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PALEOECOLOGICAL INSIGHTS ON CONSERVATION OF BIODIVERSITY: A FOCUS ON SPECIES, ECOSYSTEMS, AND LANDSCAPES

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Abstract. Environmental changes of the Quaternary have driven changes in biodiversity at every level of organization from genetic variation within populations of individual species to gradients in composition of biotic communities and heterogeneity of vegetation mosaics across landscapes. In the southern Appalachian Mountains, increased seasonality of climate during the changeover from glacial to interglacial conditions in the late Pleistocene and Holocene resulted in landscape instability that fostered a fine-grained, heterogeneous mosaic of habitats supporting a diverse biota. Ecotones between alpine, boreal, and temperate ecosystems in the Appalachians shifted dramatically through the Holocene in response to the passage of critical thresholds of temperature and changing disturbance regimes. Regional projections of future greenhouse-gas-induced climatic warming indicate that alpine tundra may be lost between 44° and 57° N and *Picea rubens–Abies fraseri* forests may become extinct in the southern Appalachians. Montane *Picea rubens–Abies balsamea* forests probably will be perpetuated between 44° and 49° N. Disjunct populations of alpine tundra species may persist below climatic treeline in small patches of open habitat. Biotic responses to late-Quaternary environmental changes indicate that a primary conservation emphasis should be to predict the effects of changes in landscape-level environmental processes on biodiversity.

Key words: Appalachian Mountains; biodiversity; climate change; greenhouse world; landscape heterogeneity.

Introduction

Current efforts to conserve biodiversity in the southeastern United States are predicated upon ecological principles that place conservation biologists in one of two positions. In the first case, management is directed toward protection of individual, often reproductively isolated populations of threatened species. A second alternative is to maintain landscape-sized reserves in hopes that rare species will be accommodated within the patchwork of the overall landscape mosaic.

Legal mandates of the United States federal government regarding recovery of threatened and endangered species encourage ecologists to place research emphasis upon genetic variation and demographics of local species populations (Schemske et al. 1994). Many of the federally listed plant and animal species currently persist in less than half a dozen populations, each numbering a thousand or fewer individuals (Hamrick et al. 1991, Wilcove et al. 1993, Schemske et al. 1994). Immediate threats to continued existence of many rare vascular plant species are primarily anthropogenic, with species losses occurring as a result of habitat loss and fragmentation of ecosystems from continued land development as well as because of direct human activities including trampling and collecting (White and Bratton 1981, Schemske et al. 1994). The focus on recovery of endangered species is based upon the presumption that the most important factor in maintaining biodiversity is alleviating near-term, direct human impacts.

Because of the seeming intractability of surveying the physiological, genetic, and life-history characteristics of each species in the complex biota in species-rich regions such as the southeastern United States (Martin et al. 1993), an alternative recommendation has been proposed that focuses conservation efforts upon higher levels of ecological organization to take into account a landscape-level context for habitat richness and biodiversity (Franklin 1993). Franklin (1988) defined compositional, structural, and functional attributes of biodiversity as ''targets'' for conservation efforts. He later (Franklin 1993) suggested that landscape heterogeneity is important in shaping patterns of biodiversity and that conservation efforts be directed at spatially explicit, landscape-level attributes. Examples include maintaining structural or functional corridors linking species metapopulations (Fahrig and Merriam

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TABLE 1. Ecotone analyses of late-Quaternary sites along a transect from 30° to 60°N, from the Gulf Coastal Plain, through the Appalachian highlands, to the Canadian Arctic. Values for ecotone positions are expressed in units of 10^3 yr BP.

Site	Latitude (°N)	Longitude (°W)	Elevation (m)	Tundra	Treeline ecotone	Boreal conifer forest
Tunica Hills, Louisiana	30.9	91.5	52	⋯	⋯	⋯
Andersonville, Georgia	32.2	84.1	92	⋯	⋯	⋯
White Pond, South Carolina	34.2	80.8	90	⋯	⋯	>19.1–12.8
Nonconnah Creek, Tennessee	35.1	89.9	76	⋯	⋯	24.0–12.5
Flat Laurel Gap, North Carolina	35.4	82.8	1475	⋯	⋯	?
Anderson Pond, Tennessee	36.0	85.5	300	⋯	⋯	20.0–12.5
Saltville, Virginia	36.9	81.7	525	⋯	⋯	>15.5–12.5
Potts Mt. Pond, Virginia	37.6	80.1	1091	⋯	⋯	?
Brown's Pond, Virginia	38.2	79.6	620	⋯	⋯	17.3–12.8
Cranberry Glades, West Virginia	38.2	80.3	1029	>20.0–13.0	13.0	13.0–12.2
Big Run Bog, West Virginia	39.1	79.6	980	>17.0–13.9	13.9	13.9–10.8
Buckles Bog, Maryland	39.6	79.3	814	>19.0–12.7	12.7	12.7–10.5
Crider's Pond, Pennsylvania	40.0	77.6	289	?	?	>15.2–11.0 (forest–tundra from >15.2–13.3)
Longswamp, Pennsylvania	40.5	75.7	192	>14.0–12.2	12.2	12.2–9.7
Tannersville, Pennsylvania	41.0	76.3	277	>14.0–13.3	13.3	13.3–10.0
Nichols Brook, New York	42.6	78.5	439	⋯	⋯	14.9–10.0
Mirror Lake, New Hampshire	43.9	71.7	213	>13.9–11.5	11.5	11.5–10.0
Deer Lake Bog, New Hampshire	44.0	71.3	1325	14.0–10.3	10.3	10.3–0.0
Kinsman Pond, New Hampshire	44.1	71.7	1140	>11.0–9.8	9.8	9.8–0.0
Lonesome Lake, New Hampshire	44.1	71.7	900	>11.0–10.6	10.6	10.6–8.0; 3.0–0.0
Heart Lake, New York	44.2	74.0	661	>12.0–10.5	10.5	10.5–9.5
Lost Pond, New Hampshire	44.3	71.2	650	>12.6–11.0	11.2	11.2–10.0
Lake of the Clouds, New Hampshire	44.3	71.3	1542	>13.0–10.3; 5.0–0.0	10.3; 5.0	10.3–5.0 (krummholz)
Moulton Pond, Maine	44.6	68.6	143	14.0–11.7	11.7	11.7–9.7
Lac Caribou, Québec	48.2	64.9	116	>13.4–10.0	10.0	10.0–8.9
Lac Du Diable, Québec	48.9	66.1	494	>10.7–10.6	10.6	10.6–0.0
Lac Turcotte, Québec	49.2	65.8	457	>10.6–10.4	10.4	10.4–0.0
Lac A Leonard, Québec	49.2	65.8	17	?	>9.4	>9.4–0.0
Moraine Lake, Labrador	52.3	58.1	385	>11.3–7.8	7.8	7.8–0.0
Lake Hope Simpson, Labrador	52.5	56.4	295	>11.0–8.0	8.0	8.0–0.0
Eagle Lake, Labrador	53.2	58.6	400	>10.6–6.2	6.2	6.2–0.0

TABLE 1. Extended.

Lower climatic spruce–fir ecotone	Edaphic populations of spruce or fir	Lower edaphic spruce–fir ecotone	References†
⋯	25.3–12.5	12.5	1; 2; 3
⋯	21.3	<21.3	2; 4
12.8	12.8–9.6	9.6	5
12.5	?	<12.5	6
>3.3	>3.3–0.0	⋯	7; 8
12.5	12.5–5.0	5.0	9
12.5	12.5–(<2.0)	<2.0	10
>11.1	>11.1–9.1	9.1	11
12.8	12.8–9.2	9.2	12
12.2	12.2–0.0	⋯	11
10.8	10.8–0.0	⋯	13
10.5	10.5–0.0	⋯	14
11.0	11.0–9.0; 0.5–0.0	9.0; 0.5	11
9.7	9.7–9.0	9.0	11
10.0	10.0–0.0	⋯	11
10.0	?	⋯	15
10.0	10.0–8.5; 2.0–0.0	8.5; 2.0	16; 17; 18
⋯	⋯	⋯	19
⋯	⋯	⋯	19
8.0; 3.0	8.0–3.0	⋯	19
9.5	9.5–6.5 1.8–0.0	6.5; 1.8	20; 21
10.0	10.0–0.0	⋯	19
⋯	⋯	⋯	16; 19
9.7	9.7–0.0	⋯	22
8.9	8.9–0.0	⋯	23
⋯	⋯	⋯	24
⋯	⋯	⋯	25
⋯	⋯	⋯	25
⋯	⋯	⋯	26; 27
⋯	⋯	⋯	26; 27
⋯	⋯	⋯	28

1994), and minimizing structural contrast between adjacent landscape units (Franklin 1993).

Environmental changes of the past 20 000 yr have affected biodiversity at every level of biological organization, from genetic differentiation within species to gradients in composition of biotic communities and landscape-scale pattern and process (Graham 1988, Hunter et al. 1988, Delcourt and Delcourt 1991). Biodiversity can be measured as the degree of genetic heterozygosity in populations (Hamrick et al. 1991), species richness (alpha diversity) of communities, species turnover along environmental gradients (beta diversity), and landscape heterogeneity (gamma diversity) (Whittaker 1975). Important processes influencing biodiversity (Noss 1990) range from demographic processes to interspecific interactions and species responses to disturbances and environmental changes. Over glacial–interglacial cycles, climatic and environmental changes have restructured biological systems, resulting in disassembly and reassembly of communities, individualistic migrations of species, and changes in genetic diversity resulting from alternate restriction and release of refugial populations (Davis 1981, Davis and Botkin 1985, Birks 1986, Cwynar and MacDonald 1987, MacDonald et al. 1993).

In this paper, we evaluate the applicability of two contrasting ecological approaches to conserving biodiversity in the Appalachian Mountains (a focus on the species populations within local ecosystems vs. an emphasis on landscape heterogeneity) in light of past and possible future shifts in the ecotones between alpine tundra, boreal coniferous forest, and temperate deciduous forest. Toward this end, we summarize available plant-fossil data from late-Quaternary sites in order to evaluate a previously developed model of changing landscape states, and then we project future shifts in ecotones in a ‘‘greenhouse world’’ based on scenarios from two different atmospheric circulation models.

METHODS

Reconstruction of late-Quaternary altitudinal shifts in ecotones

We examined published reports for radiocarbon-dated sites with detailed plant-fossil sequences along the Appalachian Mountains from North Carolina to Labrador (Table 1). For each site, we recorded the radiocarbon ages for the span of time associated with tundra, closed-canopy boreal coniferous forest, and hardwoods forest with locally persistent populations of *Picea* and *Abies*, as well as the timing of shifts between these vegetation types at each site where they occurred. To clarify the full-glacial (20 000 yr Before Present [yr BP]) southern limits of upland boreal forests and edaphically maintained *Picea* outliers along lowland, riparian corridors, we included additional plant-fossil sites from the Gulf and Atlantic Coastal Plains between 30° and 35° N (Table 1). To document Holocene fluc-

TABLE 1. Continued.

Site	Latitude (°N)	Longitude (°W)	Elevation (m)	Tundra	Treeline ecotone	Boreal conifer forest
Gravel Ridge, Labrador	55.0	62.6	565	>6.5–5.4; 0.3–0.0	5.4; 0.3	5.4–0.3 (forest–tundra)
Border Beacom, Labrador	55.3	63.2	470	>6.7–4.4; 3.0–0.0	4.4; 3.0	4.4–3.0
Caribou Hill, Labrador	55.7	63.3	475	>6.5–4.5; 1.0–0.0	4.5; 1.0	4.5–1.0
Snow Lake, Labrador	56.6	63.9	522	>5.3–0.0	···	···
Hebron Lake, Labrador	58.2	63.0	170	>7.3–0.0	···	···

† References: 1, Delcourt and Delcourt (1977); 2, Jackson and Givens (1994); 3, Delcourt and Delcourt (1996); 4, Watts (1980*a*); 5, Watts (1980*b*); 6, Delcourt et al. (1980); 7, Shafer (1986); 8, Shafer (1988); 9, Delcourt (1979); 10, Delcourt and Delcourt (1986); 11, Watts (1979); 12, Kneller and Peteet (1993); 13, Larabee (1986); 14, Maxwell and Davis (1972); 15, Calkin and McAndrews (1980); 16, Davis et al. (1980); 17, Davis et al. (1984); 18, Spear et al. (1994); 19, Spear (1989); 20, Jackson (1989); 21, Jackson and Whitehead (1991); 22, Davis et al. (1975); 23, Jette and Richard (1992); 24, Richard and Labelle (1989); 25, Labelle and Richard (1984); 26, Engstrom and Hansen (1985); 27, Hansen and Engstrom (1985); 28, Lamb (1980); 29, Lamb (1985); 30, Lamb (1984).

tuations of treeline at the altitudinal interface of alpine tundra with the latitudinal limit of arctic tundra, we examined additional sites from northeastern Canada between 55° and 60° N (Table 1).

Along the latitudinal transect of late-Quaternary sites (Figs. 1–3), we modified and generalized the topographic profile of Cogbill and White (1991) to show the elevations of the highest summits along the Appalachians north to the Canadian arctic plateaus. Modern ecotone positions are as determined by Cogbill and White (1991): (1) treeline (the lower limit of alpine tundra), extending from 1480 m elevation at 44° N to merge with the latitudinal margin of arctic tundra at 550 m, 55° N; (2) the lower limit of continuous montane *Picea–Abies* forest on well-drained, upland sites, extending from 1680 m at 35° N down to 150 m at 49°

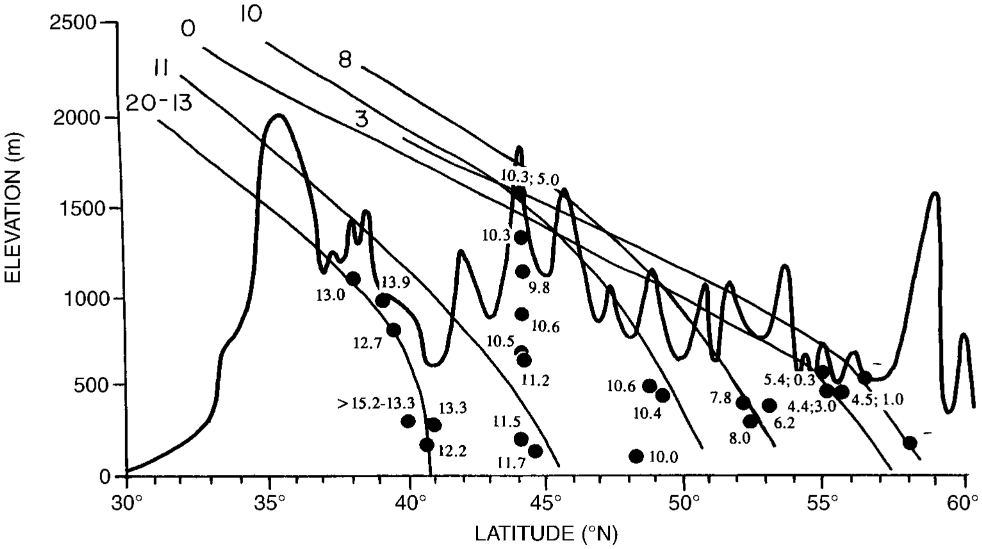

FIG. 1. Late-Quaternary positions of treeline, the ecotone between alpine tundra and montane conifer forest, in the Appalachian Mountains. The altitudinal treeline coincides with latitudinal treeline at 55° N in northeastern North America (Cogbill and White 1991). The altitudinal position for full-glacial and late-glacial treeline (20 000–13 000 yr BP; labeled as 20-13 on the graph, with numbers expressed in thousands of years Before Present [10^3 yr BP]) is documented by the lower limit for both radiocarbon-dated plant fossil evidence for alpine tundra and from relict Pleistocene evidence for nonforested periglacial landscapes (geomorphic data summarized in Mills and Delcourt [1991]). Plant-fossil sites used in documenting past ecotone positions (data from Table 1) are shown as solid dots at their altitudinal–latitudinal locations. Dashes identify plant-fossil sites with no late-Quaternary evidence for this ecotone. Both the generalized topographic profile of highest summits (the continuous elevational plot from 30° to 60° N) and the modern treeline position (the contour line for 0 yr BP on graph) are adapted from Fig. 2 in Cogbill and White (1991). Elevation is given in meters above sea level.

TABLE 1. Continued, extended.

Lower climatic spruce–fir ecotone	Edaphic populations of spruce or fir	Lower edaphic spruce–fir ecotone	References†
…	…	…	29
…	…	…	29
…	…	…	29
…	…	…	29
…	…	…	30

N; and (3) the lower limit for isolated *Picea rubens–Abies* communities, which are edaphically restricted to lowland sites, wetlands, or depressions with significant cold-air drainage, ranging from 1220 m at 35.6° N down to sea level in coastal Maine (43.7° N; Davis 1966). For each of the three ecotones, we plotted the location of each plant-fossil site as a solid dot. Ecotone positions are represented by isolines at 1000-yr intervals from 20 000 yr BP to present.

In the northern Appalachians, treeline occurs where 50% or more of the area is occupied by herbaceous or shrub tundra; krummholz thickets extend in wind-sheltered sites up to 400 m above the average treeline position. Based on least-squares linear regression, the equation for alpine elevation of treeline is ([-83 m/degree of latitude] × degree N) + 5150 m, with 1 SD ± 77 m (Cogbill and White 1991). For the latitude of the Great Smoky Mountains, the theoretical position of climatically maintained treeline is projected at 2195 m, 158 m higher than the highest summit (Cogbill and White 1991).

Cogbill and White (1991) characterized three bioclimatic thresholds for the lower altitudinal limit of alpine tundra within the northern Appalachians: (1) mean July temperature of 13°C ($\bar{X} = 12.9$°C; range 11.8°C to 13.8°C, $n = 4$); (2) mean annual temperature of -3°C ($\bar{X} = -3.4$°C; range -0.3°C to -5.2°C; $n = 4$); and (3) physiological drought accentuated by high winds and wind-driven snow (Daubenmire 1954).

Between 35° and 47.7° N, the lower ecotone for the *Picea–Abies* community is characterized by least-squares linear regression: elevation (meters) = ([-100 m/degree of latitude] × degree N) + 5229 m; $n = 19$ and 1 SD = ±80 m (Cogbill and White 1991). This ecotone corresponds with the upper transition to temperate deciduous forests and is shaped by two key bioclimatic thresholds: (1) mean July temperature of 17°C ($\bar{X} = 17.1$°C; range 16.6°C to 17.5°C; $n = 5$; Cogbill and White 1991); and (2) a consistent moisture regime coinciding with persistent cloud base, above which fog drip and rime ice occur during 10–40% of the growing season (White and Cogbill 1992).

Below the climatic *Picea–Abies*/deciduous forest ecotone, isolated montane populations of *Picea* and *Abies* persist in locales of suitable edaphic and microclimatic conditions, such as streamside ravines, topographic depressions with pockets of cold-air drainage, and wetlands and alluvial glades with impeded water flow or perched water tables. These edaphic outliers of *Picea–Abies* forest extend below their climatic ecotone by as much as 400 m in the Great Smoky Mountains (35.6° N) and by 500 m in the central Appalachians (43° N). Maritime climates steepen the montane gradients of latitude–elevation position, bringing the corresponding ecotones down to sea level along the Atlantic coast. The southern coastal limit for this edaphic community is 43.7° N (Davis 1966); the climatic limit for boreal *Picea–Abies* forest is 50.5° N (Cogbill and White 1991); and arctic treeline is ∼57.5° N (Rowe 1972).

In order to recognize past positions of ecotones between arctic–alpine vegetation, montane *Picea–Abies* forest, and deciduous forest, we used plant-fossil criteria, based upon modern assemblages of pollen grains and macroscopic remains of plants from modern lake sediments in the White Mountains of New Hampshire (Davis et al. 1980, Spear 1989, Spear et al. 1994) and in the Adirondack Mountains of New York (Jackson 1989, Whitehead and Jackson 1990, Jackson and Whitehead 1991). Total pollen influx is <2000 grains$\cdot$cm$^{-2}\cdot$yr^{-1} on mountain summits above treeline, whereas pollen influx generally exceeds 5000 grains$\cdot$cm$^{-2}\cdot$yr^{-1} within lower elevation, closed-canopy forests. Herb and shrub tundra is characterized by high percentages of nonarboreal pollen, including Cyperaceae, Gramineae, Ericaceae, Caryophyllaceae, *Lycopodium selago,* and other diagnostic taxa such as *Houstonia caerulea* (Spear 1989; nomenclature follows Fernald 1970). The lower limit of alpine tundra (the upper limit of krummholz) is identified by shrubs such as *Alnus crispa,* dwarf species of *Betula,* and *Salix uva-ursi,* along with stunted trees of *Abies* and *Picea.* Montane *Picea–Abies* forests are characterized by consistently high proportions of arboreal pollen and high concentrations of conifer needles within lake sediments (Jackson 1989). At sites below the lower climatic limit of this continuous, montane conifer forest, pollen percentages and needles of *Picea* and *Abies* decrease markedly, replaced by deciduous trees and temperate conifers such as *Pinus strobus* and *Tsuga canadensis* (Spear 1989, Jackson and Whitehead 1991).

Projection of future altitudinal shifts in ecotones

Projections of fossil fuel consumption provide the basis for predicting a doubling for concentrations of atmospheric carbon dioxide during the 21st century (Schneider 1989). Three independent general circulation models (GCMs) have simulated near-future climatic patterns of global warming in such a greenhouse world (Root and Schneider 1993). Global annual averages are anticipated to increase between 1.5° and 4.5°C (Strzepek and Smith 1995), producing a ''super-interglacial'' warming (Imbrie and Imbrie 1979) exceeding the 4°C mean global warming that occurred from 20 000 yr BP to today. Regional average values for high latitudes may increase by another 9°C (Kellogg and Schware 1982), threatening the floristic, structural, and functional integrity of tundra ecosystems (Billings 1987). For future climatic patterns simulated for a doubling of atmospheric CO_2 by AD 2100, mean July temperatures across eastern North America, are predicted to increase by 3.0°C (Goddard Institute for Space Studies [GISS] model), 3.4°C (Oregon State University [OSU] model), or 6.4°C (Geophysical Fluid Dynamics Laboratory [GFDL] model). GFDL model estimates exceed both glacial–interglacial rates and magnitudes of climatic and vegetational change documented over the past 20 000 yr (Overpeck and Bartlein 1989, Overpeck et al. 1991).

To estimate possible future shifts in key ecotones, we applied historic climatic lapse rates for the Appalachians, as calibrated by Leffler (1981), from weather stations near or on mountain summits from 35.1° to 44.5° N. For high-elevation sites, mean July temperatures represent the key bioclimatic thresholds controlling ecotone elevation (Cogbill and White 1991). The altitudinal lapse rate for the growing season is a lowering of 6.3°C average July temperature for each 1000 m increase in elevation. The corresponding latitudinal displacement of (midslope) montane ecotones is a decline of 1.06°C in mean annual temperature for each 1° latitude shift northward (Leffler 1981).

RESULTS

Late-Quaternary shifts in ecotones

Geomorphic features of sorted and patterned ground, such as stone polygons >2 m diameter, stone ellipses, and stone stripes, form by freeze–thaw action in modern areas of permafrost with mean annual temperatures colder than −4°C to −6°C (Goldthwait 1976). Relict Pleistocene features of sorted and patterned ground (with polygon diameters between 2 m and 10 m) have been identified in numerous locations on unglaciated Appalachian summits, from ~500 m elevation at 42° N to >1415 m at 35.6° N (Péwé 1983, Mills and Delcourt 1991). The corresponding linear equation of lower altitudinal position for Pleistocene-age, discontinuous permafrost south of 42° N is: elevation (meters) = ([−143 m/degree of latitude] × degrees N) + 6505 m. Between 39° N and 35° N, this permafrost zone (Mills and Delcourt 1991) is compatible with full- and late-glacial plant fossil evidence (Fig. 1; Table 1) of high-elevation alpine tundra from Cranberry Glades, West Virginia (Watts 1979), and Big Run Bog, West Virginia (Larabee 1986). Within several hundred kilometers of the glacial margin, however, a chill zone supported treeless tundra at markedly lower, unglaciated sites such as Buckles Bog, Maryland (Maxwell and Davis 1972) and at Longswamp and Tannersville Bog, Pennsylvania, the latter deglaciated before 14 000 yr BP (Watts 1979). The late-glacial position of forest–tundra was near Crider's Pond, Pennsylvania (Watts 1979), from >15 200 to 13 300 yr B.P. With glacial retreat from the northern Appalachians between 18 000 and 13 000 yr BP (Davis and Jacobson 1985), thinning glacial ice exposed montane peaks; deglaciated terrains were initially barren, periglacial deserts that were, in turn, colonized by alpine tundra (14 000–10 000 yr BP; sites from 43.9° to 44.3° N and from 213 to 1542 m; Likens and Davis 1975, Davis et al. 1980, 1984, Spear 1989, Jackson 1989, Jackson and Whitehead 1991, Spear et al. 1994). Within the White Mountains of New Hampshire, tundra was invaded by *Picea glauca* between 10 300 and 9800 yr BP, as treeline rose to form krummholz up to at least 1540 m between 10 000 and 5000 yr BP (Lake of the Clouds, Spear 1989; Fig. 1).

For reconstructed positions of alpine treeline in the northern Appalachians, Davis et al. (1980) reported that from 9000 to 5000 yr BP, *Abies* and *Picea mariana* krummholz was more extensive in high-altitude sites than today, indicating an early-Holocene warming of ~2°C above modern temperatures. Mid-Holocene warming was evidenced by anomalously high values of total pollen influx (up to 135 000 pollen grains$\cdot$cm$^{-2}\cdot$yr^{-1} at 8700 yr BP; 1976 Core B, Lake of the Clouds site, 1542 m). A corresponding peak in influx of *Picea* needle macrofossils indicated an increased number of summer freeze–thaw cycles in the alpine permafrost and accelerated colluvial transport of krummholz-plant fossils downslope to the lake basin. Subsequent lower representation for trees and increased fossil remains of herbaceous tundra plants indicate that treeline descended to its modern position between 5000 and 2000 yr BP (Spear 1989).

The full-glacial southern limits for *Picea*, *Abies*, and *Pinus banksiana* were between 33° and 34° N (Fig. 2), along a climatic ecotone between southern boreal-like forest and temperate mixed conifer–northern hardwood forest anchored by the Polar Frontal Zone (Delcourt and Delcourt 1984*a*, *b*, Delcourt et al. 1997). For example, the Atlantic Coastal Plain near White Pond in south-central South Carolina (32.2° N, 90 m elevation) supported boreal conifers from 19 100 to 12 800 yr BP, after which mesic deciduous forest became established (Watts 1980*a*, *b*). The *Picea–Abies*/deciduous forest ecotone (Fig. 2) shifted rapidly to high latitudes between 13 000 and 10 000 yr BP, and reached its farthest northward extension across eastern Canada in the mid-Holocene interval (Richard 1977, 1985, 1993). The maximum Holocene extent of the montane *Picea–Abies*/deciduous forest ecotone occurred in Quebec's Gaspé Peninsula between 7000 and 4000 yr BP (Labelle and Richard 1984, Richard and Labelle 1989,

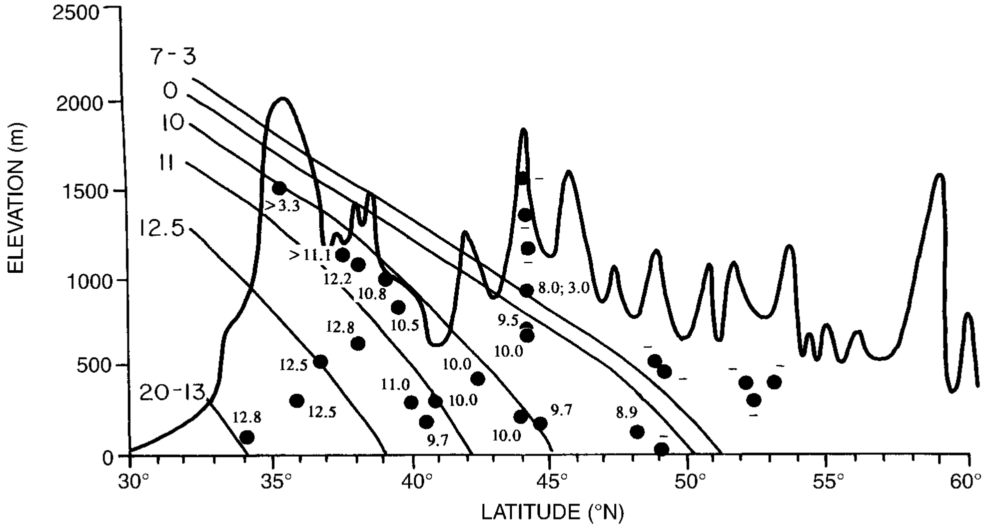

FIG. 2. Late-Quaternary positions for the lower (climatic) ecotone of montane *Picea–Abies* forest with deciduous forest (including temperate northern hardwoods and conifers such as *Tsuga*). Today, this montane ecotone corresponds with the lower limit of continuous *Picea* and/or *Abies* forest occupying well-drained uplands (Cogbill and White 1991). During the last glacial interval (from 20 000 to 13 000 yr BP, 20-13 on graph, expressed as thousands of years Before Present [10^3 yr BP]), the latitudinal limit for this *Picea–Abies* ecotone was anchored between 33° and 34° N, far south of the southernmost Appalachians. Between 13 000 and 7000 yr BP, this montane conifer ecotone shifted northward by nearly twenty degrees of latitude. Plant-fossil sites used in documenting past ecotone positions (data from Table 1) are shown as solid dots at their altitudinal-latitudinal locations; dashes indicate no late-Quaternary evidence for this ecotone. The topographic profile represents elevations of the highest Appalachian summits (adapted from Cogbill and White [1991]).

Jette and Richard 1992). Within the past 3000 yr, this lower montane ecotone of *Picea–Abies* forest has readjusted in response to graduate climatic cooling. Edaphically maintained populations expanded at some midlevel sites, such as Lost Pond (Table 1; Fig. 2), and outlier populations of *Picea rubens* and *P. mariana* reestablished in lower elevation, northern Appalachian sites (Spear 1989, Jackson and Whitehead 1991, Spear et al. 1994). The modern, lower climatic ecotone for montane *Picea–Abies* forest presented by Cogbill and White (1991; Fig. 2) agrees with plant-fossil evidence (Table 1).

After 12 500 yr BP, upland *Picea–Abies* communities experienced local extinction, as their summer bioclimatic tolerances were exceeded during heightened seasonal contrast in the early Holocene (that is, very cold winters and very hot summers; Kutzbach and Guetter 1986). Between 11 000 and 9000 yr BP, the ecotonal position for edaphically restricted, ''relict'' populations of *Picea* and *Abies* (Fig. 3) rose to modern altitudinal limits within the southern Appalachians (Watts 1979, Delcourt and Delcourt 1984*a*, Shafer 1986, 1988). In contrast, within the last 4000 to 3000 yr, outliers of relatively species-poor *Picea* communities have newly colonized midelevation wetlands in the central Appalachians. These plant-fossil sites are situated at or below the lower edaphic ecotone of Cogbill and White (1991). Marginal *Picea* populations have colonized or reoccupied suitable edaphic sites such as poorly drained, acidic wetlands, nutrient-poor or exposed rocky substrates, or topographic depressions characterized today by cold-air drainage (Delcourt and Delcourt 1986). In historic times, forest clearance and slash fires have locally eliminated edaphic populations of *Picea rubens* and *Abies fraseri* (Shafer 1986) and reduced the area of montane spruce–fir forest (Cogbill and White 1991).

Future altitudinal shifts in ecotones

Using the most conservative GISS model, a 3.0°C increase in mean July temperature would imply a warmer and longer growing season. Under this regime, the climatically limited ecotones would rise by ~480 m, and their coastal positions (0 m above sea level) could extend northward by 2.8° latitude.

Fig. 4 illustrates the consequences of future greenhouse warming: (1) loss of alpine tundra from 44° to 57° N; (2) probable extinction of upland *Picea rubens–Abies fraseri* forests in the southern Appalachians; (3) perpetuation of montane *Picea–Abies* forests from 44° to 49° N; and (4) northward displacement of conifer population centers in the restricted boreal-forest region. We speculate that under these conditions disjunct populations of alpine tundra probably would be maintained below climatic treeline in small patches of open habitat. Using the Quaternary record as a past precedent, we further speculate that rather than eliminating a host of species from the entire mountain region, this increase in temperatures might instead promote increased species richness at high elevations and midlatitudes.

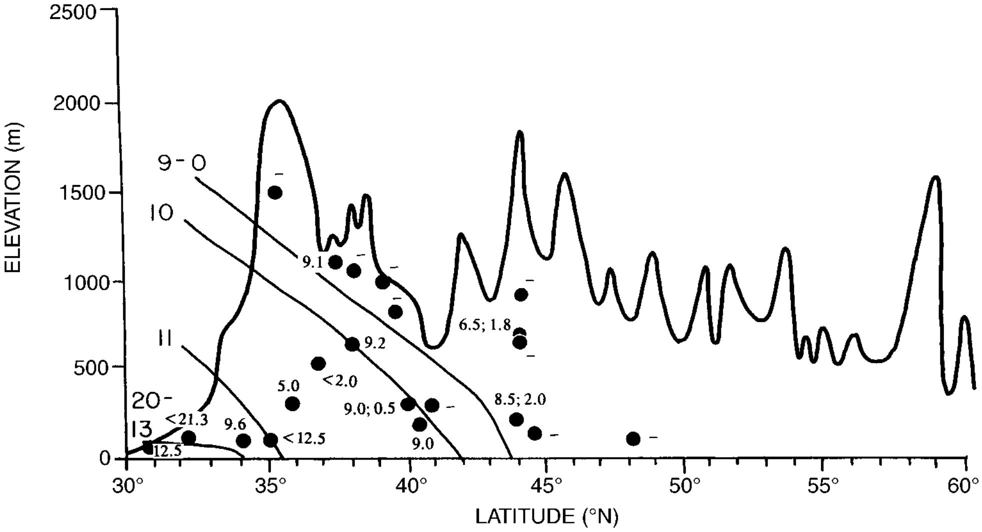

FIG. 3. Late-Quaternary positions for the lower (edaphic) ecotone for isolated montane or lowland populations of *Picea* and/or *Abies*. Today (0 yr BP), these isolated *Picea–Abies* stands occur in sites as much as 500 m below the lower (climatic) ecotone of montane spruce–fir forest within the Appalachians (Cogbill and White 1991). During full-glacial times (20 000 to 13 000 yr BP, graphed as 20-13 in terms of thousands of years Before Present [0 yr BP]), ''edaphic'' outliers of the Tunica Hills form of *Picea* extended along the Lower Mississippi Alluvial Valley south beyond the latitudinal limit of *Picea* at 33° N (Jackson and Givens 1994, Delcourt and Delcourt 1996, Delcourt et al. 1998). Plant fossil sites used in documenting past ecotone positions (data in Table 1) are shown as solid dots at their altitudinal–latitudinal locations; dashes indicate no late-Quaternary evidence for this ecotone. The topographic profile represents elevations of the highest Appalachian summits (adapted from Cogbill and White [1991]).

In contrast, for the most extreme scenario of 6.4°C summer warming by AD 2100 (Fig. 5; GFDL model), montane ecotones would be raised by ~1020 m and their coastal counterparts would be diverted northward by 6° of latitude. Both alpine and arctic tundra would be widespread only north of 63.6° N. Montane *Picea rubens–Abies fraseri* communities would survive in highlands from 51° to 55° N, and, given sufficient time

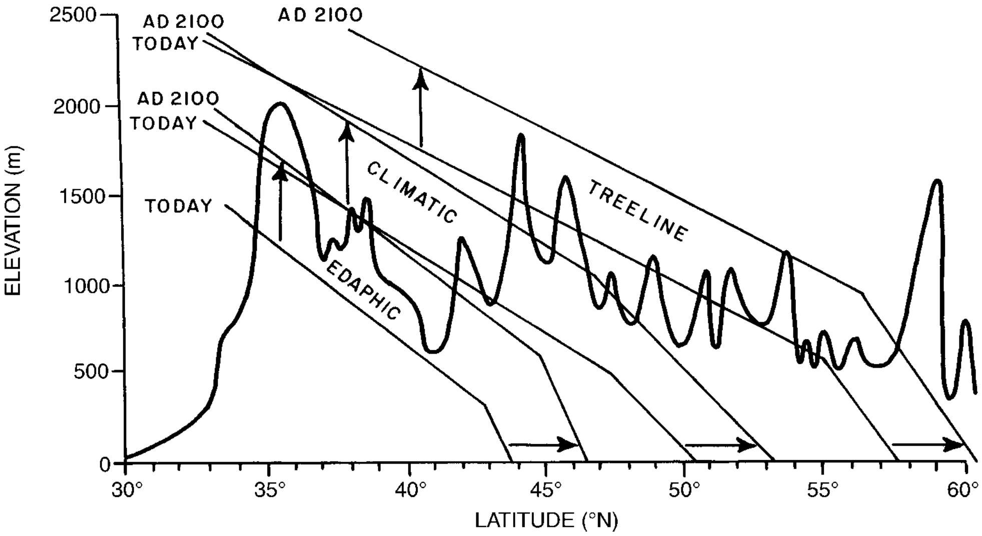

FIG. 4. Projected ecotonal shifts (of alpine treeline, the lower climatic limit of montane *Picea-Abies* forest, and the lower edaphic limit of restricted *Picea–Abies* stands) in response to accelerated summer warming by AD 2100 in a greenhouse world. The most conservative climatic model (Goddard Institute for Space Studies, GISS) simulates a 3.0°C increase in mean July temperature across eastern North America in a ''super-interglacial'' climatic regime, with a doubling in atmospheric concentrations of carbon dioxide (Overpeck et al. 1991). Based upon lapse rates observed in the Appalachians (Leffler 1981), these three ecotones could be displaced northward by a (calculated) altitudinal rise of 480 m and a latitudinal shift of 2.8° N. Modern ecotone positions and the topographic profile for the highest Appalachian summits are based upon Cogbill and White (1991).

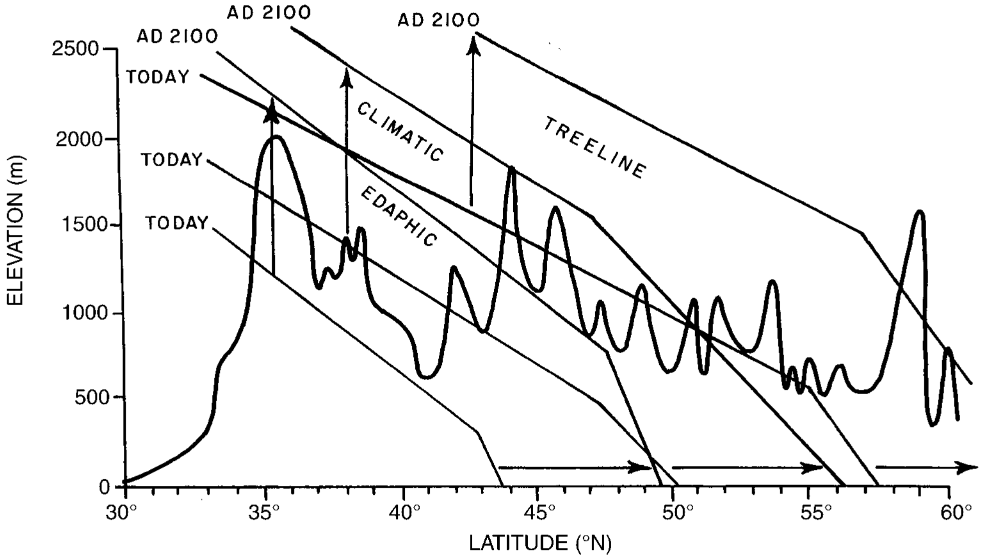

FIG. 5. Projected ecotonal shifts (of alpine treeline, the lower climatic limit of montane *Picea–Abies* forest, and lower edaphic limit of restricted *Picea–Abies* stands) in response to accelerated summer warming by AD 2100 in a greenhouse world. The most extreme climatic model (Geophysical Fluid Dynamics Laboratory, GFDL) simulates a 6.4°C increase in mean July temperature across eastern North America in a ''super-interglacial'' climatic regime, with a doubling in atmospheric concentrations of carbon dioxide (Overpeck et al. 1991). Based upon lapse rates observed in the Appalachians (Leffler 1981), these three ecotones could be displaced northward by a (calculated) altitudinal rise of 1020 m and a latitudinal shift of 6° N. Modern ecotone positions and the topographic profile for the highest Appalachian summits are based upon Cogbill and White (1991).

for species migrations, boreal forest would invade what is today the subarctic tundra region. In this extreme case, edaphically restricted *Picea–Abies* stands would persist only on northern Appalachian summits between 44° and 49° N. Even these scenarios may be minimal estimates of species displacements, as greenhouse-induced warming is expected to continue well beyond AD 2100 (Root and Schneider 1993).

DISCUSSION

In the Great Smoky Mountains of eastern Tennessee and western North Carolina, although the overall species richness of the flora diminishes with increasing elevation and with decreasing montane area available as habitat on the highest summits, the number of threatened and endangered vascular plant species increases with increasing elevation, with 14 taxa recorded from mesic, nonforested sites above 1500 m. From 33 to 50% of the rare plant species are restricted to patchy open-ground habitats of wet meadows, landslide scars, or cliff faces and constitute 42% of the high-elevation flora (White 1984). White (1984) and Wiser (1994) interpreted many of the rare plant species of high-elevation, open-ground habitats as relicts of an alpine flora, with alpine tundra communities postulated to have occupied the southern high peaks during full-glacial times. Interglacial warming, and the associated altitudinal rise in treeline above the highest summits, together with the geographic restriction and genetic isolation of tundra populations, have led to the narrow endemics and disjunct populations of rare species observed today (White 1984, Wiser et al. 1998).

Based upon geomorphic evidence, Delcourt and Delcourt (1987, 1988) and Shafer (1988) proposed a dynamic model wherein alternate landscape states are driven by passage of key climatic and geomorphic thresholds (Figs. 6 and 7). Ice-age periglacial regimes promote alpine tundra and permanent snowfields on highest summits, with mean annual temperatures as low as −8°C. In the Great Smoky Mountains, boreal coniferous forest would have occurred only below ~1450 m. Warming of mean annual temperature to near 0°C during late-glacial time, along with the heightened seasonal contrast (very cold winters, very hot summers) that characterized the transition from glacial to interglacial climates (Kutzbach and Guetter 1986), resulted in freeze–thaw churning of soils and downslope colluvial movement of earthen debris in water-saturated solifluction lobes (Shafer 1988, Mills and Delcourt 1991). Physical disturbance thus maintained patches of bare ground, favoring perpetuation of herbaceous, alpine tundra taxa even within an extensive landscape matrix of forest. With diminished seasonality of climate and sustained postglacial warming, relict Pleistocene periglacial deposits become stabilized on mountain slopes. Relict populations of alpine tundra and forest–tundra species have survived during interglacials in wet meadows of intermontane basins, on landslide scars, and along exposed cliff edges, sites kept open in part because of continuing physical disturbance in the form

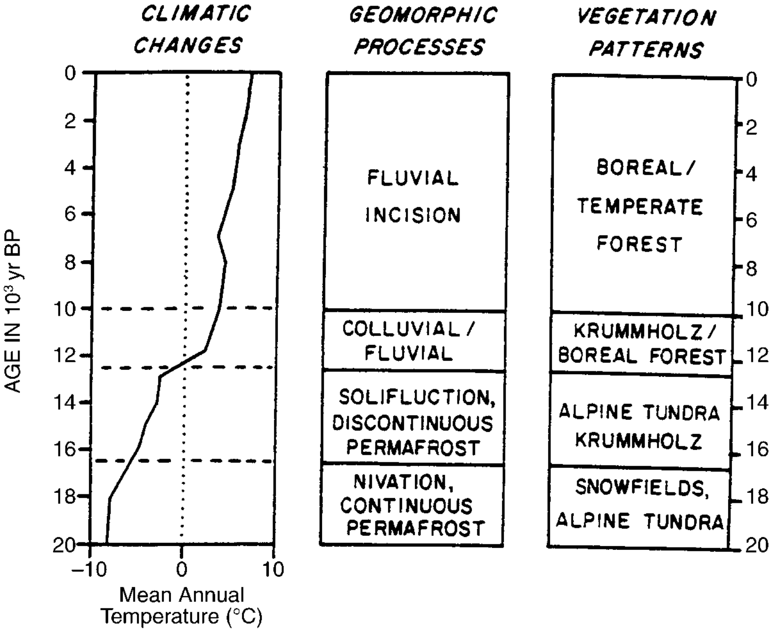

FIG. 6. Late-Quaternary model of alternate, periglacial and interglacial states of landscape dynamics, driven by the passage of key climatic, geomorphic, and vegetational thresholds between 12 500 and 10 000 yr BP in high-elevation sites of the southern Appalachian Mountains (modified from Shafer 1988; from Delcourt and Delcourt 1991).

of shifting stream channels (Delcourt 1985, Shafer 1986, 1988), catastrophic debris slides following intense rainstorm events (Clark 1987), and spalling of rock faces, respectively.

A specific example of a boreal species that has persisted in the southern Appalachians since the late Pleistocene is *Alnus crispa.* This shade-intolerant shrub is most abundant in northeastern Canada at the forest–tundra transition (Rowe 1972), where it grows on unstable upland slopes or in sheltered sites along stream or lake margins (Lamb 1984). Within the northern Appalachians, *Alnus crispa* occurs at treeline (White Mountains, New Hampshire, 44.0° N, 1300 m; Spear 1989) and in high-elevation herb–shrub tundra (Adirondack Mountains, New York, 44.1° N, above 1450 m; Jackson 1989). Disjunct populations persist in the southern Appalachians on the Roan Mountain massif, Tennessee–North Carolina (36.1° N, 1800 m; Ramseur 1960, Watts 1979). In the central Appalachians, full-glacial populations of *Alnus crispa* grew within montane conifer forests (Delcourt and Delcourt 1986, Kneller and Peteet 1993) as well as at treeline and higher in shrub tundra (Watts 1979, Larabee 1986). Early Holocene sediments record high influx of *Alnus crispa* pollen and plant macrofossils during a 2000–4000 yr interval when open-ground habitats persisted because of frequent geomorphic disturbances. The population maximum for *Alnus crispa* tracked the early-Holocene change in treeline position (Fig. 5), which shifted northward from the southern Appalachians (13 000–10 000 yr BP) to New England and the Gaspé Peninsula of Quebec (11 000–7000 yr BP), and finally to Labrador (9000–6000 yr BP). We suggest that early-Holocene landscape instability in the Appalachian Mountains fostered a fine-grained, heterogeneous landscape mosaic that included patches of open ground, which promoted the spread of this disturbance-adapted boreal species.

The present-day restriction of *Alnus crispa* to the summit of Roan Mountain is a result of the progressive restriction of its habitat in the southern Appalachian Mountains during the mid- to late Holocene. The implication of past climate changes for the future is therefore that during times of relatively rapid climate warming (i.e., early Holocene and near-future intervals), landscape instability may result from crossing both biological and geomorphic thresholds. At such times, habitat heterogeneity may increase because of increased geomorphic instability. This may promote expansions in the habitats of certain disturbance-adapted taxa, as has been demonstrated by the paleoecological record for *Alnus crispa* in the early Holocene.

CONCLUSIONS

The strong focus of many conservation biologists on immediate recovery of small populations of rare and endangered species diverts attention from the probability that widespread environmental changes in the near future may compound other, more local threats to continued existence of species that are narrowly adapted to specific habitats. Given a 60% probability that mean global temperatures will warm by 1.5° to 4.5°C

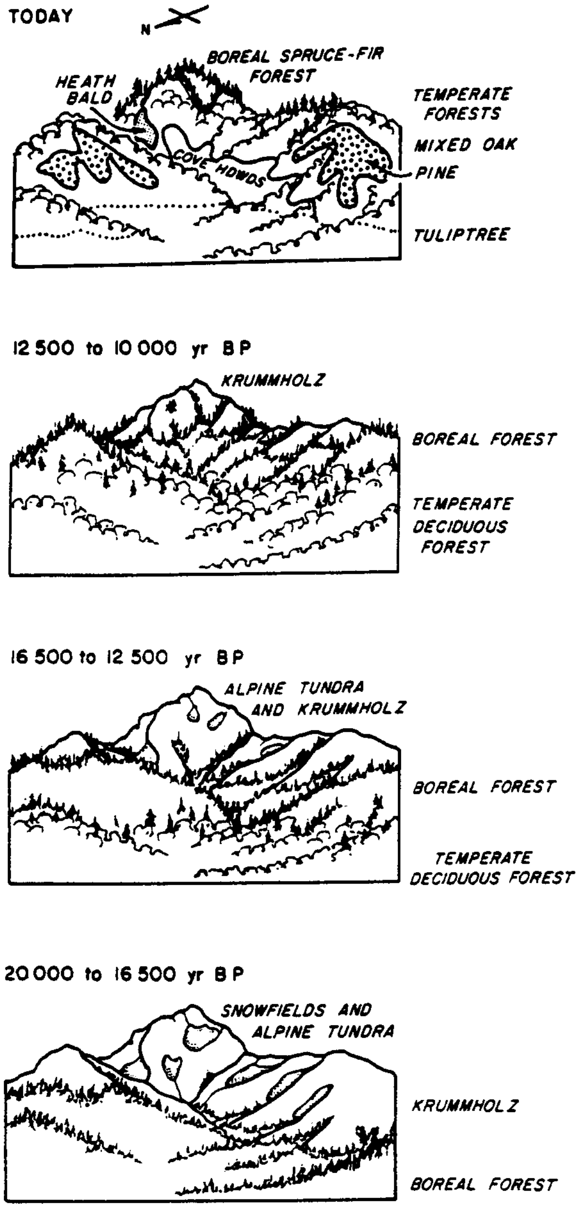

FIG. 7. Depiction of changes in vegetation within the Great Smoky Mountains, Tennessee–North Carolina, portrayed over the past 20 000 yr (from Delcourt and Delcourt 1991).

over the next century because of the carbon dioxide-induced greenhouse effect (Root and Schneider 1993), expected regional-scale climate changes include changes in the seasonal distribution of air masses, locations of storm tracks, and intensification of frequency and strength of hurricanes (Schneider 1989). Although in certain cases these environmental changes may alter prevailing disturbance regimes and locally enhance patterns of biodiversity, in many instances extinction of rare species is likely to result from loss of suitable habitat and inability of species to migrate rapidly. Even species that are now common may be vulnerable to local or global extinction if environmental changes cross physiological thresholds of tolerance (Overpeck et al. 1991, Davis and Zabinsky 1992). The combination of changing climate and disturbance regimes potentially could result in the replacement of many native species by more competitively superior exotic invasives (Delcourt and Delcourt 1992, 1993).

Species-specific and landscape-level approaches both tend to view biodiversity as a static ‘‘target’’ for conservation. But a focus solely on ‘‘targets’’ for conservation assumes that the targets are not moving. To the extent that environmental thresholds shift in space and time, biological tolerance limits will be exceeded, and individual species will either (1) adapt, (2) migrate, or (3) become extinct. An alternative viewpoint in line with contemporary paradigms in ecology is to focus on processes and dynamics responsible for community and landscape organization (Pickett and White 1985, Turner 1989, Pickett et al. 1992). Particularly in light of impending global climatic changes that may change previously existing disturbance regimes and shift competitive advantages of species along changing environmental gradients, conservation may not be successful for ecological entities such as individual species that are closely tied to specific, narrow habitats (Pickett et al. 1992). Rather, ‘‘it is the processes that have generated or that maintain species, community, ecosystem, or landscape, and the spatial context and the functional connections within that context that must be maintained’’ (Pickett et al. 1992: 84).

The Quaternary paleoecological record illustrates that a primary conservation focus should be on understanding and predicting changes in environmental processes that affect biodiversity. Given that landscape heterogeneity changes through time and that species abundances are linked to specific habitats, including their disturbance regimes, it is important to understand populations within the context of ecosystems processes (disturbance regimes, climatic thresholds) in order to predict the consequences of future environmental changes. Our evaluation of the ecological history of the Appalachian Mountains supports a two-stage management approach to conservation: (1) act to mitigate immediate anthropogenic impacts to preserve genetic diversity in populations of threatened and endangered species; and (2) act to maintain and expand the boundaries of biological reserves that constitute both altitudinal and latitudinal corridors for species migrations, thus preserving potential future habitats.

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