

The atmosphere is in continual flux, and plants are generally well-adapted to high-frequency variations in the atmospheric environment. During its lifespan, an individual tree or shrub employs a variety of mechanisms to deal with changes in air temperature, insolation, humidity, and other variables, ranging from rapid stomatal and biochemical adjustments to seasonal dormancy to long-term changes in growth rate and form. Substantial climatic variability also occurs at timescales exceeding the lifespans of individual plants. Evolutionary responses to such low-frequency ( $10^1$ - $10^5$  yr) climatic variation can occur *via* natural selection, but those responses are constrained by the extent of climatically significant genetic variability in the species population and by the rate of environmental change relative to the evolutionary response time of the species. Genecological studies indicate that, although climatically relevant phenotypic traits vary within most tree species, and that much of this variation is heritable, the magnitude of variation is not great compared to the magnitude of observed climatic variation along geographic gradients or timespans exceeding ca.  $10^4$  years. Evidently, phylogenetic constraints and adaptive tradeoffs render most trees as well as other plants incapable of expanding evolutionarily into novel climatic regimes, at least not in the short term. Furthermore, trees and other woody-plant species have relatively slow evolutionary response times owing to their long mean generation-times (typically measured in decades to centuries).

For these reasons, responses of tree species to long-term and/or high-magnitude climatic change must be manifested in population processes of recruitment, mortality, migration, and extirpation. Individual species populations may be able to withstand environmental change at a site, as long as the change does not exceed physiological tolerances. Populations may increase or decrease at a site according to environmental effects on recruitment and mortality and on interactions with competitors, consumers, and mutualists. Populations may also expand or contract at a local scale along elevational, topographic, and/or edaphic gradients.

Larger-magnitude changes in the environment can lead to local extirpation of populations, either through adult mortality or recruitment failure. However, such changes may also open up new, previously unsuitable territory that can be occupied by populations of a species provided it can disperse to the newly suitable sites. These processes can result in large-scale displacements of the geographic ranges of species, spanning  $10^2$ - $10^4$  kilometres. Conceivably, climatic changes might be of sufficient rate and/or magnitude to lead to universal extinction of a species (*via* extirpation of all existing populations, together with lack of newly suitable sites within dispersal distance).

"Climate" consists of many biologically relevant variables. Many of these variables covary in space (e.g., summer and winter temperatures along latitudinal or elevational gradients). However, spatially covarying factors may vary temporally in a more complex fashion - spatial covariance may be maintained, but the shape and slope of the relationships may change<sup>1</sup>. For example, Milankovitch forcing can result in simultaneous increase in summer temperatures and decrease in winter temperatures. The resultant changes in the shape of environmental space can lead to novel species associations. Community composition, and patterns of community composition along spatial gradients, may change dramatically with environmental change<sup>1</sup>.

Responses of plant populations and communities to environmental changes of the past 25,000 years can be observed using pollen and plant macrofossil evidence from radiocarbon-dated lake and wetland sediments<sup>2</sup>. Fossil woodrat middens from arid and semi-arid regions can also be radiocarbon-dated and analyzed for plant macrofossils<sup>3</sup>. To date, more than 1000 radiocarbon-dated pollen sequences have been documented from North America, along with macrofossil assemblages from at least 600 lake and wetland sites. More than 1200 fossil woodrat middens have been dated and analyzed from the western United States. These data are providing spatially and temporally detailed records of floristic and vegetational change, particularly in forest and woodland regions.

During the Last Glacial Maximum (LGM) 22,500 yr BP (years Before Present), temperatures in unglaciated portions of North America were -5 to -10°C lower than present<sup>4</sup>, and atmospheric CO<sub>2</sub> concentrations were ca. 65% of pre-industrial levels. Southward displacements of geographic ranges spanning as much as 1000 km are observed for many tree taxa in both eastern<sup>4</sup> and western North America<sup>3</sup> (e.g., jack pine, red pine, white spruce, Utah juniper). Many species that are now widespread and abundant (e.g., paper birch, eastern hemlock, eastern white pine, Ponderosa pine, Colorado pinyon) existed as small, widely dispersed populations on the LGM landscape<sup>2,3,4</sup>. Some species, especially montane species (Rocky Mountain juniper, limber pine, Douglas-fir) occurred in small populations in the foothills of western mountain ranges<sup>3,5</sup>. Other species (papershell pinyon, blue spruce) occurred as much as several hundred kilometers north of their modern distribution limits<sup>5,6</sup>. A now-extinct species of spruce, *Picea critchfieldii*, dominated forests in much of the lower Mississippi Valley<sup>7</sup>.

Climatic changes during the last deglaciation between ca. 18,000 and 9000 yr BP led to dramatic and often-rapid changes in plant distributions and vegetation composition. Northward spread of many plant species onto formerly glaciated territory was rapid, often exceeding 100 m/yr.<sup>8</sup> These migrations were paced primarily by climatic change and ice retreat; seed dispersal does not appear to have been limiting<sup>8</sup>. Vegetation of unusual composition (i.e., absent from modern landscapes) was widespread in parts of eastern North America during the deglaciation<sup>9</sup>. The peculiar composition was probably the result of a peculiar combination of climatic forcings (positive summer and negative winter Milankovitch anomalies, together with widespread continental ice), which led to combinations of climate variables and gradients that no longer exist<sup>10,11</sup>. *Picea critchfieldii* underwent extinction during this period, but the reasons are obscure<sup>7</sup>.

The Holocene (10,000 - 0 yr BP) was characterized by continued climatic changes, albeit of lower magnitude, and continued biotic adjustments. Many of these adjustments consisted of changes in population size and shifts along local elevational and edaphic gradients<sup>1,3</sup>. However, large-scale migrations of many taxa continued<sup>2,3,10</sup>. For example, eastern hemlock, American beech, and yellow birch have moved west in the western Great Lakes region during the past 5000 years, with range expansions occurring as recently as the past 1000 years<sup>12,13</sup>. These expansions appear to have been pulsed, and most of the migration events coincide with highstands recorded in Lakes Michigan and Superior, indicating climatic pacing of the expansions<sup>14</sup>. Stand dynamics within the past two centuries<sup>15</sup> may be related to high-frequency climatic variability.

As another example, the northward and eastward expansion of Utah juniper in Wyoming has been governed by climatic variation<sup>16,17</sup>. It colonized southwestern Wyoming ca. 8400 yr BP, and established at least two populations in northern Wyoming and adjacent Montana by long-distance dispersal (100-300 km) during a transient dry period ca. 5400 yr BP. These populations remained in place for the next 2600 years, a period characterized by relatively moist regional climate. However, with onset of warm, dry conditions 2800 yr BP, Utah juniper expanded its range rapidly over much of central and north-central Wyoming<sup>17</sup>. Utah juniper continues to invade suitable sites. During the past century, Utah juniper has begun to expand upslope, invading Rocky Mountain juniper woodlands and sagebrush steppe. Although this latter expansion has been attributed to grazing and fire management, it may be related to recent climatic changes.<sup>5</sup> Evidence also exists for similar climate-paced expansion of Ponderosa pine and pinyon pine in the central Rockies during the past few millennia as well as the past century.<sup>5</sup>

Forest and woodland sensitivity to climatic change present unique challenges to managers. "Restoration" to a 19th Century or other historical ideal may be elusive; continual environmental change provides an ever-moving target. Natural forest and woodland systems are transient both spatially and temporally. Many species are adjusting their ranges and populations to past or ongoing climatic changes. In some cases (e.g., woodland invasion of steppe or conifer invasion of hardwood forests) these adjustments may induce profound changes in ecosystem properties (soil chemistry, litter accumulation, nutrient availability, disturbance regime). All of these processes,

of course, will be influenced by future climatic change and directly or indirectly by atmospheric CO<sub>2</sub> accretion. The critical challenge we face is development of flexible management approaches that are commensurate with the complex and non-stationary nature of environmental variability and with the dynamic responses of ecological systems.

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