Evolutionary and Ecological Responses to Anthropogenic Climate Change[1]

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Strategies that enable species to persist in changing environments have historically been divided into ecological (distributional shifts and phenotypic plasticity) and evolutionary (adaptation and gene flow). However, most species will likely need to rely on a combination of approaches to mitigate extinction risks from ongoing climate change. For example, increased temporal variation in climate could favor genotypes with adaptive plasticity. Furthermore, even species capable of tracking their preferred climate via migration will encounter different abiotic and biotic conditions; plasticity and/or adaptation could facilitate establishment and population growth in new geographic ranges. The relative contributions of adaptation, migration, and plasticity to population persistence in a changing world will likely depend on characteristics such as generation time, mating system, dispersal capacity, the strength and direction of selection, the presence of ecologically relevant genetic variation, the extent of genetic correlations among traits, and the genetic architecture of adaptation. Will adaptation keep pace with rapid climate change? Here, we propose hypotheses based on ecological and evolutionary theory, discuss experimental approaches, and review results from studies that have investigated ecological and evolutionary responses to contemporary climate change. We focus our discussion on plants, but owing to the limited number of publications to date that integrate evolutionary and ecological perspectives, we draw from other taxonomic groups as necessary.

For species to survive rapid anthropogenic climate change, they must shift their distributions to track preferred conditions (Angert et al., 2011; Chen et al., 2011), adjust their phenotypes via plasticity (Nicotra et al., 2010), and/or adapt to novel stresses (Aitken et al., 2008; Hoffmann and Sgrò, 2011). In most cases, a combination of ecological and evolutionary strategies will be necessary for local and regional persistence in landscapes disturbed by habitat fragmentation, pollution, and invasive species. For example, increased climatic variation (Battisti and Naylor, 2009) could selectively favor phenotypic plasticity (Crozier et al., 2008), which, in turn, could contribute to evolutionary novelty and adaptation (Moczek et al., 2011). Furthermore, many species have already altered their distributions to more poleward and upslope regions because of increasing temperatures (Parmesan and Yohe, 2003; Hickling et al., 2006; Parmesan, 2006; Lenoir et al., 2008; Chen et al., 2011). Migrating populations will undoubtedly encounter novel abiotic and biotic conditions and will need to adjust to different photoperiods, edaphic characteristics, growing season lengths, and altered biotic communities via plasticity and/or adaptation. Gene flow and population admixture could facilitate adaptation by introducing warm- or drought-adapted alleles into populations that are locally adapted to a suite of climatic and nonclimatic variables. Finally, the rate of climate change, combined with the effects of habitat fragmentation, could surpass many species' abilities to track the climate to which they are currently adapted (Davis and Shaw, 2001). Such species will necessarily have to acclimate or adapt in situ to novel selection pressures or face a heightened probability of extinction (Aitken et al., 2008).

Evolution can proceed rapidly (Grant and Grant, 2002; Hairston et al., 2005; Franks et al., 2007), but we know little about the interplay of ecological and evolutionary processes in the context of climate change. Theoretically, adaptation could keep pace with climate change as long as genetic variation, individual fitness, and effective population sizes remain high against a backdrop of strong selection, short generation times, and minimal environmental and demographic stochasticity (Burger and Lynch, 1995; Aitken et al., 2008; Hoffmann and Sgrò, 2011). Will adaptive evolution and/or plasticity allow species to alter their phenotypes fast enough to persist despite rapidly changing conditions (Davis and Shaw, 2001; Franks et al., 2007; Crozier et al., 2008; Teplitsky et al., 2008; Nicotra et al., 2010; Hoffmann and Sgrò, 2011; Shaw and Etterson, 2012)? Can the inheritance of environmentally induced

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nongenetic modifications alter the rate and direction of species' evolutionary response to climate change? And can we make robust predictions about the relative contributions of migration, adaptation, and plasticity as a function of attributes of species or the extent of habitat degradation? This review highlights the interdependence of ecological and evolutionary processes to mitigate extinction risks. We discuss hypotheses and approaches that will illuminate the relative roles of migration, phenotypic plasticity, and adaptation in responses to global change (Table I). We encourage collaborations between ecologists and evolutionary biologists to connect studies of phenology, physiology, mating systems, and dispersal with those of ecological genetics/genomics and quantitative genetics.

RESPONSES TO CLIMATE CHANGE IN CONTEMPORARY VERSUS PALEOCOMMUNITIES

We may be able to draw from the paleoecological literature to understand extinction risks, migration rates, and potential adaptive responses to climate change (Davis and Shaw, 2001; Leakey and Lau, 2012), especially by focusing on the few geological intervals during which the rate and magnitude of naturally induced climate change were similar to contemporary climate change driven by anthropogenic processes (Willis and MacDonald, 2011). During four geological periods of rapid climate change, macrofossil and pollen records document extensive changes in species' distribution patterns, but species likely also adapted to novel climates (for review, see Willis and MacDonald, 2011). Some species experienced dramatic reductions in range size and survived rapid bouts of climate change in outlying refugia surrounded by inhospitable habitat (McLachlan et al., 2005; Willis and MacDonald, 2011).

Researchers have long turned to the fossil pollen record to examine rates of migration after the last glacial maximum in the late Pleistocene. Palynological evidence suggests that tree species migrated approximately 100 to 1,000 m year^{-1} after glaciers retreated, a rate that far exceeds average seed dispersal distances measured in natural populations (McLachlan et al., 2005). This discrepancy, known as Reid's paradox, could result from rare long-distance dispersal events and/or coarse fossil pollen records that do not adequately capture small refugial populations (McLachlan et al., 2005; Magri et al., 2006). Postglacial spread from these refugia would artificially inflate migration rates estimated from the fossil record (McLachlan et al., 2005). Instead, seed dispersal distances and life history characteristics of modern populations are more reliable predictors of the rate of possible range shifts (McLachlan et al., 2005).

Today, natural populations face myriad threats that paleocommunities did not experience, including habitat fragmentation and degradation, pollution, and invasive species. These anthropogenic stresses could hinder dispersal (Kremer et al., 2012), alter patterns of selection on complex traits (Cook et al., 2012), and reduce genetic variation (Jump and Peñuelas, 2006; Willi et al., 2007),

Table I. *Hypotheses and approaches discussed in this paper*

LS, Longitudinal studies; PT, provenance trials; RS, resurrection studies; Sim, simulating predisturbance and postdisturbance conditions experimentally. In some cases, a hypothesis needs to be tested using combined approaches, indicted here by +.

Hypothesis	Approach	Reference
1. Climate change imposes novel selection	LS, RS, PT, Sim	Etterson and Shaw (2001); Etterson (2004); Franks et al. (2007); Hoffmann and Sgrò (2011)
2. Adaptation lags behind climate change	LS, RS, PT, Sim	Etterson and Shaw (2001); Davis et al. (2005); Wang et al. (2006, 2010); Kuparinen et al. (2010)
3. Climate change can reduce fitness and population growth	LS, RS, PT, Sim	Harte et al. (2006); Willis et al. (2008)
4. Climate change disrupts local adaptation	PT, RS + PT, Sim + PT	Wang et al. (2010)
5. Climate change favors plasticity	LS, RS, PT, Sim	Nussey et al. (2005); Crozier et al. (2008)
6. Gene flow increases adaptive potential	Population genetics/genomics + LS, RS, PT, Sim	Kremer et al. (2012)
7. Admixture enables adaptation	Population genetics/genomics + LS, RS, PT, PT and/or Sim + experimentally generated crosses	A.M. Panetta and M.L. Stanton (unpublished data)
8. Adaptation is most likely at the center and leading edge of the range	LS in multiple populations across the range, RS + large-scale sampling across the landscape, RS + PT, PT, Sim + PT	Davis and Shaw (2001); Wang et al. (2006); Aitken et al. (2008); Holliday et al. (2012)
9. Fragmentation reduces adaptive potential	Population genetics/genomics + PT and Sim	Willi et al. (2007)

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thereby restricting evolutionary responses to climate change. For these reasons, the fossil record likely underestimates contemporary extinction risks and overestimates migratory potential and the capacity of species to adapt to global change.

HYPOTHESES

Since limitations exist on our ability to learn from paleocommunities, we must empirically investigate species' ecological and evolutionary responses to rapid contemporary climate change. In this section, we outline several hypotheses that warrant further exploration (Table I).

Adaptive Evolution and Global Change

Industrialization has dramatically increased atmospheric CO_2 concentration, resulting in rising temperatures and altered precipitation regimes (IPCC, 2007). However, other abiotic conditions, such as photoperiod and edaphic characteristics, will remain at historical levels, leading to future environments that have no current analog (Williams et al., 2007). Thus, it seems likely that climate change will impose strong selection on complex polygenic traits, potentially favoring phenological, ecophysiological, and morphological trait values that enable stress tolerance and avoidance (hypothesis 1: climate change imposes novel selection; Etterson, 2004; Davis et al., 2005; Hoffmann and Sgrò, 2011). Selection imposed by climate change could shift adaptive landscapes and alter the magnitude of selection gradients (see figure 1 in Anderson et al., 2012). Optimal trait values are likely to continue to change rapidly under increasingly novel conditions, becoming a moving target for natural populations to pursue (hypothesis 2: adaptation lags behind climate change; Etterson and Shaw, 2001; Davis et al., 2005; Kuparinen et al., 2010). Climate change-induced novel selection will likely reduce fitness and population growth in the short term, owing to a mismatch between current average phenotypic values and new optima (hypothesis 3: climate change can reduce fitness and population growth; Willis et al., 2008). Whether populations will be able to respond adaptively in the long run will depend on the extent of genetic variation and can be constrained by genetic correlations and tradeoffs among traits (Etterson and Shaw, 2001).

Within species, plant populations are often, but not universally, adapted to highly local conditions (Savolainen et al., 2007; Leimu and Fischer, 2008; Hereford, 2009). Few studies have teased apart the effects of abiotic and biotic agents of selection on local adaptation, but climate is clearly not the only factor that drives adaptive evolution (Lowry et al., 2009; Garrido et al., 2012). As climatic variables become decoupled from other agents of selection, genotypes may no longer have the greatest fitness in their home environments (Wang et al., 2010). Therefore, climate change could disrupt patterns of local adaptation that likely took many generations to evolve (hypothesis 4; Fig. 1; Wang et al., 2010). Locally adapted ecotypes may experience greater risk of extinction as climate change accelerates if they have narrow climatic tolerances and limited dispersal capacity (Kelly et al., 2012). In contrast, broad niche breadth and phenotypic plasticity could buffer genotypes from the immediate effects of global change (Banta et al., 2012).

We still know relatively little about the genetic basis of local adaptation. Basic research connecting genotype

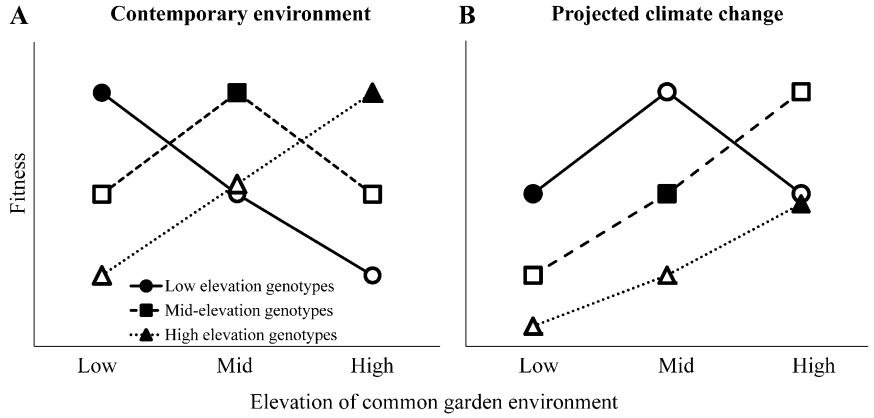


Figure 1. Climate change disrupts patterns of local adaptation (hypothesis 4). In this thought experiment, genotypes from three distinct elevations are reciprocally transplanted into gardens at each elevation. Under contemporary conditions (A), local genotypes have a fitness advantage at their home elevation, reflecting local adaptation. In contrast, future climatic conditions (B) result in local maladaptation, wherein novel conditions favor warm-adapted genotypes from lower elevations. In this case, the fitness of all genotypes is depressed at the lowest elevation. The pattern in B would be more complex if nonclimatic agents of selection, such as edaphic conditions, also contributed to local adaptation. In that case, recombinant genotypes from hybridization of local and lower elevation parents could exhibit maximum fitness in future climates (hypothesis 8). In the long run, rapid evolution could lead to adaptation to global change, restoring patterns of local adaptation. In both panels, local genotypes are represented by closed symbols.

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to phenotype, fitness, and climatic variation will eventually allow researchers to monitor allele frequency changes at loci implicated in climatic adaptation (Umina et al., 2005; Balanyá et al., 2006; Hansen et al., 2012). For example, Umina and colleagues (2005) documented a rapid shift in latitudinal clines in *Drosophila melanogaster* from 1979 to 2004 for allele frequencies at the alcohol dehydrogenase locus and a chromosomal inversion, two genomic regions associated with climatic adaptation. Concordant with changes in the climate over that time frame, tropical alleles shifted into temperate populations, potentially representing a genetic response to climate change (Umina et al., 2005). In humans, Turchin et al. (2012) found strong evidence for selective changes in allele frequencies at hundreds of height-associated loci in European populations. This study illustrates both the potential for such analyses and the massive work required for successful dissection of complex trait variation.

The genetic architecture and basis of complex traits involved in climatic adaptation remains unresolved (Aitken et al., 2008). For polygenic quantitative traits (Rockman, 2012), genomic approaches could be used to detect subtle changes at multiple loci of small effect (Hansen et al., 2012; Turchin et al., 2012). Continuing advancements in genomic technologies and bioinformatics will improve our understanding of climatic adaptation in model (Fournier-Level et al., 2011; Hancock et al., 2011) and nonmodel (Allendorf et al., 2010) organisms. For example, Eckert et al. (2010a) investigated the genetic basis of climatic adaptation in loblolly pine (*Pinus taeda*) by evaluating associations between environmental clines and allelic variation at markers genome wide. Their analysis revealed five loci that were significantly associated with aridity gradients and putatively orthologous to Arabidopsis (*Arabidopsis thaliana*) genes that confer stress tolerance (Eckert et al., 2010a). Additionally, Hancock et al. (2011) discovered a diverse series of genes and Gene Ontology categories with an excess of nonsynonymous changes that are correlated with climatic variables in Arabidopsis. Such genome-wide scans could identify candidate genes involved in climatic adaptation in other species, but they must be carefully validated experimentally (Hancock et al., 2011).

Phenotypic Plasticity

Adaptive phenotypic plasticity enables genotypes to prosper in spatially and temporally heterogeneous environments by adjusting trait values to suit specific conditions (Moczek et al., 2011). As such, plasticity is likely to play an important role in the persistence of species in rapidly changing environments (Nicotra et al., 2010). Indeed, long-term studies of pedigreed animal populations have revealed extensive plasticity and little adaptive evolution in the context of climate change, suggesting that species can alter their phenotypes much faster via plasticity than adaptation (Teplitsky et al., 2008; Ozgul et al., 2009). Nevertheless, current levels of phenotypic plasticity that are sufficient for short-term response to global change could be inadequate once temperatures and water stress exceed historical levels (Kelly et al., 2012). In some regions, climatic conditions are expected to become increasingly variable temporally (IPCC, 2007), which could selectively favor plasticity, promoting evolutionary change in reaction norms (hypothesis 5: climate change favors plasticity; Nussey et al., 2005; Etterson, 2008; Anderson et al., 2012).

Gene Flow, Dispersal, and Range Shifts

Populations routinely exchange alleles via gene flow (Savolainen et al., 2007), which can increase genetic variation and promote adaptive evolution in metapopulation settings (Yeaman and Jarvis, 2006) or constrain habitat specialization and population differentiation (Paul et al., 2011). In the context of major perturbations (e.g. climate change), intermediate levels of gene flow could replenish genetic variation and reduce inbreeding (Kremer et al., 2012), especially in fragmented populations (hypothesis 6: gene flow increases adaptive potential). Furthermore, intraspecific hybridization between residents and immigrants from downslope or more equatorial populations could produce recombinant offspring with warm- or drought-adapted alleles at loci involved in climatic tolerance and locally adapted alleles elsewhere in the genome. Consequently, admixture could speed adaptive response to global change in species that are locally adapted to both climatic and nonclimatic conditions (hypothesis 7: admixture enables adaptation).

Theoretical considerations of migration-selection balance generally presuppose equilibrium conditions in environments that do not deteriorate through time. In such situations, immigrant seeds and pollen may carry maladapted alleles. However, climate change disrupts this implicit assumption, since immigrants from some populations may actually be better adapted to novel conditions than residents. Thus, long-distance seed dispersal could enhance genetic variation and adaptation as well as facilitate migration and colonization of new habitat patches (Davis and Shaw, 2001; Alsos et al., 2012; Kremer et al., 2012). However, the rate of climate change is predicted to far outpace the rate of migration for more than 25% of the planet (Loarie et al., 2009). Species may more readily track preferred climates along elevation gradients, where short distances upslope or downslope correspond to large climatic differences, than along latitudinal gradients, where individuals must move farther geographically to remain within the same climatic region (Loarie et al., 2009; but see Chen et al., 2011). Thus, as climate change continues, in situ adaptation could become a more important pathway for survival in species that span broad latitudinal gradients than elevational gradients (but see Chen et al., 2011).

The risk of extinction from climate change likely varies across the range of a species. Effective population

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sizes and genetic variation can be greater in the center of a species' range compared with the margins, resulting in maladaptive gene flow from central to marginal populations (Kirkpatrick and Barton, 1997; Holliday et al., 2012). Such asymmetrical gene flow could accelerate adaptation to climate change in the leading edge of the range (high elevation or poleward latitudes) because of the influx of warm-adapted alleles but constrain adaptation near the trailing edge (low elevation or equatorial populations) because of the arrival of cold-adapted alleles (Aitken et al., 2008; Holliday et al., 2012). For these reasons, populations at the trailing edge could have greater risk of local extinction if the climate moves too far outside of genetic tolerances, and adaptation might be most likely in the center or leading edge of the range (hypothesis 8; Wang et al., 2006; Aitken et al., 2008; Holliday et al., 2012).

APPROACHES

We now review four powerful methods for testing hypotheses about the interactions between ecological and evolutionary processes in species' responses to climate change (Table I).

Longitudinal Approaches to Detecting Phenotypic Change

Longitudinal studies can identify long-term phenotypic shifts in natural populations and test whether those changes have a genetic basis (Hansen et al., 2012). However, even when long-term records are available, it is often difficult to disentangle the relative contributions of migration, adaptation, phenotypic plasticity, and genetic drift in population-level changes in mean phenotype. Future studies should monitor phenotypes and fitness components in natural pedigreed populations and/or experimental plantings to (1) quantify the extent of phenotypic shifts related to climatic adaptation; (2) link phenotypes to climatic variables that have also changed; (3) assess genetic variation and selection on traits relevant to adaptation to climate; and (4) evaluate whether phenotypic changes result from migration, plasticity, or genetic adaptation or are a maladaptive response to deteriorating conditions (Teplitsky et al., 2008; Ozgul et al., 2009; Hansen et al., 2012). Researchers can model whether the rate of trait changes could be consistent with random genetic drift (Hansen et al., 2012). Longitudinal studies conducted in multiple locations could test whether the adaptive potential of populations varies across the range (hypothesis 8) and whether certain microenvironments could buffer populations from the effects of climate change and potentially serve as refugia.

Randomized experimental studies have clear advantages over observational studies; replicated genotypes of known origin can provide accurate quantitative genetic data and robust tests of the mechanisms underlying temporal changes in mean phenotypes. Nevertheless, even purely observational data can provide estimates of quantitative genetic parameters based on statistical tools developed for plant and animal breeding studies and primarily used in long-term monitoring work in natural animal populations (Kruuk, 2004), thus enabling tests of hypotheses 1 to 3 and 5. This "animal model" is most informative when individuals are tagged and followed through the entire life cycle to generate data on phenotypes, life history transitions, and lifetime fitness (Kruuk, 2004). Implementing the animal model requires information on the relatedness among individuals, which can be estimated from molecular data (Kruuk, 2004; Ashley, 2010). Since observational studies can confound genetic and microenvironmental effects, spatial and temporal variation in microenvironment can and should be incorporated into models to account for environmentally induced phenotypic variation (Kruuk, 2004). Monitoring efforts in natural populations can begin to distinguish plasticity from adaptation (Gienapp et al., 2008). The few such studies done to date suggest that short-term (decades-long) responses to climate change tend to be mediated by phenotypic plasticity and not genetic adaptation (Teplitsky et al., 2008; Ozgul et al., 2009).

Evolutionary responses to climate change could also be inferred from shifts in allele frequencies over time at candidate genes associated with tolerance to temperature, drought, and other stresses imposed by global change (Hansen et al., 2012). We know of no plant-based study that documents allele frequency changes through time in loci implicated in climatic adaptation, although such studies have been conducted in *Drosophila* spp. (Umina et al., 2005; Balanyá et al., 2006). However, plant biologists could begin to explore allele frequency changes at candidate genes that have been described in model organisms. For example, the genetic basis of flowering phenology is well characterized in Arabidopsis (Wellmer and Riechmann, 2010), and orthologs of many Arabidopsis genes have conserved effects on flowering time in other species (Böhlenius et al., 2006). Furthermore, polymorphisms in various genes of the flowering time pathway can influence local adaptation to climate (Banta et al., 2012). As temperatures increase but photoperiods remain unchanged, longitudinal studies should test whether climate change alters allele frequencies more rapidly in candidate genes associated with the temperature and vernalization pathways than in genes from the photoperiod pathway or other genomic regions. Until other climate-related candidate genes and quantitative trait loci are identified in model and nonmodel organisms, researchers conducting longitudinal studies should archive tissue and seeds for future analysis of long-term trends.

Either immigration from lower elevation or more equatorial populations or in situ microevolution could result in long-term phenotypic change consistent with natural selection and underlain by adaptive shifts in allele frequencies. Data on landscape-level population genetic structure and migration rates over time could illuminate whether phenotypic change results from (1)

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replacement of local genotypes by immigrants, which are already adapted to warmer or drier conditions; (2) in situ adaptive evolution from standing genetic variation; or (3) gene flow and introgression of warm- or drought-adapted alleles from immigrants (hypotheses 6 and 7). If migrants simply replaced previous residents (possibility 1, above), we would expect to see allele frequency shifts in both putatively neutral and putatively adaptive loci across the genome. Postdisturbance genome-wide patterns of allelic variation would more closely resemble historical patterns from low-elevation/equatorial populations. However, in this case, postdisturbance populations could be maladapted to nonclimatic local conditions. In contrast, rapid in situ adaptive evolution (possibility 2, above) might only affect loci that are the targets of climate change-imposed selection and linked loci (Maynard Smith and Haigh, 1974). If trait change is a consequence of admixture (possibility 3, above), we expect a genome-wide signature of intraspecific hybridization. Next-generation sequencing will soon provide researchers with ample molecular markers even in nonmodel organisms to estimate population structure and migration rates more accurately (Allendorf et al., 2010). Although we have sketched an ambitious research program that pushes the limits of current knowledge and technology, rapid progress on similar approaches in human populations (Skoglund et al., 2012; Turchin et al., 2012) illustrates the possibilities for studying genetic responses to climate change.

Longitudinal studies can provide a wealth of information (Hansen et al., 2012); however, long-term phenotypic and genetic records are not currently available for most species. Repeated sampling of pedigreed populations over many years will be necessary before general trends become apparent. The following approaches will provide information on plastic and genetic responses to climate change in a more timely fashion.

Resurrecting Predisturbance Lineages and Following Up on Previous Studies

By comparing phenotypes, fitness components, and allelic richness in lineages derived from seeds collected before and after environmental change, Franks et al. (2007) detected rapid evolution in response to drought and Nevo et al. (2012) uncovered evolution in response to gradually changing climates. Indeed, a recent large-scale effort to store seeds has the explicit goal of providing lineages for future studies of the evolutionary response to temporal variation, especially in the context of climate change (for review, see Shaw and Etterson, 2012). This resurrection approach could also be applied to agriculturally important species through the use of germplasm repositories to assess the need to breed for specific traits and/or alter where certain crop varieties are planted as the Earth warms.

Resurrection studies can estimate the rate of trait evolution; investigate the fitness consequences of climate change; dissect the genetic basis of rapid adaptation to disturbance with mapping populations and genomic approaches; distinguish between plasticity and adaptation; and test hypotheses about how specific environmental perturbations select on complex traits and plasticity (hypotheses 1, 2, 3, and 5; see Franks et al., 2007; Nevo et al., 2012; Shaw and Etterson, 2012). These investigations could also determine whether populations can evolve to rely on new triggers for life history transitions as temperature, photoperiod and other environmental cues become decoupled from each other. With sufficient sampling across the landscape before and after disturbance, population genomics studies (Stinchcombe and Hoekstra, 2008) would allow researchers to test whether descendent lineages are immigrants, evolved in situ, or resulted from population admixture (hypotheses 6 and 7). Finally, resurrection studies that transplant lineages from across the range into multiple field environments could directly examine local adaptation and range limits (hypotheses 4 and 8).

This approach only works when propagules can be stored long term with minimal artificial selection and when previous collecting efforts provide robust sample sizes of historical lineages. When a resurrection approach is not possible, researchers could follow up on earlier studies. For example, Willis and colleagues (2008) capitalized on a 150-year record of flowering phenology and abundance patterns of 473 plant species in natural communities of Concord, Massachusetts, which were initially sampled by Henry David Thoreau in the mid-1800s and resampled between 2003 and 2007. They found a significant phylogenetic signal to the response to climate change and a strong decline in abundance among species that were unable to adjust their flowering phenology (Willis et al., 2008). Thus, climate change can have severe fitness consequences for species that are incapable of plastic or adaptive responses (hypothesis 3).

Provenance Trials

Environmental variables such as temperature, length of the growing season, and water availability change dramatically and predictably along elevational and latitudinal gradients, which can result in consistent patterns of adaptation to local climatic conditions (Byars et al., 2007; Zhen and Ungerer, 2008; Fournier-Level et al., 2011). Researchers can exploit natural climatic variation along these gradients to explore adaptation in the context of global change (Etterson and Shaw, 2001; Wang et al., 2010; Kremer et al., 2012). Future research directions include conducting multiyear studies along subtle gradients that closely simulate gradually changing conditions, manipulating the biotic environment, and incorporating the offspring of experimental transplants into the experiment in subsequent years to quantify the response to selection across generations (Shaw and Etterson, 2012).

Provenance trials established by foresters enable tests of adaptation in the context of climate change

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(hypotheses 1–8; Aitken et al., 2008; Wang et al., 2010). These experiments expose genotypes from many populations across broad climatic gradients to common gardens established in multiple locations, thereby capturing a larger range of trait values than would be found in only one population. In this way, provenance trials can test the severity of adaptational lags (hypothesis 2; Wang et al., 2010), in which case, as the climate continues to warm, native ecotypes would have suboptimal phenotypes and fitness compared with foreign genotypes from warmer locales (also hypothesis 4; Fig. 1). In conjunction with population genetic and genomic studies, provenance trials might be able to investigate interactions between gene flow and adaptive evolution (hypotheses 6–8).

Fitness can be modeled as a function of climatic variables in both the common garden site and the original provenance of a genotype. Using this approach, Wang and colleagues (2006) discovered that genotypes from populations in the center of the range of lodgepole pine (*Pinus contorta*) had the greatest performance in diverse conditions. Subsequently, Wang et al. (2010) compared predicted fitness of genotypes in their native provenance with the same genotypes at other sites and demonstrated that climate change will severely disrupt patterns of local adaptation in lodgepole pine (hypothesis 4). By the year 2080, genotypes from across the range will no longer have optimal growth patterns in their native provenances; therefore, the overall productivity of lodgepole pine will be reduced (see figure 4 of Wang et al., 2010). This landmark study also indicated that mean annual temperature had a stronger effect on the height of experimental lodgepole pine individuals than did genetic effects (Wang et al., 2010), reinforcing the hypothesis that phenotypic plasticity will play a prominent role in short-term responses to global change.

Simulate Predisturbance and Postdisturbance Conditions Experimentally

Researchers can impose experimental treatments that simulate future conditions and control treatments that represent contemporary environments (Dunne et al., 2003). Manipulative experiments that include replicated genotypes of known origin, collected from multiple populations across the range of a species, can test all of the hypotheses in Table I (Leakey and Lau, 2012), especially when combined with provenance trials or longitudinal studies. Comparisons of ancestral (pretreatment) and descendant (posttreatment) genotypes in artificial selection experiments can also be used to evaluate whether adaptation to climate change is likely, and if so, how many generations will be needed (Kelly et al., 2012).

Future experiments should factorially manipulate CO_2 concentration, temperature, growing season length (via altering snowmelt date in high-latitude and high-altitude systems), ozone, and/or drought based on specific projections for a given region (Kardol et al., 2010). Although it may be difficult to simulate future climates precisely because of uncertainties in projections (Shaw and Etterson, 2012), multifactorial manipulative experiments can tease apart the effects of different agents of selection on the evolution of complex traits, investigate the interactive effects of these variables, and more closely resemble future climatic conditions. As an example of the need for multifactorial studies, elevated atmospheric CO_2 concentration alone could enhance growth, hasten development, and increase fecundity, but reductions in performance from drought and warmer temperatures could offset those effects (Ainsworth and Long, 2005; Long et al., 2006; Ziska et al., 2012). Experiments run in controlled environmental facilities can model past, present, and future climatic conditions to test adaptation to climate in isolation from other environmental factors. However, controlled environments do not reflect the complexity of abiotic and biotic conditions that species experience in nature (Leakey and Lau, 2012). Laboratory studies often overestimate heritabilities (Etterson, 2008), thereby inflating the perceived rate of evolution. To predict species' evolutionary responses to global change, multiyear experimental studies should be conducted in realistic natural settings. Long-term experiments capture interannual variation and extreme events and can uncover general patterns rather than transient responses to short-term variation in weather (Harte et al., 2006).

Although few evolutionary genetic studies have manipulated climatic variables in the field, results to date suggest that the predominant response to elevated CO_2 concentration is physiological, not genetic (for review, see Leakey and Lau, 2012); there is a great need for additional research that exposes replicated genotypes to different climatic treatments for multiple generations. Evolutionary biologists should capitalize on long-term ongoing experiments, such as the warming meadow at the Rocky Mountain Biological Laboratory (Dunne et al., 2003), to investigate the evolutionary implications of climate change (A.M. Panetta, M. Stanton, and J. Harte, unpublished data). In cases where warming meadows have been maintained for many years, offspring of populations from control and warmed plots can be grown in each of the contrasting treatments to address hypotheses 1, 3, and 5 (A.M. Panetta, M. Stanton, and J. Harte, unpublished data).

A recent meta-analysis suggests that warming experiments might underpredict long-term shifts in phenology (Wolkovich et al., 2012). Yet, Dunne and colleagues (2003, 2004) demonstrated similar flowering phenology responses to two experimental treatments (snow removal and year-round warming) and to two natural sources of variation in climate (interannual and elevational). Thus, our best predictions of ecological and evolutionary responses to anthropogenic climate change come from studies that integrate long-term experiments with observational approaches and model phenotypes as a function of appropriate climatic factors

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(e.g. the timing of snowmelt instead of mean annual temperature; Dunne et al., 2004).

The most powerful tests of the evolutionary and ecological responses to climate change will come from combining approaches. Manipulating climatic conditions experimentally can be done in conjunction with provenance trials in the context of natural climatic gradients to test hypothesis 4 and determine whether limited genetic variation constrains adaptation, especially in the trailing edge of the range (hypothesis 8). Additionally, researchers can evaluate the importance of admixture (hypothesis 7) by outplanting offspring derived from crosses between populations at different latitudes/elevations.

FUTURE DIRECTIONS

Armed with the tools of traditional field ecology and quantitative genetics, as well as continuing technological advancements in genetics and genomics, we have substantial potential to improve our understanding of plant ecological and evolutionary responses to climate change. The following discussion highlights several emerging research directions, which could yield important insights.

Multitrait Evolution and Genetic Constraints on Adaptation

Organisms are not composed of independent traits that can freely evolve in response to novel climates (Etterson and Shaw, 2001); rather, natural selection operates on complex, integrated phenotypes. Evolutionary responses to climate change could be slow or even maladaptive if novel selection drives genetically correlated traits in antagonistic directions (Etterson, 2008). In a classic study of *Chamaecrista fasciculata*, an annual legume native to tallgrass prairies of the Great Plains, Etterson and Shaw (2001) demonstrated that genetic correlations among traits restricted adaptation to climate, even though single traits maintained substantial genetic variation. Thus, multitrait evolution depends on genetic relationships among traits, which can be subject to selection (Arnold et al., 2008). The real potential for adaptive evolution may differ substantially from expectations derived from studies of one or a few traits (Etterson and Shaw, 2001). To achieve an integrated understanding of plant evolutionary responses to global change, we recommend that researchers investigate multiple traits associated with adaptation to climate and other abiotic and biotic agents of selection (Table II; for a genomic perspective, see Hancock et al., 2011).

Functional Traits That Could Enable Adaptation

Whether a species will adapt to changing climatic conditions could depend, in part, on life history strategy, mating system, generation time, demography, and current thermal tolerances (Kuparinen et al., 2010; Alsos et al., 2012). However, tradeoffs make it difficult to predict which traits or suites of traits will be adaptive in such a complex, dynamic scenario as global change. For example, short-lived annuals and biennials will likely show faster adaptive responses to climate change than perennials, but habitat fragmentation may deplete genetic variation more rapidly in short-lived species (Aguilar et al., 2008).

Outbreeding species have seemingly clear advantages over self-pollinators for rapid adaptive responses to climate change, namely high within-population genetic variation, extensive gene flow, and limited linkage disequilibrium (Glémin et al., 2006), but a recent meta-analysis suggests that mating system does not influence patterns of local adaptation in contemporary environments (Hereford, 2010). Heritable epigenetic modifications could facilitate adaptive responses in species with little standing genetic variation, such as selfers (Pál and Miklós, 1999; Bossdorf et al., 2008; Becker and Weigel, 2012). Furthermore, outcrossers may suffer more than selfers from climate-induced disruption of pollination (Forrest and Thomson, 2011). Whether outcrossers will evolve faster than selfers likely depends on a complex interplay between existing genetic variation, the source of new genetic variation, and effective population sizes.

Seed longevity, seed dispersal, and generation time are complex functional traits that could also influence adaptive responses to changing environments. For example, long-distance dispersal could enable adaptation and migration (Kremer et al., 2012). Dispersal in time through a seed bank could moderate losses of genetic diversity attributable to habitat fragmentation, but it may impede rapid evolution by introducing genotypes that were best adapted to historical climates. Finally, trees generally have longer distance gene flow (via pollen) and seed dispersal potential than herbaceous species with similar mating systems (Petit and Hampe, 2006), possibly increasing the rates of adaptation and migration in the context of climate change. However, the long generation times of trees could slow adaptation, and low mortality rates of established adults could continuously expose local populations to maladapted pollen and seed (Kuparinen et al., 2010).

Epigenetics and Evolutionary Adaptation

Phenotypic plasticity is often studied as a within-generation phenomenon, but it can also occur across generations ("transgenerational plasticity") such that the environment experienced by the parents influences trait expression in the offspring (Bonduriansky et al., 2012). Transgenerational plasticity is mediated by nongenetic mechanisms of inheritance, such as the transmission of epigenetic variation (DNA methylation, chromatin structure, and RNA) from parents to offspring (for review, see Jablonka and Raz, 2009). Epigenetic modifications have been tied to ecologically relevant phenotypic plasticity underlying herbivore defense in natural populations of

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Table II. *Ecophysiological, morphological, and life history traits that vary as a function of climate and/or atmospheric CO_2 concentration, or proxies for climate such as elevation and latitude*

The references listed here are by no means exhaustive.

Trait	Reference
Ecophysiology	
Water use efficiency	Ward and Kelly (2004); Ainsworth and Long (2005); Edwards et al. (2012)
Photosynthesis	Ainsworth and Long (2005); Nakamura et al. (2011); Edwards et al. (2012); Leakey and Lau (2012); Ziska et al. (2012)
Chlorophyll fluorescence	Edwards et al. (2012)
Stomatal conductance	Ward and Kelly (2004); Ainsworth and Long (2005); Long et al. (2006)
Carbon-nitrogen ratio	Nakamura et al. (2011); Robinson et al. (2012)
Chlorophyll content of leaves	Nakamura et al. (2011)
Morphology	
Leaf thickness, area, length, width	Etterson and Shaw (2001); Etterson (2004); Ainsworth and Long (2005); Byars et al. (2007); Edwards et al. (2012)
Trichome density	Robinson et al. (2012)
Stomatal density	Ward and Kelly (2004)
Root-shoot ratio	Nakamura et al. (2011); Edwards et al. (2012)
Plant biomass	Edwards et al. (2012); Leakey and Lau (2012); Robinson et al. (2012)
Secondary metabolites and chemical defenses against herbivores	Robinson et al. (2012)
Physical defenses against herbivores	Robinson et al. (2012)
Floral traits (e.g., petal and organ size, reflectance)	Edwards et al. (2012); Lacey et al. (2012)
Cold/freezing tolerance	Howe et al. (2003); Savolainen et al. (2007); Zhen and Ungerer (2008)
Phenology	
Seed dormancy, germination, and seedling establishment	Donohue et al. (2010)
Bud set phenology	Howe et al. (2003); Savolainen et al. (2007)
Commencement and cessation of growth	Howe et al. (2003); Savolainen et al. (2007)
Reproductive phenology	Franks et al. (2007); Springer and Ward (2007); Inouye (2008); Anderson et al. (2012)

Viola spp. (Herrera and Bazaga, 2011) and regulation of flowering time in Arabidopsis (Bastow et al., 2004). These environmentally induced epigenetic modifications can be heritable (Richards et al., 2006; Verhoeven and van Gurp, 2012) and could potentially play an important role in species responses to rapid, directional climatic change (Bossdorf et al., 2008; Becker and Weigel, 2012).

Although empirical studies have only begun to investigate the link between epigenetic inheritance and environmental change, we know that increased temperatures can have positive transgenerational effects on germination rates, biomass, seed production, and thermal tolerance (Blödner et al., 2007). Theoretical work suggests that epigenetic inheritance can reduce lag times associated with within-generation plastic responses to environmental cues (Bonduriansky et al., 2012) and can introduce novel heritable phenotypic variation into populations with little genetic diversity (Pál and Miklós, 1999). Moreover, theory predicts that transgenerational plasticity, mediated by nongenetic inheritance, can influence both the rate and direction of adaptation (Bossdorf et al., 2008; Bonduriansky et al., 2012).

Long-term studies that track the stability of epigenetic modifications over time should be combined with artificial selection experiments to elucidate the influence of these modifications on evolutionary change (Bossdorf and Zhang, 2011; Becker and Weigel, 2012). Such studies should evaluate (1) the effects of epigenetic modifications on phenotypes, (2) the degree to which environmental change triggers heritable epigenetic modifications, and (3) the potential for selection to act on epialleles (Bossdorf and Zhang, 2011). Current methods used to sample natural variation of epigenetic inheritance in model (Schmitz and Ecker, 2012) and nonmodel (Bossdorf et al., 2008) organisms can complement many of the approaches highlighted in this review. Tools developed for evolutionary genetics can be applied to studies of epigenetic variation, including statistical measures for describing population differentiation (e.g. F_{ST}) and quantitative methods for linking genotype to phenotype (quantitative trait locus mapping; Bossdorf et al., 2008; Becker and Weigel, 2012).

The relationship between epigenetic and genetic variation ranges from complete dependency to autonomy, presenting a challenge for researchers (Richards, 2006). Studies can control for the effects of underlying genetic variation by focusing on (1) species that lack genetic variation, (2) asexual populations and/or clones generated by vegetative propagation, (3) natural epimutations or epigenetic mutants of model species, (4) induced changes in methylation by the use of demethylating agents, or (5) epigenetic recombinant inbred lines (Bossdorf et al., 2008; Schmitz and Ecker, 2012). By successfully controlling for genetic differences between individuals, researchers will uncover relationships between environmental cues, epigenetic variation, plasticity, and evolutionary responses to environmental

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change. Future research should address the stability of epialleles through multiple generations, as instability or reversions could decrease the evolutionary relevance of epigenetic modifications (Becker et al., 2011; Becker and Weigel, 2012).

Evolutionary Potential in a Fragmented World

The effects of climate change cannot be considered in isolation from pollution, habitat fragmentation, and other anthropogenic disturbances (Barnosky et al., 2012). Habitat fragmentation decreases effective population sizes and increases geographic isolation, often eroding genetic variation (Willi et al., 2007; Aguilar et al., 2008; Eckert et al., 2010b). Isolation can limit species' abilities to track climate via migration and disrupt gene flow among populations (Kremer et al., 2012), further restricting genetic variation. Thus, habitat fragmentation likely impedes adaptation to novel climates (hypothesis 9). Furthermore, maladaptive shifts in traits and allele frequencies mediated by genetic drift and/or inbreeding depression could further increase extinction risks in fragmented populations.

To date, studies of the genetic consequences of habitat fragmentation have focused almost entirely on putatively neutral molecular markers (Aguilar et al., 2008). However, neutral markers might not reflect genetic variation in polygenic traits (Carvajal-Rodriguez et al., 2005), and few studies have addressed whether fragmentation depresses variation in complex traits subject to natural selection (Willi et al., 2007). Future studies should compare genetic variation in ecologically relevant traits among populations that vary in the extent of geographical isolation and population size (Willi et al., 2007). Do large/continuous populations maintain greater adaptive genetic variation than fragmented populations? How does limited availability of pollinators and mates influence trait evolution in small and geographically isolated populations (Eckert et al., 2010b)? Does fragmentation restrict evolutionary potential in the context of climate change? These questions remain essentially unresolved, likely because they require multiyear field experiments to quantify genetic variation and selection on complex traits while simultaneously disentangling the effects of geographic isolation and population size (Fig. 2). However, such studies would provide a treasure trove of information about

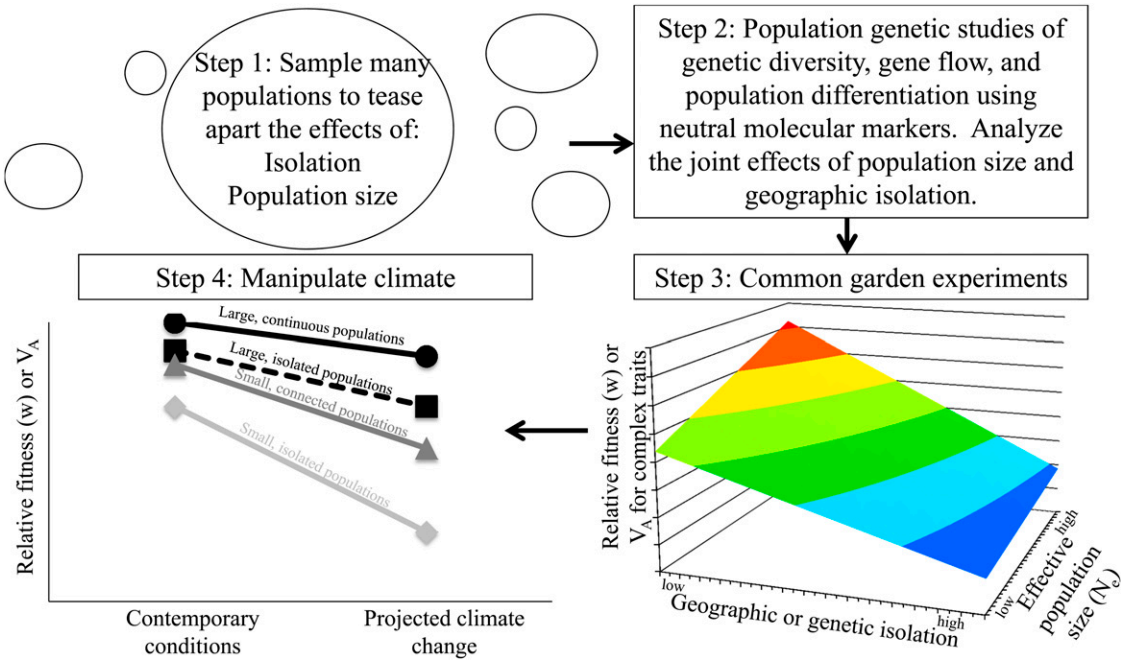


Figure 2. Schematic of steps to test the adaptive potential of fragmented populations (hypothesis 9). In step 1, future studies should sample from populations that differ in size and geographic isolation, represented here by circles of varying sizes. Step 2 assesses genetic diversity at neutral loci as a function of effective population size and geographic isolation. This step is where most studies of the genetic ramifications of habitat fragmentation have stopped. In step 3, common garden experiments quantify fitness as well as genetic variation (V_A) in multiple ecologically relevant traits. Statistical analyses should determine whether fitness and V_A vary as a function of effective population size, geographic or genetic isolation, and (if known) the time since habitat fragmentation occurred. These analyses could incorporate population genetic data (step 2). Finally, in step 4, researchers expose genotypes to contemporary versus future conditions and quantify fitness components, V_A, and predicted responses to selection. As in step 3, researchers could analyze fitness, V_A, and other response variables as a function of population size and genetic isolation. The fitness consequences of climate change could be more severe in fragmented than in unfragmented populations.

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realistic responses to novel stresses associated with anthropogenic change.

CONCLUSION

Climate change poses severe threats for biodiversity, ecosystem dynamics, and agricultural productivity (Battisti and Naylor, 2009; Barnosky et al., 2012). Models of the effects of climate change on populations and communities generally fail to consider evolutionary responses and assume that populations will respond primarily through distributional shifts (but see Kuparinen et al., 2010). Ultimately, understanding ecological and evolutionary responses to climate change will enable informed conservation decisions (Aitken et al., 2008; Banta et al., 2012). For example, Loss and colleagues (2011) propose an integrated approach to conservation, including improving habitat connectivity, managing for genetic diversity and adaptive potential, with assisted migration used as a last resort.

This review has focused on evolutionary responses of plants to changing abiotic conditions. However, climate change will continue to alter biotic communities as distribution patterns change, invasive species become more abundant, and shifts in phenology alter species interactions (Barnosky et al., 2012; Robinson et al., 2012). Interacting species might differ substantially in their responses to climate change (Davis and Shaw, 2001). Investigating the evolutionary responses of species to their changing biotic community is imperative, but it will likely be considerably more complex than studying responses to abiotic changes.

Finally, the overwhelming majority of studies of plant responses to climate change have focused on temperate systems, despite projections of severe drought, unprecedented heat, and novel climates in tropical ecosystems (IPCC, 2007; Williams et al., 2007; Battisti and Naylor, 2009). In contrast with temperate trees, tropical trees experience limited spatial and temporal variation in climate and, therefore, might maintain less genetic variation in complex traits associated with adaptation to climate (Feeley et al., 2012). We encourage international collaborations that establish large-scale projects with the objective of understanding ecological and evolutionary responses to climate change in a diversity of understudied habitats, from tropical forests to boreal, alpine, and arctic ecosystems.

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