

Adaptive Evolution in Response to Climate Change

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Why is adaptive evolution important to this discussion?

Adaptive evolution is an almost universal response of the global biota to environmental change. Theoretical models suggest that adaptive evolution can enhance the persistence of populations in a changing environment even when migration is possible (Pease et al. 1989; Lynch et al. 1991; Lynch and Lande 1993; Bürger and Lynch 1995). As climate continues to change into the future, natural selection on wild populations will be altered (Etterson 2004a). The potential of species to respond to such changes in selection depends upon a number of genetic considerations that must be examined at the population level. Species are not uniform across their ranges but comprise a series of populations that have been molded by evolutionary forces such as founder events, genetic drift, gene flow, and selection. Each population differs in the extent to which it is adapted to local conditions and each has its own ecological amplitude and evolutionary potential. Thus, the ultimate fate of a species depends upon the evolutionary response of these genetically differentiated populations across the species range, not just at the margins of climate tolerance.

In general we think of three possible responses of populations to climate change: extinction, migration and adaptation. However, all of these processes are interrelated and adaptive evolution influences both of the former. The probability of extinction is influenced by population growth rate which is higher in populations that are well-adapted to their environment. The rate of migration may be increased by selection favoring greater dispersal ability. The migratory process itself, however, may reduce the potential for adaptive evolution by eroding genetic diversity during founder events and by genetic drift in small populations at the leading edge of the migration front (Cwynar and MacDonald 1987).

What are the critical factors that determine the potential for evolutionary response to selection?

The most fundamental requirement for adaptive evolution is that populations harbor genetic variation for relevant traits (Fisher 1930). The level of genetic diversity within populations is most often inferred from measures of molecular variation (Morgan et al. 2001 and citations therein). However, molecular variation will not necessarily correspond to genetic variation in complex phenotypic traits that will most likely be the direct targets of selection with climate change (Bonnin et al. 1996; Yang et al 1996; Lynch et al. 1999; Morgan et al 2001) such as timing of reproduction, dispersal ability, and drought tolerance.

An alternative indicator of genetic variation is the quantitative genetic parameter, heritability. Heritability (h^2) estimates the fraction of the total phenotypic variance (V_P) that is genetically based (V_A) and thus can be mobilized by selection for adaptation to changing environments (Falconer and MacKay 1996) and is described by the equation:

$$h^2 = V_A/V_P \quad (1)$$

The heritability of traits is of great evolutionary significance because it reflects the degree to which progeny inherit their parents' phenotype. The speed of evolutionary response to selection (R) is a function of heritability and the strength of selection (S):

$$R = h^2S \quad (2)$$

Populations are predicted to evolve rapidly if traits under selection are highly heritable and selection is strong. However, there is little information available about the spatial distribution of quantitative genetic variation across species' ranges for traits relevant to adaptation to climate change because of the laborious and protracted nature of the research required to obtain the estimates.

Predicting the evolutionary potential of populations: A case study

In an effort to examine the potential for adaptive evolution to future climates, I conducted a quantitative genetic experiment on the native prairie legume, *Chamaecrista fasciculata* in the Great Plains of the United States. To mimic predicted temporal change in climate, three natural populations of the annual legume, *Chamaecrista fasciculata*, were sampled from a climate gradient and progeny of formal crosses were reciprocally planted back into common gardens across this climate gradient (Minnesota, Kansas, Oklahoma from north to south). Traits that influence fitness were measured, including the rate of phenological development, leaf number, and leaf thickness. In each site, native populations produced significantly more seed than the other populations providing strong evidence of local adaptation (Etterson 2004a). Clines in selection corresponding to latitude were observed and are predicted to move northward in the future (Etterson 2004a). Populations had significant heritabilities for most traits under selection, although the size the estimates varied widely and were generally lower for the northern

population at the periphery of the species range (Etterson 2004b). Despite appreciable selection and genetic variance, a multivariate analysis suggested that the rate of adaptive evolution would be slower than the anticipated rate of climate change. Slow rates of evolutionary response are attributed to genetic correlations among traits that are antagonistic to the direction selection under a changed climate (Etterson and Shaw 2001). For example, selection favored plants with many thick leaves in the southern environment but when northern plants were grown in this site, they produced either many thin leaves or few thick leaves indicating a fundamental genetic tradeoff (Figure 1b).

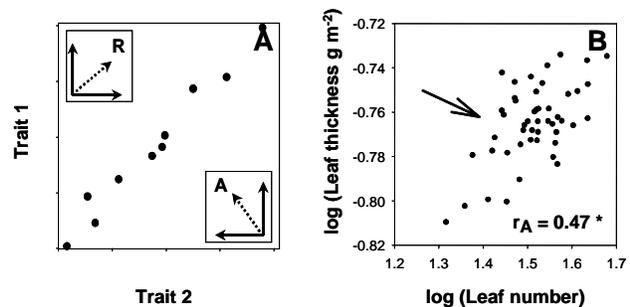


Figure 1. The influence of genetic correlations among traits on selection response. (A) Hypothetical positive genetic correlation (r_A) between two traits (each point representing a family). Two selection scenarios: "R", selection is in the same direction on traits; the depicted r_A is in accord with the direction of selection, enhancing evolutionary response; thus, the genetic correlation is "reinforcing". "A", selection is in the opposite direction for both traits; r_A is "antagonistic" to the direction of selection inhibiting evolutionary response. (B) Scatter plot of leaf thickness and leaf number of Minnesota families when grown in the southern environment in Oklahoma showing significant positive genetic correlation that is antagonistic to the negative vector of joint selection. (after Etterson and Shaw 2001)

Genetic correlations that are antagonistic to the direction of selection are due to either to pleiotropy, where an allele has positive fitness effects on one trait but negative effects on another, or linkage disequilibrium, where alleles at different loci are in close association. Antagonist genetic correlations may reduce the likelihood that the combination of traits that results in highest fitness will evolve. The lability of genetic correlations among traits and thus the severity of genetic constraint depends on the underlying cause of the correlation which is not readily determined.

In principle, populations could respond immediately to climate change, maintaining fitness by adaptive plastic responses (Bradshaw 1965; Schlichting 1986; Sultan 1987; van Tienderen 1991;

Schlichting and Pigliucci 1998; Donohue et al. 2001). For leaf number and thickness, the populations of this study exhibited substantial phenotypic plasticity that could be considered adaptive because it was in the direction of trait values favored by selection. However, even though plasticity was found to be in an adaptive direction, it did not maintain fitness across environments. Nevertheless, responses to selection on genetically based plasticity may help mitigate fitness losses as climate gradually changes.

Overall, this study suggests that if climate changes as predicted, northern populations of this species will face a severe evolutionary challenge in the future because of modest heritabilities, cross-environment genetic correlations antagonistic to selection, and demographic instability due to lower seed production in a hotter and drier climate.

Conclusions

It is uncertain whether the ongoing rate of evolution can keep pace with the rate of climate change. Rapid genetic adaptation to climate has been documented in studies of clinal variation of introduced species (Reinartz 1984; Lacey 1988; Weber and Schmid 1998; Huey et al. 2000) and a few studies have documented genetic changes in wild populations in recent decades (Bradshaw and Holzapfel 2001; Reale et al. 2003). Genetic detail is essential to furthering our understanding of the limits to adaptation. New insights into the risk of extinction may be found by coupling information on the current genetic architecture of populations, expected selection regimes in future environments, and other ecological parameters such as dispersal ability.

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