

## NEWS AND COMMENTARY

### Limitations on adaptation

# Evolutionary response to climatic change?

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There is mounting evidence to show that human activities have already left their mark on global climate, and can be expected to cause much greater changes in the global climate this century (IPCC, 1990, 1995, 2001, 2007). Increasing concern has thus focused upon how species and ecosystems will respond to these changes (Huntley *et al.*, 1997) and the likely consequences for global biodiversity (Lovejoy and Hannah, 2005). One easily detectable and early response is the adjustment of species' phenology – the timing of their annual cycle of activities – to changes in seasonal climate. Abundant evidence has already accumulated showing that numerous species have exhibited such phenological responses to the climatic changes of the past half century (Parmesan and Yohe, 2003). However, the extent to which these responses reflect adaptive genetic evolution, as opposed to phenotypic plasticity, is generally unknown. In an elegant study published recently, Franks *et al.* (2007) have demonstrated that a shift in flowering time of the naturalised annual plant *Brassica rapa* (turnip (UK), field mustard (USA)) in response to a regional multi-annual drought in southern California was an adaptive evolutionary response.

The phenological response exhibited by the species investigated by Franks *et al.* (2007) conforms to expectations for a winter annual growing in a Mediterranean-type climate and flowering in spring towards the end of the wet season. Reduced winter rainfall leads to earlier drying of the soil in spring and early summer, hence shortening the growing season. This promotes earlier flowering, increasing the likelihood that fruits are matured before the plants die as a result of water shortage. Fortunately, Franks *et al.* (2007) had collected seeds from two populations of *B. rapa* growing in contrasting sites, one 'wet' and one 'dry', in 1997 before the onset of the drought. They made a further seed collection from the same two populations in 2004, the fifth in a consecutive

series of dry years. They then performed an experiment in which plants from the two populations were grown in greenhouse conditions under one of three watering regimes designed to mimic a short, medium or long growing season. To avoid any problems that might arise from differences in seed condition, length of storage or maternal effects on seed quality, they performed their experiments using F1 seeds produced by plants grown in the greenhouse from the field-collected seeds. This enabled them to produce not only a 1997 × 1997 ('ancestors') and a 2004 × 2004 ('descendants') F1 line for each site, but also a 1997 × 2004 ('hybrids') F1 line.

Their experimental results showed that under the long season treatment, descendants flowered earlier than ancestors by a mean of 1.9 days for the dry site and 8.5 days for the wet site, both differences being statistically significant. The mean flowering dates of the hybrids did not differ significantly from the respective mid-point between ancestors and descendants, indicating a simple additive genetic basis for the observed shift in flowering date. Local site adaptation was also evident, with ancestors from the dry site flowering on average 16 days earlier than those from the wet site. In the short season treatment, wet site descendants showed a statistically significant increase in survival (75%) compared with ancestors (50%), hybrids again being intermediate (60%). Post-drought genotypes thus appear to be better adapted to shorter growing seasons than the pre-drought genotypes, a tendency that is also much more pronounced in the population from the wet site.

Despite the clarity of their results, Franks *et al.* (2007) take a generally cautious stance. They conclude their paper with a proposal that seeds or other suitable genetic materials be collected from multiple populations of a number of species. They argue that such collections will enable future research into the adaptive response of these

species to climatic change using what they term their 'resurrection protocol'. Nonetheless, they also state that 'Evolutionary adaptation to climate change may be especially important for the persistence of flowering plants, because limited dispersal ability and habitat fragmentation may prevent plants from migrating with geographic shifts in favourable climate'. A number of important objections can be raised to this statement. Foremost amongst these is the extent to which evolutionary adaptation will be of any real importance on the decade-to-century time scales of likely future climatic change, especially given the expected magnitude of these changes (IPCC, 2007). In an important early paper on this topic, Bradshaw and McNeilly (1991) argued that 'whilst some evolution is likely to occur in relation to global climatic change in some species ... in most cases this is unlikely to be sufficient to mitigate completely the effects of ... climatic change'. They reached this conclusion largely on the basis of their extensive work on the rapid evolution of heavy metal tolerance by various species (Wu *et al.*, 1975) and the evidence that not only different species but also different populations of the same species exhibited markedly different potentials for the selection of heavy metal tolerant genotypes (Symeonidis *et al.*, 1985). This evidence led them to emphasize the constraints imposed by the supply of appropriate variation upon the ability of a species, or a species' population, to show an adaptive evolutionary response to any environmental change, including climatic changes.

Although Franks *et al.* (2007) discuss the issue of the need for sufficient genetic variance to be present for a population to exhibit an adaptive response to a climatic change, they fail to point to some striking features of their own results that serve to underline this point. The contrasting responses of the *B. rapa* populations from the wet and dry sites strongly suggest that the latter population already lies close to the limit of the species' genetic variance with respect to growing season length. The dry site population exhibited no difference in survival rates between descendants and ancestors, and an advance in flowering time among descendants compared with ancestors that was only ca. 22% of that shown by the wet site, population and <12% of the difference between the ancestors from the two sites. Furthermore, in neither case was the advance in flowering date as great

as that expected on the basis of estimates of heritability of the trait and of the selection differential; the observed advance of 1.9 days for the dry site being only ca. 23% of that expected, whereas that of 8.5 days for the wet site, was less than the lower error limit of the prediction for that population. The shortest flowering time for the wet site, achieved by descendants in the short-season treatment, was significantly longer than the longest flowering time for the dry site, achieved by ancestors in the long season treatment. This strongly suggests that the genetic variance of neither population encompasses genotypes comparable to those typical of the other site. Such differential limits upon genetic variance between species' populations, as well as between species, conform to the results of Symeonidis *et al.* (1985) and support the conclusions reached by Bradshaw and McNeilly (1991). Interestingly, the observation of marked limits to genetic variance within species also parallels the few observations of apparent adaptive responses to late Quaternary glacial-interglacial climatic changes (e.g. Smith *et al.*, 1995; Rousseau, 1997). In those species where such apparent adaptive responses have been observed, the extent of the morphological adaptation seen in the past falls within the range of morphological variation found in the species today across its geographical range.

Although the demonstration of an evolutionary basis for a phenotypic response may be interesting, it is insufficient to overturn the conclusions of Bradshaw and McNeilly (1991). Evolutionary adaptation is unlikely to be of major importance in the response of

species to the climatic changes expected this century. Furthermore, even its limited potential is likely to be severely reduced as a consequence of habitat and population fragmentation, and of the rapidity and magnitude of the expected climatic changes, that together are likely to lead to rapid genetic impoverishment of many populations. A more likely outcome is that, rather as in the grasslands developed on heavy metal contaminated soils, a small number of species that happen to have the necessary genetic variance will come to dominate many plant communities, with potentially far-reaching consequences for biodiversity, ecosystem function and the ecosystem services upon which humankind depends.

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