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ECOSYSTEMS

Potential Changes in the Distributions of Western North America Tree and Shrub Taxa under Future Climate Scenarios

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ABSTRACT

Increases in atmospheric greenhouse gases are driving significant changes in global climate. To project potential vegetation response to future climate change, this study uses response surfaces to describe the relationship between bioclimatic variables and the distribution of tree and shrub taxa in western North America. The response surfaces illustrate the probability of the occurrence of a taxon at particular points in climate space. Climate space was defined using three bioclimatic variables: mean temperature of the coldest month, growing degree days, and a moisture index. Species distributions were simulated under present climate using observed data (1951–80, 30-year mean) and under future climate (2090–99, 10-year mean) using scenarios generated by three general circulation models—HADCM2, CGCM1, and CSIRO. The scenarios assume a 1% per year compound increase in greenhouse gases and changes in sulfate (SO_4) aerosols based on the Intergovernmental Panel on Climate Change (IPCC) IS92a scenario. The results indicate that under future climate conditions, potential range changes could be large for many tree and shrub taxa. Shifts in the potential ranges of species are simulated to occur not only northward but in all directions, including southward of the existing ranges of certain species. The simulated potential distributions of some species become increasingly fragmented under the future climate scenarios, while the simulated potential distributions of other species expand. The magnitudes of the simulated range changes imply significant impacts to ecosystems and shifts in patterns of species diversity in western North America.

Key words: future climate change; response surface models; western North America; trees.

INTRODUCTION

There is growing evidence that increases in atmospheric greenhouse gases are altering the Earth's climate (Houghton and others 1996). If the climate continues to change at its projected pace, it will significantly alter ecosystems and threaten the viability of many species (Watson and others 1998). Sessile organisms, such as plants, are particularly susceptible to rapid climate change because they can only migrate during certain life stages. If climate conditions become unsuitable for a plant, potential migration to areas with a more suitable climate can only occur via the dispersal and establishment of the next generation of individuals. If the rate of climate change is too fast, plants will not be able to adjust quickly enough to changing conditions, resulting in extirpations and the extinction of species along with shifts in major patterns of species diversity. For species whose migration rates are fast enough to track climate change, habitat

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fragmentation resulting from human land use could significantly impede natural dispersal and migration (Pitelka and the Plant Migration Workshop 1997).

Over the last decade, researchers have focused on developing mechanistic, biogeochemical models that simulate both equilibrium (for example, Neilson 1995; Prentice and others 1992) and transient (for example, Foley and others 1996) responses of vegetation to climate change. Ultimately, these physiologically-based models will improve our ability to accurately simulate vegetation distributions. To date, however, these models still have a number of limitations. One current drawback of biogeochemical models is that they simulate vegetation in terms of basic plant functional types. Although plant functional types are useful for many kinds of investigations, they do not provide the species-level information that is critical for understanding the impacts of climate change on biodiversity. Stand-level or patch models (for example, Burton and Cumming 1995), which are another type of physiologically-based model, can simulate the distribution of individual species, but they require species-specific physiological data, which are not available for many taxa at this time.

To project the potential impact of climate change on plant distributions, we use response surfaces to simulate shifts in potential range limits for tree and shrub taxa in North America. Response surfaces are correlative models based on the long-recognized correspondence between climate and broad-scale patterns of vegetation (Woodward 1987; Box 1981). They capture the relationship between the geographic distribution of a species and the environmental variables that are believed to limit, or be proxies for processes acting to limit, a species' range (Lenihan 1993; Bartlein and others 1986). Response surfaces have been used to examine the potential future responses of species to climate change (Huntley and others 1995; Bartlein and others 1997; Thompson and others 1998), as well as the nature of past vegetation distributions and changes over longer time periods (Bartlein and others 1998). In their application here, the response surfaces show the probability of occurrence of individual taxa at particular points in a climate space defined by three empirically derived bioclimatic variables. Other types of correlative models commonly used for simulating vegetation distributions include regression tree models (Iverson and Prasad 1998), polynomial regression models (Rehfeldt and others 1999), and climate envelopes (Box and others 1999).

Our focus in this study is on patterns of vegetation change in western North America. Response surfaces are particularly appropriate for simulating change at this scale because continental distributions for many taxa are largely controlled by macroclimatic variables (Woodward 1987). By evaluating the response of vegetation to different combinations of environmental variables, response surfaces can be useful to identify previously unrecognized mechanisms that control the distribution of particular taxa. It is important to identify these mechanisms so that we can improve the sophistication of the mechanistic models. Moreover, one of the significant advantages of response surface models is that they can be easily applied to a large number of taxa. Thus, although response surface models oversimplify physiological and ecological processes that are important in governing plant distributions, they represent a relatively economical means of evaluating the potential impacts of climate change on patterns of species diversity (Box 1995).

In this study, we describe the changes in the potential distributions of species in western North America as simulated using three climate model scenarios for the period 2090–99. Characterizing the spatial dynamics of climate change and the magnitude and direction of vegetation response is an important first step in assessing the potential impact of changing climate on natural systems. Given the complexity of the controls on vegetation, however, considerable care must be taken in interpreting the simulated responses, given that the simulations provide only a partial indication of the general character of vegetation response and are not explicit predictions of change.

Changes in Potential Range Limits under Changing Climate

Vegetation response to climate change is determined by processes that interact over multiple temporal and spatial scales. These processes range from the broad-scale bioclimatic controls limiting a taxon's distribution (Woodward 1987) to the expression of genetic variation within a taxon's subspecies (Rehfeldt and others 1999). Migration rates, changes in disturbance regimes, and interactions with other species will all be important factors in determining the distribution of species under future climates, as will transient changes in the range and viability of diseases, pests, and mutualists, such as soil mycorrhizae and rhizosphere bacteria (Perry and others 1990). Equally important are the individual responses of species to increased concentrations of atmospheric carbon dioxide (CO_2) (Mooney and others 1999). At present, the models used to simulate vegetation distributions are just beginning to address this complexity.

Interpreting Response Surface Simulations

Previous studies of vegetation response to climate change have used climatic variables such as mean annual precipitation and summer temperature (Overpeck and others 1991). For this study, we used bioclimatic variables that represent either direct physiological controls on a species or are considered proxies for other processes that limit the distribution of a species on the landscape. As applied here, the distribution limits of a species are defined by upper and lower values for each of the three bioclimatic variables: mean temperature of the coldest month (MTCO), growing degree days (GDD), and a moisture index. These particular variables were chosen because they produce a good fit between simulated and observed taxa ranges (Sykes and Prentice 1996; Sykes and others 1996). By examining the gradient of the fitted response surfaces at specific locations in climate space, it is possible to determine which bioclimatic variables are controlling the simulated range shifts for individual species. It is assumed that species are in quasi-equilibrium with climate and that the response surfaces define the potential range of a species (that is, where suitable bioclimatic habitat exists for a species). Species may be excluded from areas within their potential range by nonclimatic factors, such as unsuitable substrate or competitive interactions with other species.

Mean temperature of the coldest month. Many North American tree species are limited by low temperatures at the northern edge of their range or at high elevations. For boreal species, this limit represents absolute minimum temperatures that are cold enough to damage or kill individuals (Sakai and Weiser 1973). MTCO is correlated with absolute minimum temperatures (Prentice and others 1992) and can be used as its surrogate. For warm-temperate species, the lower limit of the MTCO is related to a species' ability to withstand frost and snow damage.

Upper limits of the MTCO often correspond to the southern or low-elevation range limits for tree species. For some species, this upper limit is correlated with a chilling requirement, which delays budburst until an individual plant has been exposed to a period of cold temperatures during winter dormancy. This chilling requirement helps a plant to avoid damage from late-spring frosts (Cannell and Smith 1986). If the coldest months of the year are too warm, a plant's chilling requirement will not be fulfilled, which in turn will affect seedling growth responses. The growth response of seedlings of *Pseudotsuga menziesii* (Douglas-fir), for example, decreases as chilling temperatures increase and as the duration of the chilling period is shortened (McCreary and others 1990). In other instances the southern or low-elevation range limit may be related to competitive exclusion by other species. In these cases, species growing farther south or at lower elevations may have a competitive advantage in that they do not need to devote energy to the metabolic costs of protection from low temperatures, such as increasing leaf thickness (Woodward 1987; Loehle 1998). However, even in instances when competitive exclusion defines a southern or low-elevation range limit, the primary indirect control may still be related to climate in that low temperatures may limit the expansion of a more competitive but less cold-tolerant species.

Growing degree days. The distribution of a species may be constrained at its northern or high-elevation range limits if the number of GDD is insufficient for accomplishing basic physiological functions, such as budburst during the growing season (Newman 1980), or if it reduces the competitive ability of a species by limiting its growth (Loehle 1998). At southern or low-elevation range boundaries, the upper GDD limit does not directly affect a species, except as GDD are related to temperature. However, the upper limit for GDD may represent competitive exclusion similar to the process described above for the upper limit of the MTCO if the expansion of the competitively superior species is limited by insufficient GDD to achieve budburst and leaf production.

Moisture index. The moisture index, calculated as annual actual evapotranspiration divided by annual potential evapotranspiration, is a simple means of representing drought stress (Prentice and others 1993). Lower limits of the moisture index represent a species' tolerance of drought; upper limits of the moisture index represent intolerance of moist conditions. Both the upper and lower moisture index limits may also represent competitive exclusion by other species more suited to particular moisture conditions.

METHODS

Climate Data

The observed climate data consist of 30-year climate normals from North America climate stations for the period 1951–80 (Thompson and others 1999). Mean monthly temperature and precipitation values from this data set were interpolated onto an equal-area 25-km grid of North America using a locally weighted trend-surface regression method with latitude, longitude, and elevation as predictors (Lipsitz 1988).

Climate data from transient experiments of three coupled atmosphere and ocean general circulation models (GCM)—HADCM2 (Mitchell and Johns 1997), CGCM1 (Boer and others 2000), and CSIRO (Gordon and O'Farrell 1997)—were used to simulate the response of vegetation to climate change. For each model, we averaged the ensemble data from the experimental runs, which included a 1% per year compound increase in greenhouse gases and changes in SO_4 aerosols matching the IPCC IS92a scenario (Houghton and others 1996). This scenario yields an atmospheric CO_2 concentration of approximately 700 ppm by the year 2100 (Houghton and other 1996). The model data were obtained from the IPCC Data Distribution Centre GCM Archive web page (http://ipcc-ddc.cru.uea.ac.uk).

Range Maps

Taxon range maps digitized from Little (1971, 1976) were applied to the 25-km grid to determine the presence or absence of a taxon for each grid cell (Thompson and others 1999). Seventy-seven tree and shrub species representing a range of North American habitat types (for example, high-elevation, low-elevation, arid, boreal, and so on) were chosen for this initial analysis. The results for the analysis of fifteen species are described here.

Bioclimatic Variables

Three bioclimatic variables were used: MTCO, GDD calculated on a 5°C base (that is, the number of degrees above 5°C of each day's temperature summed over the entire year), and a moisture index calculated as annual actual evapotranspiration divided by annual potential evapotranspiration (AE/PE) (Figure 1). The bioclimatic variables were calculated from each of the four climate data sets (modern observed climate and each of the three climate scenarios for 2090–99). To derive the moisture index, the available water-holding capacity of the soil for each 25-km grid cell was calculated using the equations of Saxton and others (1986), as applied to the Food and Agriculture Organization of the United Nations (FAO) global soil data set (FAO/UNESCO 1974) using data on soil texture and depth from Webb and others (1991). The water balance was calculated using the Thornthwaite-Mather method (Wilmott and others 1985). We are currently exploring the use of actual evapotranspiration as a moisture index to improve the fit of the response surface model (Stephenson 1998).

Response Surfaces

The relationships between taxon distributions and climate were determined using response surfaces (Bartlein and others 1986; Lenihan 1993). As implemented here, response surfaces are local regression models (Cleveland 1993; Loader 1999) that estimate the probability of a specific taxon occurring at any particular point in climate space. Climate space for this analysis is defined by the values of the three bioclimatic predictor variables at each grid point on the 25-km grid of North America.

Response surfaces for each taxon were fitted to the observed taxon presence/absence data using the bioclimatic variables derived from the modern observed climate. The probability of a species occurring at any particular point in climate space was calculated by applying a moving window through climate space with widths equal to 900 GDD for the GDD variable, 7.5°C for the MTCO variable, and 0.05 AE/PE for the moisture index variable. Each point within the window was weighted using a tri-cube function based on the distance of each point in the window from the center of the window, with points near the center of the window more heavily weighted. These weights were then applied to the taxon presence/absence data for each grid point within the window.

The arithmetic mean of the weighted taxon presence/absence data gives the proportion of the points within the window where the taxon occurs. This proportion is considered the probability of the taxon occurring in that particular region of climate space. A threshold probability for declaring a taxon to be present was determined by evaluating different probabilities of a taxon's occurrence against the modern range maps and visually choosing a threshold that maximized the number of grid cells where the presence/absence of the taxon was correctly predicted while at the same time minimizing both over- and under-prediction. If a taxon's probability of occurrence was below this threshold, the taxon was declared absent.

Climate Change Scenarios

For each climate model data set, anomalies were calculated as the change between the 2090–99 10-year mean monthly GCM climate and the 1980–89 10-year mean monthly GCM climate for each climate variable. Temperature anomalies were calcu-

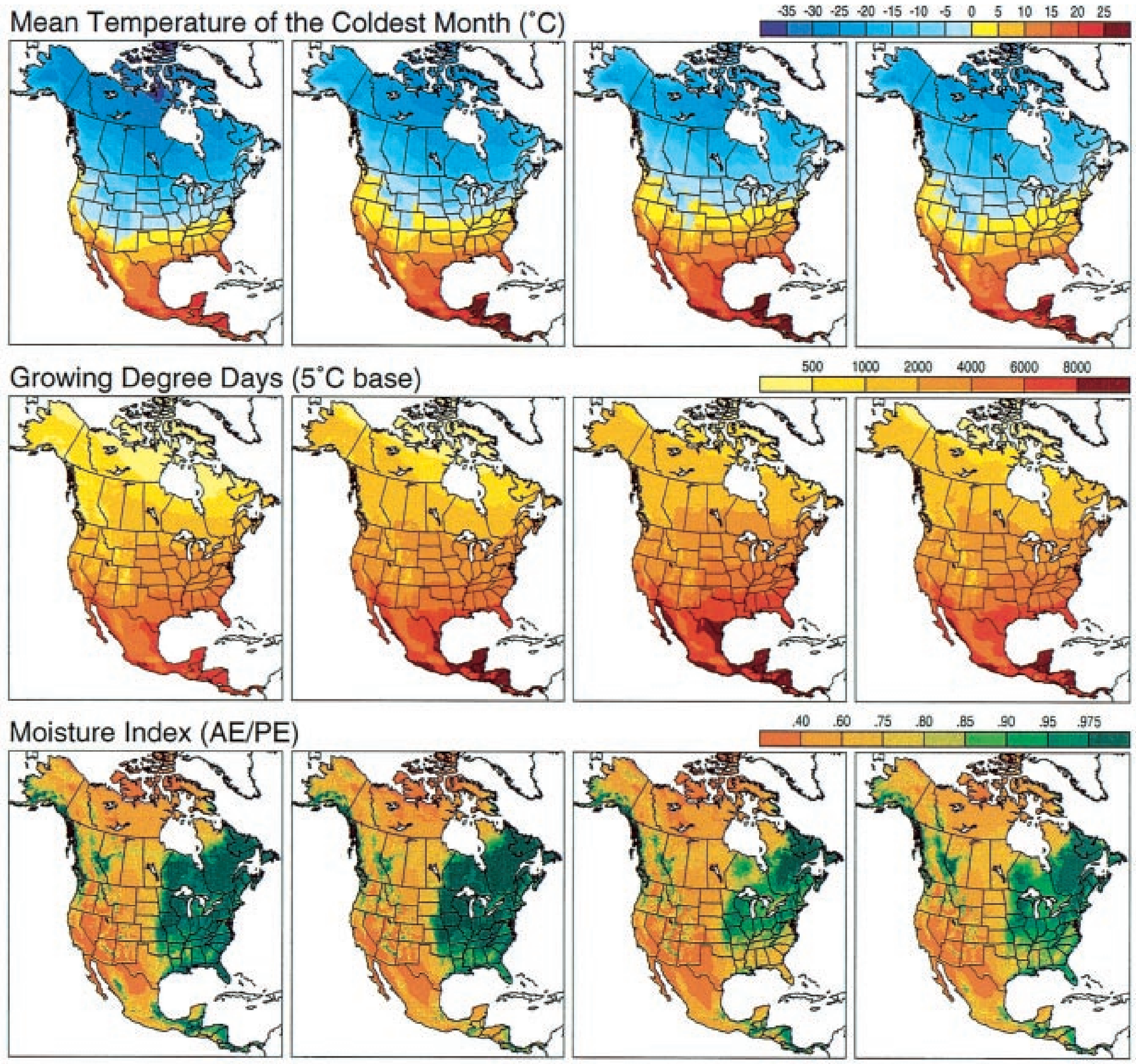

Figure 1. Maps of the three bioclimatic variables: mean temperature of the coldest month (MTCOM) (top), growing degree days (GDD) (middle), and moisture index (bottom). The first panel in each row displays the bioclimatic variable derived from the modern observed 1951–80 climate data set. The following three panels in each row display the bioclimatic variable as calculated from each of the three future-climate scenario data sets.

lated as the difference between 2090–99 and 1980–89 10-year mean monthly GCM temperature values. Precipitation anomalies were calculated as ratios of 2090–99 to 1980–89 10-year mean monthly GCM precipitation values. All of the anomalies were interpolated onto the 25-km grid using bilinear interpolation (Press and others 1992). The anomalies for each variable were then applied to the observed modern climate data to produce the future climate values for each variable.

Future Projections of Taxon Distributions

The projections of potential distributions of species under future climate were created by evaluating the response surfaces, with the climate data from each of the three future climate scenarios yielding a probability of occurrence of each taxon at each of the 25-km grid points. This process assumes that species–climate relationships can be projected into the future. Some limitations of this assumption are discussed below.

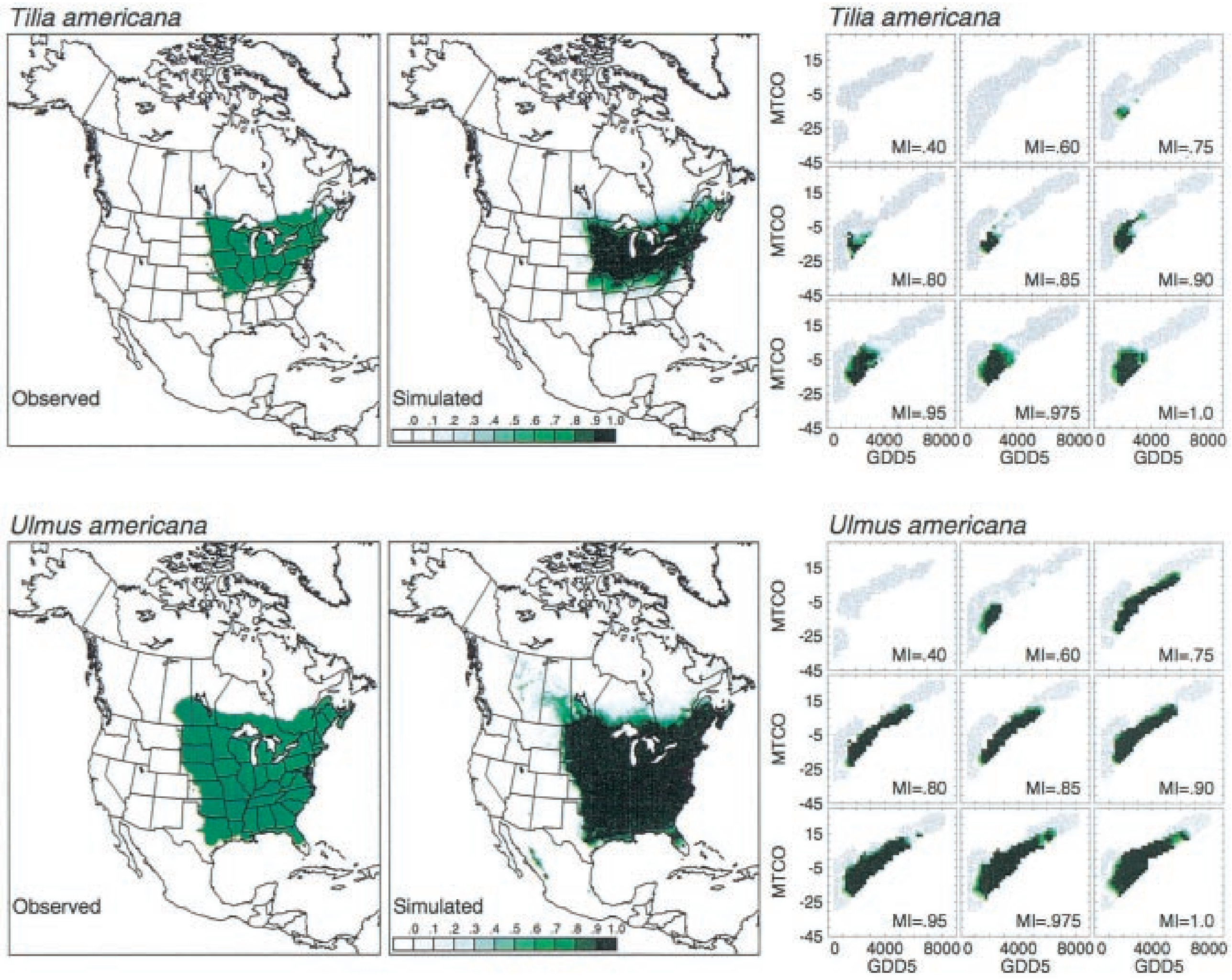

Figure 2. Response surfaces for *Tilia americana* and *Ulmus americana*. Each row shows the observed distribution of the species (left), the simulated probability of occurrence estimated using the response surface for the species and observed modern climate (middle), and the simulated probability of occurrence displayed as nine two-dimensional slices (GDD by MTCO) through a three-dimensional climate space, arranged by moisture index value (right). All the grid points in North America are displayed in the right-hand panel; gray points represent grid cells where the species is simulated to be absent, and green points (shaded by probability of occurrence) represent grid cells where the species is simulated to occur.

RESULTS AND DISCUSSION

Simulations of Observed Distributions of Species

As an illustration of the construction of response surfaces, the first column of Figure 2 displays the observed presence/absence data for *Tilia americana* (American basswood) and *Ulmus americana* (American elm) on the 25-km grid. The second column depicts the probability of occurrence for the two species obtained by evaluating each species response surface using the modern observed climate data. The third column shows the response surface itself displayed by two-dimensional slices (GDD by MTCO) through three-dimensional climate space, with the slices arranged by moisture index value. Each of the nine slices shows species presence or absence as estimated by the response surface. For most of the species examined, areas in climate space of high probability of occurrence for a particular species estimated using the response surface model correspond to the continuous core areas of the species' observed distribution in geographical space. The probability of occurrence decreases as one moves away from the core areas, representing a transition zone between the center of a species' range and peripheral areas beyond which it does not occur.

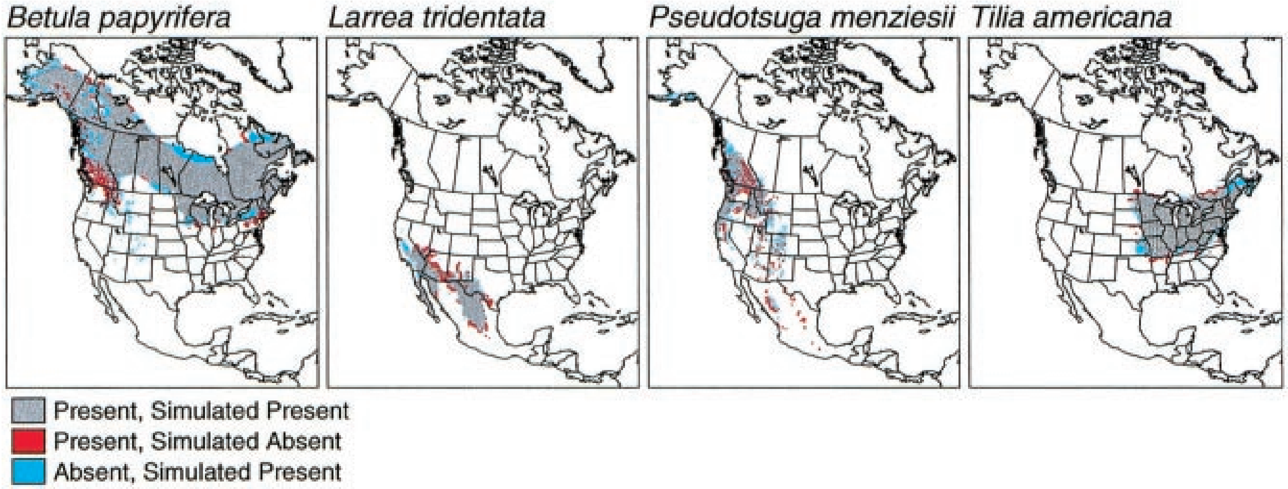

Figure 3. Estimated species occurrence simulated with observed modern climate, compared with observed range distributions for four species in North America. Gray indicates areas where the species is present and is simulated to be present by the response surface model; red indicates areas where the species is present but is simulated to be absent (underprediction); and blue indicates where the species is absent but is simulated to be present (overprediction).

The response surface slices shown in the third column of Figure 2 provide a means for evaluating the bioclimatic controls over a taxon's distribution. For example, the response surface slices for *Tilia americana* (Figure 2) show that this species does not occur at grid points with GDD values less than 1000 or where the moisture index falls below 0.6. In contrast, the response surface slices for *Ulmus americana* (Figure 2) display that species' broader range of climatic tolerances. The local gradient of the response surface provides additional information on the nature of the climatic control on different taxa by illustrating the local rates of change in taxon probability of occurrence with respect to spatial variations in climate.

The response surface models do a relatively good job of estimating the observed ranges of species. The goodness of fit between a taxon's observed range and the estimated probability of occurrence for that taxon can be evaluated in terms of the extent of overprediction (absent but simulated by the response surface to be present) and underprediction (present but simulated by the response surface to be absent) (Figure 3). Disjunct distributions can be resolved by the response surfaces even when their spatial area is relatively small, as is common in mountainous regions (for example, *Pseudotsuga menziesii*) (Figure 3).

In some cases, the response surfaces estimate a high probability of occurrence for a taxon well outside of its observed range (for example, *Betula papyrifera* [paper birch] south of Hudson Bay) (Figure 3). These areas of overprediction indicate where the bioclimatic habitat may be suitable for the species but where it does not naturally occur due to nonclimatic factors, such as inappropriate substrate (for instance, peatlands), which are not captured by the response surface method. Dispersal barriers or migrational lags could also account for these areas of overprediction. Interestingly, a number of areas of "overprediction" are locations where a species was not recorded by Little in his atlases (Little 1971, 1976) but where it does in fact occur and has been recorded in more recent range maps (for example, Burns and Honkala 1990a, 1990b). The ability of the response surface approach to capture occurrences of species in these areas accurately is a positive indication of the model's performance.

Lack of fit between observed and simulated taxon ranges may also be partly explained by the spatial resolution of the 25-km grid, which is too coarse to capture important local variations in climate space. This lack of resolution is a particular problem in mountainous regions of the West, where steep environmental gradients can yield large bioclimatic variability within an area corresponding to the size of the grid cells. A higher-resolution grid would enhance the fit of the response surfaces by resolving this variation. Another factor affecting the performance of the model is the choice of bioclimatic variables used to generate the response surfaces. The three variables chosen are not necessarily optimal predictor variables for all species. Finally, a consistent area of overprediction of distributions of species by the response surface model occurs in Alaska and northern Canada (for example, *Pseudo-*

tsuga menziesii) (Figure 3). Although these areas of overprediction may represent suitable potential habitat outside a species' current range, they may also be artifacts related to the sparse distribution of observed climate station data in this region, which prevents the interpolated climate data set from capturing important features of the regional climate.

Simulated Potential Distributions of Species under Future Climate

Figures 4, 5, and 6 display simulated potential distributions of species under each of the three climate change scenarios for 2090–99 focusing on three groups of taxa, those with (a) continental distributions (b) western North America distributions and (c) Pacific Northwest distributions. Areas of potential range contraction estimated by the response surface models indicate where one or more of the bioclimatic limits defining the distribution of a species are exceeded (red). Contraction is not meant to imply immediate mortality for the individuals of a species; rather, it indicates where the current limits of the species' bioclimatic habitat would not be met under future climate conditions. A number of additional factors will control whether the simulated potential range contraction will occur, including the particular physiological effect of the exceeded bioclimatic limit on the species in question, the life stage at which the limit is effective (for instance, seedling vs adult), the life span of the species, and the movement of other organisms into the species' range.

Areas of potential range extension are regions where suitable bioclimatic conditions will exist under each of the future climate scenarios (blue). The ability of a species to actually exploit newly available habitat will also depend on a number of additional factors, including the response to climate change of species that are already established in areas that another species is expanding into, the presence of suitable substrate, the dispersal rates of individual species, and the frequency of disturbances that facilitate species establishment (Dale and others 2000).

Overall, simulated changes in the potential distributions of species are large under all three future climate scenarios. Contractions and expansions of taxon ranges on the order of hundreds of kilometers frequently occur. Of the three climate models used here, the largest potential range changes occur under the CGCM1 scenario, the smallest changes occur under the HADCM2 scenario, and the magnitude of the changes simulated by the CSIRO model falls between that of the other two. The right-hand columns in Figures 4, 5, and 6 display model agreement for the simulated future potential distributions by showing for each grid point the number of models that simulate a species to be present or absent. Note that although the magnitude of change simulated by each of the three GCMs varies, the broad-scale geographic pattern of change is consistent among all three models.

The pattern of vegetation response to future climate change in North America is strongly mediated by topography. In the eastern and northern parts of the continent, simulated changes in potential distributions of taxa tend to be contiguous, with shifts in bioclimatic habitat occurring as broad expansions and/or contractions of the current ranges (for example, *Betula papyrifera, Tilia americana*, and *Ulmus americana*) (Figure 4). In general, the simulated potential range expansions in eastern North America, where topographic relief is relatively low, occur in a northward direction with increases in MTCO. Simulated west-to-east potential range changes along the prairie–forest border are primarily related to changes in the moisture index. In contrast, in western North America, the simulated patterns of change in potential ranges are more disjunct, often with large distances occurring between a species' current distribution and simulated areas of future potential habitat (for example, *Pseudotsuga menziesii*) (Figure 4).

A variety of patterns are reflected in the changes in the simulated potential distributions of species across western North America. *Betula papyrifera* and *Picea glauca* (white spruce) are examples of boreal species whose potential distributions are simulated to expand generally northward in response to increases in MTCO (Figure 4). This expansion of boreal trees into northern latitude shrubland and tundra areas is an anticipated response to global warming (Kirschbaum and others 1996). The simulated potential ranges for these two species also illustrate some of the complexity of species' responses to changing climate—the southern range limit of *P. glauca* contracts northward, while in contrast the southern range limit of *B. papyrifera* expands southward in the Rocky Mountains. This simulated southward expansion is due to the increase in the Rocky Mountains of both the MTCO and moisture index. The potentialranges of both species are simulated to contract in the mid-continent due to decreases in the moisture index, although drought stress could be mitigated if either species' water use efficiency increases in response to elevated atmospheric CO_2 concentrations.

Farther south in the intermountain region of the US, the potential range of *Artemisia tridentata* (big sagebrush), a major cold desert and steppe shrub

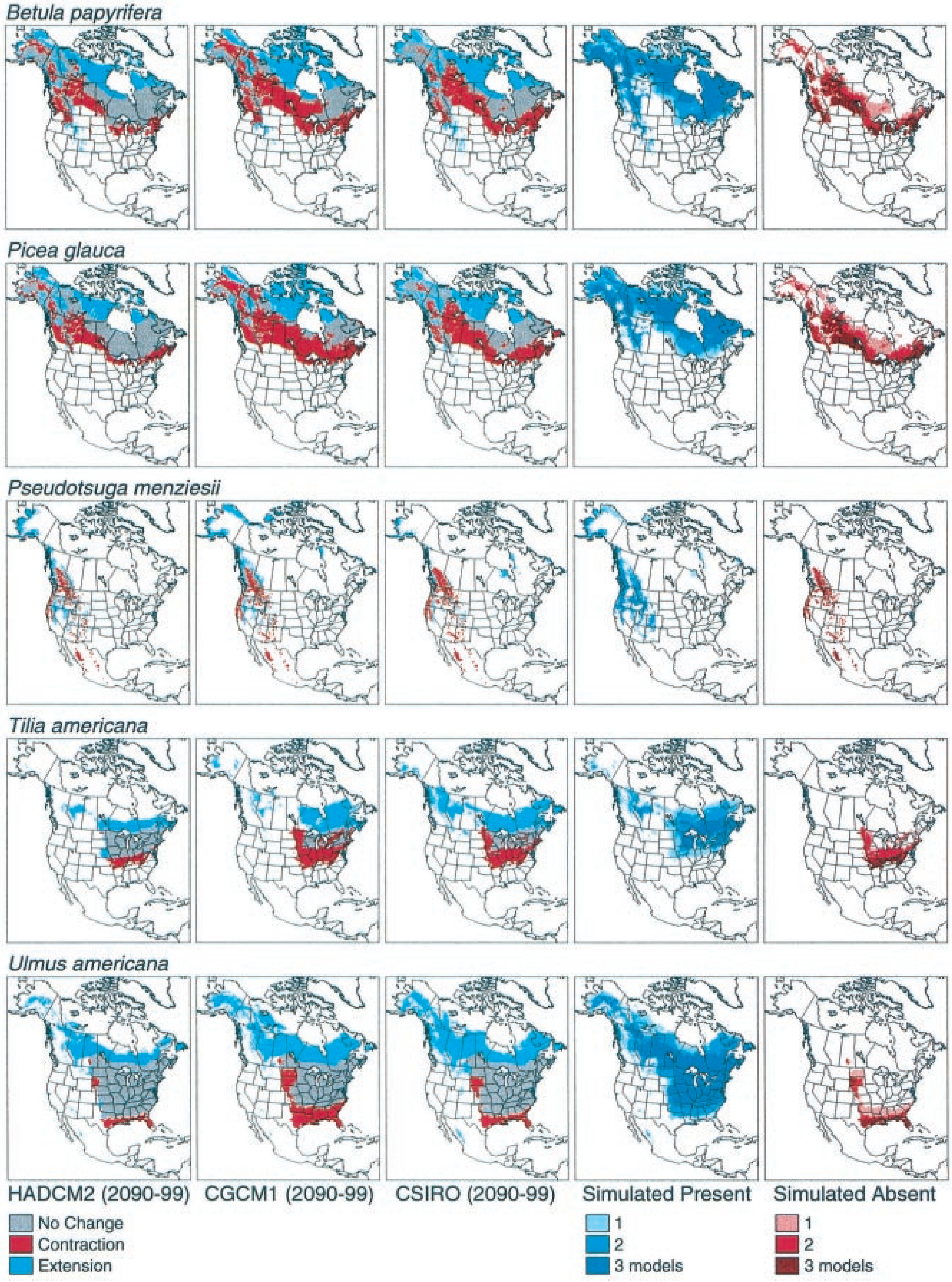

Figure 4. Comparison of observed distributions with future simulated distributions for five species in North America using climate scenarios for 2090–99 generated by the HADCM2, CGCM1, and CSIRO GCM (left three columns). "No change" indicates where the species is observed at present and is simulated to occur under future climate conditions; "contraction" indicates where the species is observed at present but is simulated to be absent under future climate conditions; and

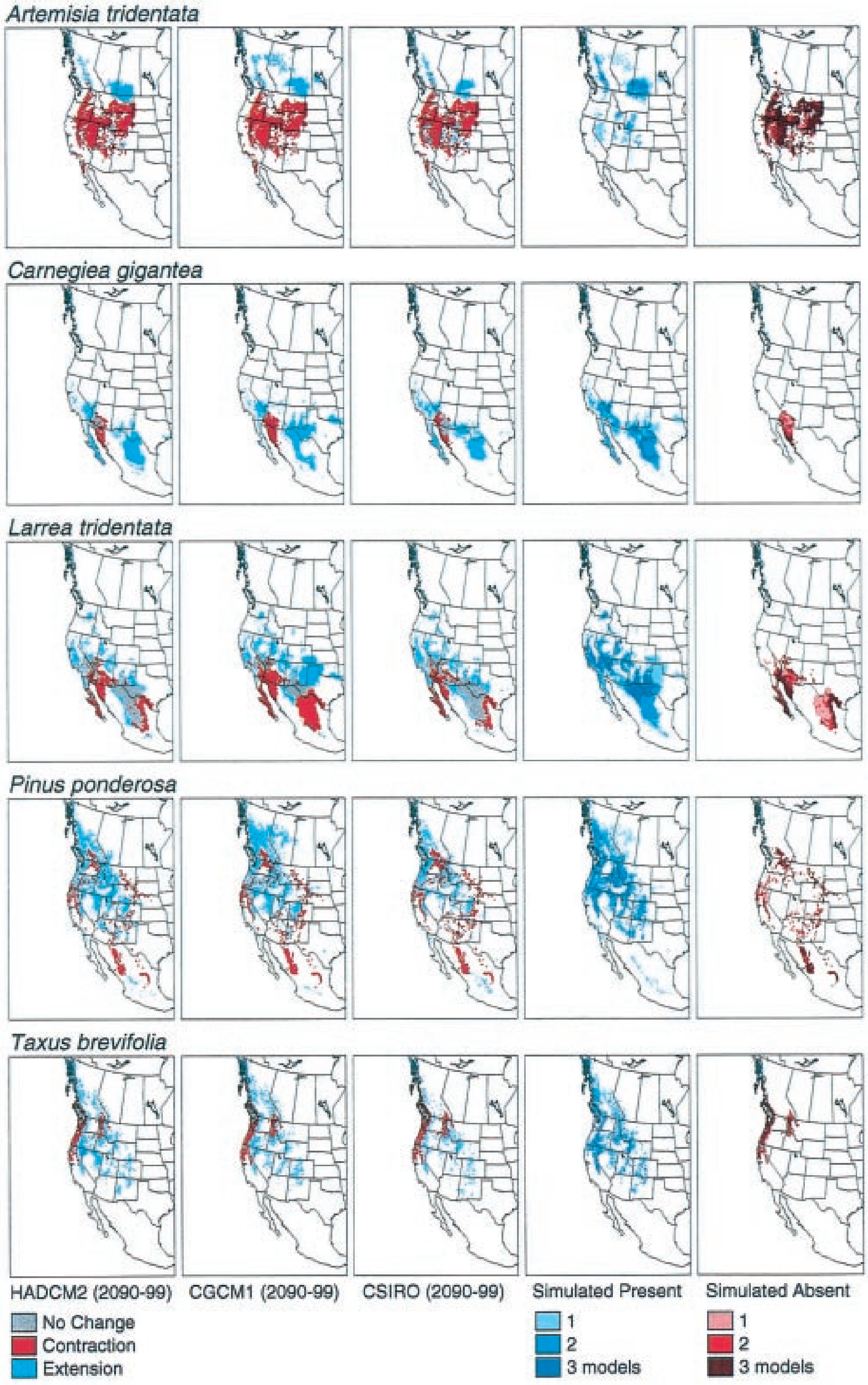

Figure 5. Comparison of observed distributions with future simulated distributions for five species in western North America using climate scenarios for 2090–99. Data as in Figure 4.

"extension" indicates where the species is not observed at present but is simulated to occur under future climate conditions. Agreement among the future distributions of each species as simulated by the three GCM scenarios is displayed by showing for each grid point the number of model scenarios that simulate a species to be present or absent (right two columns).

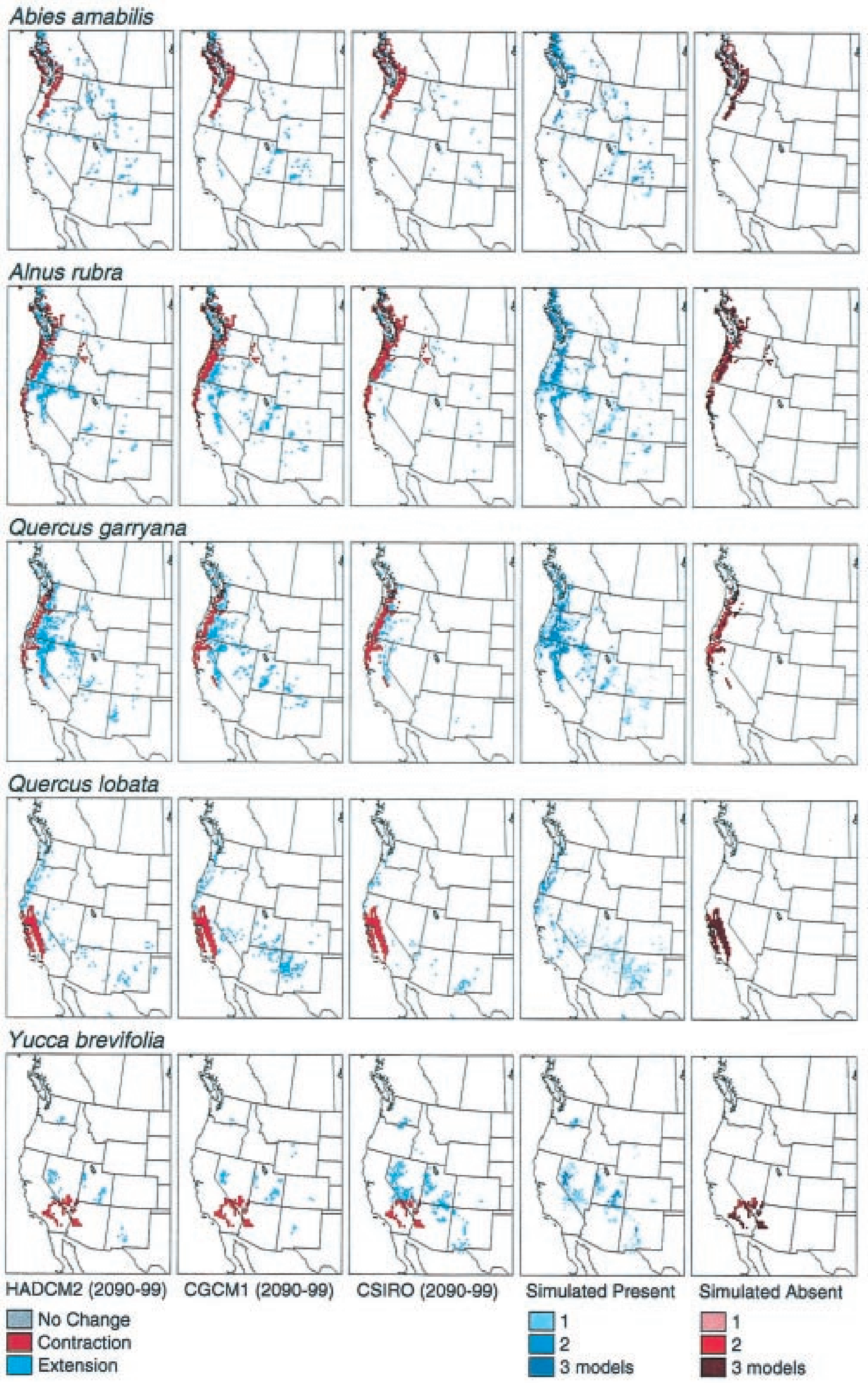

Figure 6. Comparison of observed distributions with future simulated distributions for five species located primarily in the western United States, using climate scenarios for 2090–99. Data as in Figure 4.

species, is simulated to shift northward in response to increases in the MTCO accompanied by a significant contraction of its current range (Figure 5). *A. tridentata* is limited by summer moisture stress and aridity defines its southern range limit (West and Young 2000; Smith and others 1997). Increases in the MTCO could indirectly affect the potential range of *A. tridentata* if increases in transpiration rates during the winter months combined with changes in the precipitation regime result in increased soil moisture stress during the year. Increases in the frequency of fires under the future climate scenarios would also facilitate the simulated potential range contractions because *A. tridentata* does not resprout following fire events (Smith and others 1997).

Yucca brevifolia (Joshua tree) is found in the deserts of the southwest US and northwest Mexico (MacMahon 2000). Under each of the future climate scenarios, its simulated potential range is fragmented and displaced northward and eastward (Figure 6). *Carnegiea gigantea* (saguaro, based on Little's [1976] *Cereus giganteus* map) and *Larrea tridentata* (creosote bush, based on Yang's [1970] *Larrea divaricata* map), two important desert species, also show significant simulated potential range shifts. *L. tridentata* is sensitive to freezing temperatures (Smith and others 1997); with increases in the MTCO, its potential range expands throughout the intermountain regions of the West into areas currently dominated by *A. tridentata* (Figure 5). The potential range of *C. gigantea*, a distinctive desert cactus, is simulated to expand and diverge under all three future scenarios, with new habitat occurring both west and east of its current range (Figure 5). Further south in the mountains of western Mexico, increased temperatures coupled with a lower moisture index leads to simulated potential range contractions of the southern subspecies of *Pseudotsuga menziesii* (Figure 4) and *Pinus ponderosa* (ponderosa pine) (Figure 5), two important conifers within this region.

The western mountain ranges of the Pacific Northwest are noted for their high diversity of conifer species (Ricketts and others 1999). These forests are also particularly sensitive to climate change. In the Pacific Northwest, the potential ranges of high-elevation species, such as *Abies amabilis* (Pacific silver fir), are simulated to contract due to increases in the MTCO (Figure 6). This reduction in the distributions of high-elevation species is an anticipated response to increasing temperatures (Beniston and others 1996). An unexpected response, however, is the simulated shift in the potential ranges of many Pacific Northwest species from west of the Cascades and northern Sierras to the east of these mountain ranges. This pattern occurs for both conifer species, such as *Pseudotsuga menziesii* (Figure 4) and *Taxus brevifolia* (Pacific yew) (Figure 5), as well as for broadleaf species, such as *Alnus rubra* (red alder) and *Quercus garryana* (Oregon white oak) (Figure 6). Species whose potential distributions are simulated to expand into the area west of the Cascades and northern Sierras include those species that can tolerate relatively warm and dry conditions, such as *Pinus ponderosa* (Figure 5) and *Quercus lobata* (California white oak) (Figure 6). A change in species composition of this sort would have a significant impact on the character of western forest ecosystems.

Driving this shift of the potential ranges of species from west to east is the increase in the MTCO from 0–5°C to 5–10°C along the Pacific Northwest coast (Figure 1). Although increased temperatures may not affect some species, many Pacific Northwest tree species have a winter chilling requirement that is optimally achieved with temperatures at or below approximately 5°C (Kimmins and Lavender 1992). Chilling requirements are found in many Pacific Northwest evergreen conifers, such as *Pseudotsuga menziesii* (McCreary and others 1990) and *Tsuga heterophylla* (western hemlock) (Nelson and Lavender 1979). *P. menziesii*, one of the major species of Pacific Northwest forests, has a relatively long chilling period that would not be adequately met under the simulated future increases in the MTCO (Kimmins and Lavender 1992). This increase in the MTCO is significant because, in the event of a large disturbance such as a stand-replacing fire, lack of chilling could seriously affect seedling reestablishment and could be a catalyst for major changes in the species composition of *P. menziesii*–dominated forests. The absence of below-freezing temperatures may also have an indirect effect on tree diversity as warming allows competitors that are currently excluded by freezing temperatures to move into this region.

Although western North America supports a great diversity of habitat, the spatial extent of any particular habitat type may be relatively small and separated from other similar patches of habitat by large distances. The relative isolation of many new areas of suitable bioclimatic habitat that are simulated under the future climate scenarios, coupled with their small size, would make natural dispersal to these areas difficult for many species. Migration rates for tree taxa during the Holocene were only on the order of 1000 m/y (Pitelka and the Plant Migration Workshop 1997). Even given the possibility of long-range dispersal events, habitat fragmentation resulting from human land-use activities will have a significant impact on the abilities of species to successfully disperse in response to changing climate conditions. The disjunct pattern of simulated future bioclimatic habitat, as in the case of *C. gigantea* (Figure 5), suggests that gene flow for some species may be significantly affected by changes in their potential distributions.

Challenges for Preserving Species Diversity under Changing Climate

The direction and magnitude of simulated species response to future climate change implies significant impacts to current conservation and natural resource management areas (Halpin 1997). Under each of the three future climate scenarios, the magnitude of the simulated changes in the potential distributions of species is large. Changes of this magnitude would tend to have negative consequences for species that are rare, have narrow environmental tolerances, low dispersal rates, or are less competitive than other species.

Studies of vegetation response to climate change often emphasize the anticipated movement of species northward or upward in elevation. In contrast, the response surface results indicate that potential range shifts in western North America will occur in all directions, including to the south of existing ranges for some species (for example, *Quercus lobata* (Figure 6). This pattern of change is due to the topographic complexity and steep environmental gradients of western mountain ranges, which provide a high diversity of bioclimatic habitat under each of the future climate scenarios. In selecting conservation areas to mitigate the potential effects of future climate change, the sensitivity of a conservation site's environmental gradients to changing climate will be of critical importance.

Identifying areas resilient to climate change. One strategy for conserving species and their habitat under changing climate is to identify locations that may sustain suitable habitat conditions for a species as climate changes (gray areas in Figures 4, 5, and 6). For the boreal tree species evaluated in this study, relatively large areas of their current range remain suitable under each of the future climate scenarios. In the western US, however, the steep environmental gradients, coupled with the magnitude of simulated climate change, will produce relatively few areas in this region where a species' potential range does not shift significantly under each of the future climate scenarios. One of the areas that appears more resilient to change is the southern Idaho Rocky Mountains, where bioclimatic habitat for a number of species evaluated in this study was simulated to persist under future climate conditions. Because climate change is transient, however, there is no guarantee that suitable habitat in the southern Idaho Rocky Mountains would persist into the future if anthropogenic forcing of climate change continued.

Increases in MTCO. A significant future threat to current species diversity in the mid to high latitudes of western North America is the simulated increase in the MTCO. Winter temperatures that drop below freezing are very important in determining the species composition and patterns of biodiversity in temperate North American forests (Kirschbaum and others 1996). In North America, the transition from regions where the MTCO is above freezing to areas where it drops below freezing occurs as a broad band across the southern US and along the West Coast, shown in Figure 1 as a shift from yellow to blue. Under all three future climate scenarios, large regions of the US no longer experience mean monthly temperatures that drop below freezing. In the eastern US, the area over which this shift occurs is on the order of hundreds of kilometers to the north. In western North America, the change is even more striking, as the shift from below-freezing to above-freezing mean monthly temperatures occurs for a region of the interior West stretching from northern Arizona to southern Washington (Figure 1).

A shift of mean monthly temperatures from below to above freezing does not mean that freezing temperatures will no longer occur. However, such a shift will change the duration and magnitude of below-freezing temperatures, which will have significant impacts on many species in the western US. Warm-temperate species that were previously limited by freezing temperatures may be able to spread northward. Warm-temperate pests and pathogens may be able to move northward as well, and the absence of freezing temperatures will allow some insects to reproduce throughout the year (Kirschbaum and others 1996; Ayres and Lombardero 2000). Increasing temperatures will also alter competitive interactions between deciduous and evergreen species by allowing increased rates of photosynthesis by evergreen species during winter months.

Interspecies competition. From the magnitude of the simulated potential range changes, it is clear that competitive interactions between species will change as climate changes, which could affect the viability of some species. Unfortunately, predicting areas of future competitive interactions between two species is not as simple as comparing their simulated future potential ranges. Paleoecological evidence indicates that species respond individualistically to climate change (Webb 1995; Huntley 1995); and thus, the mix of species with which any one species interacts will change as climate changes. Changing species distributions may bring a species into contact with other taxa with which it has never interacted, and entirely new competitive interactions may result. Conversely, climate change may eliminate an important predator, allowing a species to greatly expand its range. Perhaps the most significant interspecies interaction will be with humans due to the impact of our land-use activities on habitat and species distributions and abundances (Dale 1997). Response surface analyses cannot model species interactions, but they can help to identify the potential future climate space in which these interactions will occur.

Physiological Responses to Increased Atmospheric CO_2 Concentrations

An important limitation of response surface analysis, as with all other statistical models, is that it does not include the physiological response of vegetation to increases in atmospheric CO_2 concentrations. The fertilization effect of increased CO_2 concentrations could significantly alter competitive interactions among species. Elevated CO_2 concentrations may also increase a plant's water-use efficiency, which in turn may enhance its tolerance of drought conditions (Polley 1997). Because the response surfaces do not include the CO_2 fertilization effect or the enhanced drought tolerance associated with increased water-use efficiency, they may underestimate the future amount of suitable bioclimatic habitat for some species. The enhanced drought tolerance is particularly significant when attempting to project vegetation response to climate change in arid regions, such as many parts of the western US. Mooney and others (1999) found that for arid systems, CO_2-induced changes to the water balance yielded a greater plant response than the direct effects of CO_2 fertilization.

CONCLUSION

The results of this study indicate that changes in the potential distribution of tree and shrub taxa in North America in response to future climate change will be large and that ranges will shift not only northward and upward in elevation but in all directions. The response surface approach used in this study simulates changes in the potential distribution of the bioclimatic habitat of tree and shrub taxa. This approach cannot explicitly predict future ranges of species. However, to the extent that the distribution of an individual species is limited by the MTCO, GDD, and moisture index, the response surface model can simulate potential future changes in the bioclimatic habitat for individual species. In so doing, it illustrates the magnitude and direction of change we may expect to observe in the distributions of species as the climate changes, although the actual pattern of change for any individual species will be different from the pattern simulated for it by this model.

As for other correlative models, the ecological assumptions underlying response surface models are in many ways unsatisfying because they presume that there is a direct causal correlation between the distribution of a species and particular environmental variables, which is sometimes, but not always, the case. However, more robust simulations of the continental distributions of species require empirical studies of the specific controls on multiple-species distributions to determine whether range limits are controlled by climate, competition, or other factors individually or in combination. For many species, empirical studies of this sort will not be available anytime soon. In the meantime, atmospheric concentrations of CO_2 and other greenhouse gases are increasing at a rapid rate, and although there may be uncertainty in the ability of models to simulate the response of climate to the forcing of greenhouse gases, as well as uncertainty in the magnitude of the potential change, we can be certain that atmospheric increases of greenhouse gases will affect the climate. Consequently, we need to characterize the types of change that may occur as the climate changes so that we can assess the potential impact of these changes on natural systems.

The results of this study also indicate that range fragmentation may be a significant problem for some species. In western North America, the areas of future bioclimatic habitat simulated by the model are often small and disjunct, reflecting the environmental heterogeneity of the landscape. Finally, our analysis assumes that all areas of North America are available as potential future habitat but this is not the case. Land-use activities will both severely restrict the amount of suitable habitat available to species and impede their ability to successfully disperse as the climate changes.

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