Shifts in the Potential Distribution of Sky Island Plant Communities in Response to Climate Change

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Abstract—*To examine potential responses of sky island ecosystem pattern to projected climate changes, we used topographic and climatic data to develop a predictive model of plant community distribution in Saguaro National Park East, AZ. Increasing temperatures led to an upslope movement of communities and increased the area of desert scrub at the expense of montane conifer forest while increasing precipitation led to the opposite response as growth constraints imposed by arid conditions were lessened. Specific combinations of temperature and precipitation change created more or less extreme changes, with relatively little change in community area or spatial pattern occurring even in some cases where both climate variables increased. While simple, this model illustrates the complicated nature of sky island community responses to climate change and underscores the need for applications of more complex biogeographic models and targeted, field-based inventory and monitoring of plant communities.*

Introduction

Over the course of the last two decades, scientists have used a range of experimental, statistical, and mathematical techniques to explore the potential effects of projected climate changes on ecosystem pattern and function. One common prediction is that warmer temperatures resulting from increasing atmospheric concentrations of carbon dioxide and other greenhouse gases will lead to a widespread reorganization of species and community patterns (e.g., Shafer et al. 2001; Iverson and Prasad 2002). Mountains have been cited as areas where the effects of climate change may be especially noticeable because steep, elevationally structured gradients in temperature and precipitation lead to a rapid turnover of plant communities and relatively distinct community zones (Kupfer and Cairns 1996). In few places are such distinct vegetation patterns as evident as in the sky islands of the Southwestern United States and Northern Mexico, suggesting that these communities and their ecotones may be both sensitive indicators of climate change and areas of concern with respect to climate change effects. We therefore developed a predictive model of current plant community distribution in a southern Arizona sky island ecosystem based on topographic and climatic data. This model was then applied under 36 different scenarios of temperature and precipitation change to project the potential reorganization of plant communities. Our goal in doing so was not so much to predict where communities will shift given a certain trajectory of climate change, which is complicated by a range of factors other than climate, but rather to identify areas that may be most sensitive to climate change.

Study Area

The study area was the ca. 27,000 ha East Unit of Saguaro National Park (SNP-E), located immediately east of Tucson, AZ (32°N, 111°W). The park contains most of the Rincon Mountains as well as lower lying desert basins to the south and west. Elevation ranges from 818-2,620 m asl, resulting in significant gradients in temperature and precipitation. Mean annual temperatures in the desert valleys are high ($\bar{x}_{\text{July}} = 30.3$ ºC; $\bar{x}_{\text{January}} = 11.0$ ºC) (Tucson, AZ, 1948-2003; http://www.wrcc.dri.edu/), and on average, temperature decreases 6.7 ºC per 1,000 m of elevation gain. Mean annual precipitation in Tucson for the same period was 290 mm, with 51% occurring during the summer (July-September) monsoon season. Precipitation increases 24.5 cm per 1,000 m, with higher elevations receiving >750 cm yr^{-1}, some of it as snow.

Methods

Data Sets: Vegetation, Topography, Climate

Plant community types in the Rincon Mountains occur in climatically structured elevation zones and include: (1) Sonoran desert scrub, dominated by succulents and woody shrubs, (2) Sonoran grassland and savanna, dominated by herbaceous species with scattered woody individuals, (3) Madrean evergreen woodland and forest, dominated by oaks (*Quercus* spp.), alligator juniper (*Juniperus deppeana*), and pines (*Pinus* spp.), and (4) montane conifer forests, dominated by ponderosa pine (*Pinus ponderosa*), southwestern white pine (*Pinus flexilis*), and Douglas fir (*Pseudotsuga menziesii*) (Bowers and McLaughlin 1987). Two Landsat ETM+ satellite images (October 1999, June 2000; Path 36/Row 38) were used to classify land cover into five classes, including the four vegetation communities mentioned above plus rock outcrops (which are not included in this analysis). The overall classification accuracy was 85% with a Kappa

(κ) of 0.80 and accuracies for the vegetation types ranging from 75%-90%.

Six topographic variables were extracted from a USGS 7.5-minute digital elevation model (DEM) with 30 m resolution: elevation (m), slope (º), cosine-transformed aspect (cos (aspº) +1), profile curvature, planform curvature, and topographic position (1 = ridge to 5 = valley). Due to digital striping errors in the DEM that became apparent when calculating the secondary topographic variables, the topographic coverages and the land cover classification were aggregated to a 60 m resolution.

We also estimated climate variables for each 60 m pixel using a modified version of MT-CLIM, a mountain microclimate simulator designed to extrapolate routine National Weather Service data from a base station to adjacent mountainous terrain (Running et al. 1987). While the original MT-CLIM estimated climate for only a single location, it was modified to calculate conditions at multiple sites and thereby develop spatially explicit climate coverages (Cairns and Malanson 1997). The model produced estimates of ambient air temperature (mean daily high, mean daily low) and precipitation based on: (1) summarized daily high and low temperatures, precipitation, and dew point for a base station (Sabino Canyon: 805m asl), (2) the 30 m DEM (aggregated to 60 m resolution for consistency), and (3) regional climatic lapse rates. Lapse rates were calculated from daily temperature and precipitation values obtained from the National Climate Data Center for the years 1965-1980 for four weather stations in the Tucson area: Sabino Canyon, Oracle (1,375 m), Kitt Peak (2,070 m), and Palisades Range Station (2,425 m). As a rough assessment of the accuracy of the climate extrapolations, we compared, predicted, and observed mean monthly temperatures (1995 to 2000) for the Rincon Remote Automated Weather Station at Manning Camp (2,512 m), which was not used in developing the climate parameters. Predicted and observed temperatures were highly correlated ($r = 0.92$) but displayed seasonal variations in accuracy that were due to seasonality of the actual lapse rate.

Climate Scenarios

Projections from global climate models (GCMs) suggest that temperatures in the Southwest will increase 3-6 ºC over the next 100 years with a doubling of carbon dioxide while annual precipitation may increase from 50-100% (Southwest Assessment Team 2000). However, confidence in projections of temperature is higher than that for precipitation because GCMs have difficulty capturing local scale meteorological processes that cause precipitation in the Southwest (e.g., convection for thunderstorms). Further, the Southwest Monsoon and El Niño-Southern Oscillation, key factors shaping precipitation amounts in the region, are not well represented in current GCMs, introducing more uncertainty into regional precipitation predictions. Given this uncertainty, we opted to produce 36 climate change scenarios and model vegetation community response for each. We used combinations of six temperature values (mean temperature from 1961-1990; mean temperature +1 ºC, +2 ºC, +3 ºC, +4 ºC, +5 ºC) and six precipitation values (mean precipitation from 1961-1990; mean precipitation –10%, +10%, +25%, +50%, +100%). For temperature, we chose to use mean daily low temperature because: (1) it was most strongly related to vegetation patterns, and (2) most estimates of climate change suggest that the strongest temperature increase will be in overnight low temperatures.

Data Analysis

We created a predictive vegetation model (*sensu* Franklin 1995) to project potential vegetation patterns under the 36 climate scenarios by relating the current community types to matching coverages of the predictor variables using discriminant analysis. Discriminant analysis classifies cases (individual pixels) into distinct groups (vegetation classes) on the basis of a set of discriminant functions that represent combinations of predictor variables (Lachenbruch 1975). The first discriminant function maximizes between-class differences in the values of the predictor variables, and the second function is orthogonal to it and maximizes additional differences while controlling for the first factor. Analyses were performed using SPSS v. 11.5.

To build the predictive vegetation model, we extracted every fifth pixel (spatial interval = 300 m) in every fifth row from the full SNP-E raster dataset (*n = 2912 pixels*). This method decreased the amount of spatial dependence among the sample units (i.e., pixels) (*cf.* Brown 1994) and allowed us to develop an independent validation dataset for the resulting model. This second dataset (*n = 2882 pixels*), which was also manipulated to create the 36 climate change scenarios, was similarly sampled from the full SNP-E dataset at a sampling interval of five pixels but staggered from the first dataset by three pixels to the south and east. Since a regular sampling grid was used in both cases, the percentage of pixels falling into each class roughly approximated the extent of each community type within SNP-E.

Because of the high correlation between mean minimum temperature and precipitation, we used principal components analysis (PCA) to develop a single climate "variable" that incorporated both temperature and precipitation. This variable was then included, along with the five topographic variables (excluding elevation), in the discriminant analysis. The resulting predictive vegetation model was used to map the potential vegetation class for all of SNP-E under each of the climate change scenarios. We then determined the number of predicted pixels for each vegetation type and created a surface of sensitivity to potential climate change by summing the number of scenarios in which an individual pixel appeared as a different vegetation class than the current class.

Results

Discriminant Analysis

The first discriminant function (eigenvalue = 4.26) accounted for nearly 97% of the variance among community types and was almost entirely structured by the PCA-derived climate variable. The second (eigenvalue = 0.13) and third

(eigenvalue = 0.01) functions were most strongly related to slope and aspect, respectively, but collectively accounted for only 3% of the variance. When the resulting model was used both to back-predict vegetation class for the pixels used in model development and to predict vegetation class for the validation dataset, 80% of the predicted pixel classes agreed with the land cover classification (desert scrub = 92.5%; desert grassland/savanna = 74%; Madrean evergreen woodland/forest = 81%; montane conifer = 76%). The primary effect of the predictive model was to smooth out fine-scale variation that was evident in the remote sensing-based classification of SNP-E plant communities (figure 1a versus 1b).

Projected Changes in Plant Community Distribution

Changes in the extent of community types were highly dependent on the magnitude of temperature and precipitation change (table 1). As would be expected, increasing temperatures (when holding precipitation constant) led to an upslope movement of vegetation communities, substantially increasing the area of desert scrub while reducing montane conifer forest (figure 1c). Increased precipitation led to a downslope shift of communities as the growth constraints imposed by arid conditions were lessened. Thus, even a 5 °C temperature rise when coupled with doubling of precipitation resulted in a 500% increase in montane conifer and a substantial reduction in desert scrub. Specific combinations of temperature and precipitation change created more or less extreme changes. A temperature increase of 3 °C accompanied by a 25% increase in precipitation, for instance, resulted in relatively little change in community area (table 1) or spatial pattern (figure 1d). This latter finding illustrates the complicated nature of sky island community responses to climate change; that is, temperature increases may not necessarily result in upslope migration of communities if precipitation also increases.

Desert savanna/grassland and Madrean evergreen woodland/forest experienced smaller % changes in area for most scenarios. This may be a function of both their location in the middle of the mountain (with area to migrate upslope in warmer scenarios and downslope in wetter scenarios) and their relatively large current area (i.e., more area must change to evoke a similar % change for the other types). Conversely, desert scrub and montane conifer forest changed by >50% in many scenarios, most likely because they: (1) are located at the base and top of the mountain, and (2) constitute only 23% and 7% of the pixels examined, respectively. Declines in the former class, however, are of less concern because the area surrounding the park is desert and because most of the scenarios resulting in large losses of desert are unlikely to occur. Declines in montane conifer forest, however, represent regional losses that will not be offset elsewhere.

By comparing each pixel's current vegetation class to that projected under each of the climate scenarios, we identified pixels that may be most sensitive to climate change (i.e., those that change class in a wide range of scenarios) (figure 1e). While areas near current ecotones were generally more sensitive than core areas (e.g., the lowest desert areas, core montane conifer areas in Mica Mountain), the entire Madrean evergreen zone, regardless of proximity to its upslope and downslope ecotones, was highly sensitive, likely because it serves as a transition zone between grassland/savanna at lower elevations and more continuous conifer forests at higher elevations. This approach to examining sensitivity to climate change effects, however, implicitly assumes that each climate change scenario is equally likely. The most likely scenarios, given current GCM projections, would involve increases of 3-5 °C temperature and 0-50% in precipitation. In these 12 scenarios: (1) desert scrub showed moderate (10-50%) to large (>50%) increases in area in 75% of the scenarios; (2) desert grassland/savanna showed moderate increases in nearly all scenarios with a 0-25% precipitation increase and small (<10%) to moderate losses with a 25-50% increase; (3) Madrean evergreen woodland/forest declined in all scenarios; and (4) montane conifer experienced large declines in cases with little to no change in precipitation but substantial gains in cases with a 50% increase.

Discussion

There are two basic categories of biogeographic models that are used to predict the response of vegetation patterns to climate change: dynamic (time-dependent) and static (time-independent) (Peng 2000). Most static models, such as the one used in this study, are empirical and employ response surfaces or "climate envelopes" to describe the relationship between topoclimatic variables and the distributions of species or community types. Projections from GCMs are then used to map future climate patterns, and biotic distributions are re-projected based on the current relationships (e.g., Brzeziecki et al. 1995; Shafer et al. 2001). These models, by their nature, do not address transient responses of individual systems and merely represent theoretical equilibrium locations for some future time period (Kirilenko and Solomon 1998).

Static, empirical models are generally crude and limited because they do not explicitly address the underlying mechanisms that structure vegetation response to climate change, although some have incorporated a more process-based approach (Neilson 1995; Haxeltine and Prentice 1996). Among other things, these models make an untenable assumption that species or community distributions are currently in equilibrium with the variables being used to predict them and that they could not, in the absence of other species or communities, occur in a broader range of conditions. In the case of species-level models, for example, the model typically utilizes the realized niche of the species and may miss dynamics that use of their fundamental niche would show (e.g., Malanson et al. 1992; Jackson and Overpeck 2000). Further, models that exclusively address community-level responses do not operate at the scale at which response to climate change is driven (i.e., individual trees and species).

A more robust treatment of vegetation change in the sky islands needs to incorporate both greater temporal complexity (e.g., time lagged or nonlinear responses) and a broader range of factors affecting vegetation response. Most notably, community patterns may originate not only from variations

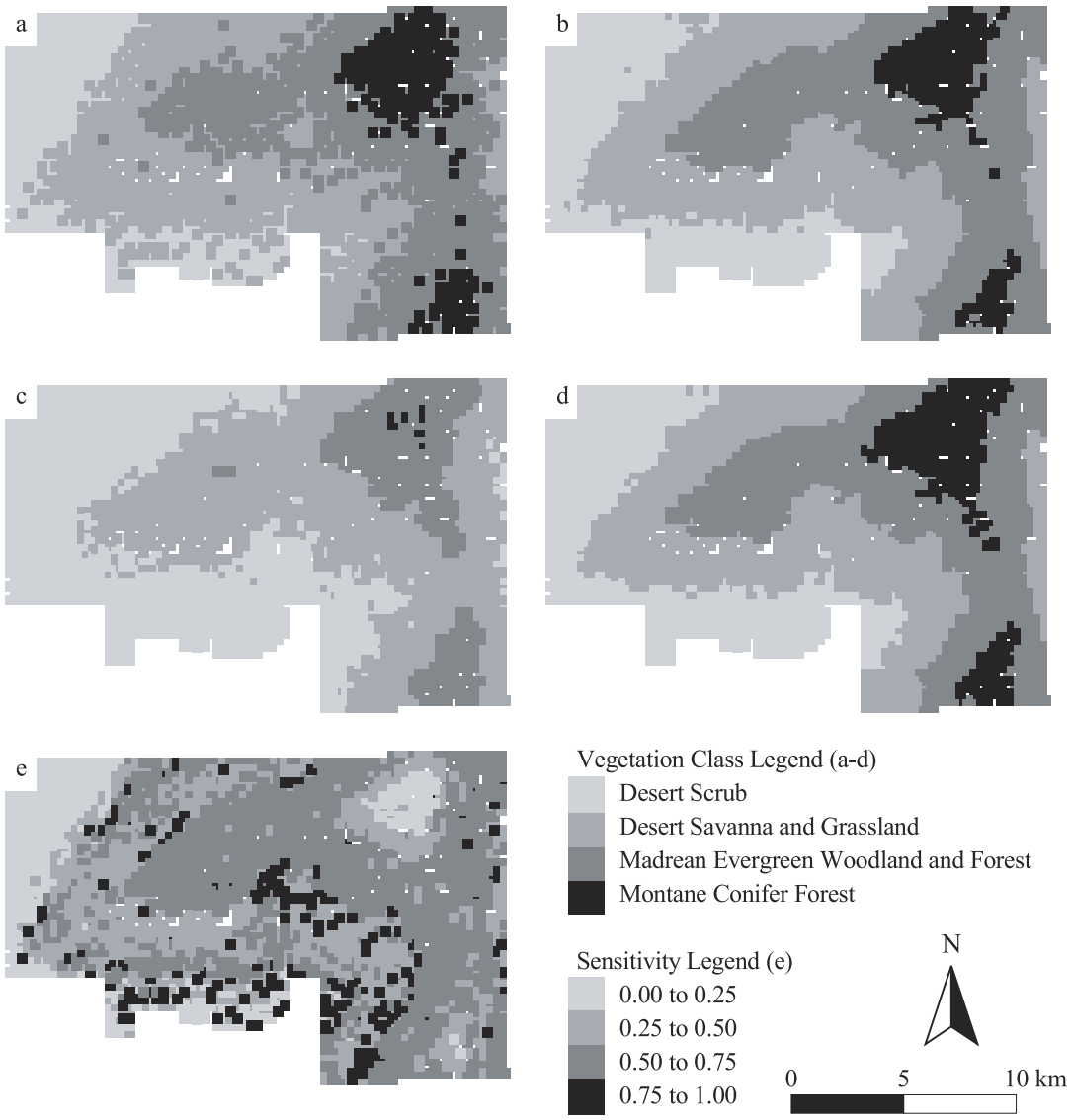

Figure 1—Current and modeled vegetation for Saguaro National Park East: (a) vegetation classification derived from Landsat ETM+ imagery; (b) modeled current vegetation; (c) projected potential vegetation with a 3 °C temperature rise and current precipitation; (d) projected potential vegetation with 3 °C rise and 25% increase in precipitation; (e) percentage of modeled climate change scenarios (n = 36 total) where vegetation in each pixel changed.

in average climate trends but also from: (1) limitations and feedbacks associated with species dispersal (e.g., Cole 1985), (2) resistance to invasion of the extant community and other interspecific interactions (e.g., Davis et al. 1998), (3) the importance of non-climatic controls on vegetation patterns (e.g., soil limitations; Kupfer and Cairns 1996), and (4) changes in the range of climate variability and the occurrence of extreme events such as prolonged droughts (e.g., Malanson 2001; Dullinger et al. 2004). Further, in the Southwest, changes in temperature and precipitation regimes will likely contribute to changes in the primary disturbance regimes, particularly fire and insect outbreaks. The ways in which altering disturbance regimes may further condition the response of sky island community pattern to climate change, especially given changes in community structure and function that have taken place with fire suppression and other human activities over the last century, is not well known.

It was in part these limitations that led us to focus not so much on the predicted output of any given climate change scenario but rather on changes in community extent along gradients of temperature and precipitation change as well as the spatial pattern of community sensitivity to a range of climate change scenarios. In this sense, the model projections become not so much predictions of vegetation change but rather neutral models of potential changes that should be examined using targeted, field-based inventory and monitoring of plant communities. This simple model also highlights the potentially complicated nature of vegetation responses and emphasizes the need for applications of more complex, dynamic biogeographic models.

Table 1—Predicted number of pixels of each vegetation class under various precipitation (columns) and temperature (rows) change scenarios. Values in parentheses represent % change with respect to current conditions (0% and +0 ºC). Bold values are changes in excess of 50% increase or decrease.

Desert scrub

	-10%	0%	10%	25%	50%	100%
+0 ºC	751 (+11%)	678 (+0%)	578 (-15%)	368 (-46%)	**135 (-80%)**	**0 (-100%)**
+1 ºC	875 (+29%)	764 (+13%)	684 (+1%)	547 (-19%)	**221 (-67%)**	**0 (-100%)**
+2 ºC	**1,070 (+58%)**	891 (+31%)	771 (+14%)	673 (-1%)	364 (-46%)	**0 (-100%)**
+3 ºC	**1,262 (+86%)**	**1,073 (+58%)**	906 (+34%)	745 (+10%)	537 (-21%)	**60 (-91%)**
+4 ºC	**1,454 (+114%)**	**1,254 (+85%)**	**1,077 (+59%)**	839 (+24%)	654 (-4%)	**148 (-78%)**
+5 ºC	**1,659 (+145%)**	**1,436 (+112%)**	**1,246 (+84%)**	1,000 (+47%)	727 (+7%)	**227 (-67%)**

Desert savanna and grassland

	-10%	0%	10%	25%	50%	100%
+0 ºC	1,232 (+19%)	1,037 (+0%)	905 (-13%)	844 (-19%)	747 (-28%)	**173 (-83%)**
+1 ºC	1,337 (+29%)	1,181 (+14%)	1,003 (-3%)	833 (-20%)	792 (-24%)	**364 (-65%)**
+2 ºC	1,324 (+28%)	1,278 (+23%)	1,140 (+10%)	876 (-16%)	771 (-26%)	592 (-43%)
+3 ºC	1,289 (+24%)	1,282 (+24%)	1,206 (+16%)	995 (-4%)	751 (-28%)	665 (-36%)
+4 ºC	1,222 (+18%)	1,249 (+20%)	1,227 (+18%)	1,108 (+7%)	779 (-25%)	690 (-33%)
+5 ºC	1,104 (+6%)	1,191 (+15%)	1,209 (+17%)	1,144 (+10%)	867 (-16%)	699 (-33%)

Madrean evergreen woodland and forest

	-10%	0%	10%	25%	50%	100%
+0 ºC	801 (-16%)	958 (+0%)	1,033 (+8%)	997 (+4%)	759 (-21%)	794 (-17%)
+1 ºC	617 (-36%)	805 (-16%)	941 (-2%)	995 (+4%)	821 (-14%)	697 (-27%)
+2 ºC	**473 (-51%)**	639 (-33%)	810 (-15%)	963 (+1%)	883 (-8%)	576 (-40%)
+3 ºC	**331 (-65%)**	495 (-48%)	672 (-30%)	881 (-8%)	898 (-6%)	579 (-40%)
+4 ºC	**206 (-78%)**	**372 (-61%)**	521 (-46%)	764 (-20%)	910 (-5%)	589 (-39%)
+5 ºC	**119 (-88%)**	**255 (-73%)**	**408 (-57%)**	628 (-34%)	878 (-8%)	629 (-34%)

Montane conifer forest

	-10%	0%	10%	25%	50%	100%
+0 ºC	**986 (-53%)**	209 (+0%)	**366 (+75%)**	**673 (+222%)**	**1,241 (+494%)**	**1,915 (+816%)**
+1 ºC	**53 (-75%)**	132 (-37%)	254 (+22%)	**507 (+143%)**	**1,048 (+401%)**	**1,821 (+771%)**
+2 ºC	**15 (-93%)**	**74 (-65%)**	161 (-23%)	**370 (+77%)**	**864 (+313%)**	**1,713 (+720%)**
+3 ºC	**0 (-100%)**	**32 (-85%)**	**98 (-53%)**	261 (+25%)	**696 (+233%)**	**1,578 (+655%)**
+4 ºC	**0 (-100%)**	**7 (-97%)**	**57 (-73%)**	171 (-18%)	**539 (+158%)**	**1,455 (+596%)**
+5 ºC	**0 (-100%)**	**0 (-100%)**	**19 (-91%)**	110 (-47%)	**410 (+96%)**	**1,327 (+535%)**

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