

MODELING FUTURE PLANT DISTRIBUTIONS ON THE COLORADO PLATEAU: AN EXAMPLE USING *PINUS EDULIS*

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The recent mortality of some plant species in the U.S. Southwest has been attributed to the ongoing drought conditions over the last decade. This mortality has been especially acute in populations of *Pinus edulis* (Colorado pinyon pine; hereafter abbreviated as pinyon), a widespread and highly visible species (Shaw 2006; Shaw et al. 2005; Mueller et al. 2005). These recent mortality events may be similar to changes expected to occur in the future because of global climate warming (Breshears et al. 2005). That is, the consequences of periodic episodes of low precipitation can be exacerbated by higher temperatures, which increase drought stress. Here we demonstrate new techniques for modeling the effect of future climates on plant species using pinyon as an example. Using the techniques described here, similar results could be generated for any plant species or for any climatically controlled environmental process.

MODELING CHANGE USING CLIMATIC ENVELOPES

As climates have changed in the past, the geographic distributions of plant species have shifted as well. Future climate change will also result in the mortality of some plant populations as the suitable climate for these species shifts to new regions. This shifting of climate and populations has occurred naturally through time, though sometimes at notably faster rates. If the rate of the climate shift exceeds the migrational capabilities of the species, it must lag the climate shift, eventually catching up through

migrational processes such as seed dispersal, maturation, succession, and equilibration within their new plant assemblages.

Through modeling it is possible, given any new climate, to predict where a species should be eliminated and where it could survive. Many models assume that a species is already present across its new potential range, waiting for the new climate to allow its seeds to sprout. In our model, we instead incorporate data on the species' past and ongoing rates of migration in order to determine which of these new potential areas the species will likely expand into, and which will remain beyond its range during that period.

We developed our computer models using the "individualistic" species approach to vegetation change. Each species is treated as an individual entity and its climate envelope is modeled using its geographic range during the late twentieth century. This approach integrates the variability within the current population including regional genetic variants and local microhabitats. The model also incorporates all of the indirect physical and biological processes influencing the range that are modulated by climate. Processes such as fire frequency, soil microfauna, and arthropod occurrences are represented in the model to the extent that they are controlled by climate and have influenced the species' range during the twentieth century. For example, if the species is susceptible to bark beetle infestations as warmer temperatures allow for increased beetle populations (Williams and Liebhold 2002), then this tem-

perature limit should be expressed somewhere as a geographic limit to the species range. But the model could not predict the effects of new beetle species recently introduced from other continents.

The incorporation of cross-correlations between these multiple limiting factors is maximized by analyzing the entire twentieth century range of the species (Jackson and Overpeck 2000). But this climate envelope model cannot predict the effect of new or unique combinations of biological and physical variables not evident near the species range. Most important, the physiological effects of higher CO₂ concentrations (Waterhouse et al. 2004) are not incorporated because the twentieth-century species range did not contain CO₂ levels as high as current or predicted future values. The results of FACE (Free Air CO₂ Enrichment) experiments and/or observations of ongoing landscape changes from permanent plots can eventually be used to incorporate this effect.

RECENT SHIFTS OF PINYON

The rate of plant migrations is determined by several factors, the most obvious of which is long-distance seed dispersal. But to be effective, these long-distance events must be frequent because seeds are rarely successful in colonizing new habitats, especially those already occupied by other species. If a seedling does survive, that individual must mature to provide a local seed source. Then this local process of further establishment and further maturation will involve additional time lags for late successional species such as pinyon. Parameterizing models of these processes requires values from observations, but the relationships between frequency and distance for long-distance dispersals cannot be measured experimentally but only inferred (Cain et al. 2000; Davis et al. 1986) because as the distance of these dispersals becomes greater, their frequency rapidly decreases below a measurable threshold. As a result, some studies retreat toward anecdotes of extreme dispersal events without information about the frequency of such events. A more promising approach toward estimating plant migra-

tions might be to observe and measure ongoing and past plant migrations, rather than to model their constituent processes.

Over the last century pinyon has been observed encroaching into grazed grasslands adjacent to existing woodlands (Rosenstock and van Riper 2001). Some researchers have observed that pinyon encroachment lags behind a more rapid juniper encroachment (Blackburn and Tueller 1970), as pinyon seedlings often become established under juniper "nurse" trees (Chambers 2001). Unfortunately, there seem to be few estimates on this rate of pinyon encroachment by distance. Instead, the rate is usually estimated as the number of years it takes for a forest to develop in a grazed or burned, or a chained area that is already adjacent to an existing forest. As a result, these estimates may be more useful as a measure of successional processes that follow the local availability of seed.

While studying woodland recovery after three stand-replacing fires near the northern limit of pinyon at Dutch John in Utah, Goodrich and Barber (1999) estimated that despite already having a rich seed source nearby, these small areas (13–82 ha in size) would take more than 200 years to return to the pre-burn mature successional pinyon woodland stage. A similar study in north-central Arizona estimated that 215 years may "underestimate" the time required for development of a mature pinyon forest (Tress and Klopatek 1987). From these estimates, it would seem that mature pinyon woodland requires a significant amount of time for development, well after it comes within the distance of abundant seed dispersal.

In order to study the issue on a much broader scale of time and space, records of paleo-migrations can be obtained from fossil pine needles in packrat middens. These records encompass the entire migration and successional cycle from mature woodland phase to mature woodland phase.

PAST CLIMATE WARMING

During the span of history most accessible for paleoecological study in the western

United States—the last 20,000 years—the most extreme climate warming occurred between about 11,700 to 11,500 years ago (Overpeck et al. 2003). This sudden temperature warming occurred at the end of the cold Younger Dryas period during the transition between the last ice age and the Holocene. During this time, temperatures increased more than 4° C in less than 200 years in the western United States (Barron et al. 2003; Cole and Arundel 2005). Uncertainties in the dating of these records probably underestimate the rapidity of this abrupt warming, shown to have happened in less than 100 years by better-dated chronologies (Severinghaus et al. 1998; Grootes and Stuiver 1997). Following this abrupt climate warming, temperatures then continued to increase more slowly, possibly reaching a maximum several thousand years later (Figure 1).

The rate and magnitude of the climate warming that occurred 11,600 years ago is remarkably similar to the warming that is expected to occur in the western United States over the next 100 years (Overpeck et al. 2003). General circulation models (GCMs) project that temperatures should warm 2–5° C over this period, depending upon many variables (Solomon et al. 2007).

Reconstructions of past temperatures are showing increasing overlap from region to region, especially in isotopic records from sea and ice cores (Barron et al. 2003; Hendy et al. 2002; Hughen et al. 2000; Grootes and Stuiver 1997). These records portray large temperature fluctuations throughout the last portions of the ice age, culminating in the rapid early Holocene warming, but then temperatures flattened out, depicting the Holocene climate as relatively stable (see Figure 1).

In contrast to sea and ice core temperature records (e.g., Grootes and Stuiver 1997), terrestrial Holocene paleoenvironmental records show much more variability and much less agreement with each other. Although broad patterns are evident on large spatial and temporal scales, there is very little correspondence in Holocene chronologies of smaller regions such as the Colorado Plateau (Thompson et al. 1993). Changes in

precipitation seasonality due to changing solar insolation complicates terrestrial records in areas with a biseasonal precipitation regime such as the southwestern United States. But biological proxy data are further affected by the complexity of ecological dynamics following times of extreme change (Cole 1985). Because of this lack of firm conclusions on Holocene climates on the Colorado Plateau, we refer to the observed migrations across the plateau as primarily a delayed (lagging) response to the climate warming at the start of the Holocene (Davis 1989). Although no two climate events can be exactly the same, these past migration rates can at least serve as a first-order estimate for the possible rate of future migration.

PAST PINYON MIGRATIONS

The past migrations of plant species on the Colorado Plateau can be retrospectively observed by analyzing plant macrofossils found in packrat middens (Betancourt et al. 1990). Individual fossil pine needles can be radiocarbon dated using accelerator mass spectrometry (AMS), which produces much more precise results (Van Devender et al. 1985) compared to conventional dating. Since each fossil pine needle probably grew within 30 m of the fossil midden (K. Cole, unpublished data), this produces a highly reliable record of the species' occurrence at a specific time and location.

A consistent application of the same criteria of AMS-dated pinyon pine needles across time should produce comparable information for calculating past migration rates. Because pine needles are not likely to be recorded until it is a dominant tree on the landscape, it is an extremely conservative record. The recorded migration rate integrates not only the geographic problem of seed dispersal into the new areas, but also the other local ecological processes of succession, maturation, and eventual dominance of pinyon in the new community.

Needles identified as *Pinus edulis* are first verified in the eastern Grand Canyon during the Younger Dryas period (Cole and Arundel 2005; Cole et al., in review). Following

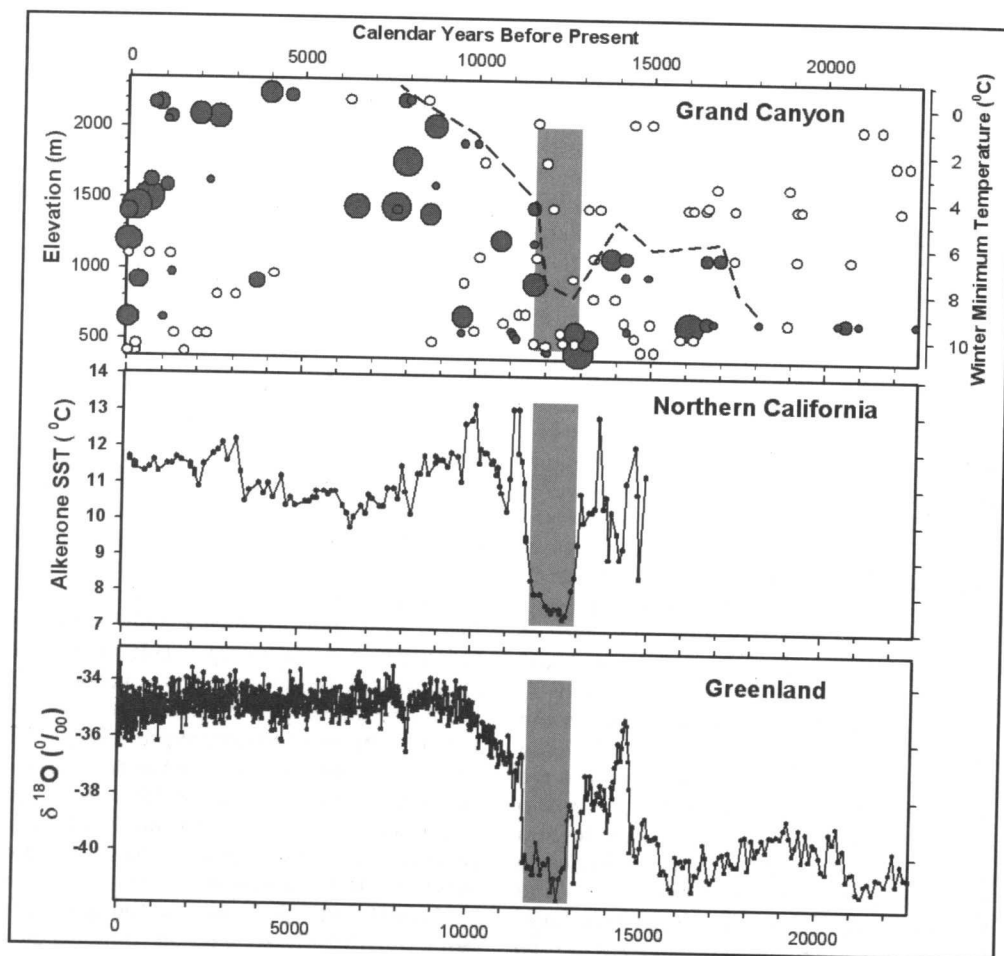


Figure 1. Indicators of temperature over the last 22,000 years illustrating the sharp warming that occurred at the end of the Younger Dryas interval (shaded zone). Top Panel: Departure of winter minimum temperature below current values (right scale), as indicated by the upper elevational limit (left scale) of Utah agave (*Agave utahensis*) in the Grand Canyon, Arizona. This upper limit is estimated as shown by the dashed line. Gray circles are scaled to represent the concentration of Utah agave fossils from packrat middens. Small open circles are packrat middens lacking Utah agave (modified from Cole and Arundel 2005). Middle Panel: Mean annual sea surface temperature estimates derived from alkenone chemistry from a sea core (ODP-1019) taken off the coast of northern California (modified from Barron et al. 2003). Bottom Panel: Oxygen isotopic record from the GRIP2 ice core from Greenland (modified from Grootes and Stuiver 1997).

the warming at the end of the Younger Dryas, these needles are then found in middens farther and farther to the north (Figure 2), suggesting a fairly continuous northward migration starting at about 11,600 years ago in the eastern Grand Canyon (Cole et al., in review) and ending in the Dutch John Mountains on the Utah-Wyoming border between 800 and 1000 years ago (Gray et al. 2006). Throughout the Holocene this northward migration from northern Arizona to southernmost Wyoming averaged 43 m/yr in latitudinal distance. Although its overall progression seems constant over the entire period, migration must have been characterized by episodic periods of relative stability interspersed with periods of rapid local invasion during decades of favorable climate, such as that described by Gray et al. (2006).

Some tree species are thought to have responded to past major warming more rapidly than others, especially in regions with low climatic and topographic variability. King and Herstram (1997) calculated migration rates of 180 and 156 m/yr for American beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*) in the deciduous forests of the eastern United States. Yansa (2006) estimated the early Holocene northward migration of white spruce (*Picea glauca*) in the northern Great Plains to have averaged 300 m/yr. Considering the magnitude of climate change expected in the near future, it is well to keep in mind that what has been called "the paradox of rapid plant migration" is only 100 to 500 m/yr (Clark et al. 1998). Even applying the most rapid migration scenario imaginable, complete species responses to climate change expected over the next 100 years could still take over 1000 years.

METHODS

In order to determine how climate controls pinyon distribution, we began with its current distribution and climate. Creating a model detailed enough to predict local changes on the landscape requires information at an extremely high resolution. We have thus integrated detailed information from sources such as the USDA's Forest

Inventory and Analysis program (Gillespie 1999), which has sampled roughly every 5 km in a systematic grid to create a highly detailed map of current tree distributions. Another important component for creating detailed models is having high-resolution information about twentieth-century climates. Using the relationships between elevation, slope aspect, and climate, monthly climate surfaces for North America were created at a ~1 km scale using data from the Global Historical Climatology Network. Species distribution and climate maps are available from our website (http://www.usgs.nau.edu/global_change).

The GCM results applied to this study use an intermediate CO₂ scenario and a high-resolution application of NCAR's CCM3 model (Duffy et al. 2003; Govindasamy et al. 2003). The results from this simulation project a warming on the Colorado Plateau of about 3.5° C (summer maximum temperature) and 2–3° C (winter minimum temperature) between now and the time when the global CO₂ reaches twice its pre-industrial concentration (2 × CO₂), roughly estimated to be the year 2100.

We next employed a program called ClimLim (Arundel 2005) to analyze geographic relationships between climate and species ranges. Because all climate variables change across space, the geographic range of any plant will encompass a range of each variable. But some of these climate variables have little influence in controlling the plant species distribution; they are merely coincidental to its geographic range. In order to determine which climate variables are the most important, ClimLim ranks each climate variable based on how well it controls the spatial distribution of the species (Arundel 2005). While some species, such as agave, are highly influenced by cold temperatures (Cole and Arundel 2005), others, such as pinyon, are highly influenced by the seasonality of precipitation (Figure 3; Cole and Arundel 2007), although temperature variables are still important.

Once the climate variables with the greatest geographic control of a species are identified, they are combined into a spatial

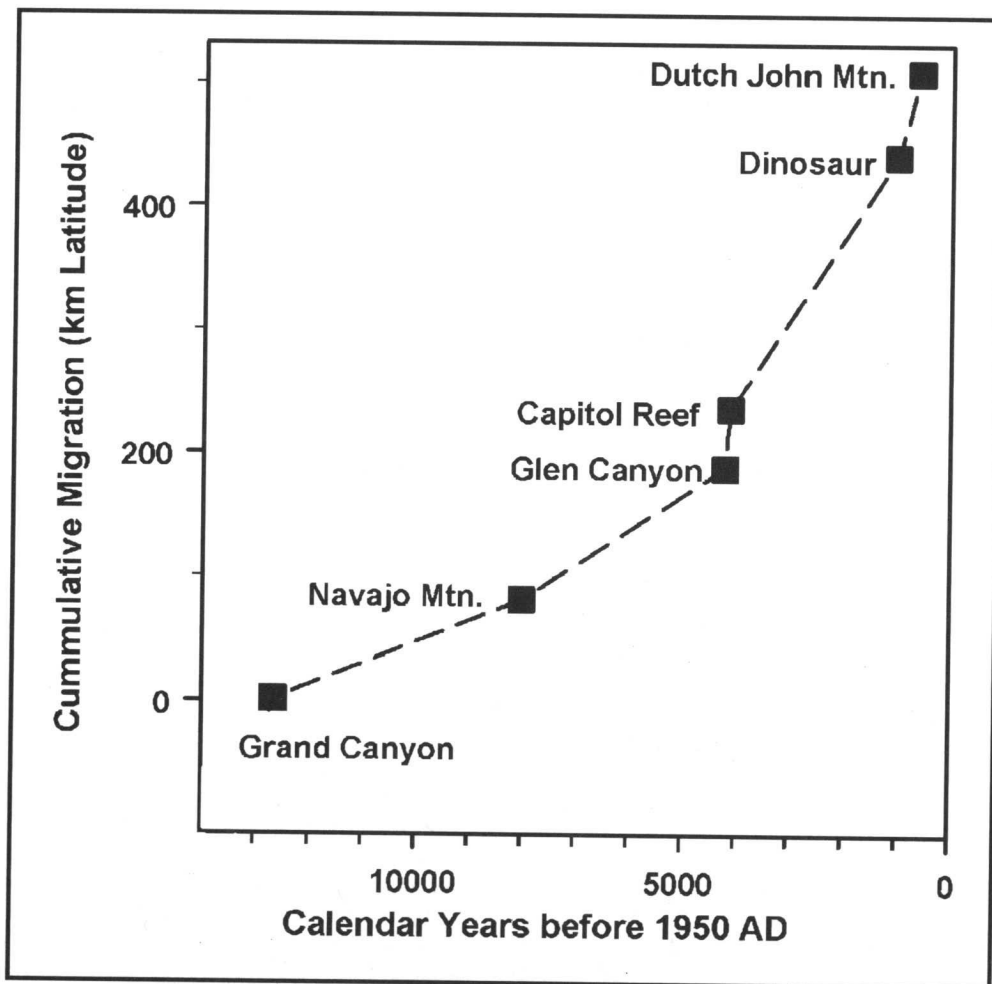


Figure 2. Northward migration of pinyon from north-central Arizona toward southern Wyoming since the last major climate warming 11,600 years ago. Names on the chart refer to packrat midden localities where the first arrival of pinyon has been documented using radiocarbon ages directly on needles (modified from Cole et al., in review).

model identifying the geographic areas that are optimal for species growth. This spatial model, called a probability surface, is generated using a multiple quadratic logistic regression of the most important variables. To create the probability surfaces for pinyon (Figure 4), variables representing January, May, June, August, and October precipitation (Figure 3) were combined with January, March, and May minimum temperatures

and June maximum temperatures.

To predict future areas of suitable climate for pinyon occupancy, we use results from general circulation models (GCMs). Most GCMs have poor resolution (approximately 310 km) because they are simulating complex atmospheric and oceanic processes for the entire globe. The GCM data that we used for predicting impacts of climate change on pinyon were produced through a special

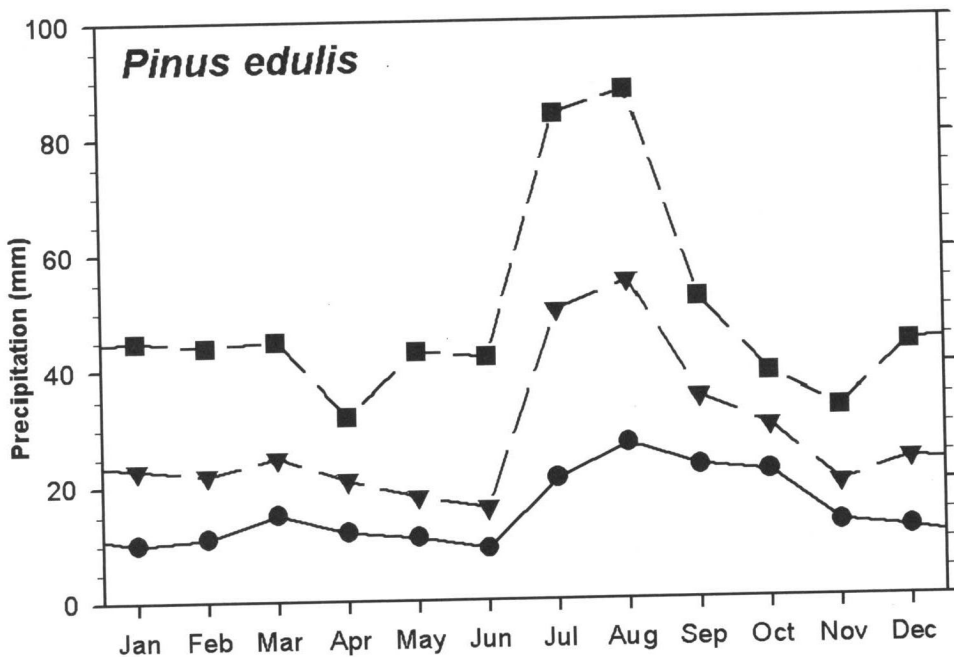


Figure 3. Precipitation seasonality over the range of pinyon. The spread between the 233,636 values representing each km² within the species range is shown by month. The bottom line (solid with circles) displays the 5th percentile, the middle line the 50th (median) percentile (dashed with triangles), and the top line the 95th percentile (long dashes with squares) of all values (modified from Cole et al., in press).

high-resolution run of the National Center for Atmospheric Research (NCAR) Community Climate Model version 3.6.6 (CCM3; Duffy et al. 2003; Govindasamy et al. 2003). Though this CCM3 data set has high spatial resolution (approximately 75 km) relative to other GCM data, this scale is still coarse for determining local changes in climate. Because of topographic diversity, climates are variable across the Colorado Plateau, and these results must be "downscaled" to show a detail level relevant to land managers. To downscale the CCM3 results, the difference between the present climate and the simulated 2 x CO₂ climate was calculated within each modeled 75 km grid square and these difference values were then applied to each 1 km grid within that larger grid using our

downscaled monthly climate surfaces for North America. This technique, sometimes called the "delta-change method" (Hay et al. 2000), takes advantage of the Colorado Plateau's high topographic diversity and low atmospheric humidity which cause temperature and precipitation to be highly correlated with local elevations.

The model predicting suitable climate for pinyon was then applied to the future climate surfaces to predict areas where it would have suitable climate in the future, approximately around 2100 AD (see Figure 4B). Information from past pinyon movements was then applied to approximate areas within its new climatic range into which it could potentially expand over such a short period.

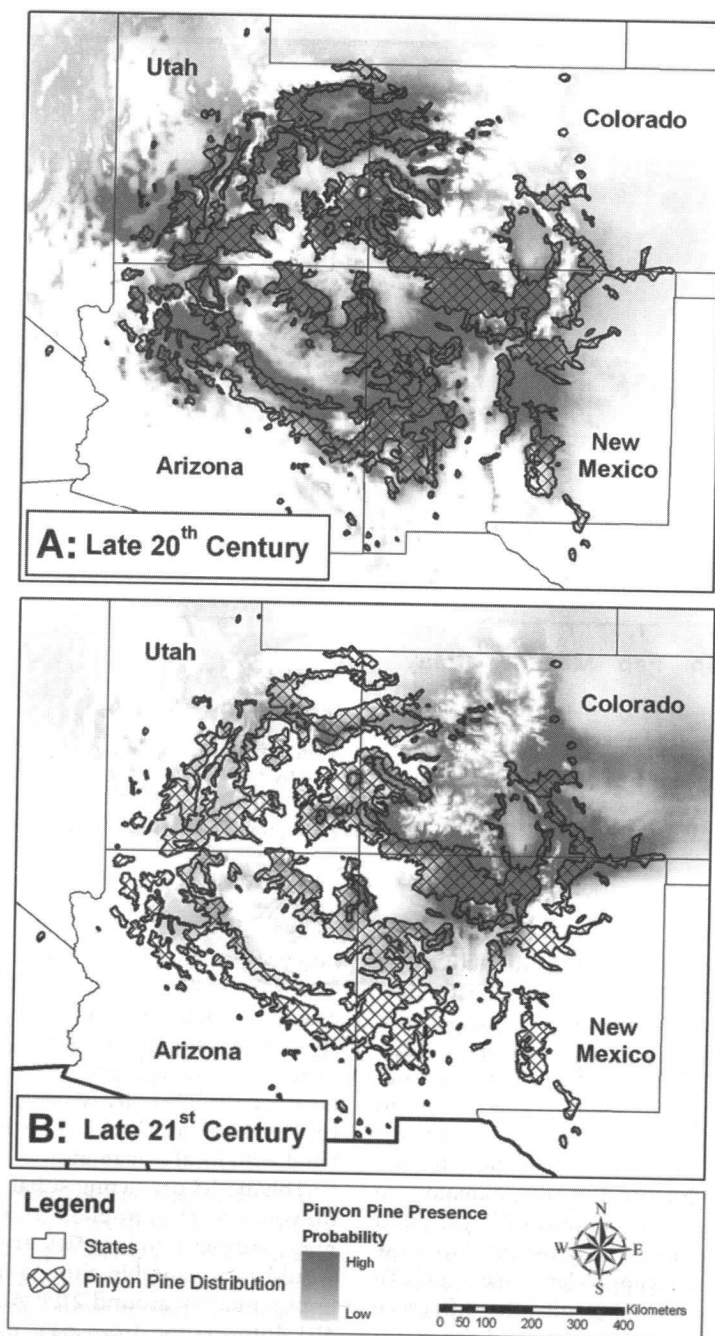


Figure 4. The current distribution of pinyon contrasted with the climate model prediction of its probability of occurring under a (a) late twentieth century climate and (b) late twenty-first century climate ($2 \times \text{CO}_2$) as generated using the CCM3 model.

RESULTS AND DISCUSSION

Our model (Figure 4A) reveals a close alignment between the present range of pinyon and model predictions. By modeling with the $2 \times \text{CO}_2$ probability surface resulting from the future GCM results, we see a proposed movement of pinyon northward (Figure 4B); the results suggest a profound shift in the potential range of pinyon over about the next 100 years. Most of pinyon's current range in Arizona and Utah will become increasingly inhospitable, but it should be able to expand northeastward and to higher elevations in Colorado and northernmost New Mexico. It is also predicted to thrive at higher elevations in the Chuska, Abajo, and La Sal Mountains, and in the Rocky Mountains (Figure 5).

Our model also predicts that pinyon would expand rapidly along the front range of the Colorado Rocky Mountains, assuming a generous future migration rate of 100 m per year over the next 100 years ($= 10 \text{ km}$) outward from existing stands. This rate is more than twice the 43 m/yr observed in fossil records (Figure 2) and is less than half the time estimated for pinyon woodland to mature where seeds are already available (Goodrich and Barber 1999; Tress and Klopatek 1987). Despite the expansion rate provided by our model, the pinyon woodland is only estimated to fill in a small percentage of its new potential range during the next 100 years (Figure 5).

Although the results shown in Figure 5 may seem extreme, they are actually more moderate than the only other published projections for this species (Thompson et al. 1998:19). Thompson's model, applying very different climate modeling methods, different GCM inputs, and coarser-resolution 15 km grid cells, predicted the elimination of pinyon from almost all of the Colorado Plateau except the highest parts of the Mogollon Rim, and projected its future range as mostly in Oregon and Wyoming.

Our results need to be further verified through the application of climate data from multiple GCMs. The modeling of multiple species will further allow more complex pre-

dictions of climate effects on plant associations to test possible plant interactions and the individualistic model of species response. Preliminary data on a major associate of pinyon in Arizona—one-seed juniper (*Juniperus monosperma*)—suggest that it will respond to these climatic changes very differently. Whereas the model portrays pinyon as persisting at the highest elevations, the same climate scenario suggests that *Juniperus monosperma* will continue its ongoing expansion into the lower elevation grasslands of northern Arizona (Ironside 2006).

Verification of the results of our model will eventually come as pinyon mortality occurs where climatic conditions are predicted to become unfavorable and establishment occurs where climatic conditions are predicted to become more favorable. The predictions of our model can be downscaled to local landscape scales, allowing land managers to monitor these predicted changes in specific plots. Because model predictions are based on quantitative probability scales, the fate of different growth classes may be best predicted at finer levels on that scale. For example, seedlings are usually far more sensitive to climate than adults.

Loss of pinyon on the Colorado Plateau due to climate change has already begun, especially in areas most affected by rising temperature. Recent droughts are causing increased pine mortality due to the higher temperatures that occur during the drought (Breshears et al. 2005). The low mortality along the Colorado front range and high mortality in Arizona and at low elevations in Utah are consistent with the CCM3 model's predictions. The recent high mortality observed in northern New Mexico was not predicted by our model, probably because the CCM3 scenario predicts increased summer monsoon precipitation for northern New Mexico, but recent summers (2000–2005) have instead been notably dry. This disparity suggests that either $2 \times \text{CO}_2$ -like precipitation scenarios are not yet evident in New Mexico or the CCM3 model is overestimating this variable. Different GCMs have greater correlation for temperature estimates

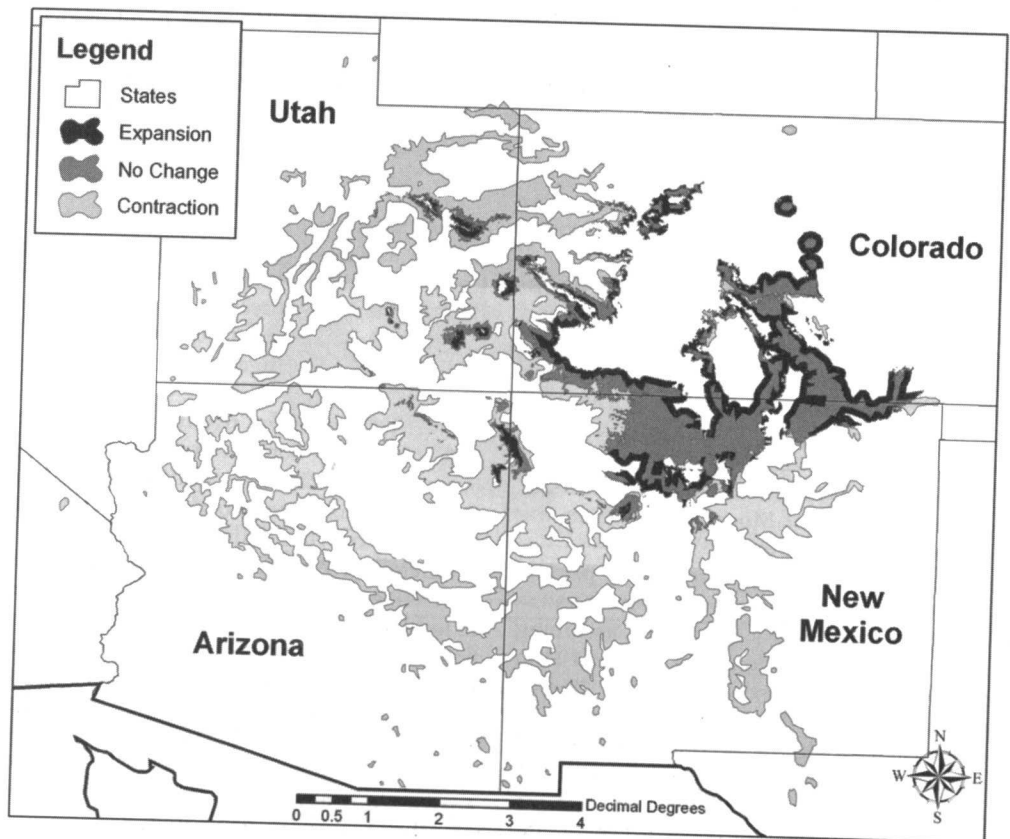


Figure 5. Areas that should experience a contraction (mortality) of pinyon over the next 100 years (light gray) are contrasted with areas where it should persist (dark gray) and areas where it should expand (black), assuming an average migration rate of 100 m/yr over the next 100 years.

than for precipitation (Coquard et al. 2004). Comparison with other GCMs will help further explore this issue.

CONCLUSIONS

Predicting the effects of future climate change on a plant species requires knowledge of the plant's current distribution, climate tolerances, and migratory response to change, as well as the geography of future climates. Using new modeling techniques and applying them to Colorado pinyon pine (*Pinus edulis*), we have found that the climatic envelope occupied by each species can be modeled through a geostatistical analysis of the twentieth-century climates over its cur-

rent range. Our model incorporates all of the climate-modulated physical and biological variables occurring near the continental range of the species during the twentieth century. We developed models of future potential geographic ranges by applying this climatic envelope to future climate predictions from general circulation model (GCM) results. Finally, in order to distinguish between this future potential climate range and the species' likely future range, we applied a spatial model of the species' observed migration rate in response to past and ongoing climate warming. Through the compilation of spatially detailed data for our twentieth-century climate model, the GCM

modeling, and the species distribution data, our results are projected to a landscape grid scale of $\sim 1 \text{ km}^2$. This detailed projection allows application of the results to individual land management areas as well as specific predictions to assist monitoring.

Our modeling results suggest that over the next 100 years the range of *Pinus edulis* will continue to profoundly contract in Arizona, Utah, and southern New Mexico, but will expand in Colorado and northernmost New Mexico. The results from this one GCM scenario imply a large magnitude of change for this species and delineate useful areas to focus future monitoring efforts.

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