estimate that could potentially be used in downstream prediction of climate adaptation. In addition, identification of loci under selection in natural populations suffers many pitfalls, including genomic coverage, demographic effects, and inability to accurately estimate phenotype and environment on relevant scales (reviewed in Hoban et al. 2016). Although estimation of genomic architecture of environmental tolerance is far from perfect, it is nonetheless clear that many of these traits are highly polygenic.

In cases where many loci contribute to environmental tolerance, changes in allele frequencies at many loci rather than fixation at a single locus may be sufficient to avert extinction (Latta 1998; Pritchard and Di Rienzo 2010). For this reason, efforts to predict the probability of adaptation to a changing environment in threatened populations will depend critically on determining the genomic architecture (the number of loci, their effects, and their distribution throughout the genome) of environmental tolerance in focal populations and translating distributions of many adaptive alleles into absolute fitness in different environments.

If environmental tolerance depends on many loci with high levels of standing variation, then quantitative trait models may be more relevant than population genetic models designed to capture fixation dynamics at a single locus (Pease et al. 1989; Lynch and Lande 1993; Gomulkiewicz and Holt 1995). However, quantitative genetic models often depend on estimates of heritable variation from common garden experiments or multigenerational field pedigrees, which are not feasible in many ecologically important species threatened by rapid environmental change, and they provide few tools for monitoring the genomic responses of populations to environmental change over time. The measurement of polygenic variation in environmental tolerance traits in natural populations remains a major challenge. When allelic effect estimates are available, patterns of polygenic variation can be measured by analyzing the distribution and abundance of alleles that affect a common trait (Berg and Coop 2014), but as mentioned above, the common gardens or pedigrees that enable such analyses are not available in many important systems.

Genotype-environment association approaches make the assumption that the distribution of alleles across space is a function of adaptation to contemporary environments, so each population is adapted to local conditions. A few studies of herbaceous plants use a combination of genotype-

environment association scans and common garden experiments to demonstrate that genetic variants associated with contemporary environmental variation can be used to predict performance under different environmental conditions (Hancock et al. 2011; Lasky et al. 2015). For example, genetic variants associated with environment in crop landraces of *Sorghum bicolor* predicted response (genotype by environment interactions [$G \times E$]) to experimental drought and aluminum toxicity (Lasky et al. 2015). Additionally, climate-associated SNPs in *Arabidopsis thaliana* were predictive of relative fitness in a common garden (Hancock et al. 2011). Measurement of polygenic variation in wild populations of species that are not amenable to lab culture or common gardening is even more challenging. Genome-environment associations and analysis of allelic covariance may provide tools to address this problem (Wellenreuther and Hansson 2016), and some advancements have been made to predict polygenic scores without estimates of allelic effects (Bourret et al. 2014; Lasky et al. 2015). Further progress in the creation of multi-locus models of genome-environment correlations will even further increase our ability to use genomic data to predict fitness in wild populations.

Although environmental tolerance traits may frequently be polygenic, the chromosomal distribution of adaptive variants will affect how selection acts on them (Tigano and Friesen 2016). If many adaptive variants are chromosomally linked—for instance, variants found on chromosomal inversions or in areas of low recombination—they may be less likely to be lost to genetic drift and more likely to contribute to rapid adaptation (Kirkpatrick and Barton 2006). In the extreme case, complex adaptations may be accomplished through the fixation of linked sets of adaptive variants, or supergenes, a case in which polygenic adaptation may be more accurately modeled with single-locus models (Schwander et al. 2014).

Spatial Distribution and Abundance of Adaptive Alleles

Predicting evolutionary responses to rapid environmental change is further complicated by environmental heterogeneity at multiple spatial and temporal scales, which in turn may alter the strength and response to selection across populations. A growing body of work studies the role that spatial heterogeneity plays in determining the rate and probability of rapid adaptation (Slatkin 1973; Ralph and Coop 2010; Uecker et al. 2014). Local adaptation to contemporary environmental extremes will in many cases maintain standing variation in environmental tolerance within species (Nagyilaki 1975; Barton 1999; Polechová and Barton 2015). Yeaman (2015) recently investigated the possibility of local adaptation by alleles of small effect in the face of gene flow. They showed that even under extremely high

gene flow, local adaptation can still evolve at the genome level if there is sufficient standing genetic variation, while no single locus makes an important contribution for long periods of time. For example, this might be the case in high gene flow marine systems: marine invertebrates inhabiting the pH gradient created by upwelling on the California coast exhibit genetic differentiation at a handful of genes despite a lack of overall structure caused by high dispersal (De Wit and Palumbi 2013; Pespeni et al. 2013). This maintenance of standing variation could contribute to adaptation to rapid environmental change.

If population fitness is reduced to below replacement by rapid environmental change, well-adapted individuals from previously extreme habitats may simply replace maladapted individuals as environmental change progresses. Under local dispersal, this will take roughly $d\sqrt{s}$ generations, where d is the distance the well-adapted alleles must travel in units of dispersal distance, and $1 + s$ is the growth rate of the well-adapted allele when rare (Fisher 1937). In addition, when gene flow brings environmental tolerance alleles to populations newly threatened by environmental change, these alleles can contribute to adaptation, a case sometimes referred to as genetic rescue (Tallmon et al. 2004; Dixon et al. 2015).

Gene flow, determined by habitat and population structure, therefore, impacts the likelihood of global or independent adaptation; when gene flow is low, populations will adapt more or less independently to the same novel environmental stress through convergent processes (Kaeuffer et al. 2012; Tenaillon et al. 2012; Roesti et al. 2014; Ralph and Coop 2015; Laporte et al. 2016; Oke et al. 2016). For example, a recent study by Laporte and colleagues (2016) combined a genetic map with a population genomic approach to assess whether parallel phenotypic changes in sympatric limnetic and benthic pairs of lake whitefish could be explained by genetic parallelism, multiple genetic routes, or both. The results revealed a highly polygenic architecture for body shape and provided evidence for both genetic parallelism and for multiple genetic routes underlying parallel phenotypic evolution in fish shape among populations occupying similar ecological niches. With sufficient gene flow, extreme populations can seed the process of evolutionary rescue across a species' range. Understanding the spatial scale across which a given adaptive process is expected to act is important for both defining the populations in which a given genomic architecture of adaptation is expected to apply and for defining units for management and monitoring of adaptation to environmental change (Schwartz et al. 2007). When populations are adapting to a patchily distributed novel environment, the transition between independent (i.e., convergent) versus shared adaptation happens at a critical distance between threatened patches, proportional to the probability of dispersal between threatened patches relative to the

selective disadvantage of an environmental tolerance allele between threatened patches (Slatkin 1973; Nagylaki 1975; Ralph and Coop 2015).

Phenotypic Plasticity

Phenotypic plasticity can play an important role in altering a population's response to rapid environmental change (Ghalambor et al. 2007; Lande 2009; Chevin et al. 2010, 2013). Plasticity can be adaptive, if it allows persistence under changed environmental conditions, or nonadaptive, if the resulting phenotype is further from the optimum (Ghalambor et al. 2007). Indeed, many of the studies documenting rapid phenotypic changes in response to environmental change reflect plasticity (Réale et al. 2003; Charmantier et al. 2008; Crozier et al. 2008; Hendry et al. 2008; Merilä and Hendry 2014). If populations can cope with rapid environmental changes via adaptive plasticity alone, it is unclear to what degree there is an opportunity for selection to result in an evolutionary response. Price et al. (2003) argue that evolutionary responses in the presence of adaptive plasticity should only occur if the phenotypic response lies below the local optimum, such that there is still an opportunity for selection. Indeed, in many cases where adaptive plasticity in gene expression has been suggested to facilitate adaptive evolution, the plastic changes appear to bring populations closer to the new optimum without reaching it (e.g., McCairns and Bernatchez 2010; Scoville and Pfrender 2010). Theoretical models of evolutionary rescue that incorporate adaptive phenotypic plasticity predict a decrease in the severity of a rapid environmental shift (i.e., a weakening of the strength of directional selection), which in turn slows the rate of population decline (Chevin et al. 2010).

Furthermore, if plasticity evolves but the phenotypic response is still below the optimum (Price et al. 2003), then the evolution of plasticity can increase the rate of adaptation (Lande 2009; Chevin et al. 2010). Alternatively, if plasticity is very costly, it may increase the probability of extinction (Chevin et al. 2010). More generally, such models confirm verbal arguments that adaptive plasticity can reduce extinction risk by increasing the range of environmental tolerance and helping populations persist in the face of environmental change (Chevin et al. 2010). However, novel environmental conditions can also induce nonadaptive or maladaptive plasticity, particularly when environment falls outside the range of historic conditions (Ghalambor et al. 2007). In such cases, nonadaptive plastic responses can potentially increase the risk of population extinction by shifting trait values further away from the new optimum and increasing the strength of directional selection. Thus, accounting for the degree to which traits respond to new environments through adaptive and or non-

adaptive plastic responses will greatly increase the ability to make more accurate predictions on when selection can rescue populations. Transcriptomic studies using gene expression to examine the interactions and trade-offs between adaptation and plasticity show great promise for identifying and quantifying adaptive and nonadaptive plasticity (Palumbi et al. 2014; Ghalambor et al. 2015). These studies show that gene expression phenotypes under different environmental conditions can be used to quantify the strength of plasticity and population-level functional variation, even when the exact physiological mechanisms of adaptation are either unknown or difficult to measure.

Empirical Tests of Evolutionary Rescue

In recent years, there has been a proliferation of laboratory experiments testing theoretical predictions regarding evolutionary rescue in response to environmental change (Martin et al. 2013; Carlson et al. 2014). These experiments generally involve introducing populations to novel environments and allowing evolution to proceed through changes in frequency of existing genetic variants or the substitution of *de novo* mutations. Adaptation is typically quantified by comparing evolved populations to their ancestors. By introducing populations to sufficiently harsh environments that mean absolute fitness is initially reduced below one, researchers can test hypotheses about the various ecological, genetic, and demographic factors that can facilitate or impede evolutionary rescue.

One of the first explicit tests of the biological plausibility of evolutionary rescue theory was conducted by Bell and Gonzalez (2009), who exposed replicate populations of *Saccharomyces cerevisiae* to normally lethal concentrations of salt. They confirmed the general predictions of the theory, observing the expected U-shaped trajectory of population size over time in rescued populations and confirming the importance of initial population size for avoiding stochastic extinction while mean absolute fitness is below one. Other experiments with yeast and bacteria have similarly shown that large population sizes serve as a key buffer to help avoid reaching critical thresholds where extinction is likely (Bell and Gonzalez 2009, 2011; Samani and Bell 2010; Ramsayer et al. 2013). In addition to the importance of population size, experiments have confirmed theoretical predictions that the amount of standing genetic variation is a critical factor influencing the likelihood of evolutionary rescue. In the first explicit experimental test of this prediction, Agashe and colleagues exposed populations of flour beetles (*Tribolium castaneum*) to a novel corn flour resource and showed that rescue was positively correlated with initial levels of genetic variation (i.e., the number of founder laboratory strains; Agashe et al. 2011). Similar results have been obtained with bacterial populations subject to antibiotic stress

and unicellular green algae exposed to high levels of salt (Perron et al. 2008; Lachapelle and Bell 2012).

As discussed in the preceding section, additional key predictions of evolutionary rescue theory are that rescue will be more likely when the initial degree of maladaptation is small or environmental change is gradual. These predictions have been tested and supported in a number of experiments (Samani and Bell 2010; Bell and Gonzalez 2011; Gonzalez and Bell 2013; Lindsey et al. 2013). For instance, yeast populations with prior experience of exposure and adaptation to salt stress show greater likelihood of rescue than those that are naïve to this stressor (Gonzalez and Bell 2013). This experiment also supported theoretical predictions that gene flow can facilitate evolutionary rescue; metapopulations of yeast exposed to variable rates of environmental change across a spatial gradient of salinity stress were more likely to persist with local dispersal, provided that the rate of environmental change was not too great.

Knowledge Gaps and Limitations of Current Models

Detecting Polygenic Variation in Environmental Tolerance

As discussed above, most environmental tolerance traits appear to be under polygenic control. Thus, it is somewhat paradoxical that the vast majority of studies that investigate signatures of selection acting on wild plant or animal populations are based on genome scan methods that are biased toward the detection of large effects at single loci (Jensen et al. 2016). Several recent empirical studies have shown that alternative methods designed to detect signals of polygenic selection on the basis of allelic covariation among many small-effect loci have proved more efficient to detect the effect of selection (Berg and Coop 2014; Bourret et al. 2014; Pavey et al. 2015). However, if different populations have different genetic architectures of adaptation due to low levels of gene flow, insights derived from one population may have limited utility in others.

If environmental tolerance is so highly polygenic that determination of a useful genetic architecture explaining a large proportion of variation in tolerance is infeasible, an alternative approach to determining adaptive potential may be to quantify genetic variation in adaptive phenotypes under experimental conditions representative of future environments. Animal and plant breeders have long employed predictions of phenotypes (specifically, breeding values) based on genetic data, an approach known as marker-assisted selection (MAS) that now includes genomic selection (GS, using all markers; Lande and Thompson 1990; Heffner et al. 2009; Meuwissen and Goddard 2010). Briefly, these approaches work by first fitting a genotype to phenotype model in a set of training genotypes and then applying that model to predict phenotypes for additional genotypes. The accuracy of

predictions from GS (Pearson's correlation r between predicted versus observed phenotypes) is proportional to the expected response from selection using these predictions (Heffner et al. 2009). A major challenge for using markers (as opposed to known causal variants) for phenotypic prediction is that predictions depend on linkage disequilibrium between markers and causal variants. As more recombination and selection events occur between the set of genotypes used to fit models and those being predicted, this linkage is likely to break down (due to recombination or fixation), necessitating recurring rounds of model fitting (Muir 2007). A combination of loci of both large effect and small effect may be important, as a result combining predictions from all markers, plus a subset of the most important markers may be most accurate (Bernardo 2014; Lasky et al. 2015; Spindel et al. 2015). If markers can be linked to absolute fitness, it might be possible to use predictions from MAS models to estimate future population persistence or decline.

Ecological Complexity of Selection

As biologists' ability to characterize molecular states has grown, their ability to measure and understand its ecological context has lagged. A central challenge in predicting evolutionary response to environmental change is that in most systems, researchers have a crude ability to tackle ecological complexity. For example, local adaptation along spatial gradients may be a poor proxy for response to future environments, if future environments do not closely match an occupied existing environment. It seems highly likely, given the high dimensionality of environmental variation (e.g., combined abiotic and biotic environments), that anthropogenic environmental change will tend to create no-analog selection regimes (i.e., that do correspond to any extant location; Williams and Jackson 2007; Fitzpatrick and Hargrove 2009).

Additionally, studies of local adaptation often use publicly available gridded estimates of climate and other variables for many populations across a species range (Hancock et al. 2011; Evans et al. 2014; Lasky et al. 2015), though these estimates can be crude and typically overlook the biotic environment. Even when selection can be measured in reciprocal transplants, it is rarely clear how applicable conditions in a given experiment are given high spatiotemporal environmental heterogeneity in nature (Ågren and Schemske 2012; Weigel and Nordborg 2015), especially for biotic conditions. Additional parameters critical to theory of evolutionary rescue, such as population growth rate, heritability, and dispersal ability are conditional on a given set of environmental conditions and can be notoriously challenging to estimate (Bjørnstad and Grenfell 2001; Clark et al. 2003).

Integrative Models: The Response Architecture

Taken together, the theoretical and empirical advances have a major implication: efforts to understand the responses of populations to environmental change will depend on an understanding of not just the genetic architecture of adaptation but also the absolute fitness consequences, the spatial distribution and abundance of adaptive alleles, and the relationship of plasticity to adaptation in the system of interest. Motivated by this emerging consensus, we strongly advocate the increased study and modeling of evolutionary response architectures (fig. 1). This program will be challenging and touches on several major outstanding questions of population genetics; however, the challenge is urgent, and as reviewed above, a good deal of progress has been made.

Genetic Architecture

The ability to model or simulate the evolution of environmental tolerance traits will depend largely on good estimates of the genetic architecture of those traits. Ideally, a thorough understanding of genetic architecture should include the number of loci associated with environmental tolerance and their effect sizes, the locations of those loci within the genome, and the linkage structure among them. Our review of climate-related population genomic studies shows that measurements of these parameters in natural populations are highly variable (table A1). Important general principles include that climate-associated traits are likely to be polygenic and distributed across a broad range of cellular functions. This may be an unsatisfying result if the goal is one smoking gun gene, characteristic of early evolutionary models. However, modern population genomic approaches for study of complex traits may lead us to focus on generalizable patterns rather than searching for a single gene of known function. As methods for identifying and interpreting the genomic basis of highly polygenic traits improve, so will our ability to use these inferences to predict evolutionary outcomes.

Spatial Distribution and Abundance of Adaptive Alleles

Although great progress is being made in characterizing the genomic architecture of environmental adaptation, this is just part of the challenge of understanding evolutionary responses to environmental change. We next need estimates of the spatial distribution and abundance of putatively adaptive alleles. This should consist of allele frequencies at all associated loci across a region of interest in order to predict the impacts of standing variation and migration on the probability of adaptation. Although for highly polygenic traits, procuring this type of data can be costly, decreases in sequenc-

ing costs and advances in genotyping from low-coverage genomes are allowing increased sample sizes and broader sampling. In addition, informative polymorphisms inferred from genomic data can be used to develop smaller, more cost-effective assays (Ruegg et al. 2014; Jones and Good 2016). Understanding the distribution of standing genetic variation will allow for population-specific simulations of future spread of adaptive genotypes.

Population Dynamics

Connecting our understanding of the genomic basis of adaptation to predictions of population persistence will require linking inferred genetic architecture of environmental tolerance with accurate estimates of fitness under different environmental conditions, both biotic and abiotic. A major gap in knowledge is the disconnect between relative fitness, which has been incorporated into the framework of population genetics for decades, and absolute fitness, which is necessary for modeling changes in population size during adaptation to novel environmental stress (Lynch and Lande 1993; Orr 2009). The best estimates are gathered from direct measures of fecundity under known conditions, but this data is not possible for all organisms. Combining measures of relative fitness inferred from genome-environment association studies with population growth rates measured during colonization of new or disturbed areas might provide us with rough estimates of absolute fitness for species that are difficult to keep in the lab or for which fecundity is not easy to measure. The development of standard methods for integrating these types of data will be an important next step toward using population genomic data to predict changes in future population size.

Plasticity

Finally, prediction of response to environmental change will necessarily include knowledge about the relative roles of adaptation and plasticity as well as interactions between these two processes. Much has been learned about the magnitude of plasticity and potential trade-offs from transplant studies in natural systems, aided by the use transcriptome data to investigate gene expression phenotypes (Palumbi et al. 2014; Ghalambor et al. 2015; Rose et al. 2016). In order to incorporate plasticity into predictions of future response, we must be able to measure how flexible environmental tolerance traits are and the effect of plasticity on the rate of adaptation. Although this is still a major outstanding question in evolutionary biology, focused experimentation in natural systems as well as in the laboratory may help measure these parameters in specific systems for incorporation into models of environmental response.

Future Directions

Some studies have already attempted to address multiple elements of this proposed response architecture in determining population responses to evolutionary change (Chevin et al. 2010; Fournier-Level et al. 2016), but very few have simultaneously measured or modeled these disparate influences on population persistence. Finally we urge increased comparison across studies and across systems. Although new genomic studies are conducted every month, results have rarely been used to search for general principles of rapid adaptation or to prioritize conservation efforts (but see Aitken et al. 2008; Shafer et al. 2015). Meta-analyses and broadly comparative studies could be highly informative for these

questions (e.g., Thurman and Barrett 2016). This requires increased transparency and sharing of data but could result in findings of extremely high utility. Combining results across multiple studies will increase our estimation accuracy for mechanisms of environmental tolerance and therefore our ability to predict the fate of species in a rapidly changing world.

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APPENDIX**Supplemental Table****Table A1:** Studies from 2014–2015 examining the genomic basis for adaptation to climate

Study	Environment/phenotype	Design	Scale (km)	Total loci	Climate loci
<i>Hordeum vulgare</i> (Abebe et al. 2015)	Altitude, rainfall, temperature	G-E	40	1,370	40
<i>Canis lupis</i> (Stronen et al. 2015)	12 climate variables	G-E	2,700	67,000	175
<i>Parus humilis</i> (Qu et al. 2015)	Altitude	G-E	3,500	3,613,365	183
<i>Homo sapiens</i> (Fumagalli et al. 2015)	Cardiometabolic phenotype	GWAS	8,400	76,872	20
<i>Iris hexagona</i> (Hamlin and Arnold 2015)	19 climate variables	G-E	1,000	750	35
<i>Corallium rubrum</i> (Pratlong et al. 2015)	Depth	G-E	.6	237,681	56
<i>Arabidopsis thaliana</i> (Raschke et al. 2015)	Temperature-associated growth	QTL	1
<i>Zea mays</i> (Takuno et al. 2015)	Altitude	G-E	200	76,989	687
<i>Sitta carolinensis</i> (Manthey and Moyle 2015)	19 climate variables	G-E	412	2,635	43
<i>Oryza glaberrima</i> (Li et al. 2015)	Thermotolerance	QTL	5
<i>Oryza rufipogon</i> (Mao et al. 2015)	Low-temperature performance	QTL	13
<i>Gadus morhua</i> (Berg et al. 2015)	Salinity, temperature, oxygen	G-E	800	8,809	234
<i>Gasterosteus aculeatus</i> (Guo et al. 2015)	Salinity, temperature	G-E	1,000	9,404	152
<i>O. rufipogon</i> (Ma et al. 2015)	Cold tolerance	QTL	5
<i>A. thaliana</i> (Lobréaux and Melodelima 2015)	Temperature	G-E	7,700	948,330	14,287
<i>Drosophila serrata</i> (Latimer et al. 2015)	Thermal performance curve	QTL	11
<i>Acropora hyacinthus</i> (Bay and Palumbi 2014)	Temperature	G-E	1	15,399	114
<i>Cryptomeria japonica</i> (Tsumura et al. 2014)	19 climate variables	G-E	900	3,930	38
<i>Ovis aries</i> (Lv et al. 2014)	105 climate variables	G-E	11,000	49,034	230
<i>Oncorhynchus gorbusha</i> (Limborg et al. 2014)	Latitude	G-E	2,800	8,036	101
<i>Alnus glutinosa</i> (De Kort et al. 2014)	8 climate variables	G-E	1,500	1,990	15
<i>Populus trichocarpa</i> (Evans et al. 2014)	20 climate variables	G-E	1,100	3,940,000	397
<i>A. thaliana</i> (Oakley et al. 2014)	Freezing tolerance	QTL	7
<i>Restio capensis</i> (Lexer et al. 2014)	19 climate variables	G-E	500	14,434	156
<i>Brassica napus</i> (Nelson et al. 2014)	Thermal time to flowering	QTL	3
<i>Eucalyptus tricarpa</i> (Steane et al. 2014)	Aridity	G-E	250	6,544	94
<i>Oncorhynchus tshawytscha</i> (Everett and Seeb 2014)	Thermal tolerance	QTL	3
<i>Sorghum bicolor</i> (Bekele et al. 2014)	Germination and growth under cold stress	QTL	61
<i>A. thaliana</i> (Li et al. 2014)	Thermal sensitivity	GWAS	...	213,000	5
<i>Rubus idaeus</i> (Molina-Bravo et al. 2014)	Chilling requirement	QTL	4

Note: Studies are listed in reverse chronological order, with newest studies first. G-E = genotype-environment association; GWAS = genome-wide association study; QTL = quantitative trait locus mapping.

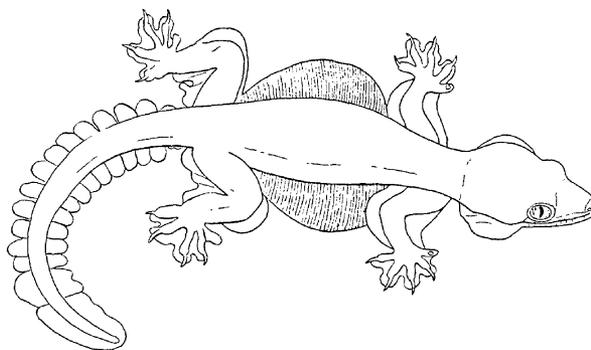
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“Among modern types two lizards have the power of soaring, though in varying degree. Of these lizards the first is of the family Geckonidæ, *Ptychozoön homalocephalum*, a remarkable form from the Malay Islands and the Malay Peninsula.” From “Volant Adaptation in Vertebrates” by Richard S. Lull (*The American Naturalist*, 1906, 40:537–566).