Plant Species Distributions under Present Conditions and Forecasted for Warmer Climates in an Arid Mountain Range

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ABSTRACT: Complex environmental gradients in the White and Inyo Mountains in eastern California produce striking variations in vegetation assemblages over short distances. Vegetation composition is dominated by elevational gradients of temperature and precipitation, but local modifications by geologic substrate, potential insolation, slope, and topographic position create finescale mosaics. Digital elevation models, geologic maps, and field data were used to map current species distributions over 6220 km^2 (622 000 ha) of the

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White and Inyo Mountains. Species–environment relationships of 88 plant species were modeled at a scale of 54 m using canonical correspondence analysis (CCA). CCA models were calibrated from 434 field plots and evaluated with 216 plots using kappa statistics. Vegetation responses to temperature increases of 1°–6°C were modeled by shifting species tolerances along the elevational gradient according to a standard lapse rate [3°C $(500\ \mathrm{m})^{-1}$] while all other factors were kept constant. Ranges of midelevations species tended to fragment onto local peaks, whereas the ranges of many desert species merged across a major pass. In several cases, local geologic features were identified as obstacles to species' upslope migration. As modeled temperatures increase, species contract to small populations around White Mountain Peak (4342 m) and its north-facing slopes. It is predicted that 10 of 18 modeled alpine and subalpine species will become locally extinct if temperatures increase by 6°C. These scenarios provide a detailed set of hypotheses on the structure of current species ranges and their ability to persist through rapid climate change.

KEYWORDS: Canonical correspondence analysis (CCA); White Mountains; California; Plant distribution models

1. Introduction

Plant species distributions are constrained by local climate, geology, soils, hydrology, disturbance, and interactions with other species, among other environmental gradients. Complex gradients formed by combinations of these factors are expressed over short distances in mountains, giving rise to finescale vegetation patterns (Whittaker and Niering 1965; Gottfried et al. 1998). However, elevation has a dominant effect in montane ecology (Walter 1984). Temperature decreases with elevation according to adiabatic lapse rates [~3°C $(500\ \mathrm{m})^{-1}$], and precipitation generally increases with elevation, particularly in arid climates. The influence of temperature and precipitation on plants is modified by slope, aspect, topographic position, and geologic substrate, giving rise to complex patterns of species distributions at finer scales. For example, species composition often differs dramatically across geologic contacts, and opposing north- and south-facing slopes commonly harbor species from contrasting elevational zones.

Higher elevations in mountain ranges are composed of ever smaller areas, so the habitat area for montane species must contract with warming as they shift upslope—this could be termed the "mountain-top squeeze scenario." Peters and Darling (Peters and Darling 1985) qualitatively illustrated warming impacts, demonstrating how alpine species may be squeezed off mountaintops, or their ranges reduced and fragmented. The isolated mountain ranges of the Great Basin constitute a natural laboratory for investigating montane biogeography (Brown 1978; Harper et al. 1978; Wilcox et al. 1986; Austin and Murphy 1987; McDonald and Brown 1992; Murphy and Weiss 1992). Murphy and Weiss (Murphy and Weiss 1992) predicted the magnitude of extinctions from a 3°C regional warming in the Great Basin by reducing the available habitat according to a 500-m rise in the lower elevations of the montane habitats, and inputting the reduced areas (approximately 30% of the original) into species–area curves. Predicted extinction rates were 44% for mammals, 23% for butterflies, and 17% for plants. Steeper species–area curves led to higher extinction rates. McDonald and Brown (McDonald and Brown 1992) not only predicted the number of mammal species lost by similar methods, but also incorporated the nested subset structure of Great Basin mammal communities to predict which species were most likely to go extinct.

Holocene climate changes in the Great Basin have driven broad- and finescale shifts in species distributions. For example, *Pinus monophylla* (pinyon pines) invaded the region from the Mojave Desert, replacing oak woodlands following postglacial warming (Mitchell 1973; Wells 1983; Lanner and Van Devender 1998). Within the White Mountains, *Pinus longaeva* (bristlecone pines) ascended ~150 m in elevation during the warm Altithermal period (6000 yr BP), retreated during the Little Ice Age, and now appear to be advancing to higher elevations (Wright and Mooney 1965; LaMarche and Mooney 1967; LaMarche 1973; Tausch et al. 1981; Graumlich 1994; Davis and Shaw 2001). In this paper, we describe future changes in species distributions with continued warming.

Gradient analysis provides a strong conceptual and empirical basis for understanding montane vegetation. Quantitative modeling of species–environment relationships can define species' tolerances along complex environmental gradients and allow for predictions as to how species will respond to environmental change. The exact forms of quantitative models are varied (see reviews by Franklin 1995; Guisan and Theurillat 2000; Guisan and Zimmermann 2000), and include diverse statistical techniques such as general linear models (GLMs), general additive models (GAMs), classifications, regression trees, and canonical ordination. These statistical models can be spatially implemented by employing geographic information systems (GIS) to produce detailed predictive maps of species distributions, the accuracies of which can be evaluated with independent data using standard statistical map accuracy assessments (Davis and Goetz 1990; Guisan et al. 1999). Another alternative for modeling species–environment relationships is mechanistic models. Mechanistic models have been tied to high-resolution (40 km) regional climate models to assess the impacts of climate change on biomes across multistate regions (Diffenbaugh et al. 2003). However, plant species have individual responses to their immediate environment and require species-specific models of processes of dispersal, recruitment, and mortality, in addition to finescale environmental and climate data. At this point, such species-specific understanding of plant processes are not adequately realized for the large numbers of species and the detailed spatial scale examined in this investigation.

Predictions at spatial scales more complex than simple elevational belts can provide insight into the factors that determine the ability of species to adjust their ranges. Conceptual models presented by Jackson and Overpeck (2000) demonstrate how a species' distribution may respond as one environmental variable changes, in this case, temperature, and others are held constant. As temperatures rise, species populations will shift toward locally cooler areas—generally to higher elevations or north-facing slopes. In Figure 1, this corresponds to a shift along the temperature/elevational gradient (horizontal axis). Species shift along the temperature gradient (axis 1), but their edaphic and other topographic affinities do not change (there is no movement along other environmental gradients such as axis 2). Even though different species have different environmental tolerances, their responses are similar—to shift toward locally cooler locations. The detailed re-

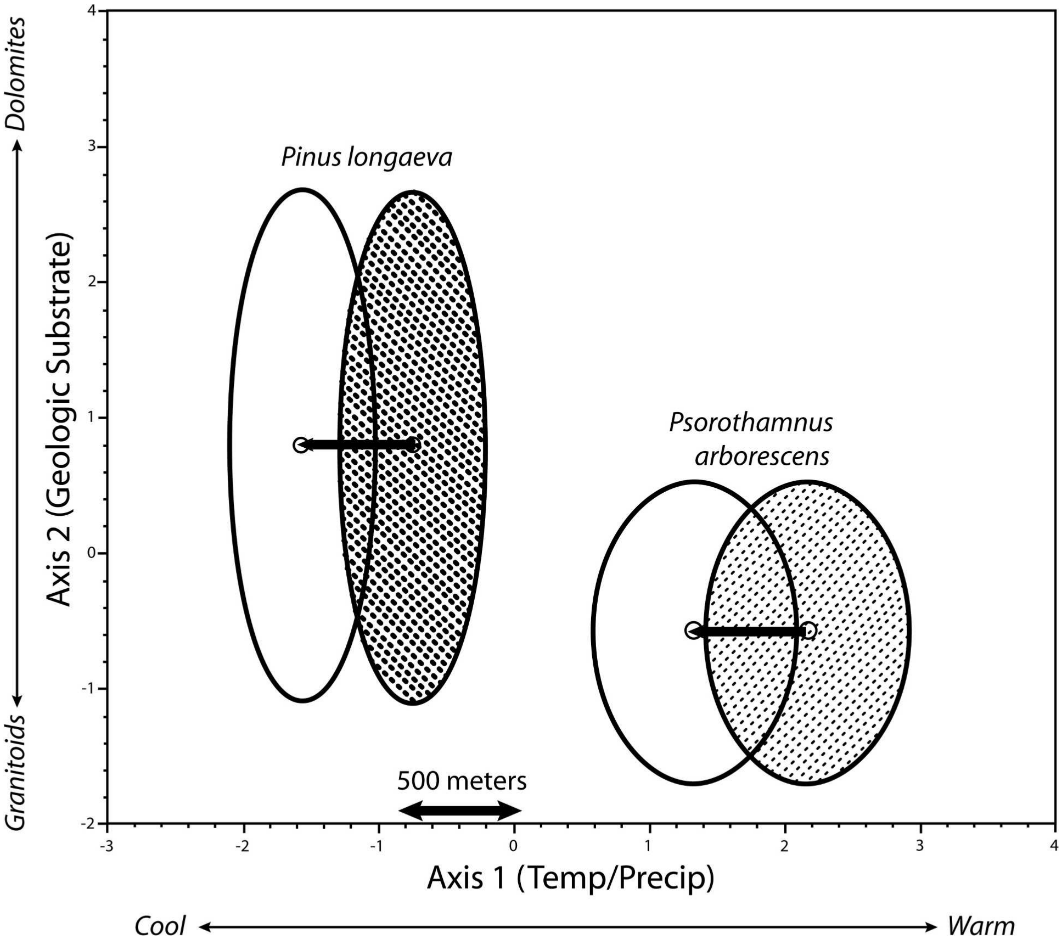


Figure 1. Species respond to an increase in temperature by moving to previously cooler locations, generally to higher elevations. A 3°C increase in temperature results in species shifting 500 m higher (toward lower values on axis 1). In these models, it is assumed that changes in temperature do not affect other environmental limitations of species, so species relationships to the underlying geologic substrate (axis 2) do not change.

sponses, however, will vary due to complex interactions with geologic and topographic gradients in the local environments.

In this paper, we analyze species–environment relationships in the southern White Mountains and northernmost Inyo Mountains of eastern California using canonical correspondence analysis (CCA), build and test finescale spatial models of the present species distributions, and simulate those distributions under successively warmer temperatures. The Intergovernmental Panel on Climate Change (Houghton et al. 2001) estimated that future global temperatures will increase by 1.4° to 5.8°C by the year 2100. Regional climate models predict monthly increases in temperature of 1.2°–4.7°C for California (Snyder et al. 2002; Snyder et al. 2004; Snyder and Sloan 2005), and overall annual temperature increases of 2.3°–5.8°C for California (Snyder et al. 2004), with greater increases at higher elevations

(Snyder et al. 2002; Hayhoe et al. 2004; Snyder and Sloan 2005). There is greater uncertainty in future precipitation estimates than for temperature, and no models show statistically significant annual changes in precipitation over the White Mountains (Houghton et al. 2001; Bell et al. 2004; Snyder et al. 2004; Snyder and Sloan 2005). Regional climate models point to a decrease in snow accumulation due to warmer winters and shifting of spring snowmelts into winter months (Bell et al. 2004; Snyder et al. 2004; Snyder and Sloan 2005). In addition, regional climate models by Diffenbaugh et al. (Diffenbaugh et al. 2005) suggest that orographic rain shadows may weaken. The effects of a weakened Sierra Nevadan rain shadow on the White Mountains are uncertain but could give rise to increased precipitation and more extreme precipitation events (Diffenbaugh et al. 2005). In this investigation, we considered increases in temperature of 1° to 6°C and modeled the changes in plant species' ranges for every 1°C of warming.

Number of hot days (temperatures greater than or equal to 32°C), number of frost days (days with temperature less than or equal to 0°C), diurnal temperature range, and a variety of precipitation parameters (total, timing, intensity, number of rain days, length of wet and dry events, etc.) are also critical to plant species distributions. Extreme weather events have significant impact over plant reproduction, establishment, and mortality. Extreme hot-weather events such as heat waves and droughts are predicted to increase in magnitude and frequency (Diffenbaugh 2005b; Bell and Sloan 2006). Snow accumulation is predicted to decrease, but total precipitation is expected to remain approximately the same (Snyder et al. 2002) or to decrease slightly (Diffenbaugh 2005a).

Study area

The White Mountains are an arid range east of the Sierra Nevada along the California–Nevada border. Geologic substrates include late Mesozoic granitoids that intrude mid-Mesozoic metavolcanics and uppermost Precambrian and Cambrian quartzites, argillites, phyllites, limestones, and dolomites. Cenozoic volcanic rocks, glacial debris, and alluvium cover smaller portions of the study area. Steeply dipping, range-bounding normal faults result in abrupt changes in elevation, from 1200 m in Owens Valley to the west, to 4342 m at White Mountain Peak, across a distance of about 12 km. Because of these topographic and geologic extremes, the White Mountains have often been used to study species–environment relationships (Billings and Thompson 1957; Wright and Mooney 1965; Brayton and Mooney 1966; Mooney 1966; Marchand 1973). The extreme topographic range provides complete transitions of species from desert scrub through alpine fell-fields. Abrupt vegetation changes across geologic contacts are common.

Vegetation associations include desert shrubs, pinyon-juniper woodlands, sagebrush meadows, subalpine bristlecone-limber pine forests, and alpine fell-fields (Mooney 1973; Thorne 1982; Hall 1991; Ernst et al. 2003). Below 2000 m, the vegetation is dominated by widely spaced, woody desert shrubs such as *Atriplex confertifolia, A. canescens, Menodora spinescens,* and *Ephedra nevadensis*, among numerous others. *Artemisia tridentata* appears at about 1220 m and gradually begins to dominate the vegetation by about 2290 m and extends to over 3000 m. The lower treeline is defined by *Pinus monophylla* and *Juniperus osteosperma* at about 2000 m. *Pinus longaeva* and *P. flexilis* compose the subalpine forest from

3000 m, up to timberline at 3500 m. Alpine fell-fields extend from timberline to the highest peaks of the range and primarily consist of small, ground-hugging and cushion plants, including *Eriogonum ovalifolium, Draba oligosperma, Phlox condensata*, and *Lewisia pygmaea*. There is a distinct break between major woodlands from 2900 to 3040 m over most of the central and southern White Mountains, between the upper limit of the pinyon-juniper woodland and the lower limit of the subalpine bristlecone-limber pine woodlands (Mooney et al. 1962; St. Andre et al. 1965; Thorne 1982; Spira 1991).

Lying within the rain shadow of the Sierra Nevada, the climate is characterized as cold and dry (Marchand 1973). Precipitation largely falls in the winter and varies with elevation, ranging from 455 mm yr^{-1} at Barcroft Research Station (3800 m) to 142 mm yr^{-1} at Bishop Airport in Owens Valley (1250 m). Temperature is also strongly dependent on elevation, with a mean annual temperature of −1.7°C at Barcroft Research Station, and 13.3°C at Bishop (Mooney et al. 1962; Wright and Mooney 1965; Powell and Klieforth 1991).

2. Methods

2.1. Field surveys

Field data were obtained in the summers of 2000–02 on a total of 650 plots (50 m × 50 m). The center of each plot was located with a GPS receiver. Up to seven investigators visually estimated percent covers of all identifiable plant species, rocks, and soils. Subsequently, each plot was arranged by elevation, rock type, aspect, and slope. Each of a total of 88 species were present in two or more sites and used in these analyses. Due to GPS errors and local inaccuracies in the digital elevation model (DEM), some sites were moved to adjacent cells to obtain better agreement between the DEM aspect and slope and field data.

2.2. Statistical modeling

Species distributions were predicted from environmental variables using CCA in CANOCO 4.0 for Windows (ter Braak and Šmilauer 1998). The environmental variables were extracted from a DEM with 18-m spatial resolution and a rasterized geologic map (Figure 2). Only environmental variables that had complete coverage of the study area were used. Elevation, slope, aspect, and curvature (plan and profile) were calculated directly from the DEM. Potential insolation, a function of aspect, slope, and topographic shading, was modeled for the spring equinox (EQsun, 21 March) and summer solstice (SSsun, 21 June) using the program Solarflux (Hetrick et al. 1993). A topographic position index (TPI) was calculated by comparing the elevation of each pixel with the mean elevation within various sized rings. TPIs with rings of 50- and 100-m radii, and 150-m-wide annuli with 300-, 1000-, and 2000-m outer radii were calculated (A. D. Weiss 2001, personal communication). Geologic maps were hand digitized from existing publications (Nelson 1966; Krauskopf 1971; Ernst and Hall 1987; Ernst et al. 1993; Ernst et al. 2002) and refined using remotely sensed imagery and field data, and additional small lenses of carbonate within metaclastic rock types were added to the geologic maps (Van de Ven et al. 2000). Rock types were aggregated to 1) granitoids/

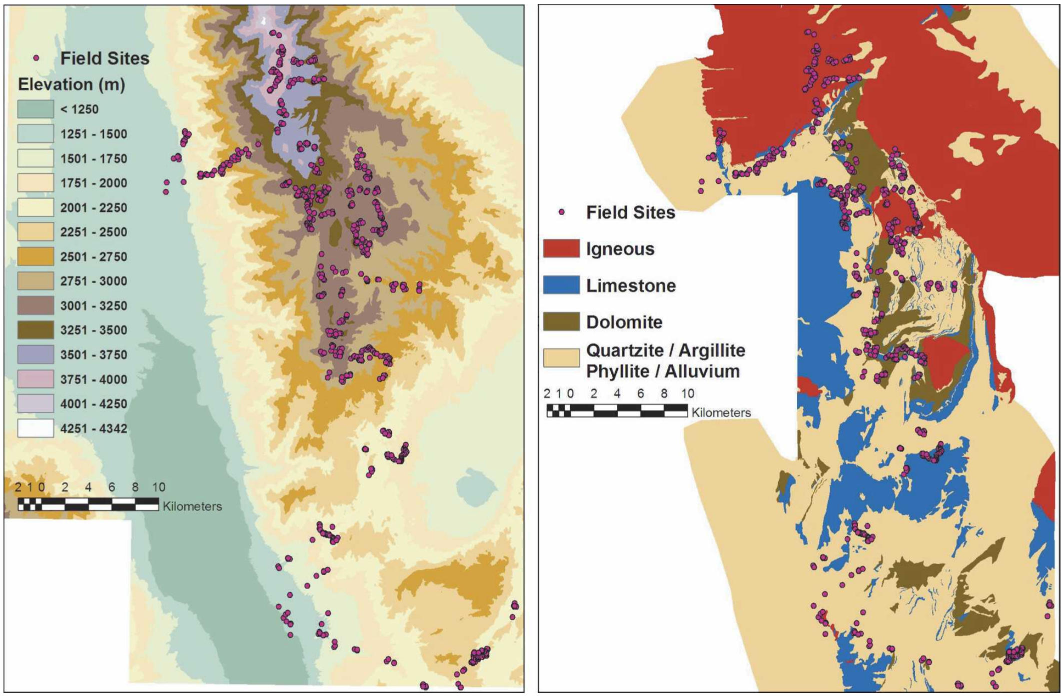


Figure 2. The two primary sources of environmental variables: (left) DEM and (right) generalized geologic map, with locations of field sites indicated on both. Slope topographic position, curvature, and insolation were derived from the DEM.

volcanics, 2) quartzite/phyllite/argillite/alluvium, 3) limestone, and 4) dolomite, and entered the analyses as nominal variables.

CCA is a direct gradient ordination that relates site/species and site/environment matrices (ter Braak and Šmilauer 1998). It extracts synthetic axes that are linear combinations of environmental variables that maximize separation of species and sites along composition gradients. CCA has been extensively used in gradient analysis (Borgegård 1990; Gottfried et al. 1998; Guisan et al. 1999), and it compared favorably with other vegetation or habitat modeling techniques such as GLMs, neural networks, and GAMs (Palmer 1993; Guisan and Zimmermann 2000).

Significant environmental variables ($p < 0.05$) were chosen by forward stepwise selection with Monte Carlo permutation tests. Four synthetic axes were derived from those variables. Maps of axes scores were generated from the regression coefficients for each standardized variable. Each species has a centroid and tolerance [standard deviation (std dev)] on each axis, defining an environmental envelope in canonical space as a multidimensional ellipsoid. The statistical distances of each pixel to each species' centroids in four-dimensional canonical space (each CCA axis being one dimension, and analyses being run to four axes) were calculated to determine the likelihood of the presence of those species. Results were expressed in species-specific std dev units—pixels closer to the species centroid have higher probability of occurrence; beyond 3 std dev was taken as absence. The species centroids and tolerances can be used to project species distributions across the landscape (Guisan et al. 1999; Torregrosa 1999).

2.3. Evaluation

Axes and species parameters were calibrated from 434 of the 650 field sites. The remaining 216 plots were used to evaluate the predicted presence or absence of 22 test species, selected from the original 88 analyzed species. The 22 species were selected to include all types of vegetation. All major tree species, abundant shrub species, and a few forbs and less common shrubs across all major environments and associations were included. To account for registration errors, predicted species distributions were smoothed with a 3 × 3 cell moving average, effectively making the final scale of predictions 54 m from an original pixel size of 18 m. Kappa statistics were calculated for each test species. The kappa statistic measures the relative improvement of a map over that expected by chance agreements (Congalton 1991; Foody 2002). A kappa statistic of 0 indicates that the predicted and observed distributions are uncorrelated, whereas a kappa value of 1 indicates that the two distributions are perfectly correlated (Congalton et al. 1983; Congalton 1991; Smits et al. 1999). The std dev that maximized kappa for each species was identified from the calibration data, and all predicted vegetation distributions were thresholded to that std dev. The kappa values of the species maps were assessed from the evaluation sites at that threshold.

3. RESULTS

3.1. CCA ordination

Axis 1 is the elevational gradient indicated by the long elevation vector, nearly parallel to axis 1 in Figure 3a. The vegetation gradient runs from low-elevation desert shrubs on the right of Figure 3a, pinyon-juniper woodlands near the center, subalpine bristlecone-limber pine forests, and alpine fell-fields to the left. Elevation is modified by equinox insolation (EQsun); greater insolation warms the ground and lowers the effective elevation. The high eigenvalue (0.67) of axis 1 indicates effective separation of species. The map of axis 1 (Figure 4) shows not only the elevational gradient (blue is higher elevation), but also finer-scale variations between the north and south sides of canyons. The extremes of axis 1 are south-facing slopes at low elevations, and north-facing slopes at the highest elevations.

Axis 2 is dominated by the geologic gradient from dolomites (top of Figure 3a), through limestones, clastic metasediments, and alluvium near the middle, and to igneous substrates at the bottom. The moderate eigenvalue for axis 2 (0.23) indicates substantial separation of species along the geologic gradient. Bristlecone pine [*Pinus longaeva* (PILO)] has a strong affinity for calcareous rocks but does occur on other substrates, whereas aspen [*Populus tremuloides* (POTR)] is confined almost exclusively to granitic substrates. Topographic position (tp1000) also influences axis 2—sites with high topographic positions (ridgetops) are driven toward the dolomite end of the geologic gradient. The extremes of the gradient are

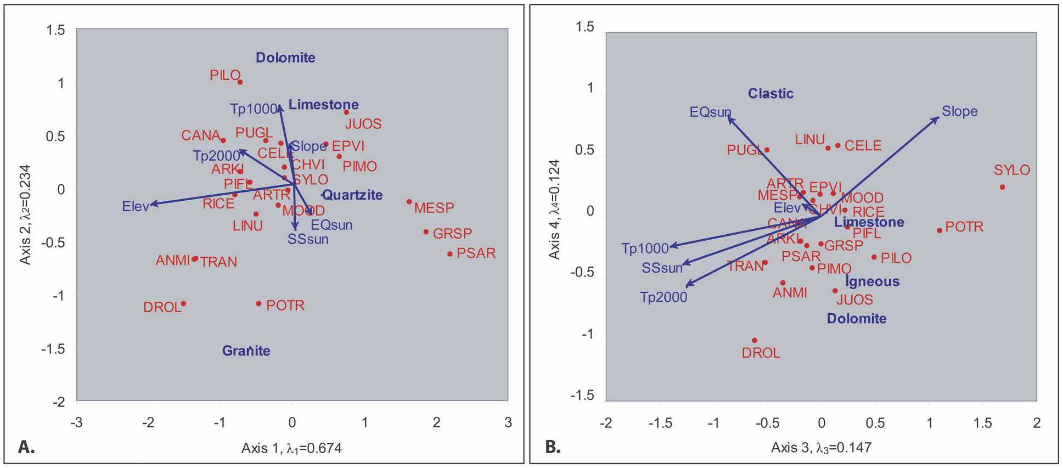


Figure 3. (a) Graphs of CCA axes 1 and 2. (b) Graphs of CCA axes 3 and 4. See text for interpretations of these graphs. Species abbreviations (red) are: ANMI = *Antennaria microphylla*, ARKI = *Arenaria kingii*, ARTR = *Artemisia tridentata*, CANA = *Castilleja nana*, CELE = *Cercocarpus ledifolius*, CHVI = *Chrysothamnus viscidiflorus*, DROL = *Draba oligosperma*, EPVI= *Ephedra viridis*, GRSP = *Grayia spinosa*, JUOS = *Juniperus osteosperma*, LINU = *Linanthus nuttallii*, MESP = *Menodora spinescens*, MOOD = *Monardella odoratissima*, PIFL = *Pinus flexilis*, PILO = *Pinus longaeva*, PIMO = *Pinus monophylla*, POTR = *Populus tremuloides*, PSAR = *Psorothamnus arborescens*, PUGL = *Purshia glandulosa*, RICE = *Ribes cereum*, SYLO = *Symphoricarpos longiflorus*, and TRAN = *Trifolium andersonii*. Environmental abbreviations (blue) are as follows: Elev = elevation, Slope = slope angle, EQsun = spring equinox insolation, SSsun = summer solstice insolation, tp1000 and tp2000 = topographic position with 1000- and 2000-m annuli, Clastic = clastic metasedimentary or alluvial substrate, Igneous = granitic or metavolcanic substrate, Dolomite = dolomite substrate, and Limestone = limestone or limestone + shale substrate.

dolomitic ridgetops in dark red, and canyon bottoms underlain by igneous rocks are in dark blue on the map of axis 2 (Figure 4).

Influential variables along axis 3 (Figure 3b) include additional topographic effects (tp1000, tp2000, slope, SSsun, and EQsun). Low eigenvalues for axes 3 and 4 (0.15 and 0.12, respectively) indicate that fewer species are separated and the gradients are relatively short and weak. For example, *Symphoricarpos longiflorus* (SYLO) is found at the bottom of canyons: low topographic position (tp1000), high slopes, and low summer solstice insolation (SSsun). *Draba oligosperma* (DROL), *Trifolium andersonii* (TRAN), and *Antennaria microphylla* (ANMI) prefer warm, sunlit flats on ridgetops (low slope, high tp1000, high EQsun, and SSsun). The extremes of the axis 3 map (Figure 4) are low-insolation, steep slopes on canyon bottoms (red) and high-insolation flats on ridgetops (blue), independent of elevation.

In addition to the topographic variables, geologic substrates are further differentiated on axis 4. *Juniperus osteosperma* (JUOS) shows a secondary affinity for

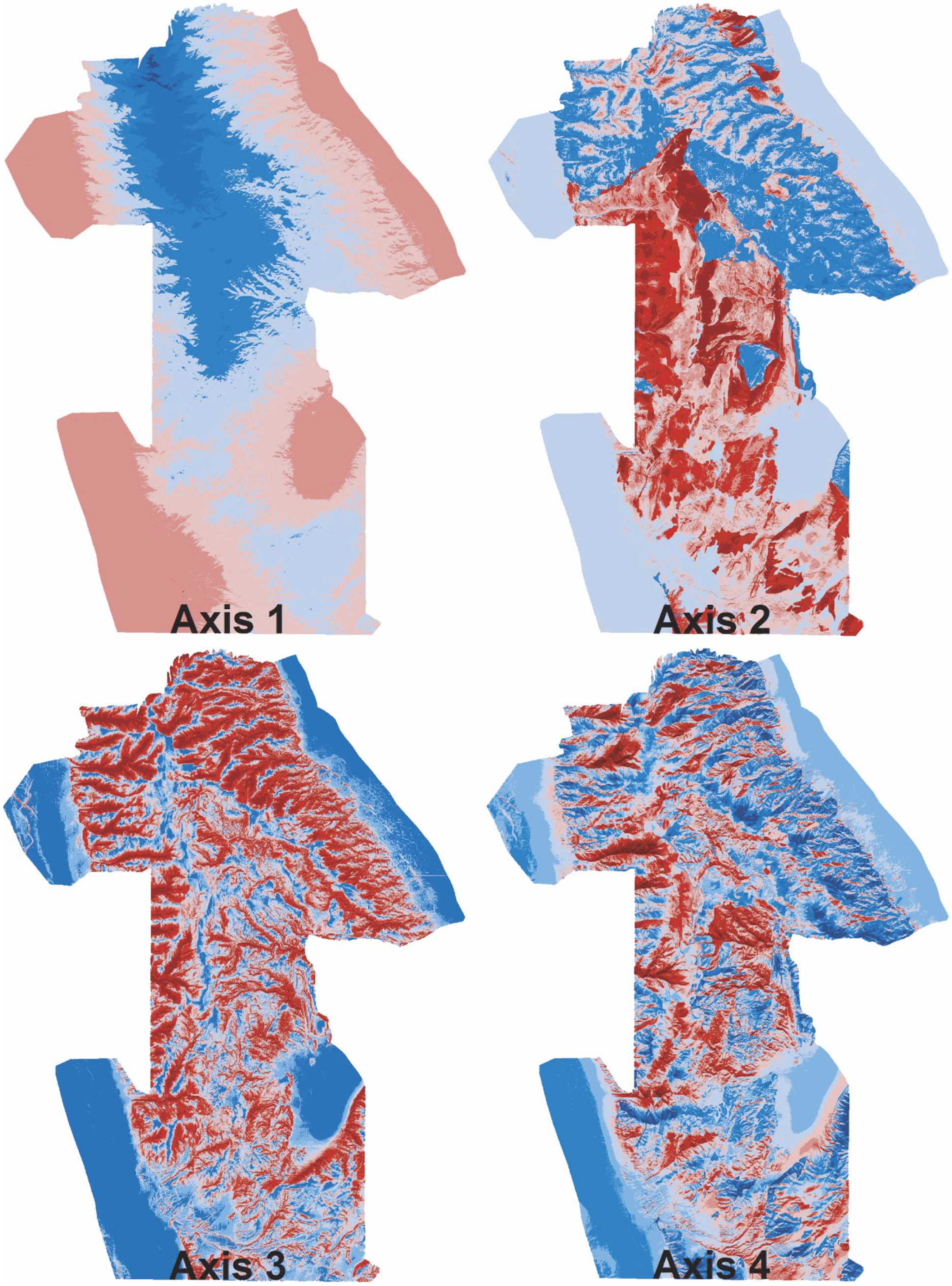


Figure 4. Axes maps show the spatial realization of the linear combinations of environmental variables. Relationships between variables are indicated on axes graphs in Figure 3. Blue indicates low axis scores, and red indicates high axis scores. See Figure 3 and the text for explanations of these axes.

igneous substrates, in addition to its preference for limestone shown on axis 2. *Linanthus nuttallii* (LINU), *Cercocarpus ledifolius* (CELE), and *Purshia glandulosa* (PUGL) exhibit preferences for clastic substrates. The overlay of the topographic effects, primarily slope, topographic position, and summer solstice insolation, on various geologic substrates accounts for the complex pattern in the map of axis 4 (Figure 4). Additional axes have lower eigenvalues and separated fewer species, so analyses were stopped at four axes.

3.2. Evaluation of the models

Kappa statistics calculated from evaluation sites ranged from 0.77 for *Psorothamnus arborescens* to 0.11 for *Purshia glandulosa*, as shown in Table 1. Four of 22 species models produced kappa statistics > 0.60, a very good improvement over a random distribution. Eight more were between 0.4 and 0.6, a moderate improvement over random. Ten species models produced poor fits (<0.40). However, in all cases, elevational ranges closely matched the field data (Figure 5). Many incorrectly predicted evaluation sites were adjacent to areas with correct predictions and may have been incorrectly located due to GPS and DEM registration errors.

The producers, users, and overall accuracies are strongly weighted by the absence of species, and are misleadingly high. Overall accuracy is simply the number of correctly identified sites, either present or absent, divided by the total number of sites. It is easily skewed by numerous absences—species that are present in very few sites usually have very high overall accuracies. Producer accuracy is a measure of omission error, and user accuracy is a measure of commission error

Table 1. Accuracy statistics from evaluation sites for 22 species.

Species	Kappa	Absence	Presence	Producer accuracy	User accuracy	Overall accuracy
Psorothamnus arborescens	0.77	194	22	0.77	0.81	0.96
Trifolium andersonii	0.67	179	37	0.68	0.78	0.91
Juniperus osteosperma	0.66	198	18	0.61	0.79	0.95
Pinus monophylla	0.63	178	38	0.82	0.62	0.88
Artemisia tridentata	0.57	64	152	0.88	0.87	0.82
Cercocarpus ledifolius	0.52	186	30	0.27	0.64	0.79
Grayia spinosa	0.51	188	28	0.71	0.50	0.87
Arenaria kingii	0.49	144	72	0.39	0.61	0.57
Menodora spinescens	0.49	187	29	0.76	0.46	0.85
Draba oligosperma	0.48	206	10	0.50	0.50	0.95
Ephedra viridis	0.46	178	38	0.84	0.45	0.79
Pinus longaeva	0.42	178	38	0.47	0.56	0.84
Linanthus nuttallii	0.31	168	48	0.67	0.40	0.70
Populus tremuloides	0.29	210	6	0.50	0.23	0.94
Ribes cereum	0.28	175	41	0.71	0.35	0.69
Pinus flexilis	0.27	191	25	0.52	0.30	0.80
Castilleja nana	0.26	195	21	0.71	0.25	0.76
Antennaria microphylla	0.24	197	19	0.37	0.28	0.86
Symphoricarpos longiflorus	0.16	208	8	0.13	0.33	0.96
Chrysothamnus viscidiflorus	0.13	92	124	0.48	0.65	0.56
Monardella odoratissima	0.12	200	16	0.81	0.14	0.60
Purshia glandulosa	0.11	207	9	0.33	0.27	0.94

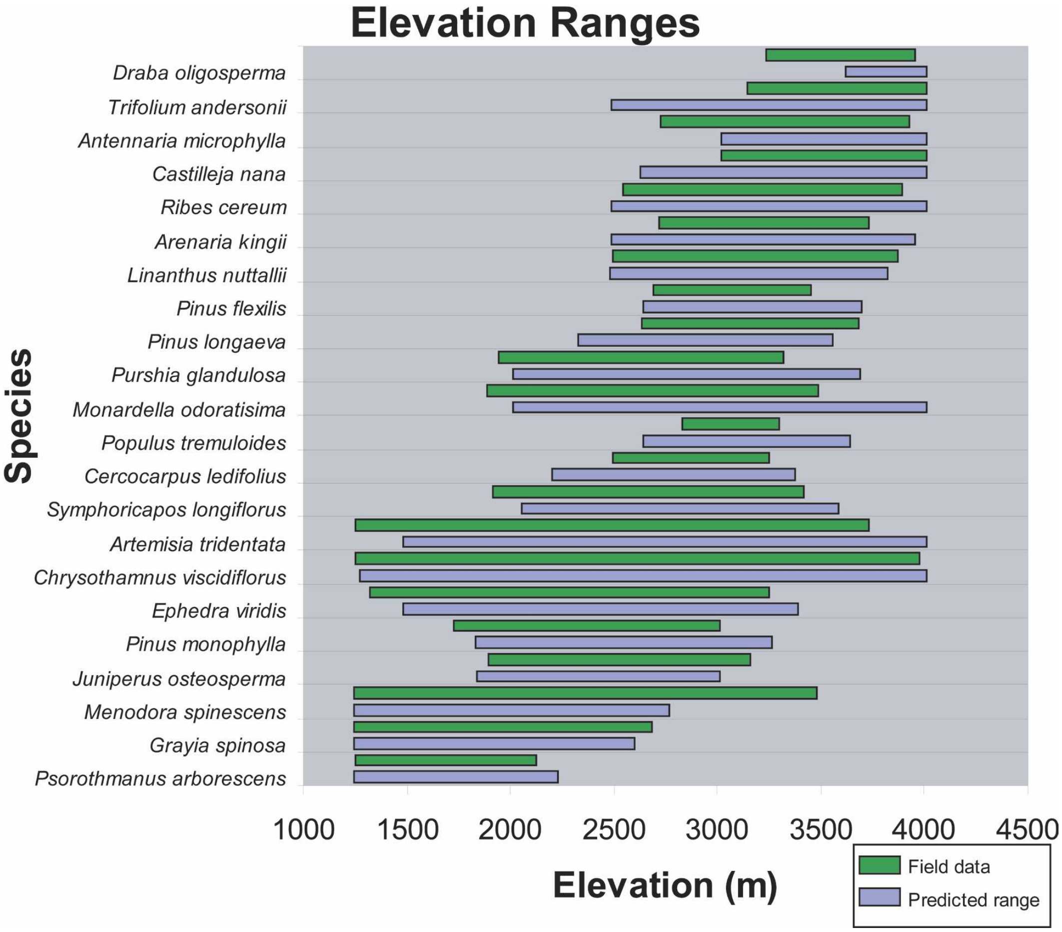


Figure 5. Graph of species presents elevational ranges for the 22 test species as determined from field data (green) and predicted distributions (blue). See also Ernst et al. (Ernst et al. 2003).

only. Kappa weighs both omission and commission errors by incorporating off-diagonal elements in the error matrix and is a better integrated measure of model success or failure (Congalton 1991; Foody 1992). In general, errors in species predictions were heavily weighted toward errors of commission (predicting presence at sites where the species was absent). This feature may be the result of the asymmetrical treatment of presence and absence in the CCA algorithm (ter Braak and Šmilauer 1998): in calibrating the environmental tolerances for each species, the CCA algorithm considers the environmental variables of each site that a species is found in but does not consider the sites in which a species is absent.

Species with very good fits include two trees, one desert shrub, and one alpine herb. The species with poorer fits include shrub species that are disturbance dependent (i.e., *Chrysothamnus viscidiflorus*), have wide environmental tolerances and poor taxonomic resolution (i.e., *Artemisia spp.*), or are less abundant species that have few occurrences for calibration and evaluation (i.e., *Populus tremuloides*, *Symphoricarpos longiflorus*, and *Purshia glandulosa*). The quality of the models, particularly at the finest spatial scales, is strongly dependent on having many presences for a given species in order to include the full environmental tolerances for model calibration and assessment. In addition, many of the species with low kappa scores performed poorly due to finescale features that are below the resolution of the DEM, such as small depressions or rocky outcrops. Historical disturbance and unmapped environmental variations will tend to confound the local distributions, so that more precise mapping across the whole mountain range at an 18–54-m scale may be impossible without more accurate DEMs, the aid of high-resolution remotely sensed data, and additional environmental parameters such as disturbance and soil conditions (e.g., soil depth, water content, and soil chemistry).

3.3. Modeling warming

Modifying the species tolerances along the elevational gradient simulated alpine and select subalpine species' responses to climate change. As shown in Figure 1, shifting the environmental envelopes of species along axis 1 has the same effect as modifying DEM elevations. The total elevational range of the field data used to calibrate the model was 2695 m (1245–3940 m). Over that elevational range, the axis 1 scores varied by 3.9308 std dev. Given a lapse rate of 3°C $(500\ \mathrm{m})^{-1}$, a change of 1°C corresponds to 167 m in elevation, which corresponds to a shift of −0.243 58 std dev for axis 1. The value is negative because higher elevations correspond to lower axis 1 scores. Each species' centroids and tolerances were shifted in 1°C increments, up to 6°C.

3.4. Species' responses to increased temperatures

Three maps of species distributions are shown in Figure 6 that demonstrate the changes from species' present distributions to their distributions after temperatures increase by 3°C. Because plant species exhibit complex finescale patterns driven by local topography and geologic substrate after temperatures rise, all species ascend in elevation, but the new ranges reflect the influence of local topography and geology, making their new distributions more complex than simple uphill migrations. Relationships illustrated in Figure 6 are as follows.

1) *Arenaria kingii* is a perennial herb broadly distributed in the subalpine zone from 2750 to 3700 m across all rock types. Under warming, it retreats from broad stretches along the crest of the range and invades the highest elevations, with a narrow zone of overlap between present and future distributions.
2) *Pinus monophylla* is the lower timberline tree in the White Mountains. It occupies south-facing slopes at its extreme upper range limit (3100 m), all aspects at midelevations (2300–2600 m), and north-facing slopes at its lower range limits (1800 m). It is sparse on granitic rocks, even in the middle of its elevation range, forming extensive stands along the southern crest of the range on metasedimentary rocks, alluvium, and limestone. Its distribution on igneous rocks is even more restricted in the warming scenario. Extensive areas below 2200 m are lost, and its originally continuous habitat becomes fragmented. However, there is substantial overlap

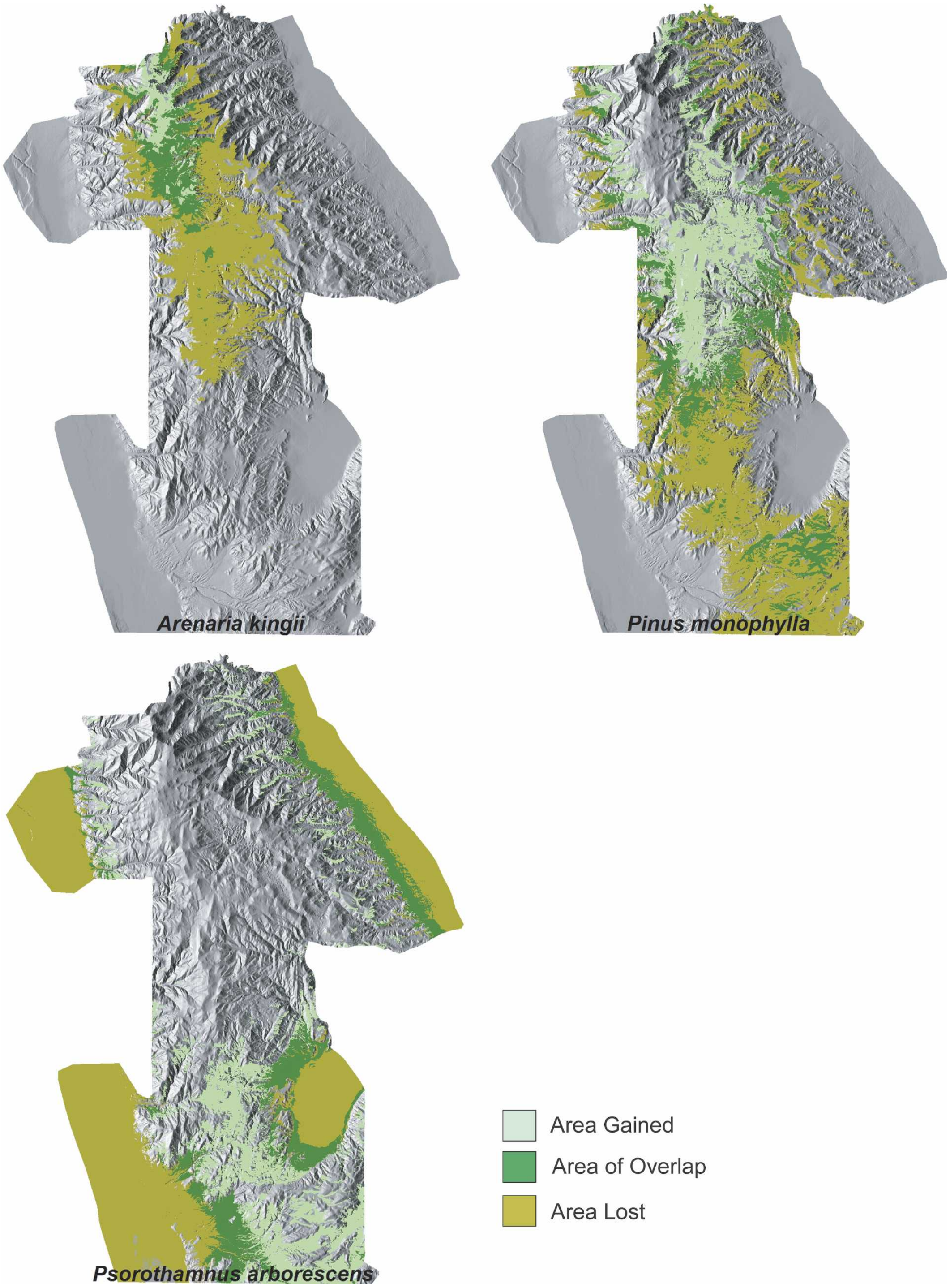


Figure 6. Predicted distributions of three species and their responses to an increase of 3°C. The current distributions are in yellow and dark green, and the predicted distributions in a 3°C warmer climate are in dark and pale green. Therefore, the area lost after warming is in yellow, the area newly gained is in pale green, and the area that overlaps the two scenarios is in dark green.

between current and future distributions. At the upper extent of the current distribution, *P. monophylla*, like many other species, is predicted to migrate from south-facing slopes to adjacent north-facing slopes, as shown in Figure 7. Its avoidance of igneous substrates prevents *P. monophylla* from colonizing the Sage Hen Flat granite beyond a few south-facing slopes.

3) *Psorothamnus arborescens* is a low-elevation desert shrub, ranging from below 1250 up to 2100 m. *Psorothamnus* displays a slight avoidance of carbonates. Its current predicted distribution is truncated at lower elevations because there were no sites below its elevational range. Therefore, a

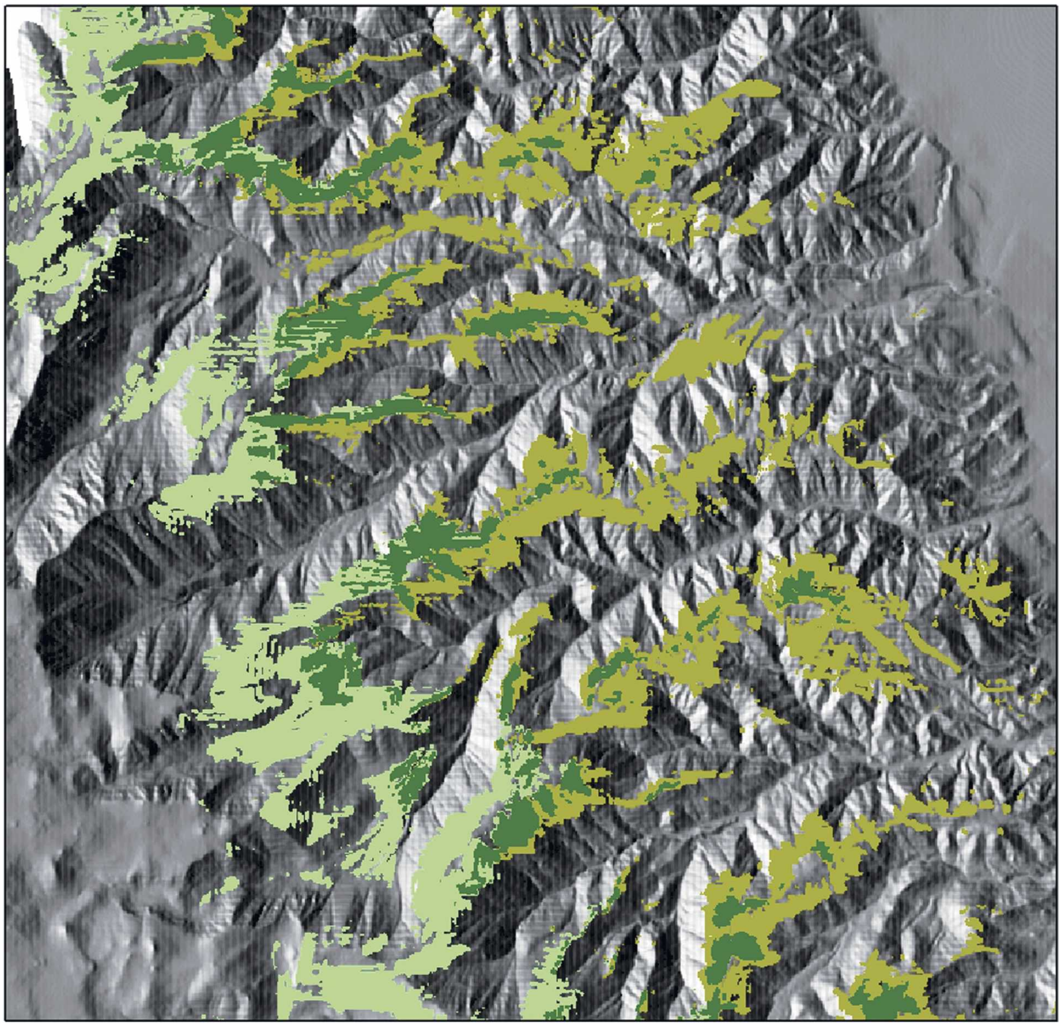


Figure 7. Present and future distributions of *Pinus monophylla*, overlaid on a shaded relief map. In addition to migrating to higher elevations, *P. monophylla* shifts from warm south-facing slopes to cooler north-facing slopes as temperatures rise by 3°C.

full environmental envelope cannot be calculated. It is common on the numerous bajadas at the base of the mountains and extends to higher elevations on south-facing slopes. The pattern of its shift includes a highly fragmented invasion of south-facing slopes up to about 2500 m. Its predicted abandonment of low-elevation alluvial fans in the warming scenario may be an artifact of its truncated environmental envelope.

3.5. Incremental temperature changes

The predicted distributions of all alpine species and select subalpine species were modeled up to an increased temperature of 6°C, in 1° increments. As before, all species shifted upslope. In some instances, they shifted from south- to north-facing slopes (like *P. monophylla* in Figure 7), and edaphic affinities limited the future distributions of some species. Figures 8–10 and Movies 1–3 show the predicted distributions of some of those species, as follows.

1) *Draba oligosperma* is a small alpine herb that occupies a small (<800 ha) range at high elevations (>3800 m). It grows on flat, high insolation meadows. As temperatures increase, its nearly continuous current distribution fragments. As shown in Figure 8 and Movie 1, after a 2°C temperature increase, *D. oligosperma* is relegated to a few very small popu-

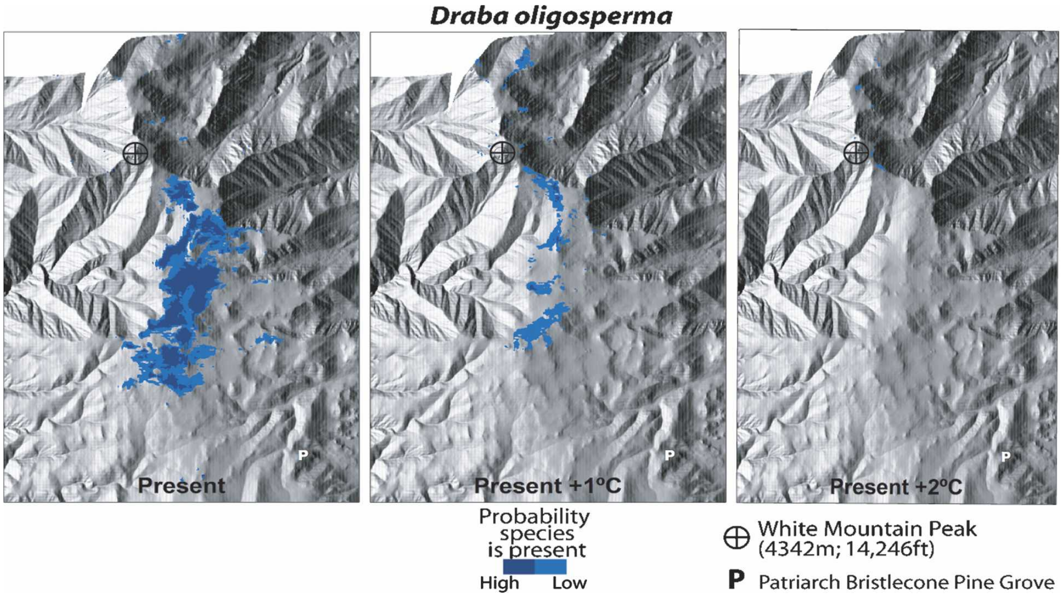
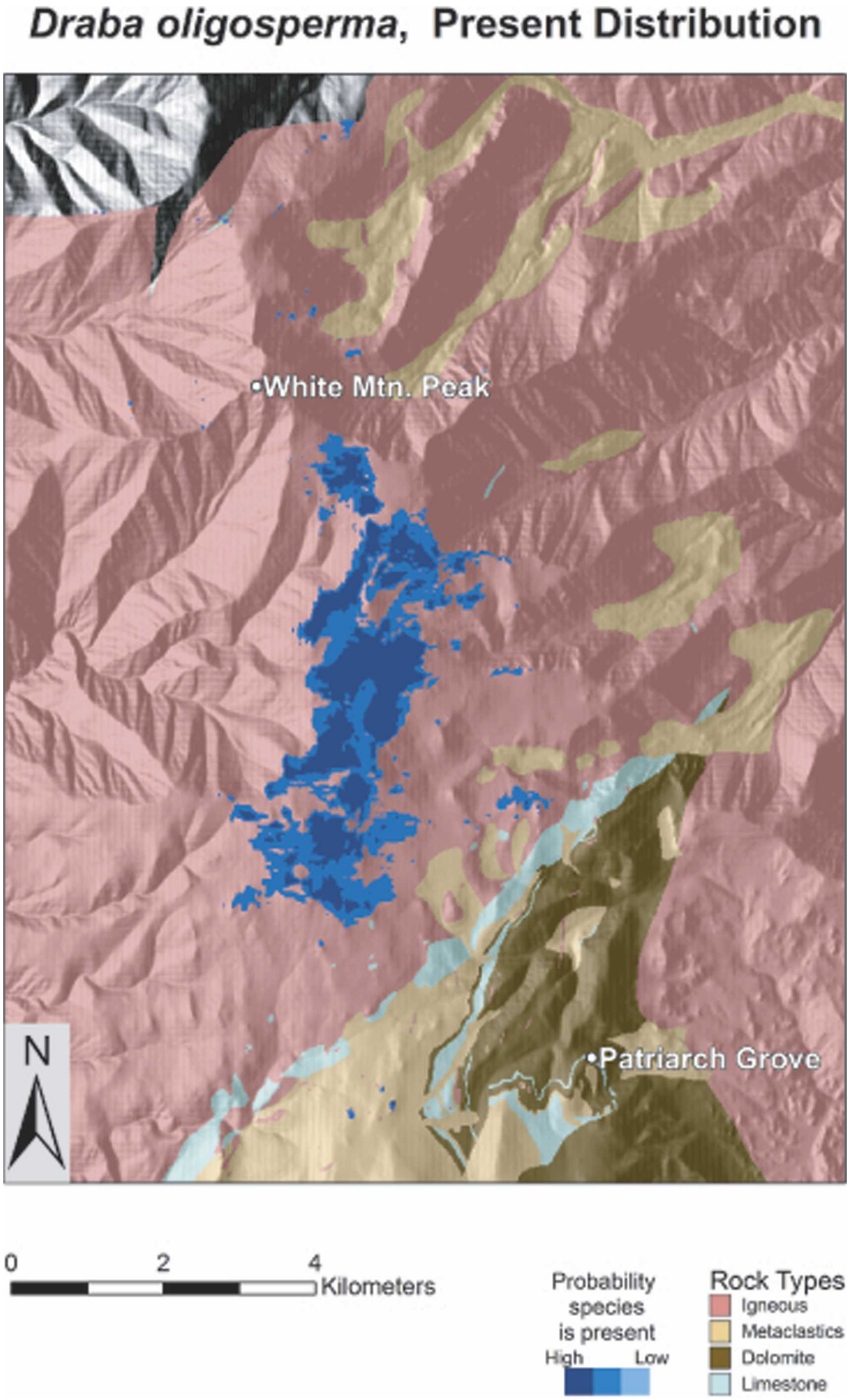


Figure 8. Predicted distributions of *Draba oligosperma* overlaid on a shaded relief map of the highest elevations in the northernmost portions of the study area. If temperatures rise more than 2°C, *D. oligosperma* is predicted to disappear from the central White Mountains. With the exception of alluvium and glacial deposits at the bases of some of the eastern canyons, the entire area is underlain by the White Mountain Peak metavolcanics and the Barcroft granodiorite. See text for discussion.



Movie 1. Response of *Draba oligosperma* to warming temperatures in 1°C increments. If temperatures warm by 3°C, *D. oligosperma* is predicated to go extinct in the White Mountains. See the online version of this paper to view animation.

lations on flat, sunlit peaks at the highest elevations. It is expected to become extinct in the study area if temperatures increase by 3°C.

2) *Pinus longaeva* dominates the subalpine woodland and is the upper timberline tree. Figure 9 and Movie 2 show that it occupies south-facing slopes at its upper range limit (3600 m), all aspects at its midelevations (3100–3400 m), and north-facing slopes at its lower range limit (2900 m). *P. longaeva* is most common on carbonate substrates but is found in limited environments on other rock types. On igneous and clastic rock types, its distribution is restricted to north-facing slopes, ridges, and peaks. As temperatures increase, it migrates to higher elevations, abandoning the Schulman and Patriarch Groves (S and P, respectively, in Figure 9) after 2° and 5°C temperature rises, respectively. *P. longaeva* does not migrate into the south-facing granitic slope in the northern part of the study area due to its aversion to granitic substrates, which limits its available habitat. If temperatures rise by 5°C, there are no carbonate substrates at high enough elevations for it to occupy; *P. longaeva* would be relegated to steep granitic slopes with northerly aspects and a few ridgetops.
3) *Trifolium andersonii* is a common herb in the alpine fell-fields. It occupies south-facing slopes at its upper range limit (4000 m), all aspects at midelevations (3700–3900 m), and north-facing slopes at its lower range limits (3600 m). As shown in Figure 10 and Movie 3, it avoids dolomite and has a fragmented distribution on several quartzite and argillite peaks south of its main population. With just a 1°C increase, it abandons its isolated southern populations. By an increase of 3°C, its formerly broad, continuous distribution on igneous substrates in the northernmost portions of the study area becomes more fragmented, and it occupies only the highest-elevation peaks and ridges. At +4°C, *T. andersonii* is predicted to occur only in the immediate vicinity of White Mountain Peak. Very small, isolated populations on the north-facing slope of White Mountain Peak remain after temperatures rise by 5°C. Any further rise in temperatures would result in the extinction of *T. andersonii* in this study area.

4. Discussion

All modeled species are predicted to decrease their ranges due to upslope range shifts. Figure 11 shows the changes in area of 14 alpine and subalpine species for incremental increases in temperature. For an increase of 6°C, 10 species are predicted to disappear from the study area. Of the remaining four species, all of their predicted ranges are expected to shrink to less than 1% of the area of their current ranges. At a more conservative temperature increase of 3°C, two species may become extinct (*Sedum roseum* and *Draba oligosperma*), the new ranges of all remaining species are 68% or less of the present areas, and four species (*Draba breweri*, *Ivesia lycopodioides*, *Lewisia glandulosa*, and *Lewisia pygmaea*) should lose over 98% of their current areas. However, some undetermined desert species will fill in the lower-elevation gaps as other species move upslope.

There are several species that are particularly rare and/or occur in extremely specialized environments that were not encountered in our field studies. These species are at greater risk than any species included in Figure 11. *Polemonium*

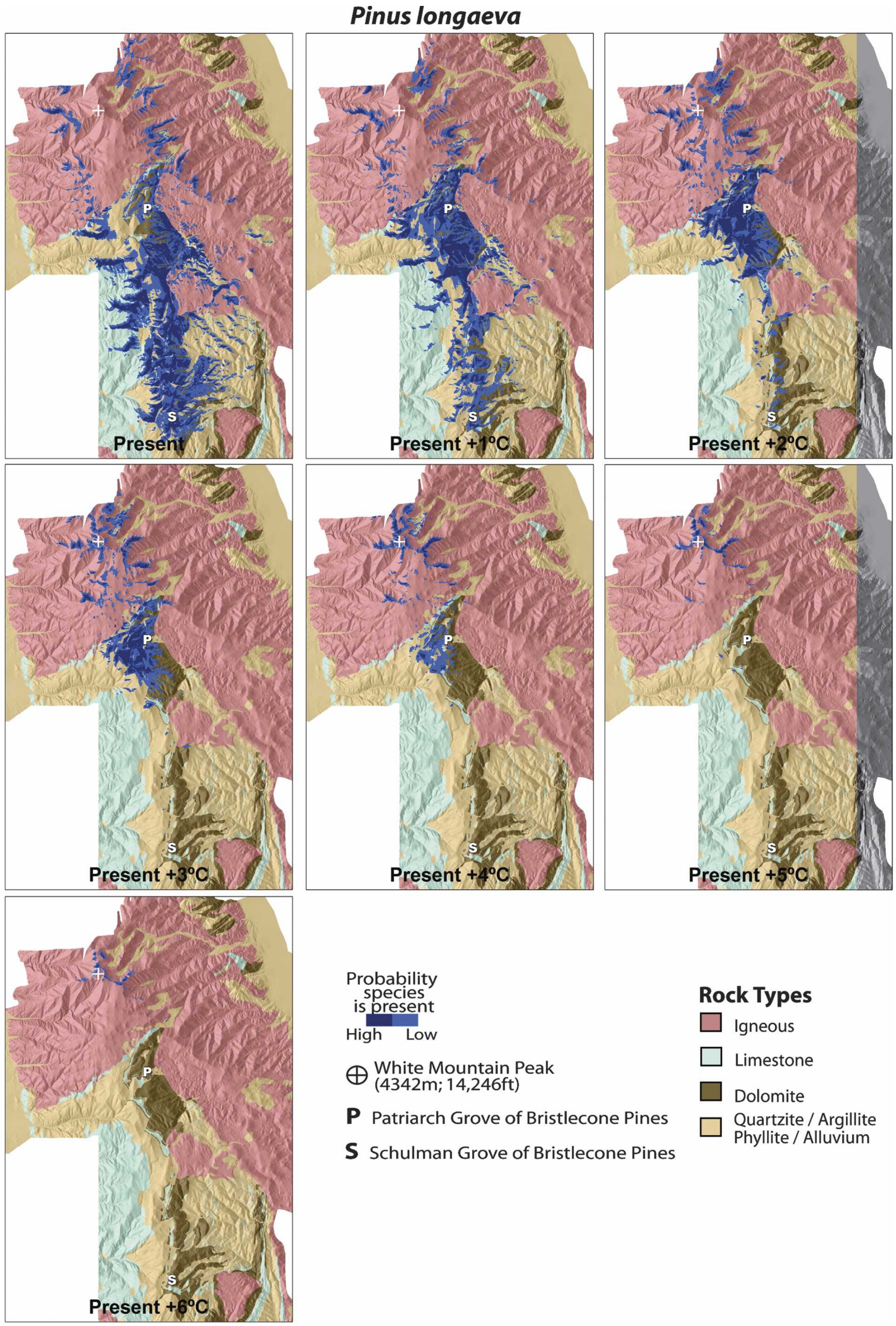
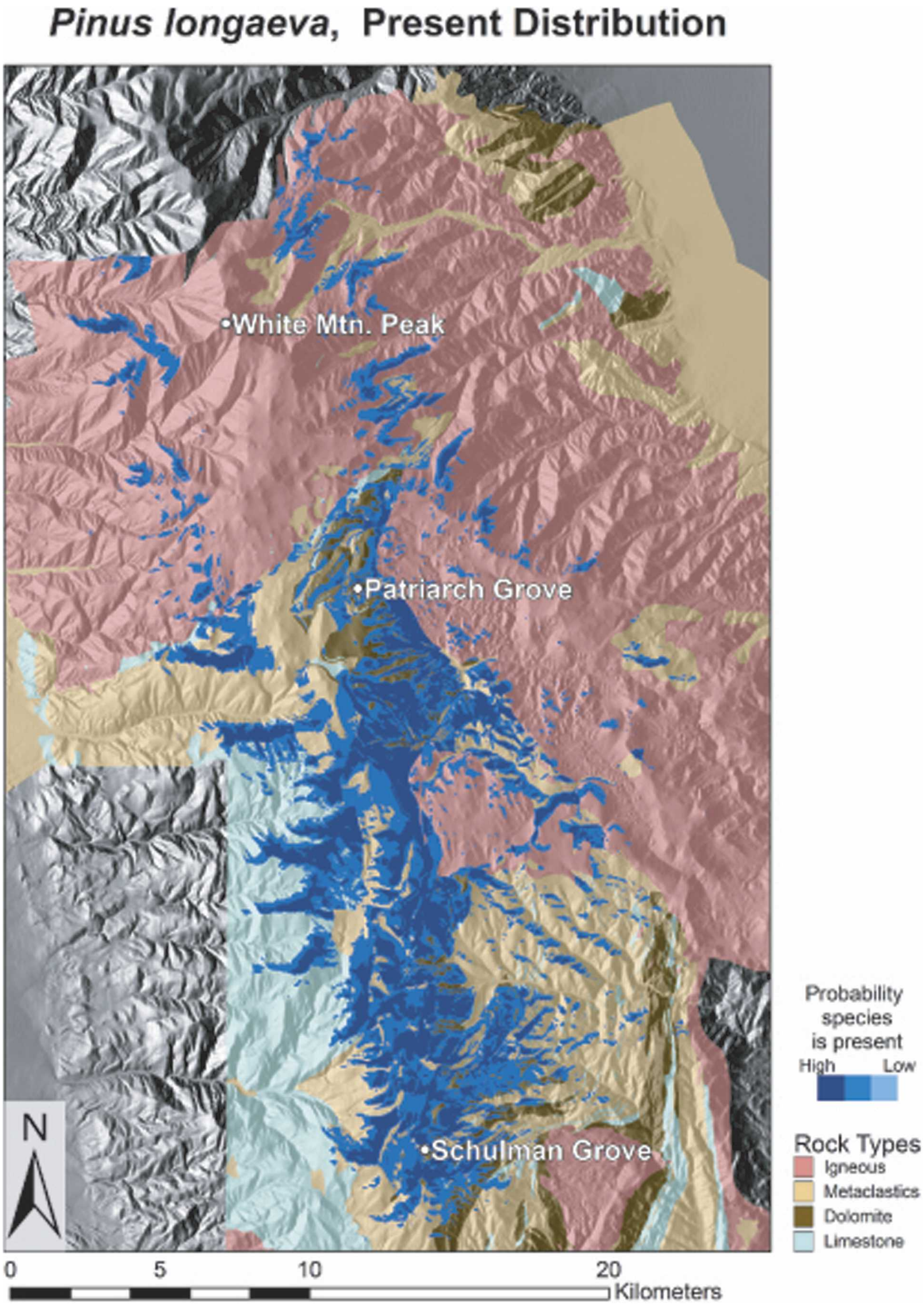


Figure 9. Predicted response of *Pinus longaeva* to increasing temperatures overlaid on a shaded relief, simplified geologic map. See text for discussion.



Movie 2. Response of *Pinus longaeva* to warming temperatures in 1°C increments. See the online version of this paper to view animation.

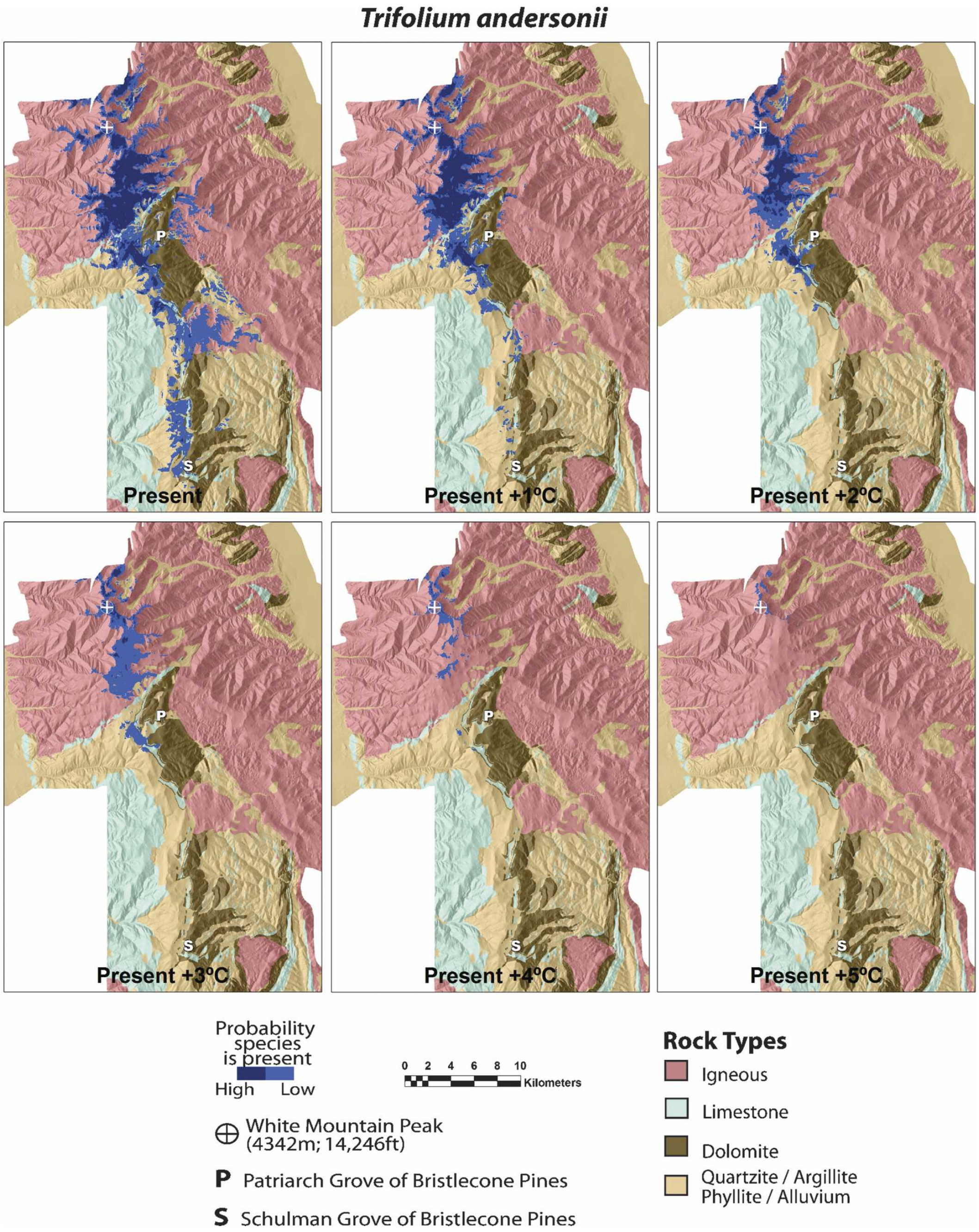
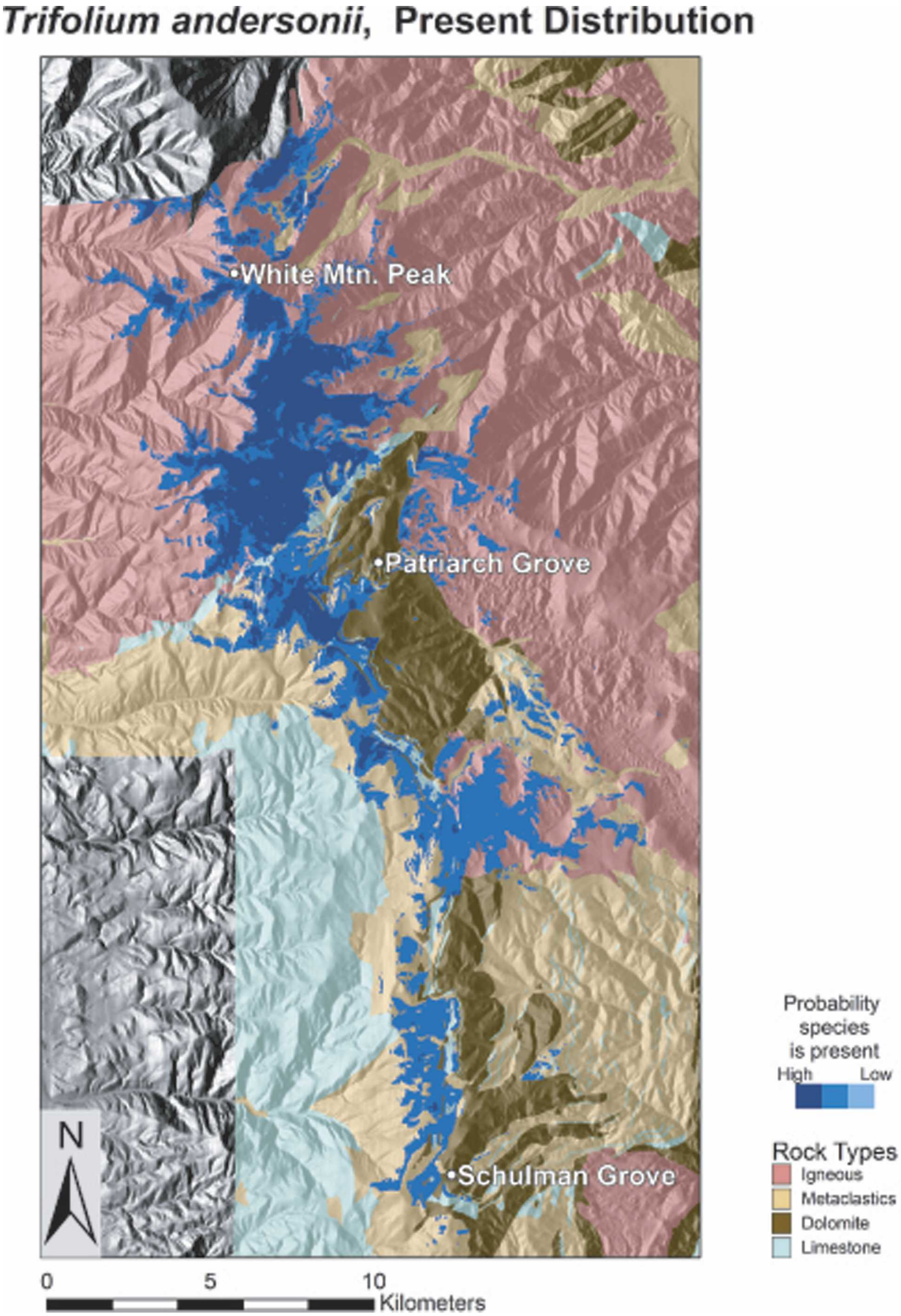


Figure 10. Predicted distribution of *Trifolium andersonii* overlaid on a shaded relief, simplified geologic map. Map legend is the same as in Figure 9. See text for discussion.

chartaceum, *Erigeron vagus,* and *Anelsonia eurycarpa* are already restricted to the highest slopes of White Mountain Peak, above 4000 m (Mooney 1973; Spira 1991), and have no higher-elevation areas to which they could retreat. Of these, *Polemonium chartaceum* has the most restricted habitat, being limited to the White



Movie 3. Response of *Trifolium andersonii* to warming temperatures in 1°C increments. See the online version of this paper to view animation.

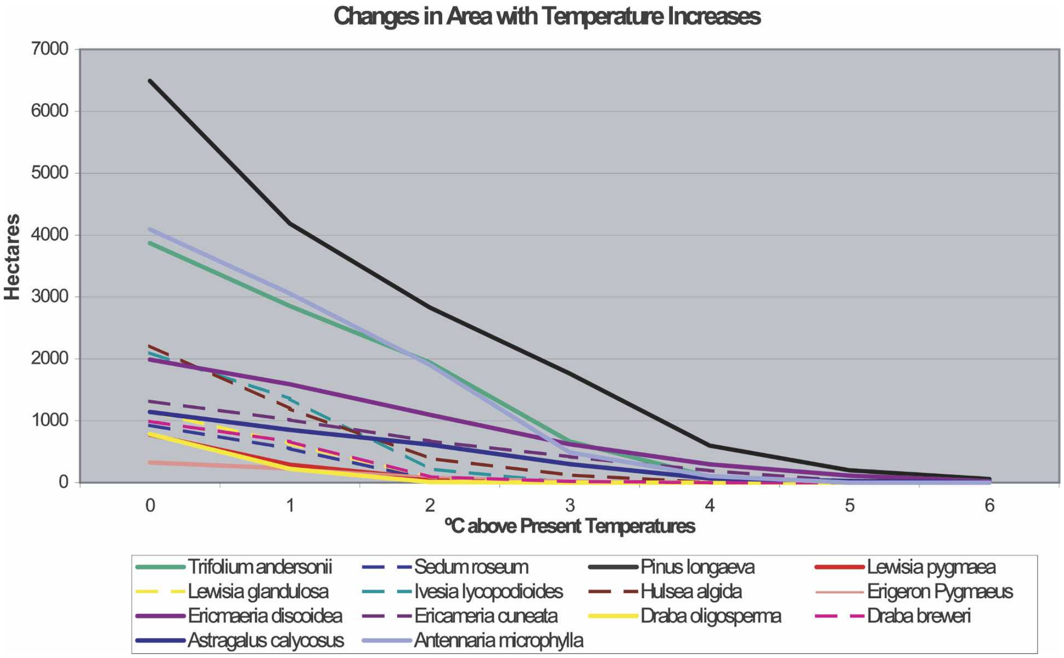


Figure 11. Graphs of changes in area for 14 modeled alpine and subalpine species. All species show a decrease in area as temperatures increase, with 10 expected to become extinct in the central White Mountains if temperatures increase by 6°C.

Mountains, Sweetwater Mountains immediately to the north, and a restricted area around a single summit in the Klamath Range. *Ranunculus eschscholtzii* is restricted to specialized environments within the alpine fellfields. It grows at the base of late-melting snow banks on north-facing slopes. Many climate models predict reduced snowpack and earlier snowmelt as a result of climate change (Leung and Ghan 1999; Snyder et al. 2002; Hayhoe et al. 2004; Snyder et al. 2004; Snyder and Sloan 2005; Bell and Sloan 2006), further shrinking *R. escholtzii* potential habitats. Due to the limited environments of these four species, they were not present in enough field sites to be included in our analyses but have a more elevated risk of extinction due to climate change than species modeled in this study.

4.1. Species–environment relationships and climate change

The CCA analysis provided a rich understanding of current species–environment relationships that can be used to predict potential range shifts with climate change. CCA axis 1, the fundamental temperature–moisture gradient, placed species within their proper elevational ranges (see Figure 5) and also predicted local aspect effects driven by insolation. Nearly all species had their lowest range limits on north-facing slopes and highest range limits on south-facing slopes due to the differences in insolation, and therefore temperature, on the different aspects. Each megajoule per meters squared of equinox (21 March) insolation had the same effect as reducing elevation by approximately 30 m. The full range of equinox insolation (EQsun) values from a steep north-facing slope to a steep south-facing slope produces the equivalent of a ~450-m elevational shift (a difference of 15 MJ m^{-2}). Furthermore, each additional megajoule per meters squared along the EQsun gradient increases average local temperature by about 0.2°C, resulting in a 3°C temperature difference between north- and south-facing slopes. These axis 1 elevation–insolation relationships are similar to CCA analyses performed by Guisan et al. (Guisan et al. 1999) and by Guisan and Theurillat (Guisan and Theurillat 2000), giving confidence that relationships with elevation provide a solid foundation for simulating warming or cooling, and that spatial shifts in the current environmental envelopes include finescale range shifts across local insolation gradients. Manipulating elevation also simulates changes in precipitation, but a change to warmer temperatures also corresponds to a change toward drier conditions, a situation tentatively predicted by the Houghton et al. (Houghton et al. 2001), and within the range of predictions made by multiple regional climate models (Bell et al. 2004; Snyder et al. 2004; Snyder and Sloan 2005).

The geologic substrate (axis 2, Figure 3) influences many species, reflecting varying amounts of edaphic endemism, and acting as local barriers to range shifts. The strong loading of topographic position on axis 2 suggests that expressions of geologic factors were higher on ridgetops than on slopes and canyon bottoms, and may reflect an erosion/deposition gradient. Meadows and valley surface soils are a more homogenous mix of foreign and local sediments and rocks, compared to the rocky, locally derived surface geology on ridges. The higher-order axes served to further differentiate some species by elucidating topographic conditions on substrate-specific relationships, such as the restriction of *Pinus longaeva* to north-facing slopes on granitoids.

4.2. Dynamics of range shifts

These models are essentially static—the current environmental envelopes of species were mapped, followed by the same envelopes shifted to higher elevations. Species ranges, however, are highly dynamic at all time scales, and ecological inertia and potential migration rates need to be considered (LaMarche and Mooney 1967; Peters and Darling 1985; Hengveld 1990; Holtmeier 1994). These mesoscale and finescale predictions do not account for the "ecological inertia" in species distributions. *Pinus longaeva* can live for 4000+ yr (Schulman 1954; Schulman 1958) and requires decades to mature. It would likely take several hundreds, perhaps thousands, of years to die back at lower elevations. Because climate change is not a smooth, linear shift to warmer temperatures, the lower-elevation populations could linger for several generations if individuals manage to reproduce and establish new recruits during colder periods. In past timberline descents, some *P. longaeva* individuals survived several hundred years after environmental change began to impact the timberline (LaMarche and Mooney 1967). *Pinus flexilis* has a somewhat shorter lifespan (1000+ yr) and likely would have slightly less inertia to overcome. However, seedlings may establish in new areas rather rapidly because seed-caching birds such as Clark's nutcrackers and pinyon jays disperse seeds, the prevalent mode of conifer migrations across the Great Basin over the last 8000 yr (Wells 1983). *P. monophylla* and *Juniperus osteosperma* live 300–500 yr, and these species are also dispersed by many of the same birds, potentially giving them rapid establishment rates, but may still require hundreds of years to die back at lower elevations. Therefore, upper-elevational limits are likely to shift more rapidly in response to changing climates, but the lower limits of a species will probably take considerably longer to adjust to new climatic conditions.

Species with wind-dispersed seeds, such as *Artemisia*, are likely to have few problems with dispersal rates and would be expected to migrate to new sites rapidly. Shrubs and perennial forbs with lifespans on the order of decades (Mozingo 1987) may rapidly respond to change, quickly establishing new sites, and abandoning warmer, low-elevation sites. Many alpine forbs only infrequently reproduce sexually (Spira 1991) and may have difficulty responding to rapid environmental change. Weedy annuals (rare in the White Mountains at present) may respond most rapidly of all, potentially resulting in increased numbers and densities, possibly at the expense of existing species. The amount of time required for these species' distributions to equilibrate into the ranges predicted here varies by orders of magnitude by species, from possibly thousands of years for some of the tree species, to a few years for weedy annuals. The differences in ecological inertia may result in new, transitory associations, as some species such as *P. longaeva* remain at low-elevation sites due to slow dieback rates and local refugia, while other species like *P. monophylla* and *J. osteosperma* rapidly migrate upslope. This combination of bristlecone–pinyon–juniper forest is currently very rare in the White Mountains but could become more commonplace as temperatures increase.

No species will make a uniform march upslope. Rather, the high-elevation outposts of all species may be the most important foci for uphill migrations. As the areas around them become more suitable, a species can spread out from local pockets of south-facing slopes across more aspects. Range shifts may then take the form of spreading foci, filling in newly suitable habitat, but die back during droughts, or cold intervals at upper-range extremes may delay the progress of upward invasion (St. Andre et al. 1965). Rare but severe events could be the ultimate driver of species range shifts. Shifts in precipitation amount and patterns may lead to more frequent and severe droughts resulting in increased plant mortality and dieback and retreat from any upslope migrations previously made (Brubaker 1986; Holtmeier 1994; Lloyd and Graumlich 1997; Allen and Breshears 1998; Breshears et al. 2005). The dispersal and establishment of new recruits would be temporarily arrested, and mortality of established species would increase for the duration of the drought. This pattern would result in an erratic series of advances and retreats, as new sites become established, only to die back after a colder interval. However, the net result of the oscillating vegetation advances will be gradual movement to higher elevations as new colonies become established and some individuals from those colonies survive to maturity.

Fire is an additional force driving range shifts that is expected to become more frequent as droughts and other extreme weather events increase in intensity and frequency. Fire kills many species outright, allowing fire-adapted species to thrive immediately after a conflagration. Following a fire, the eventual succession of species composition may lead to a different plant community than originally occupied the site. The incidence and duration of large fires and the length of the wildfire season have all increased since the 1980s in the western United States, primarily due to increased temperatures, reduced winter precipitation, earlier spring snowmelt, and longer summer dry seasons (Westerling et al. 2006). Increased fire frequency may, in turn, increase the rate of vegetation change by removing old, established vegetation and providing opportunities for new species (Overpeck et al. 1990). Extreme events such as droughts and heat waves are expected to increase in both frequency, duration, and magnitude, which could lead to increased fire activity (Bell et al. 2004; Diffenbaugh 2005b; Diffenbaugh et al. 2005; Bell and Sloan 2006). The impacts of changing fire frequency will be most important at low and intermediate elevations; at the higher elevations within the study area, modest amounts of biomass fuel and lower partial pressures of atmospheric oxygen will continue to disfavor widespread burning.

Other controls on species distributions besides topographic and geologic influences are indirectly linked to climate change. Interspecies interactions may become altered by climate change, or modify the species distributions from those predicted here (Peters and Darling 1985). For example, *P. longaeva* seems unable to compete with *Artemisia*, currently growing only where *Artemisia* is sparse or absent (Wright and Mooney 1965; LaMarche 1973). If *Artemisia* becomes established where *P. longaeva* is expected to become dominant, *Artemisia* would likely inhibit *P. longaeva* seedlings from successfully reaching maturity. There has been a downslope expansion of *P. monophylla* in much of the Great Basin, tied to grazing pressures that reduced competitively dominant grasses (Blackburn and Tueller 1970). It is uncertain what effect warmer temperatures will have on that migration—it may allow the grasses to grow faster and more dense, effectively halting *P. monophylla*. Alternatively, that downslope migration may halt simply due to the warmer temperatures. Warmer temperatures, CO_2 fertilization, and/or nitrogen deposition (the latter two a direct result of burning of fossil fuels) all have been suggested as causes for observed increases in density and growth rates of *P. longaeva*, *P. monophylla*, and *Juniperus osteosperma* in the last 150 yr (LaMarche 1973; LaMarche et al. 1984; Koniak 1986; Innes 1991). If some species are stressed or lost from areas, the vacant habitat may be filled with a variety of rapidly dispersing species in the short term, which may then sort out according to competitive abilities. Due to the complexity of interspecies interactions, they are not considered in this study—each species is allowed to migrate independently of all other species.

These models present potential outcomes to warmer temperatures. However, elevated atmospheric CO_2 concentrations are also likely to have a significant impact on plant species distributions. Elevated CO_2 concentrations increase photosynthetic and water-use efficiencies, leading regional climate models tied to ecosystem-scale vegetation models to predict high ecosystem sensitivity to elevated CO_2. These models show shifts of woody vegetation types replacing less woody vegetation types and shifts to biomes that are more suited to warmer and drier environments (Diffenbaugh et al. 2003; Diffenbaugh 2005a; Diffenbaugh 2005b). These impacts would favor shrubs over forbs, and trees over shrubs. Perhaps coincidentally, although CO_2 was not incorporated into the CCA models used in this study, this research shows subalpine trees and *Artemisia* moving upslope at the expense of the alpine fell-fields.

Changes in the vegetation will resonate among all other life forms in the White

Mountains. Rapid plant range shifts may have consequences for host plant-specific animals, such as insects. The greatly reduced ranges and possible extinctions of the highest alpine species could have drastic consequences for insects dependent on those species. A variety of animals would be significantly impacted by the dramatic changes in ecosystem function that will undoubtedly accompany replacement of woodlands with shrublands at lower elevations, replacement of shrublands with woodlands at higher elevations, and the invasion of alpine fell-fields by shrubs.

Species with broad elevational tolerances (e.g., *Pinus monophylla*) have greater overlap between current conditions and predicted future distributions, whereas species with narrower tolerances (e.g., *Pinus longaeva*) have the least overlap, as indicated in Figure 12. Inasmuch as axis 1 is the effective elevational gradient, species with greater axis 1 tolerances exist over broader elevation ranges, and therefore have greater overlap between their distributions modeled under current and projected warmer conditions. These species might be under less danger of local extinction due to their ability to survive a wider range of environments. According to the work of Peters and Darling (Peters and Darling 1985), narrow distributions were an indication that a species might be particularly vulnerable to climate change. A species with a widespread distribution will have greater overlap between current and future distributions. As a result, rapid upslope migration is less critical for the survival of that species. Species with little overlap may need to rapidly migrate upslope, as large proportions of their current ranges become unsuitable, potentially leaving unsustainably small numbers of individuals in habitats that overlap the current and future distributions. Those plants failing to track with the rate of climate change risk not having a sustainable population to expand from when (or if) the climate stabilizes at a warmer temperature. If those species with large overlaps are not able to track upslope at the rate climate changes, their larger overlap populations have more individuals for seed production, and therefore greater opportunities to establish populations in new areas.

5. Conclusions

Whereas there is consensus among scientists that global temperatures will increase, many climate change models show that the White Mountains region will have the same, or slightly less precipitation, although there is greater uncertainty in precipitation predictions (Houghton et al. 2001; Snyder and Sloan 2005; among others). This study does not separate temperature and precipitation effects. Instead, it assumes warmer temperatures, and slightly less precipitation—the same impacts as a lowering of elevation. However, different results may occur with a wetter or significantly drier future climate. For these changes, separate and very detailed temperature and precipitation maps would be needed as independent input variables, which could be modified separately for different climate models. For completeness, the impacts of a more variable climate with more frequent and severe extreme weather should be considered. For example, frequent long-term droughts may affect species differently, and their durations may impact the survivability of species that, in these models, are expected to survive only tenuously, such as many alpine species. This paper presents an initial estimate of the impacts of warmer

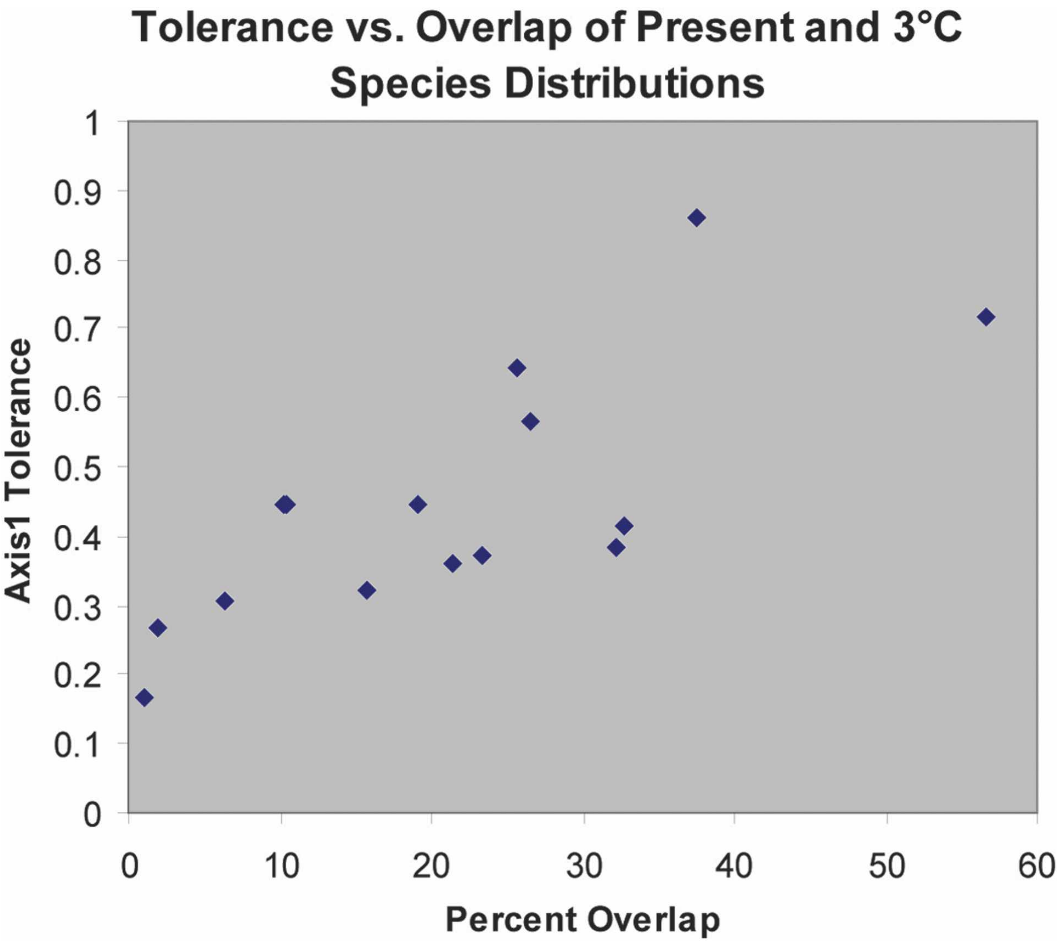


Figure 12. Graph of species' tolerances along axis 1 vs percent overlap between present and future distributions after temperatures rise by 3°C. Because axis 1 represents the effective elevational gradient (see Figure 3), the vertical axis represents the elevational ranges of species. The greater the elevational tolerance a species has, the greater area of overlap between its present distribution and its distribution in a 3°C warmer climate.

climate on vegetation species; additional study is required to understand the impacts of different climate variations.

The types of species shifts predicted here have occurred in the past. Remnant snags and logs of *Pinus longaeva* above current timberline have been dated and surveyed in other studies. These investigations show that the paleotimberline in the White Mountains during the Altithermal, about 6000 BP, was approximately 150 m above current timberline when temperatures were about 3.5°C warmer (LaMarche and Mooney 1967; LaMarche 1973). These models show similar shifts for the same temperature difference. Despite the simplicity of the climate model used, this study demonstrates the utility of modeling species-specific responses to environmental change, and impacts of topography and geology as well as climate on species' distributions at very fine spatial resolutions.

The White Mountains, like the rest of the ranges in the Great Basin, currently represent a remnant island of montane and alpine habitats that were continuous throughout the Great Basin lowlands during the cooler periods of the Pleistocene (Wells 1983). As a result of warming during the last 10 000 yr, these habitats are now restricted to the middle to high elevations, separated by desert valleys. Hence adjacent ranges are beyond reach from each other, effectively making them island ecosystems (Brown 1978; Harper et al. 1978). There is no expectation of immigration of individuals from adjacent ranges to bolster plant species' populations, with the possible exception of the lowest-elevation desert species. This study shows how warmer temperatures may affect this island biogeography. Species move upslope, subject to edaphic and topographic conditions, resulting in a reduction of habitable areas, and smaller populations. Species that currently grow at the highest elevations do not have additional upslope regions to populate and, as a result, may become extinct in this range. The effects of reduced biodiversity and shifting habitats will impact other life forms, affecting the numbers and varieties of insects, birds, and mammals within the range.

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