

3

Natural Selection and Phenotypic Plasticity in Wildlife Adaptation to Climate Change

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Climate-change models predict that during the course of the 21st century the resilience of many species is likely to be outpaced by an unprecedented combination of climate change and other global alterations (especially land-use change and overexploitation). By 2100, ecosystems will be exposed to atmospheric CO₂ levels and global temperatures substantially higher than in the past 650,000 years (Solomon et al. 2007). As a consequence, sea level rise, increased heterogeneity in weather, and associated habitat change will alter the biodiversity and functioning of most ecosystems. This understanding has led to an increase in research on the ability of wildlife populations to cope with the effects of climate change and avoid extinction (Brodie et al., this volume).

Despite increasing theoretical and empirical research on how and at what pace wildlife can adapt, we still have only limited understanding of what to expect in terms of the impacts of climate change on species and ecosystems (Heino et al. 2009). The term “adaptation” can be used broadly in wildlife management and conservation. The Intergovernmental Panel on Climate Change (IPCC) defines adaptation as an “adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities.” The US Fish and Wildlife Service and some state wildlife agencies are also developing wildlife adaptation plans in response to climate change. These different meanings and uses of adaptation require careful consideration as biologists and practitioners need be able to understand the intent of a particular action. That is, “incorporating adaptation into wildlife responses to climate change” means different things to different parties. Here we use the term “adaptation” from an evolutionary perspective (see table 3.1 for relevant terms).

Most wildlife populations are able to accommodate “normal” levels of environmental variability experienced within a lifetime. However, the predicted increase of climate-induced environmental variance may lead to variability too great for individuals to survive or reproduce successfully, so that the population begins to decline. The likely result will be

Table 3.1. Glossary of terms used in this chapter

Adaptation (evolutionary). The process of genetic change, the creation of new phenotypes from that change, and the corresponding increased fitness of individuals possessing the new genetic trait.

Canalization. The ability of an organism to produce a consistent phenotype regardless of environmental conditions. This ability often requires a developmental system with the ability to resist or buffer environmental influences on phenotypes (Stearns 1989).

Climate envelope models. A type of species distribution model in which envelopes of suitability are generated from climate data and information on known occurrence of a species. BIOCLIM is a common climate envelope model.

Coadapted gene complex. The interaction of alleles from different genes to produce viable or well-adapted phenotypes. At the intraspecific level, coadapted gene complexes are more likely to be common in species where gene flow between populations is low because high gene flow would disrupt adaptive complexes from forming.

Community genetics. A type of genetics that emphasizes evolutionary genetic processes that occur among interacting populations in communities, and which permits the evaluation of ecosystem consequences of species interactions (Antonovics 1992).

Evolution. The change in a form of phenotype that occurs over generations. Frequently a distinction is made between macroevolution and microevolution.

Fitness. In the evolutionary sense, the average greater reproductive success of an individual that can be attributed to a particular genotype.

Gene flow. The movement and incorporation (through reproduction) of alleles from conspecific populations.

Genetic drift. The alteration of populations' allele frequencies through sampling error (chance) rather than by natural selection, mutation, or immigration. In small populations genetic drift is a major factor, due to high variance in reproductive success among individuals from generation to generation.

Genetic effective population size (N_e). The number of breeding individuals in an *idealized population* that show the same amount of inbreeding or loss of diversity as the census population under consideration. The idealized population is a mathematically convenient one, having constant size through time, an even sex ratio, and equal reproductive success among individuals, among other assumptions. If a real population were to have or approach the ideal, then the N_e would be similar to the census size (N). Most natural populations have N_e far lower than N because of differential reproductive success, fluctuating population size, skewed sex ratios, and other ecological factors.

Heritability. The proportion of a phenotype's total variation that is attributable to the average effect of genes in a particular environment.

Natural selection. The process by which the relative frequency of a particular genotype changes from generation to generation because of differential fitness of phenotypes controlled by genes in question.

Ontogeny. The growth and development of an individual's anatomy from cell to maturity.

(Continued)

Table 3.1. (Continued)

Phenology. The timing of a recurring phenomenon, The phenomenon may be a response to one or more environmental factors such as photoperiod, climate, or drought.

Phenotypic integration. The correlation among certain traits, some of which may develop under natural selection. Phenotypic plasticity can evolve not only because of adaptive value, but also because of correlations with other traits (Pigliucci and Preston 2004).

Phenotypic plasticity. The ability of an organism to respond to its environment with a change in form, state, movement, or rate of activity. The broadest definition of phenotypic plasticity includes responses that are reversible and irreversible, adaptive and nonadaptive, active and passive, and continuously and discontinuously variable (West-Eberhard 2003).

Selection. As used in this chapter, natural selection: the differential fitness of genotypes that results in the change in relative frequencies of alleles over generations.

Standing genetic variation. The presence of neutral or slightly deleterious alleles found in a population, as opposed to the presence of allelic variants that appear by new mutation events.

to change patterns of population growth and abundance (Bell and Collins 2008). As a consequence, wildlife populations will respond to biotic and abiotic changes associated with increased climate variability in three fundamental ways: (1) by going extinct; (2) by expressing different behavioral or physical phenotypes under altered environmental conditions, including behavioral changes and increased dispersal to track suitable environments (phenotypic plasticity); or (3) by adaptive evolutionary responses to selection imposed by climate change (Holt 1990).

Numerous examples of distributional and phenological shifts with a changing climate have been documented for wildlife populations (e.g., Parmesan and Yohe 2003, Davis et al. 2005, Primack et al. 2009). Yet with continued habitat alteration, many species will not have the opportunity to track favorable conditions (Groom and Schumaker 1993). In these instances populations will need to adapt by evolving, responding plastically (other than dispersal), or both. For instance, although the timing of laying eggs is to some degree genetically determined, environmental cues that an individual experiences may signal the most appropriate time to lay eggs. Both evolution and phenotypic plasticity can be considered forms of adaptation in a general sense, though they have different implications for wildlife population persistence and management.

Not all species, or even populations within species, will adapt similarly to climatic (or other) variation (Young et al., this volume). Identifying and prioritizing conservation strategies will be improved with an understanding of the potential for plastic and evolutionary responses of populations. For example, recent climate-envelope models predicting large-scale extinctions (e.g., Lawler et al. 2009) often contain a high level of uncertainty. Such uncertainty will likely be reduced with a better understanding of the role of adaptation (e.g., Morin and Thuiller 2009). Finally, recent practices in climate-change management (e.g., “assisted migrations” and captive breeding) often ignore the implications of local adaptation in determining the long-term success of these management options (Popescu and Hunter, this volume).

Here we describe key evolutionary components of populations and species that are relevant to evolutionary adaptation in changing climates. We then highlight the concept of phenotypic plasticity and its relevance to climate change, as well as how the interplay of phenotypic plasticity and evolutionary adaptation may facilitate or hinder the probability of species persistence. We identify current gaps in the application of concepts of plasticity and evolution to climate-change-related biodiversity problems. Finally, we discuss some strategies for conservation and management under climate change.

Evolutionary Responses

Natural selection depends on several factors, including the rate at which new genetic material can be replenished through either *mutation* or *gene flow*, the amount of standing genetic variation in a population, the strength and consistency of selection on a particular trait, and how long selection occurs relative to the generation time and age structure of the organism in question. Given that these factors generally are nonexclusive, predicting and managing evolutionary change will be context-specific.

Adaptive evolution cannot occur without genetic-based trait variation and differential fitness among phenotypes. Mutations are the ultimate source of new variation, but their occurrence is exceedingly rare. Because of this, most adaptation in response to projected change will rely on *standing genetic variation*, as has been demonstrated from decades of research on quantitative genetics (Hill 1982, Roff 2007). Distinguishing between new mutations and standing variation is important because the process of adaptation is expected to be quite different between them. The persistence of new mutations depends on the magnitude of beneficial effect of that mutation and the effective population size (N_e). Since most new mutations are neutral or deleterious and wildlife populations are typically

small (particularly those of conservation concern), many new mutations are expected to be nonadaptive or lost through drift. In contrast, standing genetic variation reflects the cumulative effect of recurrent mutations and genetic drift acting to maintain some mutation-generated neutral variation. Given the relationship between mutation, drift, and standing genetic variation, the latter is expected to be the product of many generations of accumulation of new allelic variants. Thus, the amount of standing variation may help (if high) or hinder (if low) adaptation. Under environmental change, existing neutral variation may become advantageous, and thus allow for adaptation (Barrett and Schluter 2007).

Even when adaptive traits are predicted to respond positively to climate change, the underlying genetic architecture can constrain adaptation. Eterson and Shaw (2001) found that the multivariate adaptive response of legume plants (*Chamaecrista fasciculata*) was much slower than when adaptively important traits (fecundity, reproductive state, leaf size, and number) were considered individually. This is because negative interactions among important traits can constrain overall adaptation. Although such genetic constraints can be overcome with time, in many cases this will be too slow to avoid extinction (Gomulkiewicz and Houle 2009).

Gene flow is for many species an important means of gaining or maintaining genetic variation. As a source of new variation, a small proportion of immigrants can offset the detrimental effects of population isolation by increasing N_e (Mills and Allendorf 1996). N_e is important because it, not census size (N), predicts the rate of inbreeding and the rate of fixation or loss of neutral and (future) adaptively important alleles. However, gene flow can sometimes have negative effects on evolutionary processes when spatial patterns of natural selection result in local evolutionary adaptation. In these situations, different populations may vary in a particular trait due to local environments favoring different variations of the trait. Gene flow in these instances can inhibit local adaptation by continually introducing locally nonadapted alleles (Hendry 2004).

Environmental selection is often strong (Hereford et al. 2004) and may increase in intensity under climate change in many habitats. Selection can also frequently change direction, meaning that the selective pressures faced by parents might be very different from those faced by their offspring due to temporal or spatial variation. Such fluctuating selection pressures can result in imprecisely adapted populations (Bell and Collins 2008). From a purely natural selection perspective, environments that constantly change will keep populations “on their toes” with respect to how well they are adapted. Importantly, rapid and constant directional change (e.g., increasingly warmer mean temperatures, drier conditions)

may outpace the potential rate of adaptation for organisms with longer generation times, and high environmental variability can further impede directional selection.

Phenotypic Plasticity

Phenotypic plasticity, on the other hand, can often handle predictable and rapid changes in environmental conditions better than evolution can. Phenotypic plasticity refers to the tendency to produce different phenotypes (morphological, behavioral, or physiological) from a given genotype in response to different environments (figure 3.1). Phenotypic

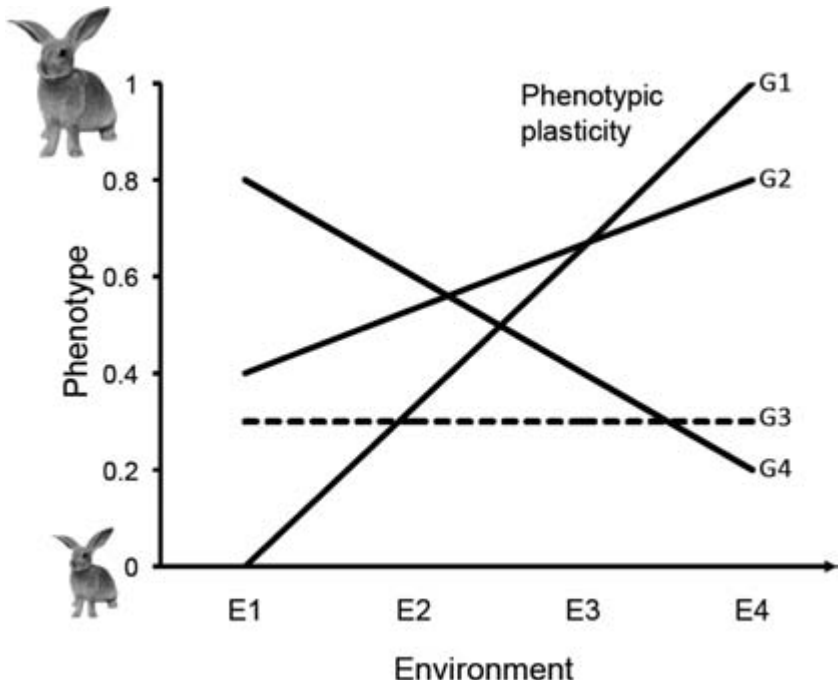


Figure 3.1. An example of phenotypic plasticity comes from the potential for genotype-by-environment interactions. Different degrees of phenotypic plasticity for a given trait are plotted as reaction norms in different environments. Plasticity occurs when the phenotype (rabbit size) produced by a given genotype (G1–G4), is determined by the environment. Note that in this example, genotypes G1, G2, and G4 converge on a similar phenotype at intermediate environments (E2 and E3) and are highly divergent at extreme environments (E1 and E4), thus representing genotype-by-environment interactions. Plasticity also varies, being greater in G1 (steeper slope) than in G2 or G4. Genotype G3 has no phenotypic plasticity and is said to be canalized. Modified from Garcia de Leaniz et al. 2007.

plasticity is best contrasted with the phenomenon of canalization, in which a particular trait will be expressed similarly under a wide range of natural environmental conditions (Stearns 1989). The role of plasticity under climate change will depend on whether the plasticity provides a fitness advantage that could allow for the persistence of populations until adaptive evolutionary change occurs (Price et al. 2003). Disentangling the relative effects of genetic background and phenotypic plasticity on behavioral or other adaptive responses can be difficult, though examples exist showing that plasticity can be used for adaptive responses under changing environmental conditions. For example, guppies adapted to low predation environments can still respond through phenotypic plasticity to predator-induced alarm pheromones (Huizinga et al. 2009).

The availability of predictive environmental cues at the correct time is crucial for the evolution and maintenance of phenotypic plasticity (Padilla and Adolph 1996, DeWitt et al. 1998). Behaviors are often immediately plastic. However, modifications in physiology and morphology require more time to occur relative to behavior. For example, geometrid moth larvae can match morphology and color to their diet and background over successive molts (Greene 1989).

Individuals are not infinitely plastic for all traits, and this is likely due to a lack of historically predictive cues or to the energy costs associated with maintaining the ability to be plastic (DeWitt et al. 1998). Nonetheless, some level of phenotypic plasticity is common for many traits in most organisms.

Evolutionary and Plastic Responses to Climate Change

Differentiating between evolutionary and plastic responses is an important component of our understanding of how and whether wildlife will adapt under climate change scenarios (Gienapp et al. 2008). Perhaps even more important, understanding the interplay of the two phenomena can lead to a richer appreciation of the ability of some species to cope with climate change. For example, phenotypic plasticity may allow species to respond immediately to change and facilitate the long-term evolutionary process (Rehfeldt et al. 2001, West-Eberhard 2003) by acting as a temporal buffer for adaptive evolution (Price et al. 2003). However, plasticity may not be able to sustain a directional response for long periods, as might be the case under long-term changes in climatic variables. Over longer periods, evolutionary change will likely be required for sustained directional responses, though at times the pace of evolution will also be insufficient for populations to sufficiently adapt (e.g., in long-lived organisms).

Plastic responses of animals under climate change will not always be

adaptive, and may at times be detrimental. Such negative responses will be more likely when environmental conditions are novel and extreme. Plasticity will promote long-term population persistence under climate change if the plastic response is well matched to the optimal phenotype, and depending upon the rate at which nonheritable, environmentally induced variation can be converted to heritable variation (Ghalambor et al. 2007).

The extent of this theoretical role of plasticity in buffering populations from climate change is still unclear, though a few examples exist. Individual great tits (*Parus major*) that are highly plastic in their timing of reproduction in response to spring temperature and prey availability have had higher average fitness over a 30-year period. As a result, greater plasticity in an ecologically important trait (timing of reproduction) has led to natural selection acting for increased plasticity of laying date correlated with changing climate (Nussey et al. 2005). Examples of phenotypic plasticity in introduced species (e.g., anoles [Losos et al. 2000] and cane toads [Phillips and Shine 2006]) suggest an important role for plasticity in the invasion of new environments, including those habitats formed under climate change.

Simply documenting phenotypic change over time does not distinguish plasticity from evolution. Many studies focusing on phenotypic characters that purport to reflect rapid microevolution have been criticized for lacking evidence of genetic change (Gienapp et al. 2008). However, it is rarely feasible to measure the genetics of adaptively important traits (particularly in nonmodel organisms) and to differentiate genetic and environmental effects. Researchers can instead use organisms where controlled breeding or pedigree analysis is possible to examine the potential for adaptation to climatic changes through evolution and plasticity. Together with predictive modeling, these efforts will serve as a guide for predicting the responses of many other species to climate change. (van Asch et al. 2007, Ghalambor et al. 2007).

While phenotypic plasticity may be an essential mechanism for allowing populations to respond to climate change, alterations in the predictability of plasticity cues can have disastrous consequences. If formerly reliable cues become disassociated with a particular environment or resource, organisms may express a maladaptive phenotype in space and/or time. Environmental sex determination (ESD) is an example in which phenotypic plasticity (the determination of sex occurring often in response to temperature; Bull 1983) can lead to evolutionary traps (Schlaepfer et al. 2002). As environments change, ESD could increase the risk of extinction by resulting in large biases in sex ratio. Species with ESD (e.g.,

reptiles; Janzen 1994) are likely to be especially sensitive to global climate change (Walther et al. 2002). However, the detrimental effects of existing plasticity may be short-lived if selection acts quickly on nest site choice—for example, in response to skewed sex ratios (McGaugh et al. 2010). Another example is the use of photoperiod to predict environmental conditions, a widespread phenomenon in animals. The tendency of large, long-lived mammals to rely on photoperiod and other cues relative to smaller mammals could mean that the former will be less likely to adapt under climate change (Bronson 2010).

Limits to plasticity and evolution may exist partly because of internal and ecological limits to adaptation (figure 3.2) that are thought to be pervasive (DeWitt et al. 1998). Tadpoles that simply possessed the *ability* to be highly plastic in response to predators experienced some costs in mass, development, and survivorship (Relyea 2002). However, negative fitness costs associated with plasticity appear to be difficult to detect in natural systems (Van Buskirk and Steiner 2009).

From a conservation and management standpoint, species that express little plasticity and/or have low genetic variation will be the most vulnerable to long-term negative effects of directional climate change (Holt 1990). While predicting evolutionary responses may prove difficult, characteristics of species and populations can provide insight into the role that evolution and plasticity may play as climate continues to change. For example, species that already use a variety of habitats, foods, and other resources have demonstrated plasticity, which will likely be beneficial. Specialists and species that require narrow sets of resources will likely suffer. Small isolated populations, already of conservation concern, may be limited in their evolutionary adaptability, due to their low N_e and low standing genetic variation. The rate of climate change may also outpace the evolutionary response of long-lived organisms, particularly those with low fecundity.

The direct impact of plasticity and evolution within a wildlife conservation and management framework is still poorly documented. However, numerous related examples illustrate their importance. For example, naive prey can quickly adapt behaviorally to the reintroduction of predators in ecosystems (Berger et al. 2001). Habitat alteration and harvest regimes have been shown to alter selection regimes on phenotypes like size at first reproduction in fish (Fukuwaka and Morita 2008). And alterations in the seasonal behavior of red squirrels (*Tamiasciurus hudsonicus*) have been shown to have a heritable component, though most of the observed shift toward earlier breeding (18 days over a decade) was due primarily to plasticity (Reale et al. 2003).

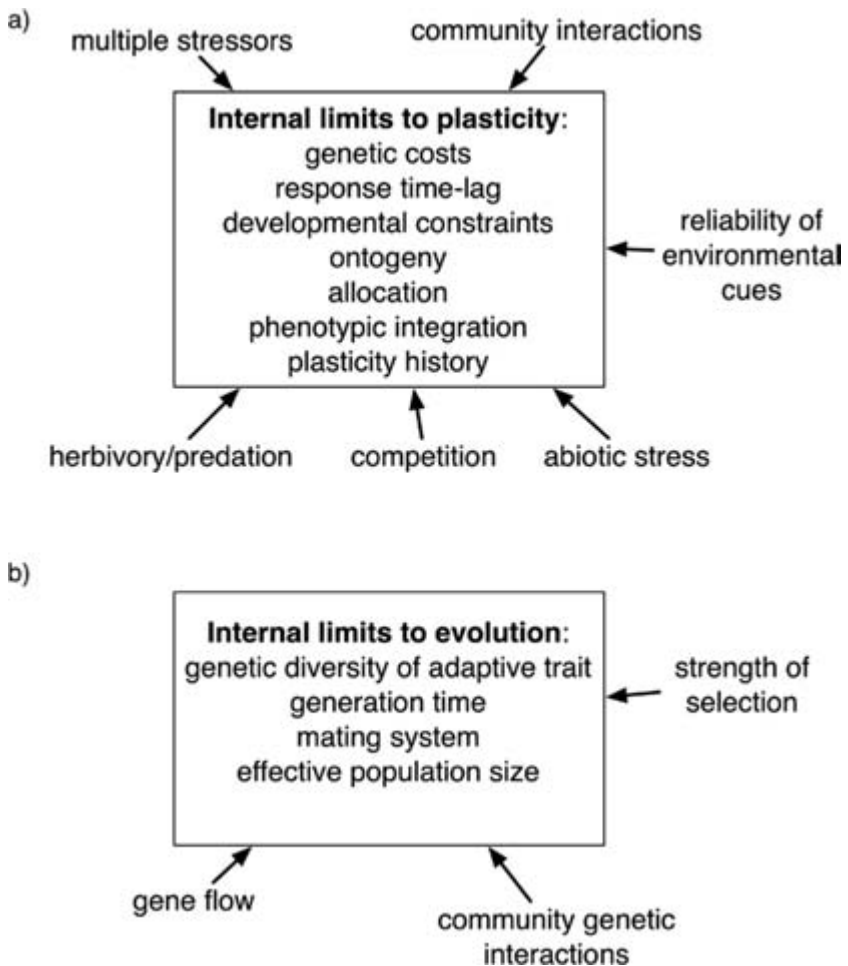


Figure 3.2. Multiple internal (*inside box*) and external (*outside box*) factors can influence the capacity of populations to respond to a given environmental factor via (a) plasticity and (b) natural selection. With plasticity, less is understood about the external or ecological limits than about the internal limits. These are the factors highly influenced by climate change. Both adaptation and plasticity are likely to be affected by dynamic changes to communities.

Applications of Evolution and Plasticity

The interpretation of climate change effects on wildlife, as well as the management strategies aimed at ameliorating those effects, can benefit by explicit consideration of phenotypic plasticity and evolutionary responses. These approaches are new to many managers and are increasingly important because adaptive change can happen rapidly, and in re-

sponse to conservation schemes (Reznick and Ghalambor 2001, Smith and Bernatchez 2008).

Interpreting Recent Effects of Climate

While there have been numerous attempts to identify the fingerprint of contemporary climate change, only recently have investigators discovered whether the trends have occurred via evolution, plasticity, or both. A recent meta-analysis on the effect of human activities (e.g., introductions, translocations, harvesting) on rates of phenotypic change in 68 studies has demonstrated that most of the rapid phenotypic response has been largely due to plasticity rather than evolutionary change (Hendry et al. 2008), a result that may apply to interpreting climate-change effects as well (e.g., Ozgul et al. 2009).

Advances in modeling now provide a better understanding of the role of evolutionary responses and phenotypic plasticity in recent climate change. For example, Knight et al. (2008) extended stage-structured matrix models to incorporate evolutionary selective pressures on demographic traits of white trillium (*Trillium grandiflorum*). Coulson and Tuljapurkar (2008) developed a novel framework that partitions the various types of selection and phenotypic plasticity within quantitative traits. Application of this model framework to a long-term dataset on red deer (*Cervus elaphus*) suggests that plasticity, rather than evolutionary responses to selection, has been a major driver in observed phenotypic change of birth weights. Such models could be applied to traits relevant to the effects of climate change, such as reproductive phenology, migration timing, or body size (Ozgul et al. 2009).

Forecasting Future Effects of Climate

Predicting how species will respond to future climate change and other rapidly occurring crises is increasingly becoming relevant not only for researchers but also for agencies, wildlife managers, and land planners. Most forecasting has focused on using bioclimatic envelopes of species-environment relationships and coupling them with projections for climate change (Lawler et al. 2009). These models have been adopted because they only require information on current distributions of species and climate variables at those locations, thereby allowing many species to be modeled across broad geographic ranges (Guisan and Thuiller 2005). Projections from these modeling attempts suggest devastating effects of climate on biodiversity in the coming decades. Although climate-envelope models of extinction probabilities have been criticized for ignoring adaptive response of organisms to perturbations (Dormann 2007,

Aitken et al. 2008), there is little for managers or policy makers to look to for guidance, particularly because adaptive responses to climate are not well understood (Davis et al. 2005) and few species have data that allow for more detailed mechanistic modeling of potential effects (but for an example of such modeling, see Rehfeldt et al. 1999).

How can these models incorporate evolution and phenotypic plasticity? Projections based on species distribution can be improved by incorporating dynamic processes and estimates of variation for data typical of species distribution models. For example, Oneill et al. (2008) incorporated population variation into modeling approaches, which substantially improved the model's performance by embracing the observed variation critical to evolutionary or plastic responses to climate change. Similarly, species distribution models that incorporate temporal variation in environmental relationships, such as variation in correlations of species occurrence in different years of variable climate, could further improve model performance and the ability to extrapolate to future climate conditions (e.g., Fletcher et al. 2011). Consequently, while it might be difficult or impossible to directly incorporate such complex processes as evolutionary response or phenotypic plasticity into data-sparse, phenomenological models of climate change, some of the dynamics necessary for such responses could be incorporated into model predictions, and could vastly improve them.

Biodiversity Conservation in a Community Context

The capacity for wildlife to respond to climate change through phenotypic plasticity does not only include the ability to respond to changing temperatures and precipitation. As climatic conditions shift, the assemblages of many plants and animals may change in a given area. A species may be able to cope with variation in temperature, but not to changes in the distribution or abundance of other species with which it interacts (e.g., Suttle et al. 2007, Post and Pedersen 2008). Thus, solely investigating the thermal tolerance of plants and animals will not give a complete picture of the potential for those species to adjust to climate change. For instance, the extinction of a major pollinator due to drought or higher temperatures may result in a domino effect, even for those plant species that themselves respond well to elevated temperatures (Hedhly et al. 2009). As communities shift in composition, selection pressures on individual species will likely change through changes in competition, predation, and mutualistic interactions. Changing selection pressures may be difficult to predict in all but the most extreme cases (e.g., obligate mutualists). Overall, understanding interactions among species will be an increasingly important

part of wildlife conservation as habitats shift and novel interactions occur (e.g., introduced species). A considerable amount of research has shown that the ubiquity of plasticity in species' responses to one another will provide expanded adaptive potential and indirect effects on biodiversity (see Agrawal 2001, Miner et al. 2005).

Connectivity Conservation

A prominent approach to wildlife conservation is in facilitating connectivity (Crooks and Sanjayan 2006). Promoting connectivity of habitats in the context of future climate change is thought to be particularly important (Cross et al. this volume). This is because as climate changes, habitats will likely shift and organisms will putatively have to track those shifts to persist. Thus, promoting current and future connectivity of habitats as a “natural” way (as opposed to assisted migration; see below) to facilitate organisms to track changing conditions in space and time will potentially be crucial to minimizing the effects of climate change.

What does the potential for evolutionary responses and plasticity to climate change tell us about future connectivity conservation? While promoting connectivity will undoubtedly be a useful conservation measure, plasticity tells us that some species may persist in the absence of tracking shifting habitat mosaics, at least for some period of time. As noted above, evolutionary perspectives also point to the role that gene flow can play in the changing ecological theater: in general, too much gene flow will swamp the potential for local adaptation, whereas too little may limit the variation available for selection to act upon.

These potential effects are complex, however, and may be highly dependent on numerous issues, including how the quality of habitats changes as climate continues to change. These changes could have profound effects on adaptive evolution. For example, theory suggests that high rates of immigration into sink habitats can facilitate adaptive niche evolution. Temporal variation in fitness, potentially driven by increased climate variation, can further facilitate adaptive evolution (Holt et al. 2004). In addition, the effects of expected asymmetric gene flow tracking favorable climate could be influenced by the quality of the habitats being connected. If these habitats function initially as source populations while previous source populations become sinks, natural selection should favor traits for the new source population (Kawecki and Holt 2002). Taken together, theoretical work on gene flow and spatiotemporal variation suggest that the effects of connectivity conservation in a changing climate may be profoundly influenced by how temporal changes in habitat quality progress.

Population genetics provides tools for estimating gene flow across changing landscapes and the role of connectivity, but the markers typically used are neutral ones, such that they are insufficient for interpreting adaptive evolutionary or phenotypic responses to connectivity conservation and climate change (Holderegger et al. 2006). Instead, interpreting these potential effects will require either a quantitative genetics approach or a focus on markers under selection (e.g., via genome scans; Holderegger and Wagner 2008).

Assisted Colonization

The past few years have seen increased focus on the merits of moving species that are potentially threatened by extinction from climate change (Mueller and Hellmann 2008; Hoegh-Guldberg et al. 2008; Popescu and Hunter, this volume). While we do not intend to contribute to the heated debate on the efficacy of assisted migrations here (Fazey and Fischer 2009), it is worth emphasizing the potential evolutionary implications associated with such strategies. As alluded to above, a high rate of migration can reduce the adaptation of recipient populations that are accustomed to different environmental conditions. This is particularly true when immigrants are from populations adapted differently from the host population. There are a number of genetic as well as demographic concerns about such management strategies, including the number and genetic makeup of colonizers, the frequency and amount of ongoing assisted migration that will be needed, and the landscape configuration of colonized populations. Quantitative approaches need to be adopted that focus on post-translocation monitoring in order to determine the factors that limit or drive successful translocations (e.g., Pelini et al. 2009).

Despite the potential positive effects of introducing novel genotypes from multiple source populations to a newly colonized small population, the disruption of coadapted gene complexes can result in overall reductions in fitness over time (Haig and Wagner 2001). Novel genotypes introduced through supplementation efforts have also been cited as a cause for native species becoming “more invasive” (Mueller and Hellmann 2008).

The viability of assisted migration efforts needs to be assessed prior to moving (or removing) individuals, to avoid detrimental impacts on source or target populations. This includes knowledge of the genetic and demographic resources available (i.e., across the native range) in order to help ascertain project viability (Haig and Wagner 2001). In other words, viability targets cannot be properly determined without an understanding of the basic population processes of intact populations. Landscape

genetic studies of neutral and adaptive variation prior to assisted colonization will be critical to this end.

Conclusions

Understanding the effects of climate change on wildlife populations, and managing for such effects, will be insufficient for protecting and maintaining wildlife population viability without an appreciation of the potential for phenotypic plasticity and evolutionary responses of wildlife to climate change. These two phenomena provide the raw essentials for wildlife to respond to climate change, and they may allow populations to persist in a rapidly changing world. Nonetheless, there has been surprisingly little direct evidence that evolution and plasticity have reduced extinction rates in wild populations (Parmesan 2006). We attribute this lack of evidence, in part, to investigators not explicitly addressing these effects and not having the appropriate tools to do so. We caution, however, that not all populations may have the evolutionary or plastic potential necessary for adapting to rapid climate change. A major challenge in the coming years will be to better identify and interpret the roles of evolutionary responses and phenotypic plasticity for wildlife in a rapidly changing climate.

Addressing this challenge and adjusting management in light of evolutionary responses and phenotypic plasticity will require incorporating new tools and approaches. The development of monitoring designs that can rigorously and efficiently estimate effects of climate change, including the potential for estimating shifting species distributions and evolutionary and plastic responses, is needed. Targeted monitoring (*sensu* Nichols and Williams 2006) that both augments surveys with relevant data on individual variation (e.g., via mark-recapture, or with genetic markers) and targets locations for observing potential changes in spatial distribution may allow for better understanding of phenotypic change in space and time. Such monitoring strategies will need to be adaptive (Lindenmayer and Likens 2009) by updating monitoring designs as data become available regarding recent climate-change effects, especially observed effects during extreme climate events (e.g., extreme drought, heat waves). Such a focus on climatically relevant traits of species may further prove informative for interpreting the potential for evolutionary or plastic changes, but clearly more work is needed in this area as responses to climate change continue to be quantified. As the roles of evolutionary responses and phenotypic plasticity in observed and future effects of climate change are better understood, management and conservation strategies will become more effective at protecting biodiversity.

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