

# Range Shifts and Adaptive Responses to Quaternary Climate Change

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Tree taxa shifted latitude or elevation range in response to changes in Quaternary climate. Because many modern trees display adaptive differentiation in relation to latitude or elevation, it is likely that ancient trees were also so differentiated, with environmental sensitivities of populations throughout the range evolving in conjunction with migrations. Rapid climate changes challenge this process by imposing stronger selection and by distancing populations from environments to which they are adapted. The unprecedented rates of climate changes anticipated to occur in the future, coupled with land use changes that impede gene flow, can be expected to disrupt the interplay of adaptation and migration, likely affecting productivity and threatening the persistence of many species.

Modern plant taxa have persisted through a long period of variable climate, including glacial-interglacial cycles with large changes in temperature, precipitation, and CO<sub>2</sub> concentration, over the past 2.5 million years. Rates of climate change varied widely: Regional temperature changes were as rapid as several degrees Celsius within a few decades or as slow as 1°C per millennium. The changes in species distribution evidenced by fossils provide a detailed record of plant responses to these changes. Hundreds of pollen diagrams, compiled in databases, provide re-

gional and continental records of tree abundances as they changed through space and time (1-3). New pollen records supplemented by macrofossils (4) and DNA recovered from fossil pollen (5) provide increasing temporal and taxonomic detail. In arid regions, where pollen-bearing sediments are less abundant, plant fragments preserved in middens made by packrats (*Neotoma*) and other rodents provide a spatially precise record of past species distributions (6). Changes in geographic distribution are so frequently documented in the fossil record that range shifts are seen as the expected plant response to future climate change (7).

Beyond changes in distribution, however, plants underwent genetic changes, adapting to changes in climate during the Quaternary.

Yet adaptation at the population level is seldom considered in the literature describing Quaternary environments nor, with some notable exceptions (8-10), in discussions of vegetation response to anticipated global change.

Here we cite evidence of genetic adaptation to climate and argue that the interplay of adaptation and migration has been central to biotic response to climate change. Moreover, we discuss how rapid climate change challenges this process, pushing populations to limits of adaptation, thus influencing regional ecosystem properties as well as the persistence of taxa.

## Range Shifts During the Late Quaternary

Range shifts are the most conspicuous, and best documented, response of woody species to Quaternary climate. As the climate warmed at the end of the last glacial interval, tree populations became established at higher latitudes. These range extensions are called "migrations," although individual plants, unlike animals, cannot move to follow changing climate. Rather, occupation of new regions occurs through passive seed dispersal and establishment of seedlings in sites where conditions permit. The patterns of migration dur-

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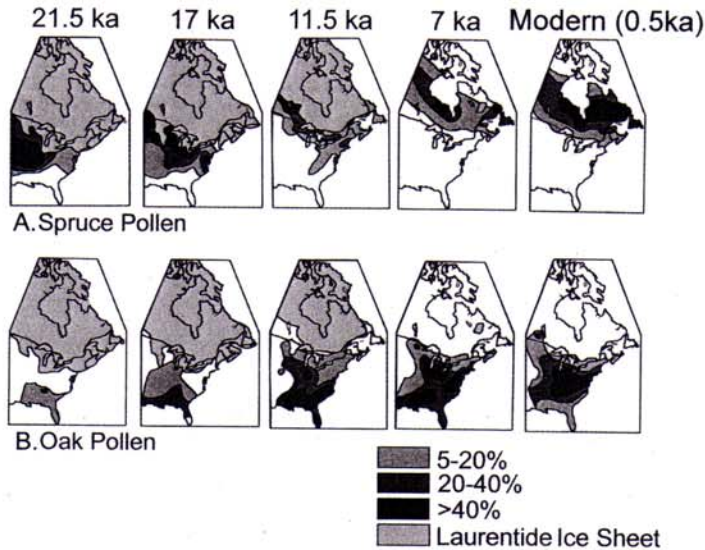
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ing the past 25,000 years are individualistic, with the entire range of some tree taxa displaced to new latitudes, e.g., spruce (*Picea* spp.) (Fig. 1A). In contrast, others expanded from glacial refuges, e.g., oak (*Quercus* spp.) (Fig. 1B). Migration rates and the routes of migration also differed among taxa (1, 11, 12). In regions that were never glaciated, many species and genera continued to grow at the same latitude, shifting from one range of elevations to another and expanding or contracting population size. In the Southern

Hemisphere, elevation shifts and expansion and coalescence from multiple refuges appear to have been the dominant responses to interglacial warming (13), but similar responses occurred in the Northern Hemisphere as well. In the arid southwest, for example, complex changes in distributions are recorded, including range shifts to new regions (e.g., *Juniperus occidentalis* and *Artemisia tridentata*), large changes in population size (e.g., *Pinus longaeva*, which declined in abundance during the past 11,000 years, and *P. ponderosa*,

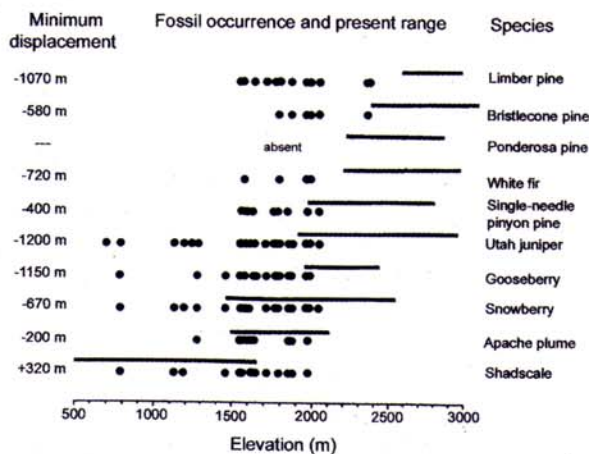
which expanded), and shifts in elevation range varying in amount and even in direction (14) (Fig. 2).

The individualistic patterns of migration and shifts in elevation have been explained by differences among species in their tolerance limits to various climate variables in the context of complex climate changes during the past 25,000 years. In the Northern Hemisphere, summer and winter temperature, seasonality, and the distribution and amount of precipitation throughout the year changed in different ways during the past 11,000 years (the Holocene interglacial), producing new combinations of climate variables. The resulting climate patterns allowed co-occurrence of species whose ranges do not overlap today (2, 15). Similarly diverse patterns of vegetation change are seen in all regions of the world where Quaternary records have been studied (1). Climate change is sufficient to explain the continental-scale patterns of plant migrations, as demonstrated by the success with which climate reconstructions by global models, coupled with transfer functions, can predict the documented patterns of pollen abundance during the late Quaternary (16). Predictions duplicate, for example, the patterns for spruce and oak pollen at the level of resolution displayed in Fig. 1.



**Fig. 1.** Ranges, as indicated by pollen percentages in sediment, of spruce and oak in eastern North America at intervals of about 5000 years during the late Quaternary (65). Dates are calibrated equivalents of radiocarbon years before present. The continental ice sheet is shown in blue; pollen proportions are shown in shades of green. The shoreline is not drawn to reflect changes in sea level. (A) Spruce (*Picea*) pollen representing three extant species plus the extinct *P. critchfieldii*. More recent data show that spruce was abundant farther south in the Mississippi valley during the Last Glacial Maximum than shown here (3, 4). Both southern and northern range boundaries of spruce shifted northward. (B) Oak (*Quercus*) pollen representing some or all of the 27 extant species in eastern United States. Oak expanded from the southeast but continued to grow near the locations of full-glacial refuges.

**Fig. 2.** Elevation ranges for 10 woody plants in the mountains of the Sheep Range, Nevada, during the last glaciation (black dots) contrasted with the present (solid line) (14, 66). The amount of elevation change and even the direction of change are different for each species.



**Adaptation During Range Shifts**

Implicit in the view that trees tracked the shifting climate space to which each species was already adapted is the assumption that taxa disperse seed and establish in new regions more readily than they evolve a new range of climate tolerances. The premise that evolutionary change occurs only on long time scales underlies recent conjecture that the tolerance range of a species remains stable as it shifts its geographic range and that variations of climate “obliterate” intraspecific adaptations to local environments (17–19). The concept of an undifferentiated species comprising individuals with broad tolerances resembles the “general purpose genotype” proposed 40 years ago for weedy plant species (20). But weedy life history does not imply that populations are undifferentiated. Numerous studies in recent decades have demonstrated local adaptation in one weedy species after another, e.g., *Poa annua* (21), *Plantago lanceolata* (22), and *Verbascum thapsus* (23), refuting the idea that weedy habit results from a “general purpose genotype.” Evolutionary theory indicates that adaptations to local environments depend on a balance between selection and gene flow. Furthermore, evolutionary models underscore the dynamic nature of a taxon’s environmental limit, which depends on the interplay of gene flow, selection, and demography (24).

Predictions of biotic response to climate, from simulations of differential growth rates and resulting stand dynamics (25) or from tolerances to bioclimatic variables (26), have also used the climate envelope spanned by the entire species, assuming, again, that the tolerance range for a species remains stable and ignoring intraspecific variation. Although none of these authors deny the reality of adaptive differentiation of populations, differences at this level are considered too small to affect model predictions. It can be argued that if this were not so, models would fail to predict past geographical patterns of pollen abundance. Model predictions of past climate are at a coarse scale of resolution both in space (300 to 400 km) and time (3000 years), however, and pollen sites are often widely spaced, separated by several hundred kilometers. Furthermore, pollen is usually identified to genus or family, rather than species. Thus, the matching of model predictions to observed historic distributions does not obviate the importance of adaptation in response to climate change.

#### Patterns of Genetic Variability

Genetic variability is the basis for evolutionary change; for this reason, considerable effort over the past half-century has been given to determining patterns of genetic variability (27). Because most allozymes (alleles at enzyme loci) and DNA markers appear to be selectively neutral, they serve as valuable indicators of gene transfer within and among populations. Widespread temperate and boreal trees, most of which shifted latitudes during the Holocene, display much allozyme variability, but little allozyme differentiation among populations (28), indicating a high degree of genetic exchange among populations. Much of the exchange occurs through pollen, as evidenced by the finding of greater population differentiation for mitochondrial DNA markers, which are typically maternally inherited, than for allozymes (e.g., 29, 30). Genetic differentiation during periods of population isolation is demonstrated by greater allozyme variability among populations of species abundant during the last glaciation (as evidenced by packrat midden records) but now confined to isolated mountain ranges than in co-occurring tree species that migrated into the Great Basin within the past few thousand years (31). Consequently, where genetic differentiation has been found among present-day populations, centers of allozyme diversity are used to infer locations of refuges during a previous period of unfavorable climate, e.g., *Chamaecyparis* (32) and *Fitzroya* (33).

Several allozyme studies of forest trees in the Northern Hemisphere show a decline in genetic variability from south to north (29, 34, 35), believed to reflect stochastic loss of

variation through repeated founder events during the course of migration (36, 37). This pattern of declining variability, if representative of the rest of the genome, would suggest that the potential for future adaptation might be limited for populations at extreme latitudes. Yet although the pattern appears quite consistent for animal populations (36), diverse patterns are found in woody plants, e.g., *Alnus rubra*, with greater numbers of alleles in northern populations (38), and *Pinus pumila*, where some genetic loci show lower diversity in northern populations whereas others show more (39). In European beech, allelic richness is greatest in the vicinity of

glacial refuges, but heterozygosity ( $H_o$ ) is greatest in peripheral populations (40). A recent model investigating the influence of migration on genetic patterns indicates that life history features of trees protect them from dramatic loss of genetic variability during migration. In the simulations, remote populations were established by a few founders, but delayed maturation allowed genetic diversity to accumulate through recruitment of additional individuals from later arriving seeds before the original founders matured sufficiently to reproduce and fill the available space (41).

Phylogeographic analyses use DNA markers to infer migration pathways (37).

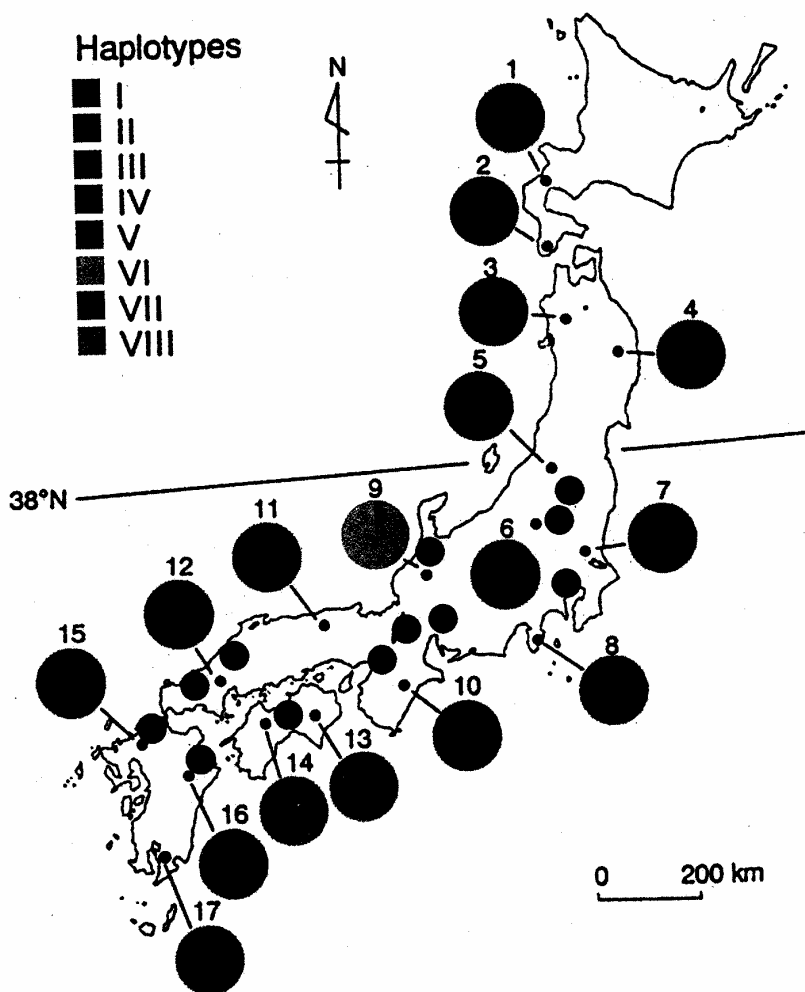


Fig. 3. Phylogeographic analysis of *Fagus crenata*, a Japanese montane beech species, based on mitochondrial DNA haplotypes (30). Beech survived the glacial interval in small populations along the coast south of the 38th parallel, but by 13,000 calibrated calendar years before present, populations had expanded at the sites indicated by black dots (62, 67). Pie diagrams indicate haplotype frequencies in 16 modern populations. Populations in the south are closely related to one another, apparently descended from populations in nearby refuges at low elevations. Northern populations appear to have descended from populations near the northern limit of beech distribution 13,000 years ago. Populations 6 and 9 are related to other northern populations but include haplotypes resulting from hybridization with eastern populations; the latter may have had their origin in refugial populations along the eastern coast.

Often the lineages of modern populations imply where refuges may have been located, e.g., *Picea abies* (42). For example, mitochondrial DNA evidence of close relationships among northern populations of Japanese beech suggests that these populations may have descended from populations in northern refuges, whereas populations along the eastern coast may have originated from refuges there and southern populations from refuges in the south (30) (Fig. 3).

**Adaptations in Modern Populations**

Given the neutrality of molecular markers, assessment of genetic adaptation to climate has relied on an experimental approach in which plants, transplanted from regions of differing climate, are grown together in common conditions (43). Such studies have demonstrated that modern populations of many species that shifted ranges in the past are adapted to the climatic conditions where they now grow. Adaptations to conditions at a range of latitudes and elevations are documented within a large number of species (44, 45). We review here a single well-studied example, Scots pine (*Pinus sylvestris*), with a pollen record that refers unambiguously (at least in northern Europe) to a single species. Fossil pollen indicates that Scots pine migrated across central Europe from the south as temperatures began to rise about 15,000 calendar years before present, expanding rapidly across the northern European plain at rates as fast as 150 km per century (12). By about 8000 years ago, Scots pine was abundant as far north as southern Sweden; it then declined in the south while continuing to expand into northern Sweden, Norway, and Finland (46). In recent millennia, populations have retreated from the upper slopes, an apparent response to cooling during the past several thousand years. Scots pine shows striking differentiation with respect to survival in

transplant trials throughout northern Sweden (47). At each site, mortality tended to be higher for trees transplanted there from lower latitudes or from lower elevations than for trees native to the site (Fig. 4A). Adaptive divergence in physiological traits has been demonstrated as well; in a common garden comparison of populations originating in 19 sites throughout Finland, the more northerly a population's origin, and the higher the elevation, the earlier it initiated winter dormancy, a process highly sensitive to photoperiod (48) (Fig. 4B). These populations differentiated at their current geographical location in the face of substantial gene flow, as revealed by allozyme loci that are weakly differentiated among populations (49).

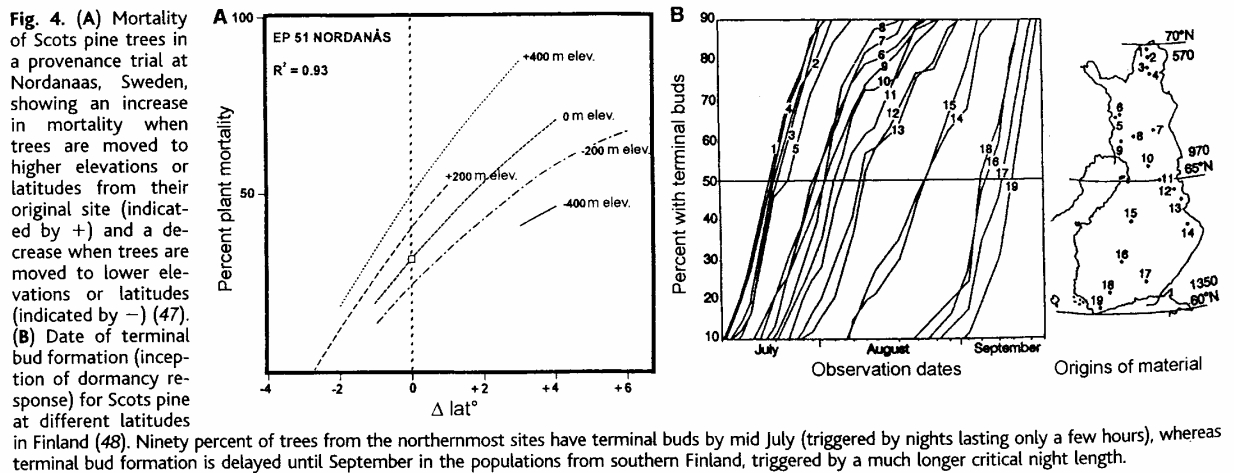
In North America, adaptive differentiation has been inferred from common garden studies of many species. Examples include white spruce (*Picea glauca*) (50), lodgepole pine (*Pinus contorta*) (10, 51), and red alder (*Alnus rubra*) (38). In the case of red alder, populations sampled from 54°N and raised in a common garden at 49°N tended to grow for fewer days during the growing season than local populations and thus failed to grow as large as trees sampled from the south, a finding similar to Scots pine in Sweden (47). Differentiation has also been found in relation to distance from the coast and, more weakly, elevation. For all three taxa, as for Scots pine in Scandinavia, the patterns of genetic differentiation with respect to quantitative aspects of the phenotype are not reflected in patterning of enzyme variation, indicating that populations diverged in relation to local climate despite gene flow.

**Adaptations During Migration**

In light of the demonstrated adaptation to local environments, migration can no longer be viewed simply as an alternative to adaptation (19), involving expansion of northern popula-

tions while those to the south contract. Instead, the range shifts occasioned by major climate changes in the past appear to have involved adaptive evolutionary change, as changing climate altered the fitness optimum for each population throughout the species range (Fig. 5, A and B). Whereas dispersal is likely to be at random with respect to a seed's adaptation to conditions where it lands, differential survival during the course of seedling establishment selectively "sieves" out genotypes that do not tolerate local conditions. Differential growth and reproduction further promote adaptation of physiological characteristics. The arrival of seeds that are somewhat "preadapted" to the novel climate (e.g., seeds from more southerly populations during periods of climate warming) may contribute to adaptation, yet selection would also promote new genetic combinations, for example, of photoperiod and temperature responses suited to the novel growing season. Building on evolutionary understanding of range limits in a static environment (24), we see that establishment of new ranges as climate changes involves a great deal more than dispersal of seed ahead of the advancing species front. It also involves selection against phenotypes that are poorly adapted to local conditions, gene migration through pollen and seed dispersal from neighboring populations, some of which are better adapted to the new climate (Fig. 5B, conditions 1 and 2), and recombination of genes influencing physiological traits. Shifts in elevation also entail adaptation, which might occur more readily, because the proximity of populations facilitates gene migration.

Until now, attention has been focused on the question of how seed dispersal extends ranges as climate changes (52, 53). Figure 5B shows, however, that dispersal of both seed and pollen is critical throughout the species range, because it can transfer genes and thus increase variability, which is the basis for evolutionary change. Adaptation of popula-





tions at the leading edge of the migrating front may be enhanced by gene transfer from the center of the range. In contrast, populations at the trailing edge of the range receive no seed or pollen from better adapted populations, because those beyond that edge are either extinct or prevented by the newly unfavorable climate from flowering and setting seed. For this reason, adaptation at the trailing edge of a species range depends largely on variation within the local population. In these areas, adaptation may occur slowly or not at all, with high mortality and/or demise of local populations resulting in contraction of the geographical range.

In the center of the species range, populations are likely to be more genetically variable, because, in addition to the genetic variation of the resident population, they receive pollen and seeds from neighboring populations that are better adapted to current local conditions as well as from populations less well adapted. Forest trees produce copious seeds, many of which germinate but die within a few years. Accordingly, intense selection could proceed without radically changing for-

est demography. A more conspicuous consequence of poorly adapted genotypes might be reduced growth rates of adult trees. Poor growth and high mortality due to evolutionary lags in adaptation could have important effects on ecosystem properties. For example, Rehfeldt *et al.* (10) project increased growth and productivity for *Pinus contorta* in western Canada under doubled CO<sub>2</sub> climate, if optimal genotypes were to grow at all latitudes and elevations. But with existing genotypes as presently distributed, the same novel climate would reduce growth and survival by 10 to 55% depending on site (10), a dramatic demonstration that intraspecific differentiation is large enough to affect predictions of biotic response to climate. In a mixed forest, competition from faster growing trees might reduce seed output, with further adverse effects on adaptation (54).

Thus, climate changes that cause range shifts can be expected to have effects throughout a species range, not just at northern and southern range limits. Furthermore, rapid climate changes, involving greater displacement along a climate gradient, challenge

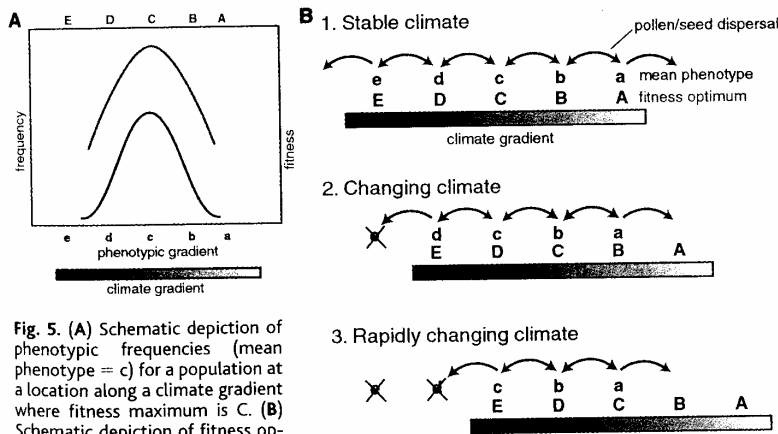
populations more than gradual change. Differences between the present phenotypic mean and the fitness optimum are larger, as are geographic distances separating genes from locations where they could contribute to climatic adaptation (Fig. 5B, condition 3).

**Limitations to the Rate of Adaptation to Changing Climate**

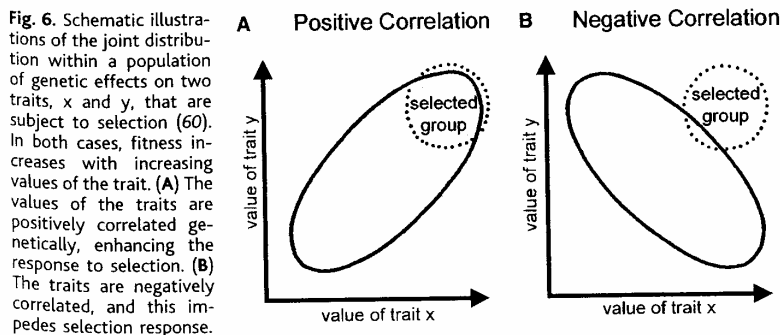
Although all the tree species that remain in our flora shifted or contracted ranges, adapting to climate changes in the past, there are reasons to question whether these processes will occur as readily during the present period of climate change. First, the extent of land currently committed to urban and agricultural use represents a considerable, novel impediment to range shifts of tree populations and in many cases to gene flow among populations. Second, although remarkably high rates of tree migration have been documented in the pollen record, predictions of rates of climate change indicate that implausibly higher migration rates would be necessary for plant populations to match climate shifts in the future (9). Current climate projections for the 21st century necessitate range shifts at rates of 300 to 500 km per century, in contrast to commonly observed migration rates in the past of 20 to 40 km per century (11, 55). Even the exceptional examples from the fossil record, 100 to 150 km per century (12, 56), are far below the rates required to track climate changes in the future.

The fitness that present-day populations would express in future climates in the absence of evolutionary change can be inferred from transplant experiments that include environments similar in as many aspects as possible to those predicted, as described by Rehfeldt *et al.* (10). Above, we noted studies in which Scots pine was transplanted to lower elevations and lower latitudes with consequent declines in mortality (47). A study of the prairie annual, *Chamaecrista fasciculata*, provides a counterexample, demonstrating fitness reduction in a warmer and drier climate. Population samples from Minnesota and Kansas were grown in sites south and west of their origin (57). Compared with their seed production when grown in their home sites, each population produced fewer seeds when growing in more southern sites. Moreover, they produced fewer seeds than the population native to the site, demonstrating adaptation of the native population to local conditions. Intense natural selection on aspects of morphology was found in the novel conditions.

The rate of evolutionary response to selection on a specific trait, for example, a morphological or physiological feature involved in drought or heat tolerance, depends on the magnitude of genetic variation in that trait and on the intensity of selection on that



**Fig. 5.** (A) Schematic depiction of phenotypic frequencies (mean phenotype = c) for a population at a location along a climate gradient where fitness maximum is C. (B) Schematic depiction of fitness optima (red) for a species that ranges across a climate gradient. Adaptive differentiation of population phenotypes is shown in black; arrows indicate gene flow through pollen and seed dispersal. Spatial distributions of the climate gradient, fitness optima, and phenotypic frequencies are shown for three conditions: 1, stable climate; 2, slowly changing climate; and 3, rapidly changing climate.



**Fig. 6.** Schematic illustrations of the joint distribution of genetic effects on two traits, x and y, that are subject to selection (60). In both cases, fitness increases with increasing values of the trait. (A) The values of the traits are positively correlated genetically, enhancing the response to selection. (B) The traits are negatively correlated, and this impedes selection response.

trait (58). The magnitude of genetic variation in natural populations for traits likely to be critical to survival and reproduction in future climates is largely unknown. When transplant experiments are coupled with quantitative genetics, they can directly assess the genetic variability of traits subject to selection under anticipated conditions. Work of this kind is demanding, but it is most directly informative of the rates of adaptation that can be expected with climate change. The above-mentioned study of *C. fasciculata* serves to illustrate this point. In the experiment, each population sample consisted of individuals of known pedigree, permitting assessment of genetic variation underlying morphological and fitness traits. The study documented substantial genetic variation underlying the selected traits, as well as reproductive fitness (59).

Rapid adaptation to changing climate might be predicted from these findings, yet whenever adaptation depends on change in multiple traits jointly, genetic interdependence among the traits may retard evolutionary response (58, 60). For example, in anticipated climates, enhanced survival and reproduction may be associated with increasing values of each of two traits. If the traits are negatively genetically correlated because genes that tend to increase one trait tend to reduce the other, then the response of both traits to selection will be slowed or stalled (Fig. 6). In the case of *C. fasciculata*, despite dramatic selection and substantial genetic variability for traits under selection, responses to selection are impeded by genetic correlations adverse to the direction of selection (59).

### The Possibility of Extinction

On one hand, examples exist of populations that adapted to change during the Quaternary, persisting in situ. For many taxa in the Northern Hemisphere, southern populations stayed in place, while northern populations expanded. Both North American and European beech, for example, still grow in the vicinity of full-glacial refuges (2, 40). The persistence of *Cryptomeria japonica* in central Japan through many glacial-interglacial cycles is well documented; populations expanded and migrated outward during each interglacial interval (61, 62)—a remarkable example of long-term persistence as the regional climate changed. On the other hand, limits to adaptation are indicated by the finding that southern populations of *Pinus banksiana* and *Pinus resinosa* in southeastern United States were extirpated at the opening of the Holocene, whereas northern populations expanded, resulting in latitudinal displacement of the ranges of both species (3, 4).

Thus, adaptation at rates sufficient to match climate change is not guaranteed (63). As we have discussed, the rapid rates projected for future decades pose a particular challenge: Taxa that fail to adapt rapidly enough

to tolerate these new and rapidly changing climate regimes will go extinct. In this connection, it seems important that the only precisely dated extinction of a tree species during the Quaternary coincided with the exceptionally rapid warming during the transition from the Last Glacial Maximum to the Holocene. *Picea critchfieldii* became extinct about 15,000 calendar years before present (64), a time when the deciduous trees with which it was associated were beginning to migrate northward. Given the limitations to migration and adaptation we have discussed, future rapid climate change could result in extinctions of many additional taxa.

### Conclusions

Range shifts can no longer be viewed as an alternative to climate adaptation. The finding of adaptive differentiation in many living species implies that species were so differentiated in the past and that adaptation accompanied migration during the many climate changes of the Quaternary. Gene flow from pollen and seed dispersal are important sources of genetic variation, not only at the leading edge of a migrating species but also throughout a species' range. Both selection against poorly adapted genotypes and genetic recombination are expected throughout a species range as it migrates to new latitudes or elevations. Although the literature has emphasized seed dispersal at the leading edge of migrating populations, we find that adaptation may be most restricted at the trailing edge, where populations are deprived of gene flow from "preadapted" populations. The fossil record shows that populations at the trailing edge are often extirpated, resulting in a latitudinal displacement of range rather than a simple expansion into newly favorable regions (Fig. 1A). Although examples of persistence through repeated periods of unfavorable climate are documented in the fossil record, the record of extirpations and extinctions suggests that limits to adaptation are greatest during periods of rapid climate change, such as predicted for the future. Genetic constraints on adaptation, together with land cover changes that impede gene flow, are likely to reduce the rate of adaptation well below the unusually rapid pace of expected future climate change.

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68. We are very grateful to C. Douglas for preparing the figures for the paper. We also thank the following for helpful criticism of the manuscript: C. Douglas, D. Lytle, K. McLaughlan, G. Wahl, S. Halpern, E. Lonsdorf, R. Zink, G. May, S. Chang, J. Hill, J. Antonovics, and three anonymous reviewers. This work was supported by the NSF.