Future Climate in the Yellowstone National Park Region and Its Potential Impact on Vegetation

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Abstract: *Biotic responses to future changes in global climate are difficult to project for a particular region because the responses involve processes that operate at many spatial scales. This difficulty is exacerbated in mountainous regions, where future vegetation changes are often portrayed as simple upward displacements of vegetation zones in response to warming. We examine the scope of future responses that may occur in a mountainous area by illustrating the potential distributions of selected tree taxa in the region of Yellowstone National Park. The output of a coarse-resolution climate model that incorporated a doubling of carbon dioxide concentration in the atmosphere was interpolated onto a 5-minute grid of topographically adjusted climate data. The output was also used as input into statistical relationships between the occurrence of individual taxa and climate. The simulated vegetation changes include a combination of elevational and directional range adjustments. The range of high-elevation species decreases, and some species become regionally extirpated. The new communities have no analogue in the present-day vegetation because they mix low-elevation montane species currently in the region with extralocal species from the northern and central Rocky Mountains and Pacific Northwest. The projected climate changes within the Yellowstone region and the individualism displayed by species in their potential range adjustments are equal or greater than the changes seen in the paleoecologic record during previous warming intervals. Although the results support conservation strategies that include habitat connectivity, the magnitude of the changes may exceed the ability of species to adjust their ranges. The predicted patterns call into question the adequacy of current management objectives to cope with the scope of future changes.*

Clima Futuro en la Región del Parque Nacional de Yellowstone y su Potencial Impacto Sobre la Vegetación

Resumen: *Para una región particular es difícil proyectar las respuestas bióticas a cambios futuros en el clima global, debido a que las respuestas involucran procesos que operan en muchas escalas espaciales. Esta dificultad incrementa en regiones montañosas, en las que los cambios futuros en la vegetación a menudo se describen como simples desplazamientos de las zonas de vegetación como respuesta al calentamiento. Examinamos el rango de futuras respuestas que pudieran ocurrir en una zona montañosa en el caso de la potencial distribución de selectos taxa de árboles en la región del Parque Nacional Yellowstone. El resultado de un modelo climático de resolución gruesa que incorporó el doble de la concentración de bióxido de carbono en la atmósfera fue interpolado a una cuadrícula de 5 minutos de datos climáticos ajustados topográficamente. El resultado también fue usado para establecer relaciones estadísticas entre la ocurrencia de taxa individuales y el clima. Los cambios simulados en la vegetación incluyen una combinación de ajustes de rango altitudinal y direccional. El rango de especies de elevaciones altas disminuye, y algunas especies se extinguen regionalmente. Las nuevas comunidades no tienen análogas en la vegetación actual porque mezclan especies montanas de elevación baja actualmente presentes en la región con especies provenientes del norte y centro de las Montañas Rocallosas y del Pacífico Noroccidental. Los cambios climáticos proyectados en la región de Yellowstone y el individualismo mostrado por especies en su potencial rango de ajustes son iguales o mayores que los cambios observados en el registro paleoecológico durante intervalos de calentamiento previos.*

Aunque los resultados fundamentan estrategias de conservación que incluyen la conectividad de habitas, la magnitud de los cambios puede exceder la habilidad de las especies para ajustar sus rangos. Los patrones predichos cuestionan la eficiencia de los objetivos de manejo actuales para enfrentar los cambios futuros.

Introduction

Climate changes resulting from human action may lead to significant disruption of species distributions in the next century and to disintegration of existing ecosystems (Houghton et al. 1996; Mellilo et al. 1996; Peters & Lovejoy 1992; U.S. Congress 1993; Kareiva et al. 1993). This prediction is based on observations that the controls of global climate, such as the concentration of carbon dioxide in the atmosphere, are undergoing significant changes (Houghton et al. 1996) and that the consequent changes in climate may amplify changes in geochemical cycles and land-surface cover (Mellilo et al. 1996; Vitousek 1994). Considerable uncertainty exists, however, as to the specific nature of future climatic changes and the potential response of biota at global and continental scales; this uncertainty is compounded at the regional-to-landscape scale (Root & Schneider 1995; Schneider 1993; Root 1993; U.S. Congress 1993). Current models are limited in their ability to resolve the spatial variability of climate and vegetation in regions of complex topography (Beniston et al. 1996; Barry 1992). Individual modeling studies have focused either on large-scale responses, as in the case of general circulation models of climate (GCMs), or on small scales, as in the case of forest stand-simulation models. In general, few studies have addressed the intermediate regional-to-landscape scales.

The nature of climate and vegetation changes that may occur on regional and subregional scales is of great concern for conservation efforts within mountainous regions. By virtue of their environmental complexity, mountainous regions are home to scenic and unique landscapes and are centers of biological diversity that include many rare and endangered species. In western North America appreciation of these attributes has led to the establishment of many federally protected wildlands. Such reserves have become central in most conservation efforts, both as biological and genetic storehouses and as examples of functioning natural ecosystems. Ecosystem management in the national parks, for example, is based on "natural regulation," which has as "a primary goal . . . that the biotic associations within each park be maintained, or where necessary recreated, as nearly as possible in the condition that prevailed when the area was first visited by the white man" (Leopold et al. 1963). Although implementation of this goal has been subject to a wide variety of interpretations, it is clear that the challenge will be even greater in the future as national parks

and other wildlands with fixed administrative boundaries face conditions of changing climate (U.S. Congress 1993). The predicted ecological disruption, as well as the best course of response, has become an issue of national concern (U.S. Congress 1993; Parsons 1991).

We examined the potential adjustments in the distributions of major tree taxa to simulated future climates in the region of Yellowstone National Park (YNP) to illustrate the scope of the biotic responses that might be expected. The Yellowstone region (broadly equivalent to the 7.3-million-hectare Greater Yellowstone Ecosystem, Keiter & Boyce 1991; Despain et al. 1986) is topographically diverse, including mountain ranges, volcanic plateaus, and intermontane basins (Fig. 1). The interaction of climate and landforms through time in this area has given rise to a mosaic of vegetation types and produced steep vegetational gradients that range from steppe and grassland at low elevations to conifer forest and alpine tundra at high elevations (Despain 1990; Whitlock 1993).
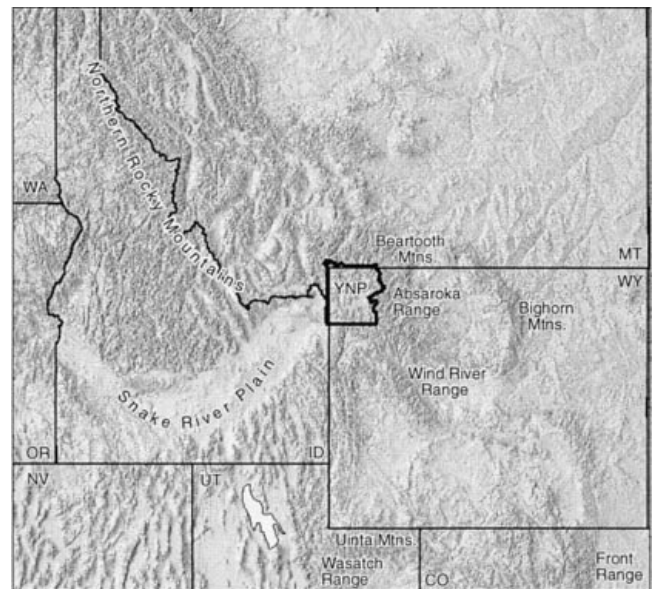

Figure 1. Shaded relief map showing the topographic complexity of the Northern Rocky Mountain region, with locations referred to in the text (YNP is Yellowstone National Park). The area extends from 40 to 48 degrees N and 104 to 118 degrees W. The map is plotted using an equirectangular projection, so scale varies across the map. (For reference, the east-west distance along the bottom edge of the map is approximately 1200 km.)

The region is also of interest because paleoecologic research reveals a complex response to climate changes in the past that probably typifies many mountainous regions. Spatial heterogeneity of climate changes and vegetation responses has been a feature of environmental change in the Yellowstone region during the Holocene (Whitlock & Bartlein 1993; Whitlock et al. 1995), and potential future changes are expected to be no less complicated.

The difficulties in estimating biotic responses at the landscape-to-regional scale in mountainous areas have led to largely subjective projections of future biotic changes from climate-model results (Franklin et al. 1992; Romme & Turner 1991; Geber & Dawson 1993). Such projections propose generalized elevational or latitudinal shifts of climate and vegetation zones (i.e., upward and northward in response to global warming), based on the broad-scale changes in climate. The paleoecologic record, however, argues against such simplistic biotic adjustments. Fossil data show that local patterns of climate have exhibited considerable spatial heterogeneity during the Quaternary (Whitlock 1993; Whitlock & Bartlein 1993; Whitlock et al. 1995). The climate history of the northern Yellowstone region has been shown to be different from that of the central and southern region. Whitlock and Bartlein (1993) attributed this difference to a trade-off between two climate regimes that are characterized by different amounts of summer precipitation and today are delimited by sharp boundaries. These differences are a local manifestation of two climate regimes that characterize the seasonal pattern of precipitation in the western U.S. (Tang & Reiter 1984; Mock 1996). The contrast between these regimes was more intense at times in the past when the large-scale controls of climate varied. The spatial patterns of contrasting regimes, however, remained relatively stationary because the location of orographic precipitation was and continues to be constrained by topography.

The paleoecologic record also provides some insight into how biota have responded to large-scale climatic changes (Webb & Bartlein 1992). The predicted magnitude of future warming, for example, is comparable to that experienced between 14,000 and 9,000 years ago during the transition from the late-Pleistocene glacial period to the Holocene interglaciation. Variations in the seasonal distribution of insolation, temperature, and precipitation during this transition led to a dismantling of glacial communities and created a series of rapidly changing biotic associations, many of which had no modern analogue. Plants, mammals, and insects adjusted their ranges independently to meet their individual climatic requirements, and the rates of response varied among taxonomic groups as a function of their ability to disperse and colonize. The individualistic response was a widespread phenomenon (Davis 1991; Webb 1992; Huntley 1991; FAUNMAP Working Group 1996; Elias 1991), and it will likely be a widespread feature of future climate changes as well.

The vegetation history of the Yellowstone region confirms the individualistic response of taxa to environmental change and illustrates the reorganization of plant assemblages, extensions or contractions of ranges, and displacements of altitudinal vegetation zones that occurred during the late Pleistocene and Holocene (Whitlock 1992, 1993; Barnosky et al. 1987). *Picea engelmannii* colonized the region following deglaciation and was later joined by *Pinus albicaulis* and *Abies lasiocarpa*. Together these taxa formed a widespread subalpine forest until 9500 years ago. *Pinus contorta* and *Pseudotsuga menziesii* expanded in the southern and central region from ca. 9500 to 5000 years ago, during a warm dry period. At the same time *Pinus flexilis* or *P. albicaulis*, *Juniperus*, and *Betula* were present in the northern region during a warm, wet interval there. In the last 7000 years, *Pseudotsuga* expanded in the northern region as conditions became drier and declined in abundance in the southern and central region, which became cooler and wetter.

Projection of Vegetation Responses at Landscape-to-Regional Scales

The projection of the influence of global-scale changes in climate on the landscape-to-regional scale requires hierarchies of both climate and vegetation models. Neither hierarchy is complete at present, but parts of each exist, and the further development of both climate and vegetation models is the subject of vigorous research and development (Mellilo et al. 1996; Kirschbaum et al. 1996). Projection of the environmental changes that may occur in response to changes in the concentration of greenhouse gases in the atmosphere requires a global-scale climate model, such as a general circulation model (GCM). A GCM has a coarse spatial resolution (e.g., grid-cell sizes on the order of a few degrees of latitude by a few degrees of longitude) and crude representations of topography. These models also generally oversimplify the simulation of those climate variables (e.g., soil moisture) that are most critical for determining plant distributions (Schneider 1993; Root 1993; Trenberth 1992). Regional, or mesoscale, climate models (RegCMs) are available that offer finer spatial resolution (e.g., grid-cell spacing on the order of 50 km) and more elaborate depiction of the climate processes that operate at the land surface (Giorgi & Mearns 1991), but these models still do not adequately resolve the spatial variability of climate in a region of complex topography. (Although large physiographic features such as the Sierra Nevada or Colorado Plateau are represented at the 50-km resolution, smaller-scale features such as the Yellowstone Plateau or the Snake River Plain are poorly resolved.) Both GCMs and RegCMs are likely to increase in resolution as climate-model development

proceeds, but until the resolution of the RegCMs falls below 10 km, additional means of "downscaling" climate-model output will be needed (Hostetler & Giorgi 1993; Gyalistras et al. 1994; Hostetler 1994).

The hierarchy of vegetation models includes models that are applicable at the landscape scale or at the global scale, but not at intermediate scales. Stand-simulation models (Solomon & Shugart 1993) portray the effect of changes in climate, disturbance regime, soil type, and biological interactions on particular forest communities, but their results are difficult to extrapolate to larger scales. At the opposite extreme of spatial resolution, biome models (Prentice et al. 1992) describe vegetation patterns at the global scale, but at low taxonomic and spatial resolution and without the dynamics included in stand models (but see Neilson 1995; Haxeltine & Prentice 1996). In light of the available models, projections of the vegetational response to future climatic variations have involved two general approaches: simulations of temporal changes in local community composition within a particular landscape (Solomon 1986; Shugart & Smith 1992; Botkin & Nisbet 1992) and global- or continental-scale estimations of the potential ranges of species or vegetation types under particular climatic conditions (Overpeck et al. 1991; Cramer & Leemans 1993; Davis & Zabinski 1992; Lenihan & Neilson 1995; Huntley et al. 1995; Sykes et al. 1996). As currently implemented, neither class of vegetation model explicitly addresses regional-scale responses of biota to future climate change or the possibility that species within a region may respond to climate change by adjusting their ranges.

Given the present incompleteness of the hierarchies of climate and vegetation models, the projection of vegetation response to future climate changes at the regional scale involves two approximations, which are rather crude and unsatisfying, but which are required in practice. The first is the "downscaling" of climate model output by the direct interpolation of the coarse-resolution "anomalies" (the differences between the simulated future climate [the experiment] and simulated present climate [the control]) onto a finer-resolution grid of observed climate. Overpeck et al. (1991), for example, interpolated anomalies from the coarse (several-degree) resolution grids of three different GCMs onto a relatively finer 100-km grid of observed present climate in eastern North America, whereas Huntley et al. (1995) did the same onto a 1-degree grid for Europe. The second approximation involves the use of empirically determined relationships between vegetation and climate. For example, Huntley et al. (1995) used statistical relationships to describe the relationship between species presence/absence and a small number of climate variables; these relationships were then used to estimate the ranges of the species under the projected future climate. As climate and vegetation models improve, both approximations will eventually become unnecessary.

Application to the Yellowstone Region

We analyzed future change in the Yellowstone region using the direct interpolation method to downscale GCM projections and an equilibrium vegetation model to project potential range displacements of selected tree taxa (Overpeck et al. 1991; Huntley et al. 1995). Relationships between present distributions of tree taxa and climate were established on a 25-km grid covering North America by interpolating present climate and by digitizing species range maps from Little (1971) onto the grid. We used "response surfaces" to infer the relationship between vegetation and climate (Bartlein et al. 1986; Lenihan 1993). As applied here, response surfaces display the probability of observing a particular taxon at a specific point in a climate space defined by four variables: mean January and July temperature and January and July precipitation. These variables were selected to represent the seasonally varying climate of the western U.S. that controls vegetation distribution. Values of the four climate variables were obtained from climate-station data and were interpolated onto the grid using a locally-weighted polynomial-regression method, with latitude, longitude, and elevation as predictors (Lipsitz 1988). This procedure produced a depiction of topographically adjusted climate values at a 25-km resolution over North America. Because the ranges of the taxa we considered extend well beyond the Yellowstone region, it was necessary to fit the response surfaces over the entire climate space occupied by the species.

We also interpolated present climate onto a 5-minute digital elevation model of the study area in order to show more clearly the effects of elevation on climate in this region. At this resolution the physiographic features that exert a strong control on surface climates and, consequently, on vegetation become evident in the topographically adjusted climate data.

The changes in climate for a doubling of carbon dioxide as simulated by the Canadian Climate Center general circulation model (CCC GCM) (Boer et al. 1992) were used to represent a potential future climate in the study region. We selected this model because it is well documented and has a relatively high spatial resolution (3.75 degree) compared with other GCMs. The anomalies (differences between the control and $2 \times CO_2$ simulations) were interpolated onto the 5-minute grid cells in a way that registers the present spatial heterogeneity in the seasonal variations of climate in the region. The modern climate variables for each 5-minute grid cell were compared with the output for the control (present) simulation of nearby GCM grid points to identify the grid points that most closely matched the modern climate of a particular cell. The distance-weighted average of the differences between the $2 \times CO_2$ and control simulations for the nearby GCM points ("$2 \times CO_2$ anomalies") were then applied to the present climate data of the

5-minute grid cells to produce the future climate values. This procedure preserves to some extent the mixture of precipitation regimes observable in the Yellowstone region (see Figs. 3 & 4 in Whitlock & Bartlein 1993).

The estimated changes in distributions of eight tree taxa were obtained by (1) evaluating the vegetation-climate relationships with the values from the 5-minute grid of present climate (which reproduces the present distributions of the taxa well); (2) evaluating the vegetation-climate relations with the values from the 5-minute grid of present climate plus the $2 \times CO_2$ anomalies to simulate potential future distributions; and (3) comparing the probabilities of occurrence of each taxon under the two climates to discern potential changes in distributions. The use of vegetation-climate relationships derived from correlations between modern species distributions and standard climate variables has limitations for predicting future species ranges (Packala & Hurtt 1993; Malanson 1993; Prentice 1992). This approach is sufficiently robust, however, for making projections about the potential magnitude and direction of future vegetation change (Overpeck et al. 1991; Davis & Zabinski 1992; Prentice et al. 1993; Prentice & Solomon 1989; Malanson 1993).

Potential Future Climate and Tree Species Distributions

A comparison of present and projected future climate reveals the nature of the simulated climate change in the Yellowstone region (Fig. 2). In general, mean January and July temperature and January precipitation increase, whereas July precipitation decreases slightly. January temperature increases from −15 to −10°C at present to −5 to 0°C in the future simulation. July temperature also increases by as much as 10°C (from 10–15°C at present to 15–20°C in the future). The Yellowstone region experiences 75–100 mm of precipitation in January at present (with up to 200 mm at higher elevations); under the simulated future conditions, January precipitation in most areas increases to 150–200 mm. In contrast, July precipitation changes little from present values of 25–50 mm, although less rainfall is received at high elevations under the future simulations. These changes, although specific to the CCC GCM, are similar to projections for western North America from other climate models (Intergovernmental Panel on Climate Change 1990).

Modern climate analogues for the future conditions in the Yellowstone region are found in the interior Pacific Northwest, the Wasatch Range of Utah, and lower elevations of the Absaroka Range of Montana and Wyoming. For example, the simulated future climate in much of the Yellowstone region (mild wet winters and warm dry summers) is similar to the present climate of northwestern Montana and northern Idaho, a region some 500 km to the northwest. Mild winters and dry summers also characterize low elevations of the Wasatch and Absaroka Ranges, and these areas provide future climate analogues for low elevations in the Yellowstone region.

The nature of the projected climate changes in the Yellowstone region can be further illustrated by mapping areas of analogous climates. These areas are identified by comparing the present and projected future climates at individual sites with those elsewhere within the study region. The comparison of the present climate at a site with the projected future climates of the region reveals where the present climate of the site will be expressed in the future. The comparison of the projected future climate at the site with the present climate elsewhere within the region reveals where the projected future climate may be found today (Fig. 3). For the Lamar Valley, a low-elevation area at the northern margin of YNP, the future locations of the present climate include the middle elevations in YNP and adjacent mountain ranges, including the Wind River Range, as well as the middle elevations of more distant ranges such as the Big Horn Mountains of Wyoming, the Uinta Mountains of Utah, and the Front Range of Colorado. The present locations of the projected future climate for the Lamar Valley occur in northwestern Montana, northern Idaho, and northeastern Oregon, about 500 km away. For the Gallatin Range, a high-elevation location at the northern edge of YNP, the present climate is projected to occur in the future at only two grid points, one in the Beartooth Mountains and one in the Absaroka Range. The present locations of the projected future climate again lie mainly far to the northwest and in a few scattered locations in nearby areas.

These analogues illustrate the general concept that high-elevation habitats will become restricted or even eliminated as warming occurs, while low-elevation habitats will expand and move to the middle elevations: the present high-elevation Gallatin Range climate is almost eliminated from the region, while the low-elevation Lamar Valley climate becomes widespread within the region. The analogues also reveal, however, that the replacement climate may be far removed from a site, particularly in the case of low-elevation locations, and that the pattern of the projected climate changes does not consist of simple upward or northward displacements of climate zones.

The projected climate conditions affect the locations of climatically suitable habitat of individual taxa to varying degrees (Fig. 2), with low-elevation taxa affected less than high-elevation ones. *Pinus contorta* and *Pseudotsuga menziesii* are representative of a group of low-elevation species that presently grow in the Yellowstone region and that experience only modest changes in range under the simulated future conditions. During the Holocene, *P. contorta* has had a competitive advantage over other conifers on the infertile rhyolite plateaus of central YNP, in areas of frequent fire, and during warm,
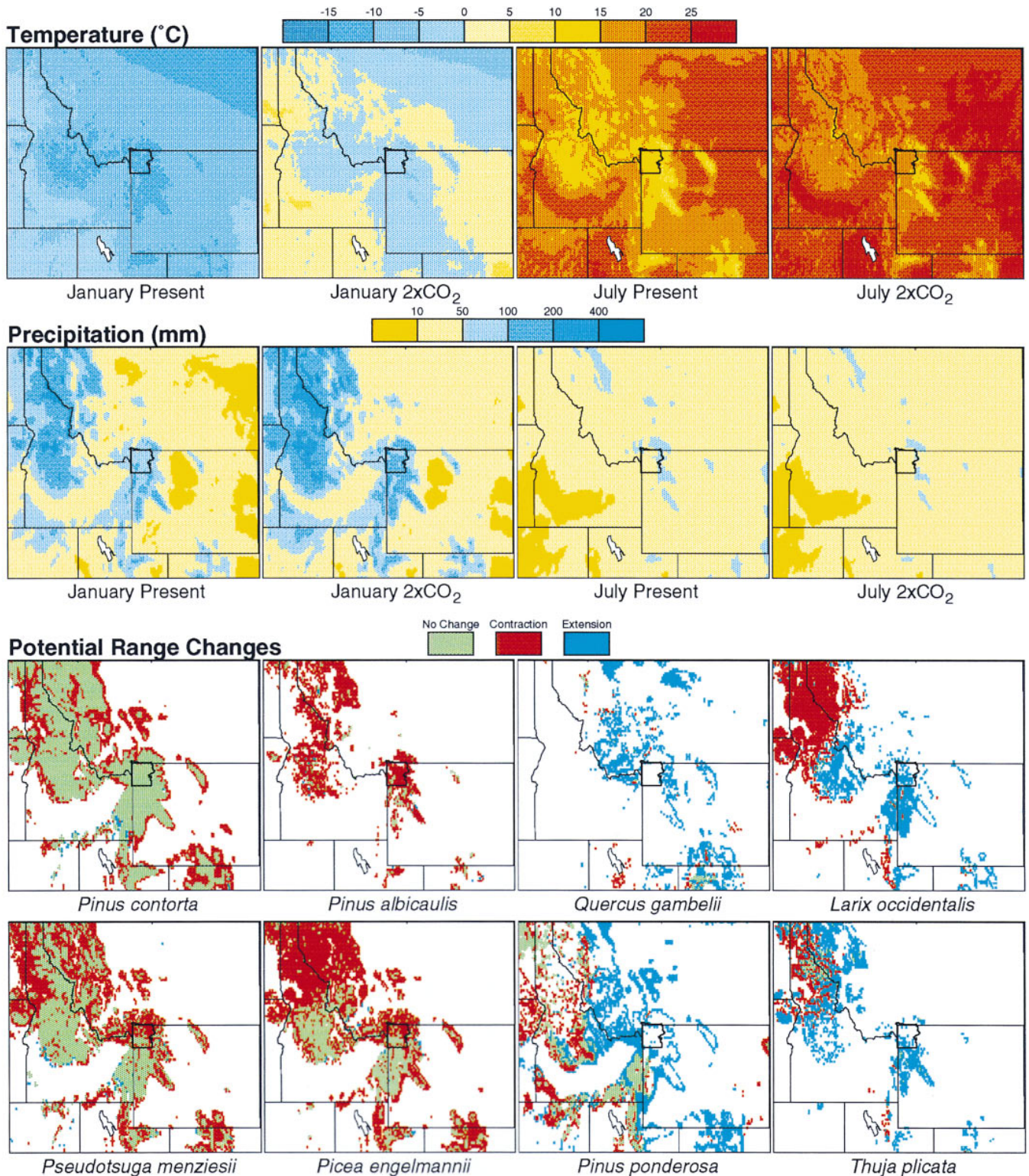
Figure 2. Climate in the northern Rocky Mountains and Yellowstone region (Yellowstone National Park is the outlined area at the center of each map) (top half). Present and simulated future (2 × CO$_2$) values of mean January and July temperature and precipitation. Present values were interpolated from standard climate station data onto a 5-minute grid. The 2 × CO$_2$ values were obtained by adding interpolated anomalies (2 × CO$_2$ experiment minus control) from the Canadian Climate Center general circulation model experiment (Boer et al. 1992). Potential range changes for selected tree taxa (bottom half). Green shading indicates grid points where a specific taxon occurs under both the present and 2 × CO$_2$ climate, red shading indicates grid points where a taxon occurs under the present climate, but does not occur under 2 × CO$_2$ climate, and blue shading indicates grid points where a taxon does not occur under the present climate, but does occur under the 2 × CO$_2$ climate.
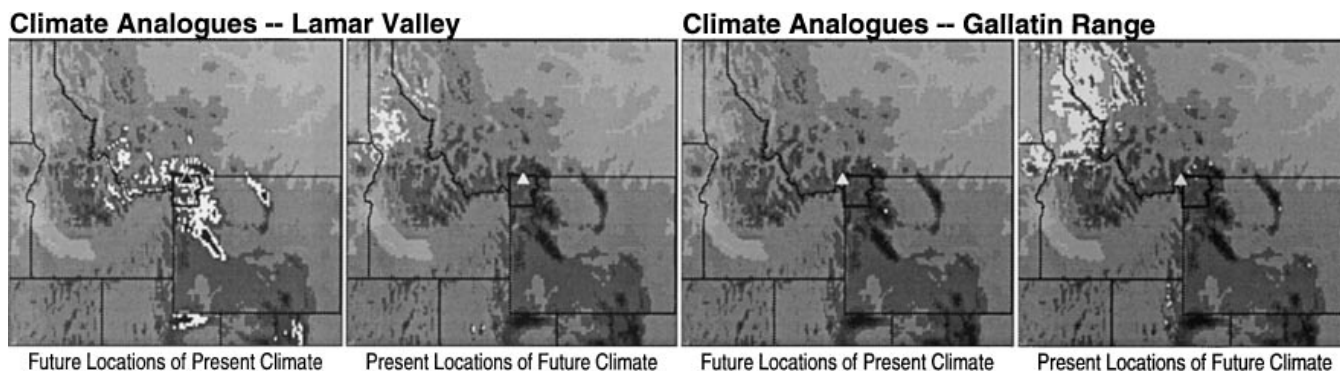
Figure 3. Climate analogues for two locations (triangles) at the northern margin of Yellowstone National Park. The left-hand panels of each pair show in white the grid points with projected future climates that are similar to the present climate at the location indicated by the triangle, whereas the right-hand panels show in white the grid points with present climates that are similar to the projected future climate at the location. The inverse-squared-Euclidian distance was used as the similarity measure, and the threshold value for indicating those grid points with climates similar to those of the target locations was determined by intercomparing the present climates at the individual grid points.

dry periods (Whitlock 1993). Future climate may allow *P. contorta* to continue to thrive on infertile soils and to become a dominant on more fertile non-rhyolite areas and at higher elevations. Climatically suitable habitat for *Pseudotsuga* is restricted to intermediate elevations in the simulations, probably because intensified summer drought limits its growth at both low and high elevations. *Pinus albicaulis*, a high-elevation species, is the most affected of the conifers studied. Its decline in YNP is consistent with the loss of the current climate conditions at high elevation that support this species. In the $2 \times CO_2$ simulation warmer temperatures and increased summer drought occur throughout its present range in the Yellowstone region and the northern Rocky Mountains.

The simulated future climate is also suitable for species that do not grow in the Yellowstone region at present. *Quercus gambelii*, *Juniperus occidentalis* (not shown), and *Acer grandidentatum* (not shown) grow today in Utah, Colorado, and southern Idaho. *Pinus ponderosa* is common in the northern and central Rocky Mountains, but conspicuously absent today in and around YNP. Warm, dry summers in the future simulation extend the potential habitats of these species to low elevations in the Yellowstone region. Projected mild, wet winters and warm, dry summers also extend the potential ranges of *Larix occidentalis*, *Tsuga heterophylla* (not shown), and *Thuja plicata* southeastward of their present limits.

Discussion

Regional-Scale Vegetation Changes

The simulated vegetation changes are based on a single projection of future climate; simulations based on other projections would likely differ in detail, but the overall character and scope of the potential changes would not change. As in eastern North America (Overpeck et al. 1991), the simulated species' range changes are large and comparable in magnitude to those that accompanied the transition from late-Pleistocene to Holocene conditions in the region (Whitlock 1993). If the taxa are considered jointly, the floristic reorganizations are of a magnitude not seen in the late-Quaternary paleoecologic record. *Pinus ponderosa* has not grown in the Yellowstone region since the last interglacial period, about 125,000 years ago; *Quercus* was last recorded in the Pliocene; and *Larix*, *Tsuga*, and *Thuja* were probably extirpated from the Yellowstone region in the Miocene (Baker 1986; Leopold & Wright 1985; Leopold & MacGinitie 1972).

Vegetation response to global warming is frequently described as a general shifting of species' ranges northward, combined with upward movement along elevational gradients toward areas of cooler conditions (U.S. Congress 1993; Peters 1992; Noss & Cooperrider 1994). These predictions are based on the results of continental-scale climate and vegetation models that simulate biotic responses to a doubling of carbon dioxide and on continental networks of paleoecologic records that disclose northward and upward range adjustments in response to Holocene warming (Davis & Zabinski 1992; Jacobson et al. 1987). The coarseness of these predictions masks the potential complexity of the vegetation response within regions. Our study indicates that at a finer scale the projected vegetation response includes a combination of elevational and directional adjustments, as the locations of suitable conditions for each taxon shift within the region. The simulated equilibrium assemblages include admixtures of low-elevation montane spe-

cies presently in the Yellowstone region, as well as extralocal species from other parts of the Rocky Mountains and Pacific Northwest. High-elevation taxa are greatly restricted in their ranges, and some are extirpated from the region.

Should the projected climatic change occur, physical and biological constraints to plant dispersal and establishment under the scenario we describe will undoubtedly impede the ability of tree taxa to keep pace with shifts in suitable climate (Davis 1989). Paleoecologic data provide some information on the speed at which Rocky Mountain taxa respond to climatic changes. Whitlock (1993) suggested that following the retreat of glaciers from YNP, *Picea engelmannii* moved into the deglaciated region at a rate of 300 m/year. Similarly, rates of 300–500 m/year have been suggested for *Picea* in eastern North America and Europe (Davis 1991; Webb 1992; Huntley 1991; see also Gear & Huntley 1991; MacDonald et al. 1993). If these migration rates are intrinsic characteristics of species that are determined by biological constraints, the ranges of extralocal taxa, such as *Larix, Pinus ponderosa*, and *Quercus,* will not be able to keep pace with projected future climatic change (Overpeck et al. 1991; Davis 1989). Even if these taxa were capable of tracking rapid climate change, the extent of current habitat fragmentation would radically slow or impede natural migration and dispersal processes (Quinn & Karr 1993).

As both community composition and climate change, elements of disturbance regimes, such as fire frequency, will also change (Franklin et al. 1992; Rind & Price 1994). The $2 \times CO_2$ scenario predicts warmer summers with little increase in summer precipitation (Fig. 1). Drier conditions would increase the frequency of fires within the study area. More frequent fires, in turn, would facilitate the migration of vegetation by creating opportunities for invading species and by limiting regeneration of fire-intolerant and late-successional ones (Clark 1993). Fire-adapted taxa, such as *Pinus contorta*, *Pseudotsuga*, and *Larix*, may expand in areas where future climates support appropriate fire regimes. Paleoecologic records support this scenario by providing evidence that *P. contorta* and *Pseudotsuga* were more abundant in YNP between 10,000 and 5,000 years ago when conditions were warmer and drier than at present and fires were more frequent (Whitlock 1993; S. H. Millspaugh and C. Whitlock, unpublished data). A return to such climates and fire regimes in the future would likely favor the expansion of these taxa.

Implications for Natural Resource Management

The magnitude of potential range changes of individual species presents a challenge to current management philosophies and conservation goals, particularly in areas where both landscape and institutional fragmenta-

tion are great (U.S. Congress 1993). Parks and preserves with geographically fixed administrative boundaries face the problem of not being able to "migrate" with the species they presently protect. As a result, cooperative management across administrative boundaries will be necessary to address the effects of climate change.

Conservation reserve theory advocates the creation and preservation of habitat corridors to connect reserves and provide pathways for migration and dispersal (Hunter et al. 1988; Shafer 1990; Noss & Cooperrider 1994). As climate changes and the areas of potentially suitable habitat for individual taxa move across the landscape, however, corridors designed to facilitate the movement of organisms across the present landscape may no longer be optimal. For example, mountain ranges along the Montana-Idaho border west of YNP provide a high-elevation route linking the Yellowstone Plateau and the northern Rocky Mountains, and conservation management of these ranges is proposed as part of the Greater Yellowstone Ecosystem (Greater Yellowstone Coalition 1994), The Wildlands Project (Noss 1992), and the Northern Rockies Ecosystem Protection Act (Bader 1992). The current ranges of *Pseudotsuga menziesii* and *Picea engelmannii* enclose this link, but projections of their potential future distributions show that the ranges of these taxa will become discontinuous across this area (Fig. 2). For such species suboptimal habitat and shrinking seed source will limit their range and their usefulness in providing corridor habitat for other species. In contrast, *Pinus ponderosa* does not grow in southwestern Montana at present but could become widespread there under future conditions. In this case the mountains to the west of YNP will become an important corridor facilitating the spread of this species and its associates into and within the greater Yellowstone region. Thus, although areas of habitat connectivity defined on the present landscape may change substantially in character, such areas will likely continue to serve as corridors for an array of species in the future.

The rapidity of the projected climate change, coupled with the size and character of the projected vegetation changes, presents a challenge to current management philosophies and preservation goals. Strategies that emphasize intensive species-level protection, such as mandated by the U.S. Endangered Species Act, will have to consider the implications of intervention and assisted migration to facilitate the movement of taxa into new ranges (Orians 1993). Strategies that promote natural regulation of ecosystems, such as practiced by many national parks, will have to consider the consequences of major extirpations and invasions as taxa adjust their range limits. Current difficulties in coordinating the management of federal, state, and private lands in the Yellowstone region only portend the scope and complexity of the debate that will ensue in formulating an appropriate response to the vegetation changes projected in the future.

Conclusions

The projected climatic changes resulting from the increases of greenhouse gasses are large and rapid, and equally dramatic is the attendant response of vegetation. In the Yellowstone region the potential range adjustments are unprecedented in magnitude during the Quaternary; they are counterintuitive, with southward and downward adjustments in the potential ranges of some taxa possible; and the potential responses of individual taxa are unique, making it likely that present assemblages of taxa will not survive into the future. The widespread extirpations, latitudinal and altitudinal displacements, and the appearance of new communities under the potential future climate may shift the location and change the character of current centers of biodiversity. This possibility complicates present efforts to protect these areas. Potential reserves and the corridors linking reserves, designed on the basis of the uniqueness of present environments or biota (Scott et al. 1993; Kareiva 1993; Prendergast et al. 1993), may not be suitable under future climate conditions. Even though future climate conditions and species ranges cannot be predicted with certainty, the results of this study suggest ways that ranges of tree taxa in the Yellowstone region may change through time. The unique responses of the species considered here supports the need for more studies of regional-scale environmental change. Such studies will help us avoid naive assumptions as to the nature of climate and biotic response on the landscape-to-region scale and will help provide the information necessary to guide specific conservation and management efforts (Root & Schneider 1993; Pitelka 1993).

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