Promoting the Science of Ecology

Managing Microevolution: Restoration in the Face of Global Change
Author(s): Kevin J. Rice and Nancy C. Emery
Source: *Frontiers in Ecology and the Environment*, Vol. 1, No. 9 (Nov., 2003), pp. 469-478
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/3868114
Accessed: 14/10/2008 16:43

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=esa.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Frontiers in Ecology and the Environment.*

http://www.jstor.org

Managing microevolution: restoration in the face of global change

Kevin J Rice[1,2] and Nancy C Emery[2]

Evidence is mounting that evolutionary change can occur rapidly and may be an important means by which species escape extinction in the face of global change. Consequently, biologists need to incorporate evolutionary thinking into management decisions in conservation and restoration ecology. Here, we review the genetic and demographic properties that influence the ability of populations to adapt to rapidly changing selective pressures. To illustrate how evolutionary thinking can influence conservation and restoration strategies, we compare the potential of two California plant communities (vernal pools and blue oak woodlands) to evolve in response to global change. We then suggest ways in which restoration biologists can manipulate the genetic architecture of target populations to increase their ability to adapt to changing conditions. While there may not be any universal rules regarding the adaptive potential of species, an understanding of the various processes involved in microevolution will increase the short- and long-term success of conservation and restoration efforts.

Front Ecol Environ **2003; 1(9): 469–478**

Open any undergraduate biology textbook, turn to the chapter on evolution, and you will probably encounter the story of Dr Kettlewell's moths. In the sooty forests of industrialized England, the rise of a dirty gray color morph in populations of the peppered moth (*Biston betularia*) is a classic tale of rapid adaptation to environmental change (Kettlewell 1972; Figure 1). This story of industrial melanism in Birmingham supposedly showed that microevolutionary change – evolution within species and populations – can occur rapidly in response to human impacts on the environment. In many ways, this "selection by smokestack" signaled the beginning of the current age of human-induced global change.

Despite this early example, an evolutionary perspective is rare in current discussions and research on the effects of global change (Travis and Futuyma 1993). A search of articles in *Global Change Biology* from the past 10 years found that only 2% of the papers considered microevolutionary questions or topics. In predicting the biotic effects of global change, it appears that an ecological rather than an evolutionary orientation currently dominates the scene. Speculations on whether species will avoid extinction often focus primarily on their capacity to migrate in response to climate change (Peters and Darling 1985). This ecological viewpoint discounts the potential to avoid extinction by in situ adaptation to climate change by microevolutionary processes (Geber and Dawson 1993). A purely ecological perspective would have predicted (incorrectly) that the conspicuousness of a white peppered moth against a sooty tree trunk in a forest full of hungry birds would drive the species to local extinction. Evolution, not just ecology, explains the species' persistence. A more complete understanding of the role of evolution in shaping populations and species will help conservation biologists and restoration ecologists make management decisions that facilitate the persistence of diversity in the face of global change.

In a nutshell:

- Evidence that evolution can occur over ecological time scales suggests that adaptation to global change may be critical for species to escape extinction
- Genetic variation, correlations between traits, gene flow, plasticity, and demography all influence the ability of a population to adapt to environmental change
- Consideration of relevant evolutionary processes will enable restoration biologists to manipulate the genetic structure of source populations to maximize the adaptive potential of restored populations

■ The time scale of adaptation

Why are evolutionary processes largely ignored in restoration and conservation management? A primary explanation is the assumption that evolution takes a long time, a view based on observations of slow rates of change over long periods of time in the fossil record. The fossil record not only indicates that evolutionary change (in preserved morphological traits) occurs slowly, but that species have responded to global change in the past primarily by migrating. Unfortunately, migration may not be a viable option for today's global biota, given the current rate of habitat destruction (Geber and Dawson 1993). Despite abundant evidence that artificial selection can cause dramatic evolutionary changes in just a few generations in

---

[1]*Department of Agronomy and Range Science, University of California, Davis, CA 95616 (kjrice@ucdavis.edu);* [2]*Center for Population Biology, Department of Evolution and Ecology, University of California, Davis, CA 95616*

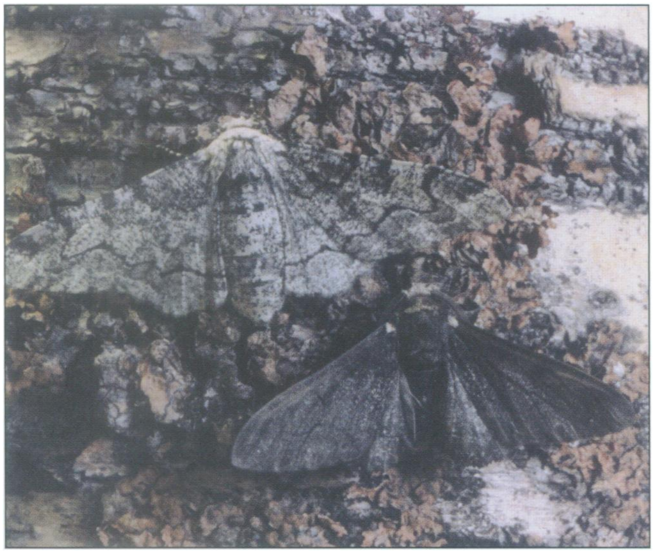


Figure 1. Prior to the industrial revolution, trees in Birmingham, UK were covered with white lichens, giving the trees a mottled appearance. Against this background, the lighter morph of the peppered moth was camouflaged (left). As pollution levels rose and killed the lichen, bird predators exerted strong selection for the sooty colored morph (right) that was now better camouflaged against the darker tree trunks (Grant 2002).

domesticated plants and animals, even Darwin (1859) concluded that "natural" selective pressures are too weak to do so in the wild (Reznick and Ghalambor 2001).

In the past few decades, studies by evolutionary biologists have revealed that selection in natural populations can be quite strong, and can cause evolutionary shifts within a few generations (Endler 1986; Kinnison and Hendry 2001). Not surprisingly, the majority of rapid evolutionary changes in natural populations involve responses to anthropogenic pressures (Ashley *et al.* 2003). Adaptive responses have occurred in a broad variety of traits spanning morphology, physiology, life history, phenology, and behavior (Reznick and Ghalambor 2001; Table 1). The emerging recognition of "contemporary evolution" – observable evolutionary change that occurs within decades – has stimulated awareness that evolutionary concepts need to be incorporated in conservation thinking and management practices (Stockwell *et al.* 2003).

Intraspecific genetic variation is "where the action is" in terms of microevolution. Genetic differences between populations reflect the past actions of selection and gene flow, and genetic variation within populations represents the potential for further adaptive change in response to new selective challenges such as global warming. A lack of a microevolutionary perspective in global change research may result from a research agenda focused at the species level, with little consideration of intraspecific variation. In fact, we believe this minimization of the importance of intraspecific genetic variation in ecological studies goes far beyond just global change research. For reasons that are not entirely clear, many ecologists assume that intraspecific genetic variation is not very important in most ecological interactions. For example, we surveyed experimental studies on plant competition published in *Ecology* over the past 10 years. Of the 56 studies we identified, 51 (over 90%) did not consider the effects of intraspecific genetic variation on competition at the species level. We inferred a lack of interest in intraspecific variation if only a single population was used, or the author failed to provide any information on the sources of plant material. We suspect that a lack of appreciation for the impact of evolutionary processes on ecological interactions is widespread in the field of ecology, although there have been some encouraging signs recently that this may be changing (Agrawal 2003).

Microevolutionary processes can have important consequences for species conservation, management, and restoration (Ashley *et al.* 2003). However, one cannot assume that adaptation will "rescue" species from global change; evidence from mass extinctions during past periods of climate change (ie glaciation), as well as contemporary restrictions to species ranges, suggest that there are limits to adaptation (Hoffmann and Blows 1993). So, what are the factors limiting the potential for rapid evolutionary change to save species from extinction in the face of global climate change? Are there certain characteristics of species or particular environmental conditions that make adaptive responses more or less likely? How can restoration and management practices account for, and even use, evolutionary processes in conservation efforts? To begin to answer these questions, we examine some of the relevant evolutionary theory on adaptation, and discuss the potential for evolutionary processes to influence species responses to global change. To provide examples for putting conservation and restoration into an evolutionary context, we examine two classic California plant communities – vernal pools and blue oak woodlands. Finally, and perhaps most importantly, we explore several means by which human intervention can incorporate evolutionary thinking into translocation and restoration practices, to increase the probability of species adapting to global change before going extinct.

■ The adaptive race against extinction

The selective pressures imposed by humans on the environment go far beyond the industrial pollution experienced by Kettlewell's moths. Human impact ranges from over-harvesting and habitat reduction to direct modification of the earth's atmosphere, waters, and soils, and the alteration of global geochemical cycles and temperature (Western 2001). Under what conditions will populations adapt to these changes? Under what conditions will they go extinct? While difficult to address empirically, these questions have been explored explicitly in theoretical models (Lynch and Lande 1993; Gomulkiewicz and Holt 1995). Furthermore, insight into the factors determining the evolution of species' ranges can be used to understand limits to adaptation in general (Antonovics 1976;

Table 1. Examples of rapid evolutionary responses of natural populations to human-induced environmental change

Selective pressure	Organism	Response	Reference
Harvesting patterns, overharvesting	Various fish species, including Pacific salmon, cod, Atlantic silversides, European grayling	Life-history evolution (eg juvenile growth rate, age and size at maturity, fecundity)	Haugen and Vøllestad (2001), Law (2000), Conover (2000), Conover and Munch (2002)
Industrial pollution	Peppered moth *(Biston betularia)*	Change in pigmentation	Kettlewell (1972)
Heavy metal pollution in mine tailings	Various plant species, oligochaetes (earthworms)	Heavy metal tolerance	Antonovics *et al.* (1971), Klerks (1989)
Extinction of food source	Hawaiian honeycreeper *(Vestiaria coccinea)*	Selection for shorter bills (access to alternative nectar source)	Smith *et al.* (1995)
Heavy effluent from nuclear reactor deposited into reservoir	Lepomis bluegill	Change in thermal tolerance	Holland *et al.* (1974)
Eutrophication of lakes	African cichlids *(Haplochromis* sp)	Reduced coloration and species diversity (via reduction in capacity for mate choice and sexual selection)	Seehausen *et al.* (1997)
Introduction of novel host species through logging and cattle ranching	Checkerspot butterflies *(Euphydryas editha)*	Diet shift to new host	Singer *et al.* (1993)
Global warming	Pitcher-plant mosquito *(Wyeomyia smithii)*	Shift in photoperiodic response	Bradshaw and Holzapfel (2001)
High ozone	Common plantain (*Plantago major)*	Ozone resistance	Davison and Reiling (1995)
Introduction of exotic host species	Soapberry bug *(Jadera haematoloma)*	Change in mouthparts, body size, body size, and development time	Carroll *et al.* (2001)
Introduction of exotic seed predator (red squirrel, *Tamiasciurus hudsonicus*)	Limber pine (*Pinus flexilis*)	Shift in energy allocation from seeds to cone defenses	Benkman (1995)

Full references for source papers can be found in the Web-only version of this table

Hoffmann and Blows 1993). Together, these models indicate that adaptation to changing environments depends heavily on the interactions between genetic and demographic responses of populations to the changing selective pressures.

Genetic variation

The presence of substantial heritable genetic variation plays a critical role in the adaptive potential of a population. In the simplest case, the evolutionary response of a population to a changing environment is a function of heritable variation in the population and the intensity of selection. In a constant environment, evolutionary theory predicts that stabilizing selection removes non-optimum genotypes from the population, reducing the genetic load – the number of harmful genes maintained in a population – and "fine-tuning" the population to its environment (Figure 2, left). Consequently, in a static environment, a population that exhibits the optimum mean phenotype and low genetic variation will have a higher mean fitness than a population with the same mean phenotype and higher amounts of genetic variation (Figure 2, right).

However, although the reduction of genetic load by stabilizing selection allows finely tuned adaptation in constant environments, tight adaptation has a cost when environments change, thereby making the optimum a moving target (Figure 3. left). When the optimum shifts, a narrowly adapted population with low levels of heritable genetic variation will contain few genotypes with the new optimal phenotype (Figure 3, right). A population with higher levels of heritable genetic variation has a better chance of evolving towards the new optimum, because it has a greater number of genotypes with the "correct" phenotype (Gilpin and Soulé 1986). During the lag between the environmental change and adaptation, selection will cause a reduction in population fitness, because the environmental change increases the proportion of maladapted individuals in the group (Lynch and Lande 1993). The probability that a population will persist through this lag and adapt to the new phenotypic optimum depends upon the spread of genetic variation in the population, as well as the degree of plasticity and the growth rate of the individuals.

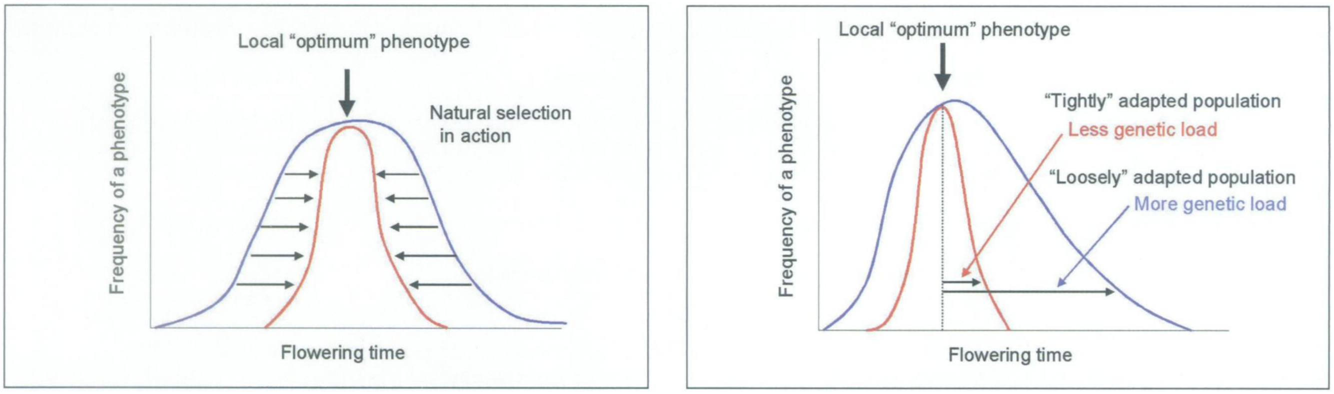


Figure 2. *(left) In a constant environment, natural selection favors the optimum phenotype (eg intermediate flowering time), and selection against extremes in that trait reduces the variance around the optimum. (right) Individuals that deviate from the optimum phenotype have lower fitness and thus reduce the mean fitness of the population, imposing a "genetic load". In a constant environment, populations with lower levels of genetic variation contain fewer maladapted individuals, and consequently experience less genetic load (and thus higher mean fitness) than populations with more genetic variation.*

Correlations among traits

Genetic interactions can drive correlations among traits, so that those traits respond to selection in concert rather than independently. Correlations among traits may substantially influence adaptation to global change (Antonovics 1976; Hoffmann and Blows 1993). If adaptation to a changing environment requires changes in several independent characters, positive correlations among those traits will increase the rate of adaptation. Alternatively, traits that are adaptive to a particular environmental change may be negatively correlated with other fitness-related traits (eg heat tolerance may be negatively correlated with competitive ability). As a result, the costs and benefits cancel each other out, yielding no net fitness change and preventing individuals from expressing the optimal phenotype (Hoffmann and Blows 1993). Trade-offs may also exist across the distribution of a species such that adaptive traits in one environment are maladaptive in others.

Antagonistic gene flow

The importance of "connectedness" between reserves has been emphasized in the management of rare species, under the assumption that gene flow always enhances the probability of persistence. However, the effects of gene flow on adaptation to changing environments are complex. Gene flow from large populations can "rescue" small, peripheral ones that may otherwise go extinct due to random demographic processes (Brown and Kodric-Brown 1977) and/or reduced fitness from inbreeding (Frankham 1995). On the other hand, gene flow can also inhibit the ability of populations to adapt to local conditions if traits that are locally adaptive are not favored at the source of the gene flow (Storfer 1999). When such "gene swamping" occurs, migration between habitats can lead to the accumulation of genetic load in the populations receiving non-local propagules (Lenormand 2002).

Haldane (1956) first proposed the concept of "antagonistic gene flow" in a discussion of the evolutionary limits of species distributions. He reasoned that species borders represent an equilibrium at which adaptive expansion in marginal populations is balanced by antagonistic gene flow from the central population. Several recent models have examined how gene flow may swamp local adaptation to marginal habitat and thus limit species range expansion (Holt and Gomulkiewicz 1997; Kirkpatrick and Barton 1997; Case and Taper 2000; Ronce and Kirkpatrick 2001). Kirkpatrick and Barton (1997) modeled this process and found that distribution limits were produced under strict conditions of density-dependent population growth, relatively long dispersal distances, steep environmental gradients, and low genetic variation. Case and Taper (2000) incorporated the effects of interspecific competition at species boundaries and showed that competition at the boundary makes it easier to obtain stable range limits.

An interesting result of these models is that dispersal can theoretically cause marginal populations to collapse and the overall distribution of a population or species to shrink (Ronce and Kirkpatrick 2001). This occurs because long-distance dispersal from high-density, central populations into low-density, marginal environments results in a net flux of non-adapted genotypes repeatedly invading peripheral habitat. This inhibits the ability of genotypes adaptive in marginal environments to rise in frequency, and consequently the marginal population maintains a constant or increasing level of genetic load. In cases of high gene flow and large fitness differences between central and peripheral populations, enough antagonistic gene flow can cause the marginal population to crash, a process called "migrational meltdown" (Ronce and Kirkpatrick 2001).

Plasticity

Although heritable genetic variation is the focus of most theoretical work, it is not the only evolutionary factor that may help a population avoid extinction under a changing selective regime. Phenotypic plasticity, or the

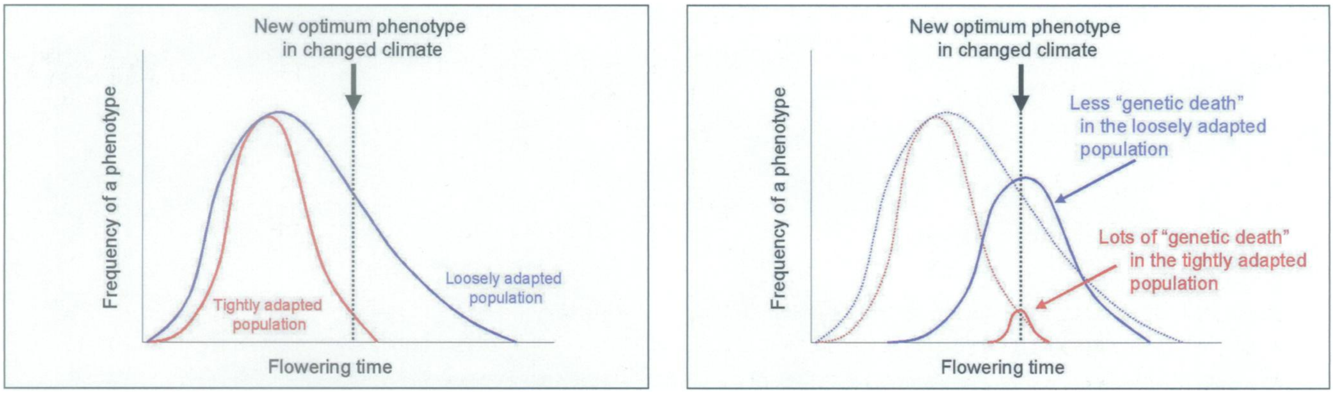


Figure 3. *(left) In a changing environment, populations with higher levels of genetic variation for a trait under selection will contain more individuals with the "right" phenotype than a less variable population. (right) Consequently, relatively more individuals survive changing selective pressures in a population with higher initial levels of genetic variation, increasing the potential for the population to adapt to the new conditions. In contrast, a less variable population is more likely to go extinct.*

capacity of a genotype to express varying phenotypes depending on environmental conditions, may often reduce the effectiveness of selection in winnowing out maladapted genotypes (Sultan 1987). Selection can only operate on genetic variation expressed in the phenotype, and if plastic responses in genotypes produce the optimal phenotypes for a new selection regime, there is no genetic load. By shifting phenotypic expression in response to global change, adaptive phenotypic plasticity in genotypes exposed to a changing environment could allow a population to rapidly track the moving selective optimum. Initially, this buffering against selection would reduce declines in population fitness while adaptation is (hopefully) occurring under a less stringent selection regime. Adaptive phenotypic plasticity, by reducing the genetic load, may "soften" selection and allow a population to adapt to changing conditions without going extinct.

Demography

Generation time is a demographic parameter that should strongly influence the rate at which a species will evolve, although this is often difficult to estimate. All else being equal, an annual plant population should be able to respond much more rapidly to a changing climate than a stand of long-lived trees. This is not to say that longer lived species cannot demonstrate contemporary evolution. In the calculation of generation time, the time of first reproduction and the distribution of reproductive output over the life span of an organism are important factors. For example, if most reproduction occurs early in the life span of a tree species, then it may have the capacity to respond rapidly to selection. Range shifts of tree species in response to the many climate changes of the Quaternary suggest that relatively rapid adaptive differentiation may have accompanied migration (Davis and Shaw 2001).

A high population growth rate can reduce the chance of extinction in the changing selective regime. Rapid population expansion following an introduction event can replenish genetic variation and counteract the decline in mean fitness that may arise due to genetic bottlenecks and/or genetic load imposed by a changing environment. Furthermore, a high growth rate reduces the chance of extinction due to random events (ie demographic stochasticity). This theoretical prediction was borne out by a review of rapid adaptive change which found that this often occurs in populations with opportunities for growth (Reznick and Ghalambor 2001).

■ Vernal pools and sylvan glades: an evolutionary perspective

Vernal pools and blue oak woodlands are two habitats at the focus of conservation concern and restoration efforts in California (Pavlik *et al.* 1991; Black and Zedler 1996). Although occurring in the same general climate, it is hard to imagine two plant communities that differ more in structure and floristic composition. Contrasting the ephemeral, annual-dominated flora of vernal pools with blue oak trees that can live for centuries nicely illustrates some of the factors that may increase or reduce the capacity of plant species to evolve in the face of global change.

Islands of endemism in a sea of invaders

California vernal pools are ephemeral wetlands scattered throughout the grasslands of California's Central Valley. The pools form in shallow depressions underlain by impervious soil that allows water to accumulate during the rainy winter season. In the warmer months, the water recedes and the soggy environment transforms into one of severe drought (Figure 4). The extreme cycles of submersion followed by desiccation create a unique abiotic environment in which only native plants are able to flourish (Holland and Jain 1981). The community of vernal pool-adapted plants consists primarily of endemic annuals, many of which are restricted to distinct depth zones and appear as striking concentric rings around the pools when they flower in early spring. The persistence and structure

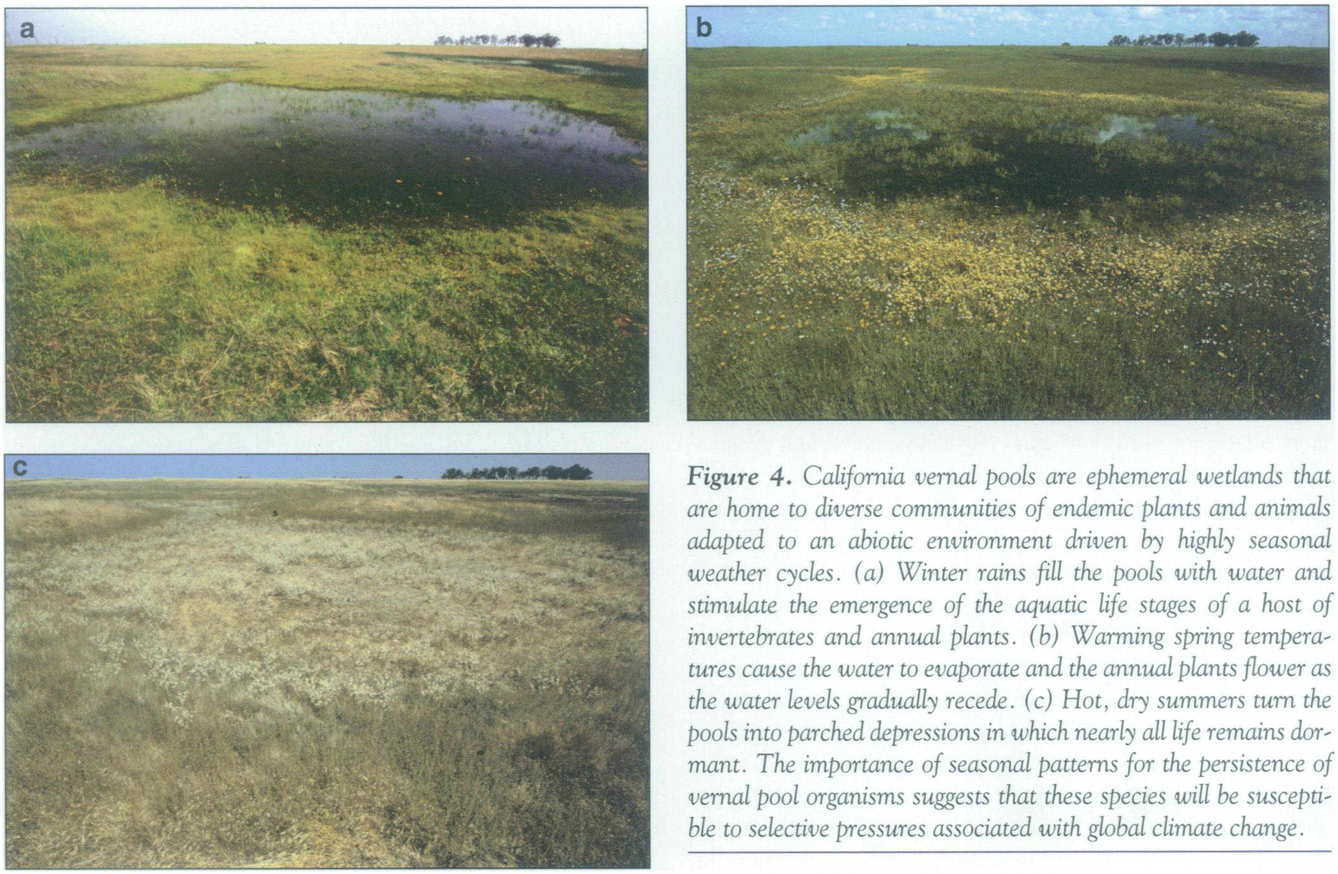


Figure 4. *California vernal pools are ephemeral wetlands that are home to diverse communities of endemic plants and animals adapted to an abiotic environment driven by highly seasonal weather cycles. (a) Winter rains fill the pools with water and stimulate the emergence of the aquatic life stages of a host of invertebrates and annual plants. (b) Warming spring temperatures cause the water to evaporate and the annual plants flower as the water levels gradually recede. (c) Hot, dry summers turn the pools into parched depressions in which nearly all life remains dormant. The importance of seasonal patterns for the persistence of vernal pool organisms suggests that these species will be susceptible to selective pressures associated with global climate change.*

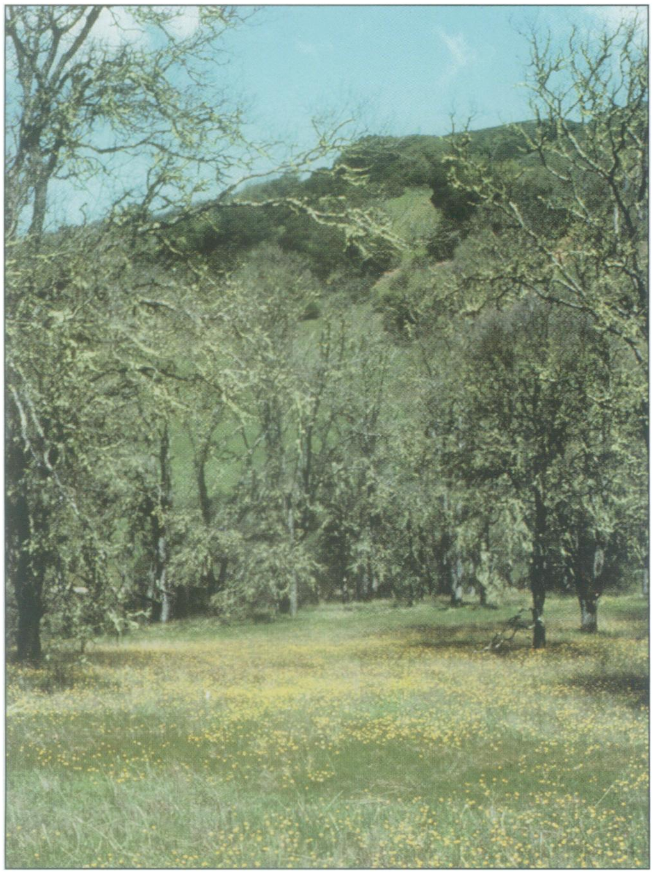
© David Rosen

of these plant communities are heavily dependent on temperature and rainfall patterns each year (Alexander and Schlising 1996), so this system is probably already experiencing new selective pressures associated with global change.

Several observations suggest that evolutionary forces may heavily influence the persistence of vernal pool plant communities in the face of global change. The annual habit of most plant species probably facilitates rapid adaptive response to changing selective pressures. In fact, adaptive genetic differentiation across small-scale moisture gradients was found in purslane speedwell (*Veronica peregrina*) (Linhart 1988), illustrating the potential for adaptive shifts in the resident taxa. Large year-to-year variation in rainfall patterns, which somewhat mimics the increased climatic variability expected to occur with global change, may have provided the selective pressure for plant seed banks and invertebrate egg banks as demographic buffers against the unpredictable environment. By maintaining a large population below ground, these dormant propagules reduce the potential for losing genetic variation through population bottlenecks and represent a storehouse of heritable genetic variation that might foster adaptive shifts (Levin 1990). The patchy nature of these pools results in naturally fragmented populations that may restrict antagonistic gene flow between pools experiencing different selective regimes. Thus, in many ways we might expect these vernal pool communities to be "pre-adapted" to show a rapid evolutionary response to global change.

Of course, these and other aspects of vernal pools may constrain the capacity of resident annual populations to respond to global change. First, vernal pool habitat has been drastically reduced over the past 150 years in the Central Valley of California; one can only guess at the effect of this massive habitat destruction on genetic diversity within the remaining pool populations. Further, although vernal pools are patchy in the landscape, it is not at all clear how the human-imposed fragmentation of pool complexes has affected natural gene flow patterns and thus the capacity for pools to "share" genetic variation important for adaptive shifts. The genetic storehouse of seed and egg banks also represents one of those "good news/bad news" aspects of gene flow. In a rapidly changing environment, a large, persistent seed bank that contains genotypes adapted to previous environments may represent a pool of maladaptation rather than a storehouse of genetic innovation. Germination of these maladapted individuals into the aboveground population represents a kind of antagonistic "gene flow from the past" that may hinder adaptive responses to the current selective regime.

It is important to remember that insect pollinators are crucial to many of the outcrossing vernal pool plant species. Solitary burrowing bees, highly specialized in their pollination behavior, are important pollinators of many vernal pool plant species (Thorp and Leong 1996). Given that new species of these bees are still being discovered (R Thorp pers comm), it is not surprising that we do not know whether these pollinators will be able to adapt to



Courtesy of E Knapp

Figure 5. *(left) Blue oak (*Quercus douglassi*) woodlands are an important but declining habitat type in California that is home to a wide range of native plant and animal species. (above) Because of exceedingly low sapling recruitment, blue oak populations are not regenerating and stands are in decline throughout California. Whether this is caused in part by global change is unknown.*

global climate change. Although usually not considered in the discussion about adaptation to global warming, this example of burrowing bees and flowers in vernal pools highlights the under-appreciated importance of coevolution between taxa in the face of climate change. In addition to plant–pollinator associations, other interspecific interactions, such as competition and predator–prey dynamics, represent important biotic selective factors that may evolve in response to global change (Holt 1990).

Blue oaks: majestic but evolutionarily challenged?

If news on the evolutionary potential of vernal pools is somewhat mixed, the prognosis for evolutionary change in blue oak (*Quercus douglasii;* Figure 5, left) seems downright grim. Oaks, famed for their longevity, might be expected to have exceptionally long generation times and thus exhibit a slow adaptive response to climate change. Even when grown under optimal conditions in an orchard setting, time to first reproduction in blue oaks is usually greater than 15–20 years (K Rice pers obs). Given the slow growth of blue oaks under natural field conditions (Adams and McDougald 1995), the time required for an acorn to produce another blue oak acorn in the foothills of the Sierra Nevada is probably well over 20 years.

Hay fever sufferers probably think that oak pollen gets everywhere. One would therefore expect high levels of antagonistic (and allergenic) gene flow to limit the capacity of oaks to adapt to a changing climate. Surprisingly, recent work suggests that gene flow in oaks may be rather limited (Koenig and Ashley 2003). Ecological genetic studies with blue oak seedlings collected along rainfall gradients in California reveal the existence of regional ecotypes (Rice *et al.* 1993). This ecotypic variation provides additional evidence that gene flow is not overwhelming in its influence, and suggests that oak populations can respond to climatic variation. These results are further supported by stable isotope studies indicating that there is heritable genetic variation within and among blue oak populations in seedling water use efficiency (K Rice unpublished), a trait with obvious implications for adaptive responses to climate change.

Evidence that blue oak populations can differentiate into locally adapted ecotypes along rainfall gradients might suggest that even blue oaks may evolve in response to global warming. However, recruitment of saplings into many blue oak populations is often vanishingly small (Figure 5). Sapling surveys in blue oak stands in the southern Sierra Nevada foothills predict landscape-level losses of this distinctive woodland habitat and extreme fragmentation of any remaining stands (Adams and McDougald 1995; Standiford *et al.* 1997). The ecological reasons for this lack of regeneration in blue oak populations throughout their California range are still speculative, but probably include the cumulative effects of factors ranging from strip mall development and deer and cattle browsing to the introduction of highly competitive exotic annual grasses. Whatever the cause, this extreme demographic limitation almost renders evolutionary speculations moot. It is difficult to imagine how blue oaks will adapt to climate change if there is essentially no "next generation" for selection to act upon. Perhaps the populations that are exhibiting adequate sapling recruitment reflect this selection in action, and the saplings surviving in these stands represent the hope for future survival of blue oaks in California.

The emerging field of restoration genetics

In a time of gloomy forecasts of global climate change and massive species extinctions, one bright spot has been the prediction that ecological restoration will be a critical factor for saving planetary biodiversity (Young 2000). As a response to concerns about the vagaries and inadequacies of chance migration, ecological restoration has been proposed as a way to augment natural species migration and establishment (Stockwell *et al.* 2003; Hufford and Mazer 2003). On the other hand, restoration practitioners are constrained by budgets and often have to make difficult decisions about where to obtain the material to augment extant populations or establish new ones. They are well aware that it is not the entire species that is moved during restoration, but only a subset of populations within a species.

Although the science of restoration has yet to develop a substantial focus on genetic and evolutionary issues (Young 2000), reputable restoration practitioners have begun to voice concerns about how their actions may be influencing the long-term evolutionary "health" of restored populations. The emerging field of restoration genetics represents an important application of ecological genetics and microevolutionary theory that addresses these concerns (Hufford and Mazer 2003). Restoration geneticists try to address scales of local adaptation, the effects of gene flow on adaptation, and the importance of genetic variation in promoting adaptive response. All of these topics are of critical importance in trying to understand how human manipulation of microevolution may facilitate or foil the capacity of organisms to evolve and adapt to climate change.

One of the first tenets of ecological restoration is to consider the option of doing nothing. Rather than spending time and money on the introduction and establishment of species at a restoration site, it may be cost effective to allow natural recruitment processes to take place. The decision for no action may also be preferable in restoration genetics. If populations seem demographically viable and probably contain enough heritable variation in traits that are important for adaptation, then the best course of action may be monitoring rather than active intervention. A recent meta-analysis of phenological shifts of several broad taxa in response to global warming suggests that plant and animal populations may already be evolving in response to climatic shifts (Root *et al.* 2003). A triage approach could focus restoration efforts on those taxa that are not adapting at all, especially if they appear to be demographically imperiled.

If some sort of intervention is necessary, then it is clear that we have the capacity to exert a major influence on evolutionary processes. The history of biological invasions has taught us that, either by accident or design, humans are great vectors for the dispersal of all kinds of plant and animal propagules. Aided by time, money, and determination, we have a huge potential to change patterns and rates of gene flow and modify the genetic structure and adaptive capacity of existing or newly created populations.

Humans as gene dispersers

Human introduction of a large number of propagules to a site to create a "ready-made" population is a rather unnatural process. This human-facilitated "en masse" migration is very different from the scenario typically envisioned for natural founder events, where just a few individuals colonize a site. In theory, large introductions from appropriate source populations can reduce the probability that adaptation to climate change will be hindered by a lack of adaptive genetic variation. Although this type of large introduction is biologically unusual, it reduces the chance of genetic bottlenecks if there is substantial genetic variation within the introduced population. A determined restoration practitioner can further reduce the chances for bottlenecks and demographic extinction by repeated introductions at a site. After initial introduction, a management strategy that reduces temporal fluctuations in population size will also decrease the loss of genetic variation through drift. Furthermore, the source of the introduced genotypes can be targeted and not left to chance.

Easing the genetic load

When restoration biologists attempt to restore a population to an area from which it has been extirpated, they determine the genetic properties and thus the evolutionary potential of the initial population. Unfortunately, restoration propagules are often introduced without any consideration of the genetic variation and history of selection in the source populations. Although necessary for an adaptive response to selective challenges, a large amount of heritable genetic variation can be "too much of a good thing", and can cause a severe genetic load if many of the individuals in a population deviate greatly from the current optimum phenotype. On the other hand, a population with low levels of heritable genetic variation, finely tuned to the current selective optimum, will have little capacity to adapt to new conditions. This is especially true if the new environment has a phenotypic optimum far from the native environment's optimum, or if the optimum shifts rapidly with global change. By manipulating the genetic constitution of restored populations, it might be possible to strike a balance between an acceptable level of genetic load and the capacity for further adaptive shifts. In essence, this type of "coarse selective tuning" adjusts the balance between existing adaptation and potential adaptation. An example in plant restoration might be the creation of regional seed mixes that are delineated by climate zones but also contain genotypes collected from a variety of microenvironments within each zone. By matching seed sources to climate, one reduces the chance that completely maladapted genotypes will be introduced (ie reducing the initial genetic load), while the genetic diversity present within the mixture allows fine-scaled adaptive tuning to take place in the future.

Another approach would be to collect planting material from the edges of a species range. Although these marginal populations may contain reduced levels of genetic variation because of small population sizes and/or past founder effects, they may possess novel adaptations to environmental extremes that could be important for evolutionary response to climate change (Hoffmann and Blows 1993). For that matter, any extreme microenvironments within a species range (eg hot, dry slopes) might yield genotypes with useful adaptations.

■ A risky business

Our ability to effectively manage microevolution and facilitate adaptive response to climate change is severely hampered by our current lack of knowledge of scales of adaptation and patterns of gene flow for most species. In the past, estimates of gene flow and outcrossing rates in plant species have often been based on floral morphology and reproductive characters such as pollen/ovule ratios (Cruden 1977). In the absence of anything better, restorationists can still use this type of information to get very rough estimates of breeding systems. However, recent advances in the development of molecular genetic markers should make the capacity to accurately determine patterns of gene flow easier for both ecologists and managers. Much better reconstruction of historical gene flow is now possible with the use of "coalescence" techniques (Beerli and Felsenstein 2001) and estimates of current gene flow patterns are possible with new non-equilibrium approaches (Rannala and Mountain 1997). By combining these methods, restorationists will be able to understand how factors such as habitat fragmentation may have changed patterns of gene flow and thus the potential for evolutionary response. This knowledge can be used to help restore altered gene flow so managers can mimic or even augment natural patterns of gene flow among fragmented populations.

Despite the power and increased accessibility of these new molecular techniques, it is important to remember that molecular markers usually do not reflect patterns of selection (Reed and Frankham 2001; McKay and Latta 2002). The fact that variation in molecular markers is usually "invisible" to natural selection is precisely why isozymes, amplified fragment length polymorphisms, and microsatellites are used to independently estimate gene flow and genetic drift "uncontaminated" by the effects of selection. As a result, these molecular markers, often called "neutral markers", cannot be used to infer scales of adaptation or patterns of variation in traits that might be important in adapting to climate change (Ashley *et al.* 2003). That type of information lies in the realm of quantitative genetics and comes from time-honored techniques such as common garden experiments and reciprocal transplants. In an ideal world, a wide range of population samples from each species would be tested by researchers in carefully designed gardens across a range of environments in order to understand patterns of adaptive genetic variation within and among populations as well as patterns of adaptive plasticity. Clearly, however, it will not be possible to conduct extensive garden and transplant experiments for even a small subset of species that will be affected by global change. Unfortunately, in addition to being time-consuming and labor intensive, it is difficult, if not impossible, to effectively apply these techniques to many animal species or to long-lived plant species such as blue oaks.

What might be an alternate, more realistic strategy? It is possible that information on scales of adaptation could be gleaned from the large number of ongoing restoration projects both in the US and abroad. Although these projects often leave a lot to be desired in terms of experimental design, they could represent a large untapped source of information on what does and does not work (genetically) during restoration (Stockwell *et al.* 2003). If reasonable records of the genetic sources of material used in the restoration project are available, at least some rough estimates of adaptive zones might be inferred.

The use of existing environmental data to better understand the selective regime within the range of a species can also go a long way towards predicting potential patterns of adaptation. Genetic distances in adaptive traits between population are often correlated with the environmental distances among the home sites of the populations (Knapp and Rice 1998). Horticultural climate zones found in most gardening guides are probably excellent indicators of climatically distinct selection regimes, and this type of environmental information is increasingly available on the Internet.

Holt (1990) warned that "predicting the microevolutionary consequences of climate change for even a single species is dauntingly complex". Because we know so little about contemporary gene flow and selection, restoration genetics is still a very inexact science. Admittedly, manipulating evolutionary processes to foster adaptive response to climate change is inherently risky. It is an unfortunate reality that difficult decisions in genetic restoration will have to be made, based on incomplete knowledge. However, we hope that a better appreciation of the importance and potential for rapid adaptive change might provide scientists and managers with evolutionary options that have not been widely recognized. For the great global "damage control" operation that will be needed in the next century, we can use all the help we can get.

■ References

Adams TE and McDougald NK. 1995. Planted blue oaks may need help to survive in southern Sierras. *Calif Agr* **49**: 13–17.

Agrawal AG. 2003. Community genetics: new insights into community ecology by integrating population genetics. *Ecology* **84**: 545–46.

Alexander DG and Schlising RA. 1996. Patterns in time and space for rare macroinvertebrates and vascular plants in vernal pool ecosystems at the Vina Plains Preserve, and implications for pool landscape management. In: Witham CW, Bauder ET, Belk D, *et al.* (Eds). Ecology, conservation and management of vernal pool ecosystems: proceedings from a 1996 conference. Sacramento, CA: California Native Plant Society.

Antonovics JA. 1976. The nature of limits to natural selection. *Ann Mo Bot Gard* **63**: 224–247.

Ashley MV, Wilson MF, Pergams ORW, *et al.* 2003. Evolutionarily enlightened management. *Biol Conserv* **111**: 115–23.

Beerli P and Felsenstein J. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in subpopulations by using a coalescent approach. *P Natl Acad Sci USA* **98**: 4563–68

Black C and Zedler PH. 1996. An overview of 15 years of vernal pool restoration and conservation activities in San Diego County, California. In: Witham CW, Bauder ET, Belk D, *et al.* (Eds). Ecology, conservation and management of vernal pool ecosystems: proceedings from a 1996 conference. Sacramento, CA: California Native Plant Society.

Brown JH and Kodric-Brown A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**: 445–49.

Case TJ and Taper ML. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am Nat* **155**: 583–605.

Cruden RW. 1977. Pollen–ovule ratios: a conservative indicator of breeding systems in plants. *Evolution* **31**: 32–46.

Darwin CR. 1859. On the origin of species. London, UK: John Murray.

Davis MB and Shaw RG. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* **292**: 673–79.

Endler JA. 1986. Natural selection in the wild. Princeton, NJ: Princeton University Press.

Frankham R. 1995. Conservation genetics. *Annu Rev Genet* **29**: 305–27.

Geber MA and Dawson TE. 1993. Evolutionary responses of plants to global change. In: Kareiva PM, Kingsolver JG, and Huey RB (Eds). Biotic interactions and global change. Sunderland, MA: Sinauer.

Gilpin ME and Soulé ME. 1986. Minimum viable populations: processes of species extinction. In: Soulé ME. (Ed). Conservation biology: the science and scarcity of diversity. Sunderland, MA: Sinauer.

Gomulkiewicz R and Holt RD. 1995. When does evolution by natural selection prevent extinction? *Evolution* **49**: 201–07.

Grant BC and Wisenman LC. 2002. Recent history of melanism in American peppered moths. *J Hered* **93**: 86–90.

Haldane JBS. 1956. The relation between density regulation and natural selection. *P Roy Soc Lond B Biol* **45**: 306–08.

Hoffmann AA and Blows MW. 1993. Evolutionary genetics and climate change: will animals adapt to global warming? In: Kareiva PM, Kingsolver JG, and Huey RB (Eds). Biotic interactions and global change. Sunderland, MA: Sinauer.

Holland RF and Jain SK. 1981. Insular biogeography of vernal pools in the central valley of California. *Am Nat* **117**: 25–37.

Holt RD. 1990. The microevolutionary consequences of climate change. *Trends Ecol Evol* **5**: 311–15.

Holt RD and R Gomulkiewicz. 1997. How does immigration influence local adaptation? A reexamination of a familiar paradigm. *Am Nat* **19**: 563–72.

Hufford KM and Mazer SJ. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends Ecol Evol* **18**: 147–55.

Kettlewell MG. 1972. The evolution of melanism. Oxford, UK: Oxford University Press.

Kinnison MT and Hendry AP. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112–13**: 145–64.

Kirkpatrick M and Barton NH. 1997. Evolution of a species' range. *Am Nat* **150**: 1–23.

Knapp EE and Rice KJ. 1998. Comparisons of isozymes and quantitative traits for evaluating patterns of genetic variation in purple needlegrass (*Nassella pulchra*). *Conserv Biol* **12**: 1031–41.

Koenig WD and Ashley MV. 2003. Is pollen limited? The answer is blowin' in the wind. *Trends Ecol Evol* **18**: 157–59.

Lenormand T. 2002. Gene flow and the limits to natural selection. *Trends Ecol Evol* **17**: 183–89.

Levin DA. 1990. The seed bank as a source of genetic novelty in plants. *Am Nat* **135**: 563–72.

Linhart YB. 1988. Intrapopulation differentiation in annual plants. III. The contrasting effects of intra- and interspecific competition. *Evolution* **42**: 1047–64.

Lynch M and Lande R. 1993. Evolution and extinction in response to environmental change. In: Kareiva PM, Kingsolver JG, and Huey RB (Eds). Biotic interactions and global change. Sunderland, MA: Sinauer.

McKay JK and Latta RG. 2002. Adaptive population divergence: markers, QTL and traits. *Trends Ecol Evol* **17**: 285–91.

Pavlik BM, Muick PC, Johnson S, and Popper M. 1991. Oaks of California. Los Olivos, CA: Cachuma Press.

Peters RL and Darling JDS. 1985. The greenhouse effect and nature reserves. *Bioscience* **35**: 707–17.

Rannala B and Mountain JL. 1997. Detecting immigration using multi-locus genotypes. *P Natl Acad Sci USA* **94**: 9197–201.

Reed DH and Frankham R. 2001. How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution* **55**: 1095–103.

Reznick DN and Ghalambor CK. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112–13**: 183–98.

Rice KJ, Gordon DR, Hardison JL, and Welker JM. 1993. Phenotypic variation in seedlings of a "keystone" tree species (*Quercus douglasii*): the interactive effects of acorn source and competitive environment. *Oecologia* **96**: 537–47.

Root TL, Price JT, Hall KR, *et al.* 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.

Ronce O and Kirkpatrick M. 2001. When sources become sinks: migrational meltdown in heterogeneous habitats. *Evolution* **55**: 1520–31.

Standiford TB, McDougald N, Frost W, and Phillips R. 1997. Factors influencing the probability of oak regeneration on southern Sierra Nevada woodlands. *Madrono* **44**: 170–83.

Stockwell CA, Hendry AP, and Kinnison MT. 2003. Contemporary evolution meets conservation biology. *Trends Ecol Evol* **18**: 94–101.

Storfer A. 1999. Gene flow and endangered species translocations: a topic revisited. *Biol Conserv* **87**: 173–80.

Sultan SE. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evol Biol* **21**: 127–78.

Thorp RW and Leong JM. 1996. Specialist bee pollinators of showy vernal pool flowers. In: Witham CW, Bauder ET, Belk D, *et al.* (Eds). Ecology, conservation and management of vernal pool ecosystems: proceedings from a 1996 conference. Sacramento, CA: California Native Plant Society.

Travis J and Futuyma DJ. 1993. Global change: lessons from and for evolutionary biology. In: Kareiva PM, Kingsolver JG, and Huey RB (Eds). Biotic interactions and global change. Sunderland, MA: Sinauer.

Western D. 2001. Human-modified ecosystems and future evolution. *P Natl Acad Sci USA* **98**: 5458–65.

Young TP. 2000. Restoration ecology and conservation biology. *Biol Conserv* **92**: 73–83.