

Evolutionary Responses to Climate Change

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Advanced article

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Biological responses to contemporary climate change are abundantly documented. We know that many species are shifting their geographic range and altering traits, including the timing of critical life history events such as birth, flowering and diapause. We also know from comparative studies of species found across the earth that a strong relationship exists between a species trait and the climatic conditions in which it is found. Together, these observations suggest that ongoing climate change may lead to evolutionary responses. Where examined, evolutionary responses have been uncovered in most cases. The effort needed to disentangle these genetic contributions to responses is substantial and so examples are few. In general, the documented evolutionary responses feature traits that are likely to alter responses to seasonal change or to change tolerance to environmental conditions. Currently available research provides hints that climate-mediated evolutionary responses are likely to be enormously diverse. It is clear, that the current presumption of many climate change scientists, that evolution can be safely ignored, does not have a basis in evidence.

Introduction

Climate is well known as a mediator of evolutionary change. Related species that inhabit different climate regimes differ in characteristic ways that are repeated across taxonomic groups (e.g. Huey and Kingsolver, 1993).

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Everything from heat tolerance, body shape and size, and water use physiology of plants is strongly related to the climate conditions within a species range. From these observations, a natural assumption would be that a great deal of research on the role of contemporary climate change in driving evolutionary responses has taken place. Although there has been an increasing amount of research very recently, in fact there is relatively little known about the links between contemporary climate change and evolution. The reasons for this are not hard to determine. There is abundant documentation of biological responses to climate change (Parmesan, 2006). Species distributions are moving poleward, the timing of life history events are shifting to reflect lengthened growing seasons and traits such as body size are changing. The problem, explored in more detail later, is that these changes may or may not have an evolutionary component. The implicit assumption has been that there is none (e.g. Thomas *et al.*, 2004) and that any observed phenotypic changes are the product of phenotypic plasticity. **See also: [Biotic Response to Climatic Change](#)**

In part, this is because plasticity is known to be widespread and can be readily documented using experiments in which organisms are raised under various conditions. It is much more challenging to parse the relative contributions of plastic and evolved responses. By adding organisms from multiple population origins to experiments aimed at documenting responses to a changing environment, we can first determine whether populations have diverged in their responses. Verifying whether such divergence has a genetic basis then requires an additional step. The most straightforward possibility involves directly documenting relevant genetic change. However, in many cases, that will not be possible and we will be left with a situation in which divergence among populations could be explained by a genetic effect, by an inherited nongenetic effect or by some combination. One of many possible examples of a nongenetic effect is the influence mothers can have on their offspring by better provisioning their eggs. Such maternal or paternal effects can be bred out of offspring by rearing them under common conditions for multiple generations. Following such treatment, we can attribute observed divergence to a genetic origin. Alternatively, we can estimate the size of genetic effects relative to estimated

inherited nongenetic effects through half-sib mating designs (Gienapp *et al.*, 2008). Given these challenges, it is perhaps not surprising that, in the great majority of cases for which we know changes are taking place, the potential for an evolutionary basis to changing climate is unexplored.

Here, we focus on what we do know about microevolution in response to contemporary climate change. Given the recent nature of the efforts, the evidence is impressive. Even when confronted by large-scale, multifaceted and rapid change in climate, there is evidence from various organisms that evolution takes place. In many cases, these changes are detectable in just a few generations. A larger problem is that we know little about the consequences of these responses. Do they help to protect species from further impacts of climate change? In what senses does evolutionary response represent a type of impact? And when we look to the future, can we expect the significance of evolutionary responses to magnify? Later, we document what is known about evolutionary responses to contemporary climate change and lay out some challenges and opportunities for future researchers.

Observed Genetic Changes

Observations of genetic change associated with changing climate provide critical evidence for evolutionary responses. Genetic evidence is also difficult to collect and can be challenging to interpret. It is no accident that much of the evidence we discuss in this section comes from fruit flies. These model organisms have been well characterised genetically, and the relationship between genotype, phenotype and performance is as well understood as it is for any organism on earth. This immense background knowledge has given fly biologists the motivation and perspective from which to sample field populations. For the most part, long-term genetic monitoring was not initiated with climate change in mind. Nevertheless, these data sets are now invaluable for the insights they offer to those understanding how, and how fast, species respond genetically to climate change.

Chromosomal inversions

Balanya *et al.* (2006) analysed global patterns of chromosomal inversion frequencies in *Drosophila subobscura*. Data were collected for a half-century in the species native range, stretching from northern Europe to north Africa. Additional data in their introduced range (North and South America) go back to shortly after their introduction in 1979. It has long been known that inversion genotypes sorted with latitude. Compared with historical samples, researchers found that warm-associated inversions in contemporary samples had moved poleward. This was true in both old and new world latitudinal clines and was resolvable when historical and contemporary samples were separated by as little as two decades. Whereas the genetic response to a warming environment is clearly detectable in

this species, it is not clear what type of selection pressure (e.g. thermal or seasonal selection) is causing it.

Alcohol dehydrogenase

The fruit fly, *Drosophila melanogaster*, is polymorphic for an enzyme, alcohol dehydrogenase (*Adh*), that metabolises alcohol. *Adh* exhibits a strong latitudinal cline. In laboratory experiments, temperature is one of the factors that influences *Adh* allele frequencies. In one study (Umina *et al.*, 2005), researchers resampled sites in coastal Australia for which historical data were available (collected in 1979 and 1982). Across the sampled latitudinal cline, the allele associated with warmer climates had increased in frequency. Here again, as in the previous example, we have a species with a known genetic latitudinal cline shifting frequencies in response to a changing environment.

Mosquito diapause

At the end of the growing season based on a daylength cue, the pitcher plant mosquito (*Wyeomyia smithii*) produces diapausing larvae (Bradshaw and Holzapfel, 2001). The mosquito is polymorphic for the daylength cue. Comparison of contemporary samples with historic ones revealed that the shorter critical daylength morph has increased.

Salamander colour polymorphism

The salamander *Plethodon cinereus* has a genetically based colour polymorphism (Highton, 1975). Red-backed forms tend to be more common in cooler microclimates, whereas a grey, or lead-backed form increases in frequency in warmer microclimates. Gibbs and Karraker (2005) examined over 50 000 individuals collected between 1908 and 2004 from a range of latitudes and altitudes at 558 sites. Their results showed that the frequency of the lead-backed form increased over the course of a century during which temperature increased by approximately 0.7°C.

Adaptations to Climate Change

Reviews of biological responses to contemporary climate change have emphasised two patterns: species are moving and, within a given location, timing of life history events is shifting (Parmesan, 2006). In one review, nearly 60% of more than 1500 species examined had undergone measurable changes in either phenology or distribution during the course of long-term observations (Parmesan and Yohe, 2003; Root *et al.*, 2003). In the majority of cases, responses were in directions expected under changing climate. Among species showing changes, reviews estimated an average poleward movement of 6.1 km per decade and an average spring advancement in phenology of 5.1 days per decade (Parmesan and Yohe, 2003; Root *et al.*, 2003). Both the diversity of responding species and the consistency of response are surprising given the relatively modest extent

of climate change to date. **See also:** [Adaptation and Natural Selection: Overview](#)

Although responses are well characterised in many species, they are still known primarily as natural history observations. We have very little information on the evolutionary basis, if there is one, for changes to phenology and distribution. In the absence of information, there has been a presumption that evolutionary responses are absent or unimportant (e.g. Parmesan, 2006; Williams *et al.*, 2008). Under this view, distributional changes could reflect plasticity in phenology responding to changes in climate cues, whereas distributional shifts could mean nothing more than habitat tracking (Williams *et al.*, 2008). However, for the small number of species where responses have been investigated in greater detail, there is in fact evidence of evolutionary contributions to both phenological and distributional changes.

Phenology

An example of the evolution of phenology comes from a long-term study of red squirrels in the Canadian Arctic (Reale *et al.*, 2003; Berteaux *et al.*, 2004). Over a 13-year period, researchers measured the date on which a total of 664 marked females gave birth. Confronted with warming temperatures and greatly increased food supply (an indirect consequence of warmer temperatures), females gave birth 18 days earlier at the end of the study compared with the beginning (Figure 1). The researchers then used responses from the same females across different (warmer and colder) years to estimate the relative contributions of phenotypic plasticity and evolutionary response to the overall shift. They concluded that most of the attributable variation (3.7 days per generation) was due to plasticity. They also concluded that there was a significant evolutionary response during the 13-year study (0.8 days

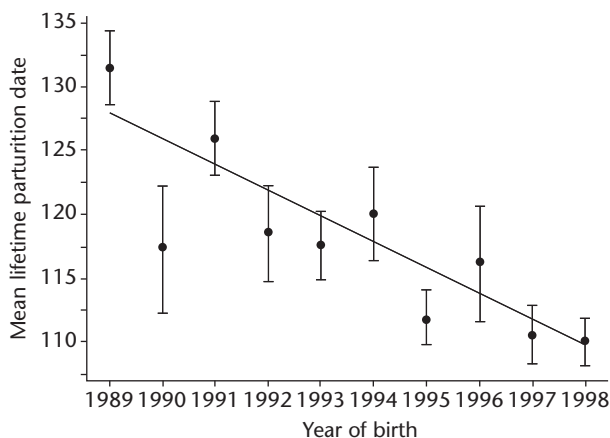


Figure 1 Average parturition date (Julian date \pm 1 SE) for cohorts of female red squirrels at Kluane, Yukon, Canada. Each point represents the average lifetime parturition date of females from a given cohort corrected for age effects. Reproduced from Reale *et al.* (2003), with permission from the Royal Society.

per generation). In one of the few instances for which we can make such an evaluation, a phenological shift was the result of both plastic and evolved responses. In this instance, the evolved response over this short time span was on the order of one-fifth the size of the plastic response.

A second case of phenological evolution involves the pitcher plant mosquito *W. smithii* (Bradshaw and Holzapfel, 2001). Comparing results from common garden experiments conducted across a 24-year period, the geographic distribution of daylengths associated with the production of diapausing larvae had shifted to shorter daylengths. These changes, which were resolvable over durations as small as 5 years, imply an evolved response to longer growing seasons in temperate sites. In the northernmost sites sampled, the observed change corresponds to a 9-day shift in the onset of diapause.

Movement

Distributional shifts in response to changing climate are a form of biological invasion. During invasion, a selective advantage accrues to those individuals colonising an area first. Their offspring get first crack at local resources, can breed earlier than offspring of late arrivers and then move on first to colonise new sites. Studies of invasive species have shown that the evolution of traits related to movement can occur within decades of introduction to a new environment (Phillips *et al.*, 2006) and that the changes can be associated with increases in expected range (Urban *et al.*, 2007).

In the context of climate change, there has been very little study of trait evolution at expanding range edges, but even this much of study suggests similar processes may be at work. A study of two British bush cricket species (*Conocephalus discolor* and *Metrioptera roeselii*) focused on genetically based wing polymorphisms (Thomas *et al.*, 2001). In both species, a shorter winged or wingless form has reduced dispersal abilities relative to a longer winged form. As climate has warmed, both species have spread northward and inland from southern coastal regions. In newly colonised areas, frequencies of long-winged forms are higher than in source regions.

In addition to traits that can directly facilitate movement, warming conditions may have less straightforward effects that can promote range expansion. Thomas *et al.* (2001) also report on two British butterflies that have undergone range expansions over the course of two decades. In the first case, the silver skipper butterfly (*Hesperia comma*) was restricted to south-facing slopes at its northern range limit. As the climate warmed, the butterfly colonised a wider range of slope aspects, in effect greatly increasing the number of sites for reproduction and reducing the distance among them. Within metapopulations, a large increase in breeding sites can facilitate a regional increase in population density and fuel range expansion (see also Werner *et al.*, 2009).

In a second butterfly species, the brown argis (*Aricia agestis*), populations at the northern range limit were confined to a host species found in warmer microclimates. As the climate warmed, the researchers postulate that a second host species located in relatively cooler sites became warm enough to support successful development.

Body size

A New Zealand-based study (Teplitsky *et al.*, 2008) examined changes in body size of red-billed gulls (*Larus novaehollandiae scopulinus*). The study took advantage of data from more than 16 000 marked gulls recorded over a 47-year period. As temperature increased during the study, body size declined. This change is consistent with 'Bergmann's Rule' that states that body size tends to increase with latitude. Using an approach similar to that employed in the red squirrel study (Reale *et al.*, 2003), the researchers evaluated the relative contributions of phenotypic plasticity and evolution to the body size shift. In this case, they found no evidence for an evolutionary contribution.

Changes in Selection Pressures

Natural selection related to changing climate is likely to manifest itself in a diversity of forms. In many cases, changes in natural selection imposed by changing climate can be inferred from the adaptations discussed in the previous section. In this section, we go beyond those examples to highlight nonintuitive shifts that may occur. The examples are not numerous, but they make the point that because climate is so fundamental to ecological processes, the ways in which selection responds to changing climate will likely reflect the full range of those ecological processes.

Gene flow

By shifting species distributions and by altering the timing of life history events like flowering, climate change can alter the effective isolation of populations within a species. In one example (Franks and Weis, 2009), decreased isolation following a climate shift led to greater synchrony in flowering among populations of *Brassica rapa* and greater opportunities for gene flow. Gene flow itself can change the genetic composition of a population, leading to evolutionary change that may or may not enhance fitness. In another instance, changing climate was associated with decreased gene flow among populations of *Daphnia* water fleas because a local population evolved traits that made it less vulnerable to introgression by invaders (Van Doorslaer *et al.*, 2009).

Hybridisation

Changing climate is already leading to range shifts that move some species away from each other and place others in contact. When closely related species come into contact,

opportunities for interbreeding can lead to the creation of hybrids. These hybrid forms will themselves be subject to natural selection on new suites of traits that result from the combination of parental stocks. The appearance of grolar bears, the hybrids resulting from matings between polar bears (*Ursus maritimus*) and grizzly bears (*Ursus arctos*), may offer one such example (Roach, 2006).

Species invasion

Movement of species from climate change will alter the composition of communities and result in changes in the complement of interspecific competitors, predators and prey with which a species will interact. Rapid evolution in response to invasions into communities has been documented. Although the example we highlight here is associated with an intentional introduction as opposed to a climate-mediated range shift, it is illustrative. In 1935, cane toads were introduced into coastal Queensland, Australia, for pest control in cane fields. The toads began expanding their range, slowly at first and then more rapidly (Urban *et al.*, 2007). Recent evidence suggests this acceleration in the pace of invasion may be associated with evolution of novel traits, including greater hind limb length (Phillips *et al.*, 2006). As they moved into less-developed landscapes, cane toads came into contact with Australia's many native predators including snakes. Australia's snakes are generally ill-equipped to deal with toad venom. As the wave of invading toads passed through, snake populations would decline but recover somewhat afterwards. When scientists compared snakes collected before and after snake invasion, they discovered evidence that they too had evolved (Phillips and Shine, 2004). Post invasion snakes have smaller relative head sizes that may help prevent them from getting large doses of toxin associated with eating larger toads.

Rate of Evolution versus Rate of Climate Change

The influence of contemporary evolution on patterns of biological response to changing climate depends critically on the rates of evolution on the one hand and climate change on the other. In the early 1990s, when biologists first paid serious attention to the consequences of climate change, evolutionary considerations were not a prominent part of the discussion in part because of the widespread belief that evolutionary rates were too slow. Distinctions had long been drawn between ecological and evolutionary timescales (Slobodkin, 1961; Pianka, 2000). Reviews of contemporary evolution published beginning just over a decade ago have greatly influenced our understanding of evolutionary rate (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001; Reznick and Ghalambor, 2001; Hendry *et al.*, 2008). Analyses within these studies showed that rates of phenotypic change were typically much higher than had been appreciated. It also appeared that cyclical

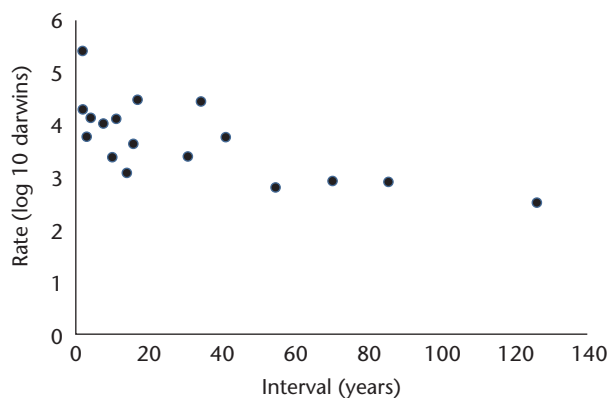


Figure 2 Estimated evolutionary rates from a review by Kinnison and Hendry (2001). Rate is measured in darwins and expressed in terms of the interval over which the measurement took place. Adapted from Kinnison and Hendry (2001), with permission from Springer.

changes in the environment could mask estimates of evolutionary rate. Rate estimates were generally higher when examining shorter time scales (Figure 2; Kinnison and Hendry, 2001) or in situations where anthropogenic change was implicated (Hendry *et al.*, 2008).

Evolution happens when there is differential survival and contribution to future generations. For this reason, generation time is a key to understanding how species will respond to changing climate. Rates of contemporary evolution are scaled by generation. Climate change is not. All else equal, species with shorter generation times will be better able to respond to changing climate. In fact, most species with genetic responses to changing climate are shorter lived. However, this could be an artefact of study system choices made by researchers also favouring species with shorter generation times. It is also possible that longer lived species may be better equipped to handle changing climate without evolving. In part, this could occur because lifespan is linked to body size that may, in turn, confer resistance to some effects of altered climate. Nevertheless, evidence exists that even species as long lived as beech trees (*Fagus sylvatica*) may be responding evolutionarily to changing climate, in this case through directional selection on a temperature-induced polymorphism (Jump *et al.*, 2006).

Another factor affecting evolutionary rate is the degree of variation in critical traits. Natural selection can act only on existing variation. If a trait is under selection, but there is no relevant variation, then no evolution can occur whatever the generation time. This is not just a hypothetical case. In a species of rainforest fly, there is no heritable variation for a trait related to desiccation resistance that is known to be under selection in related species (Hoffmann *et al.*, 2003). Assuming variation exists, the bigger challenge for researchers is identifying traits that are under selection. Whereas climate change is often expressed in terms of a certain degree rise in average temperature, most documented responses to changing climate are related to shifts in seasonality (Parmesan, 2006). Where temperature does matter, it may be affecting traits that help species cope

with extreme temperature events that become more frequent and more intense. Other traits may have nothing directly to do with temperature. Shifts in the timing and amount of precipitation may be critical for many species.

Extinction Risks

Extinction is the most extreme potential biological consequence of climate change. It is also a difficult phenomenon to study let alone predict. The evidence that contemporary climate change has already led to extinction is equivocal at best (Pounds *et al.*, 2006; Lips *et al.*, 2008); yet models of future extinctions include dire projections of 30% of all species committed to extinction by the middle of the twenty-first century (e.g. Thomas *et al.*, 2004). Whether or not such models provide a reliable forecast (Skelly *et al.*, 2007), the threat of extinction for many species is evident. Can evolution save some species that would otherwise go extinct due to changing climate? In one sense, extinction can be defined as the failure to respond adaptively fast enough in a changing environment (Kinnison and Hairston, 2007). Indeed, both fossil and historical records contain abundant evidence of extinction.

Gomulkiewicz and Holt (1995) provided an attempt to resolve the conditions under which adaptive evolution could forestall extinction within a population. A key insight was the recognition that the distinction between ecological and evolutionary effects of a changing environment may be unduly artificial: population declines may be likely to promote natural selection in proportion to their severity. A population would persist if allowed sufficient time to evolve traits that conferred positive population growth.

Many species at risk of extinction from changing climate are distributed among numerous populations whose persistence depends on the ability to colonise new environments as local populations wink out. In such cases, the extinction of a local population does not signal overall extinction as long as a species can colonise new environments. Given that human-modified landscapes have proliferated around the globe, some of the most critical adaptations to climate change may involve the ability to disperse farther (between habitats isolated by habitat destruction) and to traverse developed landscapes. If such traits emerge within populations undergoing climate-induced range shifts, evolutionary response could prevent population extinction even in the absence of a large-scale decline. Although increased tendencies to disperse may be favoured as climate changes, it is worth noting that fragmentation of habitat can have a countervailing influence. When human-altered environments with little capacity to support a species are interspersed with relict habitat patches, some types of organisms may be prevented from successfully dispersing unaided. **See also:** [Ecological Genetics](#)

Finally, it is also possible that evolutionary change could accelerate extinction. Rapid climate change that leads to fast migration of species tracking their habitat can be associated with genetic impoverishment and an increase in homozygosity

(Hewitt, 2000). Even species that apparently are responding ecologically to changing climate may be at enhanced risk for extinction if declining genetic diversity impedes their ability to deal with future change in their new range.

Future Prospects

The influence of ongoing climate change on the phenotypes of plants and animals is widespread. What we still do not know is the prevalence of evolutionary responses underlying these changes. Although some scientists have argued that most of what we see is plasticity (Parmesan, 2006; Gienapp *et al.*, 2008; Hendry *et al.*, 2008), the fact is that we simply do not know in most cases. Interestingly, in the specific cases outlined here in which researchers have taken the considerable time and effort required to investigate evolutionary mechanisms, most have revealed a role for evolutionary response. This is telling because unlike plastic responses, which can be instantaneous, evolution takes time. The degree of climate change experienced during the twentieth century has been modest compared with that expected in coming centuries. As climate continues to change, scientists will continue to learn more about its evolutionary implications.

Progress on this front will be aided by modifying a perspective that still pervades the literature on climate change. When discussing the potential responses of species to changing climate, scientists often nominate three alternatives: be plastic, move or evolve (e.g. Jackson and Overpeck, 2000; Reusch and Wood, 2007). Because these alternatives are synergistic in their action, this view oversimplifies the situation of a species affected by climate change and may lead to missed opportunities to avert extinctions and other harms. As one example, a plastic response can alter selection on a species, especially if the relationship between plastic response and environmental condition is based on an environment that is no longer present (Berteaux *et al.*, 2004; Visser, 2008). In this case, environment may offer misleading cues, and one response can be evolution in norms of reaction. Such a response could be all but invisible to researchers who were not looking for it, and the role of evolution discounted in spite of its importance. It is also clear that the great increase in attention to climate change is resulting in more and better monitoring, including genetic monitoring of populations (Berteaux *et al.*, 2004; Hoffmann and Willi, 2008). These data will clarify the role of evolutionary responses as they accumulate.

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