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Evolutionary Responses to Climate Change

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In their paper Malcolm et al. (2006) use climate-warming scenarios to estimate up to 43% loss of species within biodiversity hotspots. This prediction is based on a climate-envelope approach that assumes the distribution, and hence extinction, probability of every species is predicted by climate alone. We agree that global climate change will have substantial effects on biodiversity and will cause extinctions (Crowley & North 1990; Hoffman et al. 2003). Nevertheless, the climate-envelope approach presents a distorted estimate of extinction probabilities. Most notably, the approach does not consider evolution and therefore implicitly assumes that species cannot evolve in response to changing climate.

Current empirical evidence suggests that evolution is responsive to climate variation and occurs at rates that make it relevant for consideration of current and projected responses to climate change. For a wide variety of taxa, thermal performance varies within species' geographic ranges, suggesting both genetic variation in critical traits and localized evolution in response to climate variation (Conover & Schultz 1995; Gilchrist et al. 2004). Many examples of contemporary evolution in response to climate change exist. In less than 40 years, populations of the frog *Rana sylvatica* have undergone localized evolution in thermal tolerance (Skelly & Freidenburg 2000), temperature-specific development rate (Skelly 2004), and thermal preference (Freidenburg & Skelly 2004) in response to altered temperature in their wetlands. Laboratory studies of insects show that thermal tolerance can change markedly after as few as 10 generations (Good 1993). Studies of microevolution in plants show substantial trait evolution in response to climate manipulations (Bone & Farres 2001). Collectively, these findings show

that genetic variation for traits related to thermal performance is common and evolutionary response to changing climate has been the typical finding in experimental and observational studies (Hendry & Kinnison 1999; Kinnison & Hendry 2001).

As one estimate of the potential for evolutionary response to climate warming, we considered evolved change in critical thermal maximum (CTM), an important indicator of thermal performance, for a hypothetical species. CTM varies within species and is associated with differences in climate (e.g., Witz 2001). During the 100-year period of interest defined by Malcolm et al. (2006), the cumulative change in CTM was estimated (Hendry & Kinnison 1999) as the product of the phenotypic standard deviation and the estimated per-generation evolutionary rate (measured in units of standard deviation). This product was multiplied by the number of generations elapsed. We assumed a generation time of 5 years. We based our estimate of phenotypic standard deviation for CTM on three prior studies of herpetofauna (Du et al. 2000; Witz 2001; D.K.S., unpublished data). In each study of CTM individual animals were placed in a test environment in which the temperature was steadily raised until the individual exhibited behavior indicative of imminent demise. We collected the standard deviation in CTM from each study (sample sizes ranged from 10 to 60 individuals per study) and averaged it for our estimate of phenotypic standard deviation: 0.62. We then used data from a review of previously published studies on evolution during directional environmental change (T.J.F. et al., unpublished data; $n = 113$ rates) to estimate an average evolutionary rate of 0.255 haldanes (a haldane is equal to a change of one phenotypic standard deviation per generation). Across

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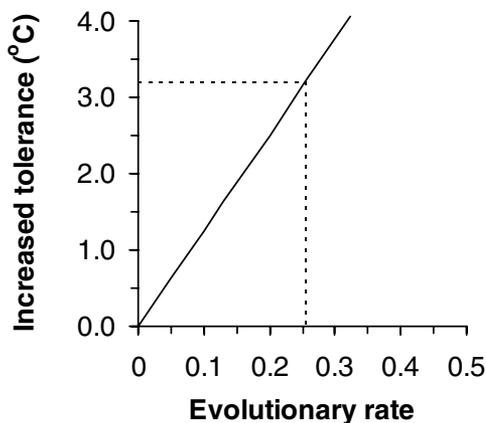


Figure 1. Relationship between evolutionary rate (baldanes) and increased thermal tolerance (estimated by critical thermal maximum [CTM], degrees C). Published work on evolutionary rates during directional environmental change was used to estimate evolutionary rate over 100 years for a species with a 5-year generation time (0.255). We assumed a phenotypic standard deviation in CTM of 0.62 based on published values.

10 generations, we predicted an increase in CTM of 3.2°C (Fig. 1). This evolutionary response matches or exceeds midrange predictions for increases in global temperature during the coming century.

Does this result mean that we expect all species to evolve in synchrony with changing climate? No. Although not often studied with specific reference to climate change, the factors limiting evolutionary response to a changing environment have been considered closely by evolutionary biologists. There are several potential constraints on evolutionary response. We focus on three that are likely to be critical: time lag between change and response, lack of genetic variation, and erosion of genetic variation. Some species will not be able to respond rapidly enough to keep up with climate change (Davis et al. 2005). Long generation times are the norm in some groups, including important conservation targets (e.g., forest vegetation, large mammals). Abundant evidence of past changes in climate show that some species can take hundreds or even thousands of years to respond demographically to a new climate regime.

Many populations of conservation concern have small effective population sizes. Small population size can influence evolutionary response through multiple mechanisms (Burger & Lynch 1995; Willi et al. 2006). Small populations can have low initial genetic variation. A lack of response can simply reflect a lack of grist for selection to act on. Small populations are also subject to large influences from genetic drift, which can limit natural selection (Burger & Lynch 1995). In addition, small populations may have higher rates of inbreeding, leading to genetic

problems that can limit evolutionary response (Futuyma 2006).

Although some species may show large initial responses to a changing environment, the rate of evolution can decay over time (Kinnison & Hendry 2001), perhaps due to a loss of genetic variation (Rodríguez-Trelles & Rodríguez 1998). In this case initial responses to a changing environment can indicate a contemporaneous evolutionary response, but this reaction will not be a good predictor of the long-term response to selection.

In highlighting the potential limits on evolutionary response to climate change, we point to one of its most salient features: context dependence. Both the species of interest and the specific environmental context will affect evolutionary responses, and one should expect a range of outcomes. Nevertheless, the approach typically adopted by conservation biologists and ecologists focuses exclusively on demographic effects in estimating extinction risk. This approach sidesteps the fact that a directionally changing environment capable of provoking massive shifts in demography is also capable of producing a massive selection event. The earliest considerations of the biological effects of climate change (e.g., Holt 1990; Kareiva et al. 1993) recognize this relationship and conclude that evolutionary responses deserve close consideration. During the ensuing years, the case for such rapid responses has grown much stronger (e.g., Stockwell et al. 2003; Berteaux et al. 2004; Hairston et al. 2005; Bradshaw & Holzapfel 2006; Schwartz et al. 2006; Urban et al. 2007). Ironically, several recent papers considering the consequences of climate change do not acknowledge the role of evolutionary responses (Thomas et al. 2004; Malcolm et al. 2006) or do so only in passing (Araujo & Rahbek 2006; Ibanez et al. 2006). Understanding the contexts in which evolution should be considered versus those in which it can be ignored remains a critical challenge for scientists who study climate change. Specifically, it is critical to understand when dispersal and other means, such as behavioral plasticity, either cannot or will not provide species with adequate means to avoid population collapse and extinction.

On the basis of the present knowledge of genetic variation in performance traits and species' capacity for evolutionary response, it can be concluded that evolutionary change will often occur concomitantly with changes in climate as well as other environmental changes (e.g., Grant & Grant 2002; Stockwell et al. 2003; Balanya et al. 2006; Jump et al. 2006; Pelletier et al. 2007). We cannot ignore that, in many instances, adaptation is likely to mitigate the impacts predicted by models that take into account only one of the two major modalities of biotic response. Although the study of Malcolm et al. and its antecedents (e.g., Thomas et al. 2004) have likely overestimated extinction probabilities, few conservation biologists have focused on what may be the most pervasive effect of climate change: as species evolve in a changing

world, genetic responses may render them forever different. Such within-species changes in biodiversity remain deserving of close study if we are to fully comprehend and accurately communicate the consequences of global change.

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