A PALEOECOLOGIC PERSPECTIVE ON PAST PLANT INVASIONS IN YELLOWSTONE

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ABSTRACT.—The role of climate and natural disturbance in the past provides a context for understanding present and future changes in biota. The vegetation history of the Yellowstone region, like that of North America as a whole, is largely one of plant invasions and extinctions in response to changes in climate and environment. When Holocene plant migrations are examined on multiple spatial and temporal scales, several generalities are apparent. First, at a continental and regional scale, plant migration patterns followed the direction of climate change, whereas at local scales plant colonization was governed by site-specific conditions and possibly by biotic interactions. Second, species were individualistic in their response to climate change, and, as their ranges shifted across the landscape, existing communities were dismantled and new ones were formed. Individual species met little resistance from existing communities. Third, rates of species invasion were astonishingly rapid, suggesting that rare long-distance dispersal events were critical. Fourth, fire during periods of climate change was an important catalyst in allowing the invasion of new species, but it is unlikely that a single fire event triggered irreversible vegetation change.

Regional climate and biotic changes in response to projected increases in atmospheric CO_2 in the next century suggest an even more complex picture than in the past. Model simulations portray changes in temperature and precipitation in the Yellowstone region that have not occurred in the last 20,000 years. Likewise, projected changes in species ranges, including latitudinal, longitudinal, and elevational shifts, require faster rates than anything observed in the fossil record. Increased fire occurrence may help maintain some native taxa but promote the decline of others. Thus, future conditions are likely to create evermore opportunities for exotic species to invade and establish within the Yellowstone region.

Key words: *Yellowstone, past plant migrations, paleoecology, fire history, invasive species.*

Exotic species are those that occur in a given place as a result of direct or indirect, deliberate or accidental action by humans (not including deliberate reintroduction). . . . The exotic species introduced because of such human actions would not have evolved with the species native to the place in question, and, therefore, would not be a natural component of the ecological system characteristic of the place (National Park Service 1988).

This definition of exotic species emphasizes the fact that human actions are responsible for the introduction of new species that pose considerable threat to the health of native ecosystems. The definition also implicitly raises questions about the natural state of ecosystems on long time scales and the relative importance of biotic invasions and range expansions prior to extensive Euro-American activity. To address these issues requires an examination of the paleoecological record, inasmuch as such data disclose the response of biota in the face of past environmental changes (Millar and Woolfenden

1999) and provide a natural baseline against which to measure present conditions (Swetnam et al. 1999). A long-term perspective also allows us to consider the role of climate and natural disturbance in accomplishing major biogeographic changes. Paleoecologic data thus offer a context by which to evaluate present invasions and their ecological consequences.

Information on past changes in species distributions is also relevant in assessing the potential impact of rising concentrations of atmospheric CO_2 and other "greenhouse" gases on ecosystems in the future. Land managers around the world are engaged in complicated and expensive efforts to combat the introduction and expansion of alien species, and several studies have noted that projected climate changes will accelerate the success of these invasions (e.g., Vitousek et al. 1996, Dukes and Mooney 1999, Mooney and Hofgaard 1999). Rates of exotic species spread are alarming, particularly in areas of highly altered habitat and human-mediated disturbance, but even

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seemingly pristine places, like Yellowstone National Park, are not immune to the assault. At present, over 170 species of nonnative plants have been identified in Yellowstone, and additional invasions are imminent (Olliff et al. 2001, Whipple 2001).

The objectives of this paper are to (1) provide some examples of past plant migrations in North America and Europe, as well as in the Yellowstone region, during the Holocene (the last 10,000 years of earth history), (2) describe the role of natural disturbance as a trigger of past vegetation change, and (3) compare past and present biogeographic changes in Yellowstone with projections of ecosystem changes in the future.

BIOTIC INVASIONS IN THE PAST

Pattern of Plant Migrations

An "invasive species" has been defined as one whose introduction does or is likely to cause economic or environmental harm or harm to human health (President's Executive Order EO13112 of February 3, 1999). Certainly, this narrow definition does not fit the spread of native species in the past, but current invasions and past "migrations" both require species to colonize, establish, and reproduce in new plant communities. The paleoecologic record therefore offers insights into the ecological consequences of introducing new species into established communities, as well as the potential rate of species spread.

The paleoecologic record of the last 20,000 years provides evidence of significant adjustments in the geographic distribution of plants and animals since the last ice age. These biogeographic changes involved displacements that ranged from a few to hundreds of kilometers (see Webb et al. 1983, Huntley 1988, Webb 1988, Elias 1991, FAUNMAP Working Group 1996), and they were accomplished by a series of biological invasions in which new species moved into and potentially disrupted existing ecosystems. The paleoecologic record indicates that species were highly individualistic in the direction and rate of migration because each had particular environmental requirements that dictated their pattern of colonization. As a result, the ranges of species shifted in no single direction, and communities were continually formed and dismantled in the process. To accomplish the long-term patterns of migration,

the rates of invasion for most species were breathtakingly fast, e.g., on the order of 200–1500 m · yr^{-1} for major tree taxa (Huntley 1988, Birks 1989). Long-distance dispersal was apparently critical in the past, and the process was probably similar to exotic species invasions in this century that begin with a quiescent phase of little discernible range change and are followed by an active phase of explosive expansion (Mack 1986, Pitelka et al. 1997).

The large-scale picture of past tree invasions comes from examining networks of radiocarbon-dated pollen records. One approach for analyzing pollen data is to determine the timing of the first appearance of species at individual pollen sites and compile these "first appearance" dates to construct a map of range limits for different time intervals (pollen isochrone maps; see Davis 1981a, 1983, Gaudreau and Webb 1985). Another approach is to plot the abundance of particular pollen types at specific locations and develop pollen percentage contour maps (isopoll maps; see Huntley and Birks 1983, Webb et al. 1983, Bartlein et al. 1986, Huntley 1988, Webb 1988). Changes in the spatial patterns of pollen abundance are then used to track the distribution of the species at different times.

The pollen record of spruce in North America and Europe provides an example of the range shifts that occurred in the last 18,000 years[2] (Webb and Bartlein 1992; Fig. 1). In North America a network of pollen records indicates that spruce (*Picea glauca* and *P. mariana*) resided in the southern and central Great Plains during the last ice age. As the climate warmed, spruce shifted its range northward and eastward into deglaciated regions. By 12,000 years ago, it occupied a broad region along the southern margin of the retreating ice sheet. The advance of spruce in interior Canada was particularly rapid from 12,000 to 9000 years ago and has been attributed to strong southeasterly winds off the ice sheet that may have transported seeds exceptional distances (Ritchie and MacDonald 1986). At 6000 years ago, the northern limit of spruce lay north of its present position as a result of higher-than-

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[2]Ages are given in radiocarbon year, except where noted, because most of the literature cited uses radiocarbon year. Radiocarbon ages depart from true calendar year for some periods of the Holocene (Stuiver et al. 1998) and affect calculation of rates of change. The general picture of invasion is unchanged by using radiocarbon dates; however, the rates of change are different.

Spruce (Based on Pollen Data)

18,000 ^{14}C yr BP   15,000 ^{14}C yr BP   12,000 ^{14}C yr BP   9000 ^{14}C yr BP   6000 ^{14}C yr BP   3000 ^{14}C yr BP   Present
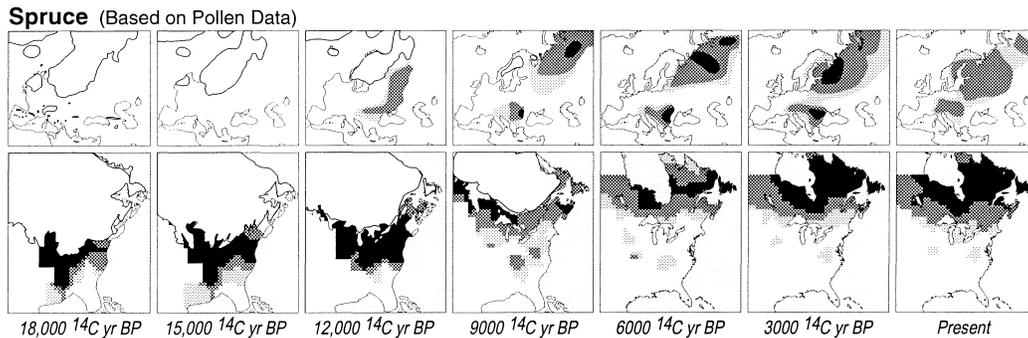
Fig. 1. Geographic variations in the abundance of spruce (*Picea*) pollen in Europe (top row) and eastern North America (bottom row). Darkest shading represents >20% spruce, medium shading represents 5–20%, and light shading represents <1% (after Webb and Bartlein 1992).

present temperatures. In the last 6000 years, the limit of spruce has shifted southward because of cooler conditions. The modern boreal forest formed in only the last 3000 years when the ranges of white spruce (*Picea glauca*), black spruce (*P. mariana*), jack pine (*Pinus banksiana*), tamarack (*Larix laricina*), and balsam fir (*Abies balsamifera*) overlapped. The present distribution of boreal mammals was also attained at this time (FAUNMAP Working Group 1996). In Europe, Norway spruce (*Picea abies*) moved from its glacial range in northwestern Russia westward into Fennoscandia and eventually into the Baltic region and Sweden. Some researchers have suggested late-Holocene deforestation as the cause of the spruce expansion in Fennoscandia; however, climate-model results indicating lower winter temperatures and increased winter precipitation may better explain the pattern (Huntley 1988).

An example of a prehistoric pathogen invasion that had large ecological consequences comes from eastern North America. The invasion occurred 4650 ± 300 years ago when forests of hardwoods and conifers extended across the eastern and central U.S. (Gaudreau and Webb 1985). At this time populations of eastern hemlock (*Tsuga canadensis*) declined precipitously in the forest, as evidenced by the sharp drop in hemlock pollen percentages at most sites. The demise was rapid, widespread, and showed no discernible geographic pattern. Hemlock was the only victim detected in the fossil record, but organisms that relied on hemlock probably also declined. Davis (1981b) attributed the "hemlock decline" to the effects

of a pathogen, not unlike the European chestnut blight of the 1900–1920s that killed American chestnut (*Castanea dentata*) in the same forests. Competing theories, such as climate change or widespread natural disturbance, do not adequately account for the abrupt decline of a single species over such a large area. A recent study (Bhiry and Filion 1996) suggests that a series of defoliating events between 4900 and 4200 years ago led to the loss of hemlock; hemlock looper (*Lambdina fiscellaria*) and other lepidopteran defoliators, including spruce budworm (*Choristoneura fumiferana*), were the likely culprits. These insects have their greatest impact during warm, dry conditions, as was the case at the time of the hemlock decline.

How long did it take for hemlock to recover following its decline? Pollen records suggest 500–1000 years, but forests in most places were never the same (Davis 1981b). In the absence of hemlock, tree species like maple (*Acer*) and beech (*Fagus*) expanded their range and presumably took over the ecological space occupied by hemlock. Moreover, the climate 1000 years later was cooler in many areas than it had been before, and this probably shifted the ecological balance (Bartlein et al. 1986). Although hemlock survives to the present, one could argue that the legacy of the pathogen(s) is still evident.

When past invasions are examined at the local scale, the pattern of colonization seems to be shaped by the interplay of soil characteristics and disturbance regimes at the site level and the overarching control of climate at the regional scale (Brubaker 1975, Graumlich and

Davis 1993, Davis et al. 1994). Stratigraphic changes evident in individual pollen diagrams suggest that most sites experienced long periods of vegetation stability, which are designated as pollen zones, interrupted by periods of relatively rapid change, marked by pollen zone boundaries. Periods of invasion span 500–1000 years at most sites, whereas periods of relative stability often last for millennia (Watts 1973). The transition periods thus represent several generations of the invading species, which implies that past invasions of native tree taxa were gradual but fairly opportunistic events. A species' success depended on the ability of seedlings to establish and survive during a phase of initial low population density. Stable populations within the existing communities seem to have offered little resistance to these tree invasions; instead, the important controls appear to be habitat conditions and intraspecific biological constraints (Watts 1973).

Opportunism modulated by habitat conditions is also evident on longer time scales when the vegetation history of other interglacial periods is examined. In northeastern Europe, for example, subtle variations in the sequence and direction of plant migrations distinguish each interglacial period and attest to the fact that plant associations are not persistent in time (Watts 1988). For example, *Abies* was more widespread and moved more rapidly in the Holsteinian interglacial period than in the younger Eemian or Holocene interglacial periods. Differences in migration history are attributed to variations in the location of glacial refugial populations and the climate of each interglacial period.

In the western United States, the density of fossil sites is too sparse to describe the pattern of postglacial plant migrations in detail. Regional descriptions of vegetation history, however, are available from several regions, including the American Southwest (Betancourt et al. 1990), Pacific Northwest (Whitlock 1992), Colorado Rockies (Fall 1997), and Sierra Nevada (Anderson 1990). In the Yellowstone and Grand Teton region, a series of pollen records from the former ice margin to the center of glaciation (Whitlock 1993, Whitlock et al. 1995) provides information on the movement of conifers during deglaciation. For example, the spread of Engelmann spruce (*Picea engelmannii*) is estimated from the first increase in spruce pollen and presence of needles in a series of
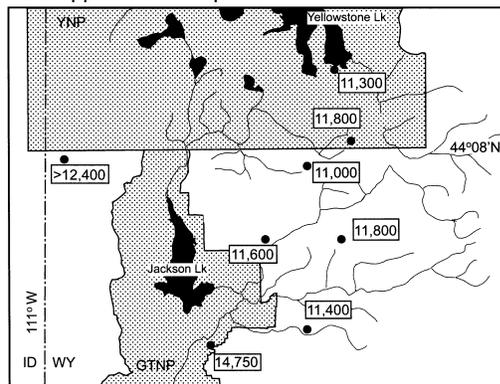

Fig. 2. Age (in radiocarbon years before present) of the first appearance of Engelmann spruce (*Picea engelmannii*) in Grand Teton National Park (GTNP) and southern Yellowstone National Park (YNP) based on the initial increase in *Picea* pollen in a network of pollen records. All sites lie within the area that was glaciated by the Yellowstone ice cap, and the center of glaciation was in the Yellowstone Lake region (after Whitlock 1993). Large lakes are shown in black.

Yellowstone sites (Fig. 2). The evidence suggests that spruce survived close to the ice margin in northwestern Wyoming and southeastern Idaho, probably as small populations in protected areas. As the climate warmed and glaciers receded, the range of spruce shifted northward and eastward into northern Jackson Hole. Spruce was present in northern Jackson Hole by 14,750 years ago and reached the Yellowstone Lake region by about 11,300 years ago. The pattern of spruce invasion within the deglaciated region was not unidirectional, and elevation, soil development, and environmental conditions probably complicated colonization at the local scale. Nonetheless, a simple calculation of the invasion rate from its arrival at the former ice margin to its appearance near Yellowstone Lake (the former ice center) is $\sim$100 m · yr^{-1}, which is consistent with rates estimated for spruce in eastern North America and Europe (Davis 1981a, Huntley 1988). Although pace of climate change and availability of suitable habitats limited the migration of all, the similarity among widely separated species of *Picea* is remarkable. It suggests that spruce may have an intrinsic rate of response determined by its biological constraints to produce and disperse seeds, establish seedlings and saplings, and grow to reproductive age. If so, this characteristic has probably

been acquired as part of a long-term evolutionary strategy for surviving the climate changes that accompany glacial/interglacial cycles (Barnosky 1987, Bartlein 1997, Bennett 1997, Jackson and Overpeck 2000).

Several plant species in the western United States have experienced recent expansions that may be either a continuation of Holocene range changes or a response to recent human activities (Swetnam et al. 1999). The appearance of pinyon pine in northern Colorado 400–500 years ago, for example, seems to be a part of a general expansion from Mexico that has been underway since the last ice age (Betancourt et al. 1991). Climate change has also been implicated in the recent spread of creosote bush (*Larrea tridentata*) in the middle Rio Grande Basin and Borderlands of Arizona and New Mexico (Grover and Musick 1990), single needle pinyon (*Pinus monophylla*) in northern Nevada (Nowak et al. 1994), Utah juniper (*Juniperus osteosperma*) in Wyoming (Swetnam et al. 1999), and western juniper (*Juniperus occidentalis*) in eastern Oregon, (Miller and Wigand 1994, Miller and Rose 1995). Paleoecologic data show that these taxa have undergone considerable adjustment in their ranges during the Holocene and may still be migrating in response to long-term climate changes. However, the impact of such Euro-American activities as grazing, agriculture, and fire suppression on their recent spread is difficult to disentangle from the impact of longer processes.

Importance of Natural Disturbance

Disturbance, particularly fire, is considered an important catalyst in the spread of exotic species at present (Vitousek et al. 1996). Exotic grassland species, for example, have been shown to initiate and maintain a fire regime that prevents the regeneration of native woody and grassland species (D'Antonio and Vitousek 1992). Paleoecologic records, on the other hand, suggest that fires have been a major form of natural disturbance in temperate ecosystems throughout the Holocene and have helped maintain particular vegetation types for long periods. Such records also show that the frequency and ecological importance of fires have varied in association with past climate changes (see Clark et al. 1996, Millspaugh et al. 2000, Whitlock and Larsen in press).

Yellowstone National Park is one location where climate-vegetation-fire relationships have been studied on both short and long time scales, and thus the role of fire in biotic change can be assessed. Fire reconstructions of the last 500 years come from dendrochronological records (Romme and Despain 1989, Barrett 1994), including fire-scarred tree-ring data and forest-stand ages. Holocene records of fire occurrence are available from high-resolution charcoal records obtained from lake sediments (Millspaugh and Whitlock 1995, Millspaugh et al. 2000[3]. Both tree-ring and charcoal data indicate that a combination of small, frequent fires and large, infrequent fires characterizes the current fire regime. For example, the period from 1690 to 1750 A.D. experienced extensive fires, but several decades with small or no fires followed it. This regime led to the development of extensive old-growth forest in the late 20th century and large accumulations of burnable biomass. Unusual weather and fuel conditions triggered large fires in 1988, which affected 395,600 ha of the park (Schullery 1989, Balling et al. 1992). Although these fires have no precedence in recorded history, they seem to be well within the natural range of variation documented in the dendrochronological and charcoal record.

Long charcoal records from Yellowstone reveal the relationship between fire, vegetation, and climate on millennial time scales (Fig. 3). At Cygnet Lake in the Central Plateau region, a sharp increase in fire frequency occurred at the beginning of the Holocene. The change in fire regime coincided with the onset of warm conditions and the establishment of lodgepole pine forest in an area that was previously covered by tundra vegetation. Local fires were most frequent between 11,000 and 7000 years ago[4] (>10 fires $\cdot$ 1000 yr^{-1}). Paleoenvironmental records from southern and central Yellowstone and Grand Teton national parks suggest that summer temperatures were higher than today and drought was more severe at this time (Millspaugh et al. 2000). Fire occurrence decreased to the present frequency of

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[3]Charcoal analysis is based on evidence that charcoal particles are introduced to lakes during and shortly after a fire. Sedimentary layers with abundant large charcoal particles provide a record of past fire events in the watershed (Whitlock and Millspaugh 1996, Whitlock and Larsen in press). In a study of 4 small lakes, charcoal peaks dated by the lead-210 method matched well with timing of fires identified by historic documents and dendrochronologic studies (Millspaugh and Whitlock 1995).

[4]These dates are given in calendar year (see Millspaugh 1997).

Northern YNP

Slough Creek Lake
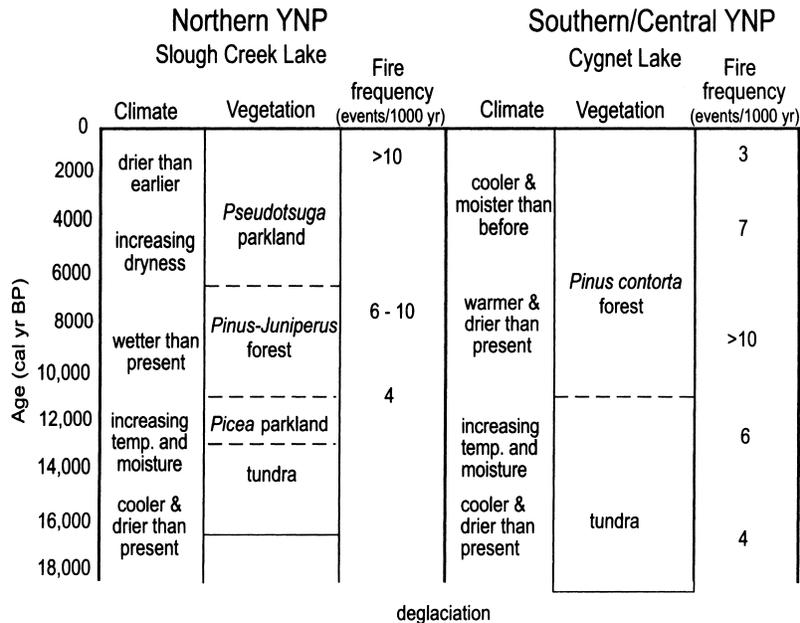
Southern/Central YNP

Cygnet Lake

Fig. 3. Comparison of climate, vegetation, and fire history in 2 regions of Yellowstone with contrasting Holocene climate histories (after Millspaugh 1997). Ages in this figure represent calendar years before present.

2–$3 \cdot 1000$ yr^{-1} in the last 7000 years as the climate become cooler and wetter. Despite these changes in fire regime and climate, the forest continued to be dominated by lodgepole pine, probably because the infertile soils of the Central Plateau have limited the establishment of other conifers (Whitlock 1993).

Pollen and charcoal data from Slough Creek Lake in northern Yellowstone, in contrast, show changes in both vegetation and fire regime as a result of Holocene climatic change. A period of pine-juniper (*Pinus-Juniperus*) forest and low fire frequency occurred between 11,000 and 7000 years ago, when the climate was warmer and wetter than present. Wetter-than-present conditions in this region have been attributed to a strengthening of summer monsoonal circulation in the early Holocene (Whitlock and Bartlein 1993). Fire frequency has increased from 4 fires $\cdot$ 1000 yr^{-1} to >10 fires $\cdot$ 1000 yr^{-1} in the last 7000 years, and Douglas-fir (*Pseudotsuga menziesii*) parkland has established as a result of cooler, drier conditions and increased fire activity (Millspaugh 1997).

A comparison of the Cygnet and Slough Creek records on a finer time scale reveals short periods when both sites burned despite their long-term climate differences; 1988 was such a year, and another period occurred about 1000 years ago during a warm, dry interval known as the Medieval Warm Period (Millspaugh 1997). At these times, short-term climate variations apparently overrode the influence of the slowly varying climate changes and led to fires in both summer-wet and summer-dry regions. The pollen record suggests that such short-term variations are not accompanied by major changes in vegetation composition or by the appearance of new species.

General Observations

Past changes in the ranges of native taxa invite a few comparisons with the spread of exotic species at present (Table 1).

First, plant migrations on long time scales have been governed primarily by climate change and the attendant effect of climate on the physical and biotic environment (Bartlein et al. 1986). In contrast, exotic species invasions at present are largely determined by the direct and indirect actions of humans. This difference contributes to the unprecedented nature of current invasions.

Second, the pattern and rate of invasion vary among species. The paleoecological record

TABLE 1. Characteristics of biological invasion: past, present, and future.

	Holocene time scales	Last few centuries	Next century
Mode of dispersal	irrelevant	human, wind, animal vectors	human (dispersal may require deliberate assistance)
Rate of movement[a]	$<1 \text{ km} \cdot \text{yr}^{-1}$	$>10 \text{ km} \cdot \text{yr}^{-1}$	$>40–50 \text{ km} \cdot \text{yr}^{-1}$
Primary cause of invasion	climate change	human activities	climate/human activities
Proximal cause of invasion	natural disturbance	natural and human disturbance	natural and human disturbance
Limits to invasion	major biogeographic barriers (mountain ranges, oceans, deserts)	characteristics of invading species, human activities, landscape pattern	uncertain

[a]Based on Mack 1986, Huntley 1988, Webb 1988, Bartlein et al. 1997

from Yellowstone and elsewhere suggests that species adjusted their range during the Holocene according to their individual requirements. Features such as soil and disturbance regime helped guide the local pattern of invasion, but, at regional and continental scales, climate conditions governed species limits. Physical barriers have not been significant obstacles to invasion in the past or at present. The Great Lakes and the deserts and mountains of the western United States did not slow climatic-driven Holocene plant migrations in North America (Thompson 1988, Betancourt et al. 1990, Davis et al. 1994). Likewise, mountain ranges, deserts, and oceans have been easily breached by exotic species in recent times as a result of human-assisted dispersal (Vitousek et al. 1996, Cox 1999, Mack et al. 2000).

Third, much debate focuses on the significance of species richness and community structure on the invasibility of present-day communities (Elton 1958, Tilman and Downing 1994, Stohlgren et al. 1999, Levine 2000). On long time scales these attributes seem to have little importance because patterns of plant migration at continental and even local scales have been strongly mediated by environmental conditions (Davis et al. 1994). Indeed, paleoecological records indicate that invading species meet little resistance from existing ones. As a result, communities have been dismantled and reorganized continually through the Holocene. The observation that present-day communities have no long history suggests that species richness and structural complexity may ultimately prove irrelevant to the success of exotic species.

Fourth, the ecological mechanisms that enable most tree taxa to move presently operate too slowly to account for the rates of movement observed on Holocene time scales (Huntley 1988, Birks 1989, Clark et al. 1998; Table 1). This mismatch between present and past observations points to the importance of rare events, including long-distance dispersal, in shaping present-day geographic distributions (Cox and Moore 2000). Waif dispersal is a poorly understood process in modern ecology; yet, it may be key in explaining major expansions in geographic range over the long term (Clark et al. 1998).

Finally, paleoecological records clearly show that climate, fire, and vegetation are interrelated elements of the earth system, and their variation and interaction through time have shaped the modern landscape. On century and millennial temporal scales, large changes in climate determine fire regime and vegetation composition. Yellowstone studies indicate that periods of major climate change, such as transitions from the late-glacial period to Holocene and the early Holocene to late Holocene, were accompanied by changes in fire frequency. This shift in fire regime undoubtedly contributed to vegetation changes recorded in the pollen records of specific sites. In the absence of climate change, fires should be considered an intrinsic component of the ecosystem, whereas during periods of climate change, fires are significant catalysts that allow the invasion of new species. The role of fire at present is further accentuated by nonclimatic disturbances, such as human-caused habitat alteration and landscape fragmentation.

BIOTIC INVASIONS IN THE FUTURE

An issue of great concern and debate is how past and current species invasions compare with those that may occur in the future (Vitousek et al. 1996, Pitelka et al. 1997, Dukes and Mooney 1999, Davis and Shaw 2001). Efforts to address this question rely on results of climate and ecological model simulations that examine ecosystem responses under elevated greenhouse gases (Houghton et al. 1996). In the western United States, atmospheric general circulation models (AGCMs) and regional climate models have been used to compare changes in climate arising from a doubling of atmospheric carbon dioxide (referred to as the $2xCO_2$ climate) with those simulated for the present day (Bartlein et al. 1997, Thompson et al. 1998). The output of climate models has also been introduced into ecological models to consider the response of particular taxa to changes in seasonal and annual temperature and precipitation. Comparison of present and future species ranges identifies where suitable habitat will be lost, gained, or remain unchanged in the future. These projected range changes, like those in climate, represent a comparison of equilibrium conditions (i.e., how the species ranges or regional climate in a $2xCO_2$ climate compares with simulations of present conditions).

Climate and ecological models are continually under refinement. AGCMs and regional climate models improve as spatial resolution, physics of atmospheric circulation, and interactions of the atmosphere and Earth's surface become better constrained. Ecological models are becoming more realistic by incorporating bioclimatic variables, such as growing degree days, minimum temperature, effective moisture, and the biophysical effects of CO_2 on plant growth. Nonetheless, model simulations should be considered projections of potential climate-vegetation relationships under equilibrium conditions; they are not predictions of what will actually occur.

Most climate projections of the future indicate warmer, wetter conditions in the northwestern United States (Bartlein et al. 1997, Thompson et al. 1998). Differences between $2xCO_2$ and present-day simulations in the Yellowstone region include an increase in January and July temperatures of more than ~5°C, a substantial increase in January precipitation, and less extreme and spatially more variable changes in July precipitation. Modern climate analogues for projected changes in the Yellowstone region are found in the interior Pacific Northwest, the Wasatch Range, and lower elevations of the Absaroka Range (Bartlein et al. 1997). Other model simulations suggest a greater role for fire in the future, both in terms of more convectional activity (Price and Rind 1994) and reduced water surpluses in summer (S. Shafer unpublished data 2000).

The location of suitable climate for particular species changes dramatically in future simulations, but, in general, low-elevation taxa are less impacted than high-elevation species (Bartlein et al. 1997). For example, the future range of low-elevation lodgepole pine (*Pinus contorta*) in Yellowstone is little changed from its present distribution (Fig. 4). The climate suitable for Douglas-fir, another low-elevation species, shifts to intermediate elevations in future simulations, probably because drought conditions at low elevations limit its growth.

In contrast, projected future conditions in most of Yellowstone and the Northern Rocky Mountains are not suitable for current high-elevation species. Whitebark pine (*Pinus albicaulis*) is a subalpine species that provides food for grizzly bear, Clarks Nutcracker, and red squirrel in Yellowstone (Despain 1990). Its range is nearly eliminated in Yellowstone in the $2xCO_2$ scenario. This keystone species has declined already with the spread of white pine blister rust (*Cronartium ribicola*) in the late 20th century (Kendall et al. 1999). The additional impact of projected climate changes on whitebark pine has not fully been considered in conservation plans aimed at protecting grizzly bear habitat.

Current models are not able to consider transient conditions that might determine whether species could keep pace with projected climate changes, nor do they address the importance of habitat connectivity, competition, and disturbance in influencing biotic responses. These factors will be critical in predicting the response of native and exotic species. For example, the attendant changes in fire regime toward more frequent and/or more intense fires will undoubtedly complicate vegetation adjustments. The ability of lodgepole pine to grow on infertile soils and reproduce following fire (neither of which is considered in model experiments) should help perpetuate
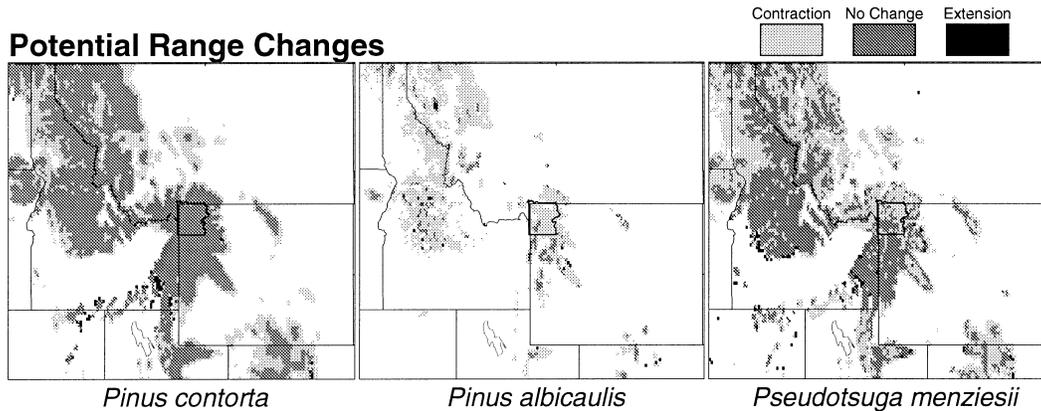
Potential Range Changes

Fig. 4. Potential range changes for 3 tree taxa. Medium shading indicates grid points where a specific taxon occurs under both the present and $2xCO_2$ climate; light shading indicates grid points where a taxon occurs under the present climate, but does not occur under $2xCO_2$ climate; and dark shading indicates grid points where a taxon does not occur under the present climate, but is present under $2xCO_2$ climate conditions (after Bartlein et al. 1997).

it as a forest dominant in the future. Fires may also encourage the spread of Douglas-fir into new areas, since its seedlings require light and mineral soil to become established (Burns and Honkala 1990). On the other hand, the thick bark of mature Douglas-fir trees is an adaptation to fire, and increased fire occurrence may delay the decline of old-growth Douglas-fir forest and the invasion of new tree species. Fires will likely accelerate the decline of whitebark pine, given its sensitivity to intense fires. Added to this picture is the role of opportunistic exotic species that thrive in areas of disturbance.

The message of future climate studies for conservationists and land managers is not whether the simulations are correct in detail (they probably are not). Rather, the point is the model results consistently suggest that large biogeographic adjustments will be required if species are to maintain equilibrium with future climate conditions. Current simulations indicate complex changes in mountain regions that include north- and southward shifts as well as altitudinal adjustments of species ranges. The rates of movement required of species to keep pace with projected climate changes are greater than anything observed in the fossil record of the last 20,000 years. Predicted increases in fire frequency and intensity will affect species differently. A shift toward more frequent or intense fires will create ecological opportunities for some taxa, but, in other cases,

fire may retard vegetation changes by helping to maintain existing communities.

CONCLUSIONS

The process of invasion looks different depending on whether one uses Holocene time scales, the last few centuries, or the next 100 years as the time scale of interest. The relative importance of biological versus climatic constraints on invasion also varies with time scale. When invasion is studied on long time scales, the specific mechanism of dispersal and the role of natural disturbance are generally unimportant because large-scale climate change is the primary driver. During the Holocene, rates of migration for most tree species were <1 km · yr^{-1}, and, although fire and other natural disturbances may have promoted invasion at the local scale, no single fire led to unidirectional ecological change.

Exotic plants in recent centuries have been largely introduced by the deliberate and accidental actions of humans, but their success as invaders is constrained by the characteristics of the species and habitat. Successful invaders include species that can colonize disturbed areas, have rapid growth, reach maturity early, and reproduce prolifically. The most aggressive colonizers are often those with superior mechanisms for dispersal by human, wind, or animal vectors. Current rates of exotic species invasion seem rapid, ~10 km · yr^{-1} (Mack

1986, Vitousek et al. 1996, Pitelka et al. 1997), but if considered on longer time scales, these rates would probably appear slower.

Invasions in the next 100 years will likely combine elements of short-term and long-term patterns and processes discussed above because both human actions and climate change are involved. Humans will be the primary agent of dispersal, and human-assisted migration may be a necessary conservation strategy for the survival of some native plant species. Climate will determine the potential limits for plants and animals, and current biogeographic barriers, like oceans and mountain ranges, may not be significant. The rapid rate of future climate change exceeds anything seen in the Holocene, and simple calculations suggest that native species will have to move or disperse at rates 40–50× faster than those observed in the paleoecologic record if they are to maintain equilbrium with the climate. It seems unlikely that most species will be able to do so, and disturbances, such as fire, may tip the balance in enabling their spread or extinction. Unfortunately, disturbance in the face of climate change will also create opportunities for non-native species to establish and flourish.

Although the past provides a key to the present and perhaps to the future, the past also highlights the unprecedented nature of the present and future. We have seen species in the past adapt to the magnitude of climate change projected in the next century but not at the projected rate (Overpeck et al. 1991). It is not clear that native species will be able to move across highly fragmented landscapes fast enough to survive, and management strategies will have to consider what level of intervention is acceptable. The projected ecological disruption also paves the way for exotic species invasions. Because future invasions stand as outliers to those witnessed in the past and present, managers and conservationists need to consider climate change explicitly in their planning efforts. As Hobbs and Huenneke (1992:333) observed:

> Nearly all systems are likely to be nonequilibrial in the future; we must be activists in determining which species to encourage and which to discourage. We cannot just manage passively, or for maximal diversity, but must be selective and tailor management to specific goals.

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