Forecasting Alpine Vegetation Change Using Repeat Sampling and a Novel Modeling Approach

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Abstract Global change affects alpine ecosystems by, among many effects, by altering plant distributions and community composition. However, forecasting alpine vegetation change is challenged by a scarcity of studies observing change in fixed plots spanning decadal-time scales. We present in this article a probabilistic modeling approach that forecasts vegetation change on Niwot Ridge, CO using plant abundance data collected from marked plots established in 1971 and resampled in 1991 and 2001. Assuming future change can be inferred from past change, we extrapolate change for 100 years from 1971 and correlate trends for each plant community with time series environmental data (1971–2001). Models predict a decreased extent of Snowbed vegetation and an increased extent of Shrub Tundra by 2071. Mean annual maximum temperature and nitrogen deposition were the primary a posteriori correlates of plant community change. This modeling effort is useful for generating hypotheses of future vegetation change that can be tested with future sampling efforts.

Keywords Probabilistic modeling · Alpine vegetation change · Snowbeds · Climate warming · Plant community change

INTRODUCTION

Experimental manipulations of temperature (Walker et al. 2006), snow (Wipf and Rixen 2010), and nutrients (Suding et al. 2006) as well as resampling of historic surveys (Hedenås et al. 2011 [this issue]) suggest that alpine tundra is sensitive to environmental change. High mountain landscapes are forecast to undergo among the most dramatic changes in climate over the next century (Körner 1999), and several studies of observed changes in the European

(e.g., Cannone et al. 2007), Fennoscandian (e.g., Hedenås et al. 2011 [this issue]) and North American alpine (e.g., Crimmins et al. 2011) plant communities suggest such forecasts are on track for many alpine areas. Such change has the potential to alter a range of factors including regional biodiversity and land–atmosphere feedbacks such as radiative forcing potential (Costa and Wilson 2000). Some studies suggest that alpine systems are likely indicators of change in lower elevation ecosystems and stress an urgency for further understanding ecosystem dynamics in these systems (Pauli et al. 1999). To date, however, few studies have described decadal time scale changes in alpine ecosystem structure and function (sensu Schultz and Mooney 1993) and even fewer studies forecast future states of alpine ecosystems (sensu Körner 1999).

Alpine ecosystems represent some of the most marginal ecosystems of the global system (Körner 1995). The biophysical factors typically associated with high altitude systems, combined with wide topographic variation over short distances create a spatiotemporally heterogeneous and dynamic environment relative to other ecosystems (Körner 1999). For example, high relief causes extreme variation in both temperature and precipitation over short geographical distances resulting in a high degree of specialization and adaptation in plant species (Körner 1999). Species must withstand wide fluctuations in both temperature and precipitation, and some plant communities in physiologically extreme environments can be climatically decoupled from others nearby (Körner 1999). Because alpine plant species are highly adapted to localized micro-environments, they are predicted to be responsive to climate change (Lesica and Steele 1996). Changes in these micro-environments may result in reduced survival due directly as a result of events such as slope instability, wind/ice damage (Körner 1999) or herbivory (Olofsson et al.

2009). In contrast, Scherrer and Körner (2011) argue that this adaptation to the many alpine micro-environments may result in resilience to change. Plants may respond by either increasing or decreasing carbon uptake (e.g., Volk et al. 2011) and/or altering vegetative and reproductive capacity (e.g., Dunne et al. 2003). Thus, some alpine plant communities have the capacity to respond to environmental perturbation, such as warming nonlinearly, especially if they are close to physiological thresholds such as their temperature tolerance (Pauli et al. 1999).

Understanding and determining change in alpine ecosystems is challenging—largely due to the bioclimatic and landscape heterogeneity of these environments. Local climate stations may not adequately measure all conditions experienced along sharp elevation gradients (Greenland and Losleben 2001), and only recently has the thermo-environment of plant communities in alpine ecosystems been modeled successfully using remote-sensing techniques (Scherrer and Körner 2010). Despite these challenges, several patterns of climatically driven change among alpine ecosystems have emerged. These include upward elevational range shifts, such as an advance of treeline (e.g., Kullman 2010; Van Bogaert et al. 2011), increases in the cover of shrub species (Pauli et al. 2007; Erschhammer et al. 2009; Hallinger et al. 2010), and downward elevational range shifts of some species in response to changes in water availability (Crimmens et al. 2011). At elevations greater than 2500 m above sea level, and in more exposed areas, species richness also appears to have decreased because of reduced water availability associated with warmer temperatures (Cannone et al. 2007).

As with many other alpine ecosystems, the alpine tundra at Niwot Ridge, CO is structured by the combined interactions of topography, wind, and snow (Ebert-May and Webber 1982; Walker et al. 1994). Sparsely vegetated Fell-field and Dry Meadow plant communities are typically found in exposed locations that experience cold winter temperatures, strong winds, and low snow cover. Topographically sheltered areas have deeper snow cover and more diverse meadow and Shrub Tundra communities (Komárková and Webber 1978). In these relatively sheltered locations, the timing of snowmelt and duration of snow cover are the primary determinants of plant community composition (Ebert-May 1973; Walker et al. 1994). Owing to the close proximity of Denver, Niwot Ridge has received substantial nitrogen (N) deposition with few other anthropogenic impacts such as changes in land use (Bowman et al. 2006). A modest increase in Dry Meadow biomass appears to have resulted from the combined impacts of ammonium (NH_4^+) and nitrate (NO_3^-) deposition (Bowman et al. 2006). While it is unclear what the impact

increased N-deposition has had on vegetation composition, species removal, N fertilization, altered snow depth, and warming result in profound differences in ecosystem function in manipulative experiments (Williams et al. 1998; Suding et al. 2006; Walker et al. 2006; Volk et al. 2011;) all of which together with results from modeling studies (e.g., Litaor et al. 2008) illustrate the sensitivity of alpine tundra on Niwot Ridge to global change.

For many alpine ecosystems, long-term datasets are lacking. In the absence of long-term monitoring, rescuing data, revisiting, and resampling historic research sites may be the only means of detecting decadal-scale change in tundra plant communities (Callaghan et al. 2011 [this issue]). Because of the lack of sustained monitoring efforts, forecasting vegetation scenarios are difficult and prone to unacceptable levels of uncertainty (Finzi et al. 2011). Although a variety of vegetation models have been developed (see review by Woodward and Lomas 2004) incorporating both correlative and mechanistic approaches (e.g., Voinov et al. 2004), application of these are problematic for alpine ecosystems for a few key reasons. Because alpine communities can be climatically decoupled from those nearby (Körner 1999), parameterizing both correlative and mechanistic models may be difficult if the specific environmental variables at the plot level are not described accurately through space and time. Correlative approaches depend on the relationship between vegetation and environmental variables such as temperature and precipitation (e.g., Grant and French 1990), whereas mechanistic approaches rely on the fundamental understanding of bio-physical processes and relationships to derive predictive models of change (e.g., Epstein et al. 2007). In addition, novel system states and tipping points are hard to detect with both these modeling approaches because new environmental conditions are likely to be outside levels for which the models were parameterized (Woodward and Lomas 2004).

In this article, we present a novel probabilistic modeling approach to generate hypotheses of plant community change on Niwot Ridge using data from repeat sampling of marked vegetation plots spanning three decades (1971–2001). Model simulations were employed to predict which plant communities are increasing and which are decreasing. Using these rates of change, future plant community change on Niwot Ridge was forecast for 2071 based on the assumption that past change is likely to be indicative of future change. This approach differs from other approaches in that species cover and abundance are the only data used as model inputs. Our model results represent hypotheses that can be tested with future resampling or utilized to refine future monitoring efforts.

MATERIALS AND METHODS

Study Site

Plant community data used for this study were collected in the Saddle of Niwot Ridge, CO, which is one of the oldest continuing alpine ecological study locations in North America (Marr 1961). It was the U.S. alpine site for the International Biological Programme (IBP) Tundra Biome Project from 1971 to 1974 (see Tieszen 1978), and has been a Long-Term Ecological Research (LTER) site since 1980 (Bowman and Seastedt 2001). It is located at 40°3'20"N 105°35'22"W (approximately 3000 m above sea level, Fig. 1). Niwot Ridge is home to an excellent example of mid-latitude alpine tundra in North America. The Ridge is free of direct anthropogenic disturbance (apart from sheep grazing in summer prior to 1948) and is geomorphically an old well-weathered Pleistocene surface with acid substrates (Marr 1961). It has a mean annual air temperature of -4.1°C and a mean annual precipitation of 993 mm (for the period 1961–1990, Greenland and Losleben 2001). In 1971 and as a contribution to the IBP,

30 sites were established across the range of vegetation occurring in the Saddle. In a Master's thesis completed by Ebert-May (1973), these plots were utilized to examine the relationship between plant communities and a range of environmental parameters. Exposure and topography were found to be the dominant drivers of vegetation structure. Fell-field and Dry Meadow vegetation occupy exposed landscapes where wind prevents snowbanks from forming, exposing vegetation to low temperatures in winter. Where snow accumulates, the timing of snowmelt was found to be the primary control of plant communities, with Moist Meadow vegetation being located in areas where spring snowmelt is the earliest followed by Wet Meadow, Shrub Tundra, and Snowbed vegetation along a complex moisture and snowmelt gradient.

Vegetation Field Sampling and Classification

Vascular plant species cover and abundance were estimated using a method established elsewhere by Webber (1971) for a number of arctic sites. Each site was 1×10 m in size and consisted of ten contiguous 1 m^2 plots. Within

Fig. 1 Topographic map of Niwot Ridge, CO, USA, along with the location of the “the Saddle” (rectangular inset labeled “IBP” along the crest of the east west trending Niwot Ridge) where plant

community sites used in this study are located. Contours lines are in feet above sea level. From Ebert-May (1973)

each plot, community composition was measured by visually estimating species percentage cover within a 10 cm × 100 cm strip along one edge of each 1 m² plot. Species presence was also recorded for species that occurred outside the 10 cm × 100 cm strip but within the plot. Sites were marked with permanent stakes and resampled using the same sampling methods used in 1971 in 1991 and 2001, 20 and 30 years respectively, after site establishment. All data were collected in early-to-early July to mid-August of the sampling years.

For a given sampling date, estimates for the species cover and the presence were standardized by dividing values for each species by the total cover and the presence for each plot and multiplying by 100. Relative cover and relative presence within each plot were then summed and divided by 2 to obtain an importance value for each species in a plot (Webber 1971). A classification of plant communities in 1971 was derived from a hierarchical cluster analysis performed in PCORD version 5.10 using Euclidian distance measure and Ward's linkage method. This classification served as a baseline from which plot-level change in plant community type from one sampling period to another was determined using Pearson's correlation in PCORD. Plant communities for 1991 and 2001 plots were assigned according to the classification of the 1971 plot with which they best correlated. Where a plot sampled in 1991 or 2001 remained correlated with a 1971 plot in the same plant community, no change in plant community was noted. However, where a plot became more highly correlated with a 1971 plot from a different plant community, the direction of change was noted. It was assumed that no new plant communities had appeared since 1971, although these are predicted with climate warming (Wookey et al. 2009). The relatively high Pearson's correlation coefficients suggest this assumption was valid. The probability of a given plot at a respective sampling time (1991 or 2001) changing from one plant community to another within a normalized time period between sampling times was used as input to the probability model described below.

Model Development

The modeling approach used is similar to that used in probabilistic population models (e.g., Callaghan 1976), except that instead of modeling transitions from one life history or demographic stage to another (e.g., sub-adult to breeding adult), we modeled the probability a given plot changing from one plant community to another between sampling times (Fig. 2). The software Stella (v9.0.3 ISEE Systems) was employed to create the models (Costanza and Voinov 2001) using the following equation to simulate the state of each plant community at each iteration:

Fig. 2 A two-dimensional ecological sequence diagram (sensu Gams 1961) showing the inferred positions of the principal plant communities of the Niwot Ridge Saddle within the principal complex environmental gradients. This conceptual framework, adapted from Webber et al. (1976), represents the transition probabilities of plots from one plant community to another using output from model 1 of this study. Values represent the probability for any one plot in a given model iteration (year) transitioning from one plant community to another based on the difference between individual plot classification in 1971 and its classification in 1991

$$\frac{dV_i}{dt} = V_i(t-1) + C_{ji} \cdot C_{ki} \dots C_{ni} - C_{ij} \cdot C_{ik} \dots C_{in}$$

where V_i is the number of plots classified for plant community $i, j, k, \dots$ at time t , C_{ji} is the probability of one plot from V_i transitioning to V_j at $t+1$, and C_{ij} is the probability of one plot from V_j transitioning to V_i at time $t+1$. Thus, the number of plots in each plant community for a given iteration (time step) is a function of the number of plots at the end of the prior iteration plus the exchange among the other five plant communities at that iteration.

We formulated four models to simulate changes among plant communities. The first model was based on the probabilities of change among plots of different vegetation types observed between 1971 and 1991. For example, in 1971 there were 56 Fell-field and 44 Dry Meadow plots (Table 1). In 1991, ten Fell-field plots correlated with plots classified as Dry Meadow in 1971 and four Dry Meadow plots correlated with plots classified as Fell-field in 1971. Thus, in 1991 there were 62 Fell-field plots and 38 Dry Meadow plots (Table 1) and the probability for any given Fell-field plot transitioning to Dry Meadow using the 1971–1991 rate at any given year is approximately 0.2 and the probability of any given Dry Meadow plot transitioning

Table 1 Summary of the distribution of plots among respective plant communities for each sampling date. Characteristic species are according to Ebert-May (1973)

Plant communities	Characteristic species	1971	1991	2001
Fell-field	<i>Trifolium dasyphyllum</i> <i>Silene acaulis</i> <i>Carex rupestris</i>	56	62	58
Dry Meadow	<i>Kobresia myosuroides</i> <i>Selaginella densa</i>	44	38	43
Moist Meadow	<i>Acomostylis rossii</i> <i>Deschamsia caespitosa</i>	69	70	72
Snowbed	<i>Sibbaldia procumbens</i> <i>Carex pyrenaica</i>	56	41	30
Wet Meadow	<i>Caltha leptosepala</i> <i>Carex scopulorum</i>	55	62	67
Shrub Tundra	<i>Salix planifolia</i>	20	27	30
		300	300	300

to Fell-field is approximately 0.5 (Table 2). At every iteration, this probability was compared against a randomly generated number resulting in a transition if the random number was less than the probability value, thereby allowing for confidence intervals to be generated for the forecast change between two time periods. A second model was developed using probabilities of change among plots of different vegetation types observed between 1991 and 2001, and the third between 1971 and 2001. In addition, we formulated a fourth model which used the probabilities of change between 1971 and 1991 for the first 20 iterations, and the probabilities of change observed between 1991 and 2001 for the remaining iterations. Each model iteration (t , $t + 1$, ...) represented 1 year, and we determined 100-year forecasts for each model for 100 iterations from 1971 using a fourth-order Runge–Kutta algorithm to calculate the integral between iterations. To assess the likelihood of nonlinear change, we compared the slope of the mean model output for models 1 and model 2. Forecast rates of change represent the likely change in the presence of a given plant community within the 300 plots making up the 30 monitoring sites established in 1971, not the relative presence of a given plant community on Niwot Ridge, which is outside the scope of this study.

Model Exploration

We used two methods to explore the implication of the model results. First, we correlated mean forecasts of change in each plant community with environmental time series data spanning the sampling period (1971–2001) from EcoTrends (Servilla et al. 2008). These included mean annual temperature, mean annual maximum and minimum

Table 2 Probabilities of a plot in a given plant community transitioning to another community during a specified sampling interval

Initial state	Final state	Rates		
		1971–1991	1991–2001	1971–2001
Fell-field	Dry Meadow	0.2	0.6	0.167
Dry Meadow	Fell-field	0.5	0.2	0.03
Moist Meadow	Snowbed	0.05	0.3	0.067
Moist Meadow	Wet Meadow	0.1	–	0.067
Moist Meadow	Shrub Tundra	0.05	–	0.03
Snowbed	Dry Meadow	–	0.1	–
Snowbed	Moist Meadow	0.2	0.4	0.167
Snowbed	Wet Meadow	0.5	1.0	0.43
Snowbed	Shrub Tundra	0.35	0.2	0.23
Wet Meadow	Moist Meadow	0.05	0.1	0.03
Wet Meadow	Snowbed	0.15	0.3	0.167
Wet Meadow	Shrub Tundra	0.15	0.100	0.13
Shrub Tundra	Snowbed	0.1	–	0.033
Shrub Tundra	Wet Meadow	0.1	–	–

“Initial” represents the classification of a given plot at the beginning of a sampling period and “final” represents the classification of the plot at the end of a sampling period

temperature, annual ammonium and calcium cation wet deposition, and annual nitrate deposition. In addition, mean annual precipitation, drought severity index, sulfate wet deposition, chlorine anion wet deposition, and pH were also correlated; however, these were not significant and are not reported here. Second, we used 1946- and 2002-georeferenced aerial photographs of Niwot Ridge (Manley et al. 2009) in a Geographic Information System (ArcGIS V9.2) to determine whether changes predicted from the model were notable at the landscape scale. Site coordinates from a hand held Garmin GPS (± 4 m horizontal accuracy 90% of the time) collected in 2010 were imported into a geographic information system and viewed as a layer on the aerial imagery. Locations of Dry Meadow, Shrub Tundra, and Snowbed vegetation were used for qualitatively assessing changes in these land cover types between the aerial photos at a scale of 1:350.

RESULTS

Classification and Correlations

Hierarchical classification of the 300 plot data collected in 1971 resulted in a very similar classification to that

previously described by Ebert-May (1973). Six plant communities were identified: Fell-field, Dry Meadow, Moist Meadow, Snowbed, Wet Meadow, and Shrub Tundra (Fig. 3, Table 1). The majority of plots resampled in 1991 and 2001 correlated well ($R^2 > 0.9$) with the 1971 classification given to the same plot, and although there were some plots with correlation coefficients lower than 0.9, all were above 0.5, suggesting that the plant community classification derived from 1971 field data is valid and

adequate for describing plant communities present in 1991 and 2001.

Model Simulations

Of the six plant communities, the driest types (Fell-field and Dry Meadow) were the only types to show wide variation between the four different models (Fig. 4a, b) as a result of different patterns of change detected between

Fig. 3 Photographs of the six plant communities documented at Niwot Ridge, CO. Photographs taken in July 2001 (*Top left to right*: Fell-field, Dry Meadow, Moist Meadow, *bottom left to right*: Snowbed, Wet Meadow, and Shrub Tundra)

Fig. 4 Model forecasts of the proportion of plots (relative to the initial counts in 1971) in different alpine plant communities at Niwot Ridge, CO. *Solid lines* represent the mean of 100 simulations over 100 iterations and *dashed lines* represent 95% confidence intervals. Four different model simulations are represented by *red* (rate of

change between 1971 and 1991), *blue* (rate of change between 1991 and 2001), *green* (rate of change between 1971 and 2001), and *orange* lines (a model which combines the 1971–1991 rate of change and the rate of change between 1991 and 2001)

resampling periods. Between 1971 and 1991, more Dry Meadow plots transitioned to Fell-field plots than Fell-field plots transitioned to Dry Meadow, whereas, between 1991 and 2001, the opposite was true. Thus, the 100-year forecasts for Fell-field varied between a forecast of 80 and 60% loss and gain, respectively, whereas Dry Meadow varied between a forecast of 75 and 120% loss and gain, respectively (Fig. 4a, b). Three of the four models predicted an overall increase in Dry Meadow at the expense of Fell-field. All plots classified as Fell-field in 1971 remained as Fell-field or shifted to becoming Dry Meadow in 1991 and 2001. Only one Snowbed plot transitioned to Dry Meadow

between 1991 and 2001. There was no other transition recorded for plots classified as Dry Meadow, suggesting Dry Meadow and Fell-field plant communities are relatively decoupled from other plant communities and have been relatively stable over time.

Moist Meadow vegetation also appeared to be relatively stable over time with the mean 100 year forecasts for this plant community varying between an 8% loss to a 20% gain among the four models (Fig. 4c). Forecasts for Snowbed, Wet Meadow, and Shrub Tundra were consistent among all the four models. In addition, the model based on the change between 1991 and 2001 predicts the loss of

Snowbed vegetation as early as 2021 (Fig. 4d). All the four models predicted increases in both Wet Meadow (Fig. 4e) and Shrub Tundra (Fig. 4f). Wet Meadow is forecast to increase between 20 and 50% by 2071 depending on the model, and Shrub Tundra is predicted to increase between 90 and 200%.

Correlation with Environmental Variables

Almost all the model simulations were well correlated with environmental data as reported in EcoTrends (Table 3) except for Fell-field and Dry Meadow vegetations in the fourth model (combined model including both for 1971–1991 and 1991–2001). These had the highest correlations with wet ammonia deposition (Fell-field $R^2 = 0.1$, $p < 0.05$, Dry Meadow $R^2 = 0.14$, $p < 0.05$). Mean maximum temperature had the highest correlations with all model runs ($R^2 = 0.5$, $p < 0.05$) followed by mean temperature

(R^2 approximately 0.45, $p < 0.05$), and ammonia wet deposition (R^2 approximately 0.31, $p < 0.05$).

Comparison with Air Photo Time Series

Examination of vegetation change derived from aerial photography suggests Moist Meadow, Wet Meadow, and Fell-field changed relatively little between 1946 and 2002. Similarly, Dry Meadow appears to be relatively stable between the 1946 and 2002 air photos (Fig. 5). However, there appears to be a decrease of Snowbed vegetation in 2002 compared to 1946. The most obvious change was the dramatic expansion of Shrub Tundra between 1946 and 2002. Although these images were taken at different times in the growing season (Fig. 5), the presence of shrubs in the later images is a categorical evidence of this change. One other caveat to note, however, is that domestic sheep grazing was a regular occurrence during the summer

Table 3 Correlation coefficients (R^2) correlations between model simulations (mean of 100 runs) and environmental variables

Model	Period	Plant communities	Mean T	Max T	Min T	NO ₃ [−]	NH ₄ ⁺	Ca ²⁺
1	1971–1991	Fell-field	0.46	0.49	0.28	0.18	0.3	0.16
		Dry Meadow	0.44	0.49	0.28	0.17	0.3	0.15
		Moist Meadow	0.49	0.53	0.32	0.18	0.33	0.18
		Snowbed	0.47	0.5	0.28	0.18	0.31	0.15
		Wet Meadow	0.45	0.5	0.28	0.18	0.31	0.15
		Shrub Tundra	0.45	0.5	0.28	0.18	0.31	0.15
2	1991–2001	Fell-field	0.44	0.49	0.26	0.18	0.31	0.16
		Dry Meadow	0.45	0.49	0.28	0.18	0.31	0.16
		Moist Meadow	0.45	0.5	0.28	0.18	0.31	0.15
		Snowbed	0.45	0.5	0.28	0.18	0.31	0.16
		Wet Meadow	0.45	0.5	0.28	0.18	0.32	0.16
		Shrub Tundra	0.45	0.5	0.28	0.18	0.31	0.16
3	1971–2001	Fell-field	0.46	0.51	0.29	0.19	0.32	0.16
		Dry Meadow	0.45	0.5	0.28	0.19	0.31	0.16
		Moist Meadow	0.31	0.34	0.2	–	0.22	–
		Snowbed	0.44	0.5	0.27	0.18	0.31	0.15
		Wet Meadow	0.46	0.5	0.29	0.18	0.31	0.16
		Shrub Tundra	0.45	0.5	0.28	0.18	0.31	0.15
4	Model 1 for the first 20 iterations	Fell-field	–	–	–	–	0.1	–
		Dry Meadow	–	–	0.06	–	0.14	–
		Moist Meadow	0.43	0.45	0.32	0.13	0.25	0.12
	Model 2 thereafter	Snowbed	0.44	0.48	0.29	0.16	0.29	0.15
		Wet Meadow	0.45	0.48	0.29	0.16	0.29	0.14
		Shrub Tundra	0.45	0.5	0.27	0.19	0.32	0.16

Only significant ($p < 0.05$) correlations are shown and red values indicate negative relationships

Environmental data were obtained from the EcoTrends Project (<http://www.ecotrends.info>) funded by the National Science Foundation and the USDA Agricultural Research Service. Temperature data are from Niwot Ridge (<http://culter.colorado.edu/NWT/>), Climate and Hydrology Database Projects (CLIMDB/HYDRODB) (<http://www.fsl.orst.edu/climdb/>); ecotrends.6073.1 (mean temperature; Mean T); ecotrends.9718.1 (mean maximum T; Max T); ecotrends.7387.1 (mean minimum temperature; Min T). Chemistry data are from National Atmospheric Deposition Program (<http://nadp.sws.uiuc.edu/>); ecotrends.13952.1 (nitrate wet deposition; NO₃[−]); ecotrends.3410.1 (ammonium wet deposition; NH₄⁺); ecotrends.3793.1 (calcium wet deposition Ca²⁺)

Fig. 5 Aerial photograph time series of Niwot Ridge, CO from 1946 (*left*) and 2002 (*right*). The 1946 image was taken in September 1946, and the 2002 image was taken in spring 2002 (Manley et al. 2009).

The scale of the imagery is 1:350 and the *scale bar* and *north arrow* in the *bottom left panel* is applicable to all the images

months until 1948 (Marr 1961); thus, caution must be taken when interpreting change in these images.

DISCUSSION

This study presents a novel modeling approach that appears to be well-suited to generating hypotheses of future vegetation change from decadal time scale repeat sampling of marked sites. While our approach does not include the

adaptive modeling capacity of incorporating exterior climate predictions that otherwise provide mechanistic drivers of change to be derived (e.g., Epstein et al. 2007), the approach is relatively simple, and could be used for refining long-term monitoring efforts. Results from this study suggest, for example, that Snowbed vegetation may not be represented within the study sites in a few decades, and, therefore, increasing the number of Snowbed sites to better understand future change in this plant community may be necessary.

The model's output documented changes similar to those found in other alpine ecosystems worldwide (e.g., Hedenås et al. 2011 [this issue]), but there are several caveats that guide our interpretation of results reported above. The vegetation classification, which underpins the model, was derived from plots chosen to be representative of the Niwot Ridge Saddle vegetation in 1971. Thus, changes predicted by the model are relative to the vegetation present at site initiation and the patterns of change that have occurred at these sites between 1971, 1991, and 2001. Thus, other possible changes in plant communities, including species range shifts, such as the upslope advancement of treeline (e.g., Van Bogaert et al. 2011), may be occurring but are not adequately captured within the modeling framework we have employed. Also, inter-annual variability is common in many alpine and subalpine plant species (e.g., Ebert-May 1976), and results of this study are based on three sampling dates, and we suggest that there could be some level of uncertainty introduced into our analyses because of this. In addition, our modeling approach does not account for any other biotic factors, such as the importance of herbivores, which can be important drivers of vegetation dynamics in alpine ecosystems (Sherrod et al. 2005). For example, the snow-covered communities at Niwot Ridge support both pikas and pocket gophers (Armstrong et al. 2001), and recent evidence suggests that the abundance of a preferred forage plant species of pikas *Acomastylis rossii* is becoming less abundant (M. Williams, pers. comm.). This suggests the potential for a change in trophic interactions could be occurring and that changes in herbivory are driving plant community change (Olofsson et al. 2009; Van Bogaert et al. 2011). Regardless, the approach is relatively simple and focused on the generation of hypotheses of change that can be tested with future monitoring and experimental studies.

Interestingly, model forecasts clearly show a decoupling of dry and wet plant communities. The lack of strong directional change in Dry Meadows and Fell-field is unsurprising. Dry communities, in particular Fell-field, are windswept in winter and despite the long growing season have low productivity, relative to plant communities with deeper later melting snow cover (Walker et al. 1994). Thus, these communities are controlled primarily by factors that do not appear to have changed to the extent that these vegetation types respond. The dominant controls of dry plant communities on Niwot Ridge are wind and evapotranspiration (Walker et al. 2001). Therefore, there is the possibility that under sustained drying, possibly exacerbated by Snowbank loss, dry plant communities may advance downslope into formerly wetter areas. Although such a scenario is counterintuitive to the dominant theme of upslope range expansion of vegetation with climate warming, it is consistent with recent reports of down-slope movement of species in northern California since the

1930s, which appears to be correlated with plant responses to water availability (Crimmens et al. 2011).

The decrease in the prevalence of Snowbed vegetation in the monitoring sites is somewhat expected (Björk and Molau 2007) despite evidence suggesting winter snow-depth has not changed (Litaor et al. 2008). Snowmelt, however, is occurring earlier (Chow 2010). Snow distributions, snow-depth and the timing of melt have long been known to control the distributions of alpine plant species and plant communities at Niwot Ridge and other alpine locations (Körner 1999; Walker et al. 1994, 2001). Alpine snowbeds may be one of the most vulnerable plant communities to climate warming because temperature directly affects a critical tipping point—the freezing point of water, and therefore, the prevalence of snowbanks (Schob et al. 2009) and plant available light. Snow manipulation experiments have shown that the phenology and biomass of many plant species are sensitive to changes in snow depth and distribution (Wipf et al. 2009; Wipf and Rixen 2010). Interestingly, the strongest environmental correlation with the modeled change was an increase in mean maximum temperature, suggesting that long lasting snowbanks are becoming rare which would lead to the loss of Snowbed species.

Increases in Shrub Tundra predicted from our model are similar to trends and long-term observations documented for alpine ecosystems worldwide (Cannone et al. 2007; Erschhammer et al. 2009). This study is, however, one of the first to document such trends for Niwot Ridge. As with the forecast decrease in Snowbed vegetation, an increase in the prevalence of shrubs on Niwot Ridge has been predicted for more than a decade (Williams et al. 1998) and is a well-recognized response to both warming and snow additions in manipulative experiments (Wipf and Rixen 2010). The documented increase in N-deposition could also have catalyzed the prevalence of Shrub Tundra as alpine shrubs have been shown to respond to increased nitrogen availability in fertilization experiments through increased growth and biomass (e.g., Gerdol et al. 2002). This supports other studies suggesting that N-deposition at Niwot Ridge is already a driver of plant community change (Bowman et al. 2006). Herbivory may also explain the increase in shrubs, as this mechanism is well documented in alpine systems (Olofsson et al. 2009).

CONCLUDING REMARKS

Our modeling effort of the plant communities of Niwot Ridge, CO revealed the strong decoupling of dry vegetation types from wetter vegetation types and forecasts suggest the prevalence of Snowbed vegetation will decrease, Shrub Tundra will increase, and that Moist Meadow will change little by 2071. These results should be seen as hypotheses

that can be tested by future resampling efforts and experimental studies. Primarily because of the low sample size of the study site, we did not seek to validate this model by splitting the sample, or by some other method. The ultimate validation of this effort will be the resampling of these plots. This will allow for the testing of these hypotheses, in particular, to establish that Snowbed vegetation is decreasing and Shrub Tundra is increasing. Understanding these patterns has important implications for understanding changes in ecosystem structure and function, particularly, biodiversity, surface energy budgets, and cyclings of water, carbon, and other plant nutrients.

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REFERENCES

- Armstrong, D.M., J.C. Halfpenny, and C.H. Southwick. 2001. Vertebrates. In *Structure and function of an alpine ecosystem*, ed. W.D. Bowman, and T.R. Seastedt, 128–156. New York: Oxford University Press.
- Björk, R.G., and U. Molau. 2007. Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic, and Alpine Research* 39: 34–43.
- Bowman, W.D., J.R. Garner, K. Holland, and M. Wiedermann. 2006. Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: Are we there yet? *Ecological Applications* 16: 1183–1193.
- Bowman, W.D., and T.R. Seastedt. 2001. *Structure and function of an alpine ecosystem: Niwot Ridge, Colorado*. Long-term ecological research network series. New York: Oxford University Press.
- Callaghan, T.V. 1976. Strategies of growth and population dynamics of tundra plants. 3. Growth and population dynamics of *Carex bigelowii* in an alpine environment. *Oikos* 27: 402–413.
- Callaghan, T.V., C.E. Tweedie, and P.J. Webber. 2011. Multi-decadal changes in tundra environments and ecosystems: The International Polar Year Back to the Future project (IPY-BTF). *Ambio*. doi:10.1007/s13280-011-0162-4.
- Cannone, N., S. Sgorbatti, and M. Guglielmin. 2007. Unexpected impacts of climate change on alpine vegetation. *Frontiers in Ecology and Environment* 5: 360–364.
- Chow, D.W. 2010. Changes in the timing of snowmelt and stream flow in Colorado: A response to recent warming. *Journal of Climate Research* 23: 2293–2306.
- Costa, P.M., and C. Wilson. 2000. An equivalence factor between CO₂ avoided emissions and sequestration—description and applications in forestry. *Mitigation and Adaptation Strategies for Global Change* 5: 51–60.
- Costanza, R., and A. Voinov. 2001. Modeling ecological and economic systems with STELLA: Part III. *Ecological Modeling* 143: 1–7.
- Crimmins, S.M., S.Z. Dobrowski, J.A. Greenberg, J.T. Abatzoglou, and A.R. Mynsberge. 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* 331: 324–327.
- Dunne, J.A., J. Harte, and K.J. Taylor. 2003. Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. *Ecological Monographs* 73: 69–86.
- Ebert-May, D. 1973. Models for predicting composition and production of alpine tundra vegetation from Niwot Ridge, Colorado. MS Thesis, University of Colorado, Boulder, CO.
- Ebert-May, D. 1976. The response of alpine tundra vegetation in Colorado to environmental variation. PhD Thesis, University of Colorado, Boulder, CO.
- Ebert-May, D., and P.J. Webber. 1982. Spatial and temporal variation of vegetation and its productivity on Niwot Ridge, Colorado. In *Ecological studies in the Colorado alpine, a festschrift for John W. Marr* (Occasional paper number 37), ed. J. Halfpenny. Boulder: Institute of Arctic and Alpine Research, University of Colorado.
- Epstein, H.E., Q. Yu, J.O. Kaplan, and H. Liscike. 2007. Simulating future changes in arctic and subarctic vegetation. *Computing in Science and Engineering* 9: 12–23.
- Erschhammer, B., T. Kiebach, M. Mallaun, and P. Unterluggauer. 2009. Short-term signals of climate change along an altitudinal gradient in the Southern Alps. *Plant Ecology* 202: 79–89.
- Finzi, A.C., A.T. Austin, E.E. Cleland, S.D. Frey, B.Z. Houlton, and M.D. Wallenstein. 2011. Responses and feedbacks of coupled biogeochemical cycles to climate change: Examples from terrestrial ecosystems. *Frontiers in Ecology and the Environment* 9: 61–67.
- Gams, H. 1961. Erfassung und Darstellung mehrdimensional verwandtschaftsbeziehungen von Sippen und Lebensgemeinschaften. *Berichte des Geobotanischen Institutes der Eidgenössische Technische Hochschule, Stiftung Rübel Zurich* 1960(32): 96–115.
- Gerdol, R., L. Brancalion, R. Marchesini, and L. Bragazza. 2002. Nutrient and carbon relations in subalpine dwarf shrubs after neighbor removal or fertilization in northern Italy. *Oecologia* 130: 476–783.
- Grant, W.E., and N.R. French. 1990. Responses of alpine tundra to a changing climate: A hierarchical simulation model. *Ecological Modeling* 49: 205–227.
- Greenland, D., and M. Losleben. 2001. Climate. In *Structure and function of an alpine ecosystem*, ed. W.D. Bowman, and T.R. Seastedt, 15–31. New York: Oxford University Press.
- Hallinger, M., M. Manthey, and M. Wilmking. 2010. Establishing a missing link: Warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist* 186: 890–899.
- Hedenäs, H., H. Olsson, C. Jonasson, J. Bergstedt, U. Dahlberg, and T.V. Callaghan. 2011. Tree growth, biomass and vegetation changes over a thirteen-year period in the Swedish sub-arctic. *Ambio*. doi:10.1007/s13280-011-0173-1.
- Komárková, V., and P.J. Webber. 1978. An alpine vegetation map of Niwot Ridge, Colorado. *Arctic and Alpine Research* 10: 1–29.
- Körner, C. 1995. Alpine plant diversity: A global survey and functional interpretations. In *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences*, ed. F.S. Chapin III, and C. Körner, 45–62. New York: Springer.
- Körner, C. 1999. *Alpine plant life: Functional plant ecology of high mountain ecosystems*. New York: Springer.
- Kullman, L. 2010. A richer, greener and smaller alpine world: Review and projection of warming-induced plant cover change in the Swedish Scandes. *Ambio* 39: 159–169.
- Lesica, P., and B.M. Steele. 1996. A method for monitoring long-term population trends: An example using arctic and alpine plants. *Ecological Applications* 6: 879–887.
- Litaor, M.I., M. Williams, and T.R. Seastedt. 2008. Topographic controls on snow distribution, soil moisture, and species

- diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. *Journal of Geophysical Research* 113: G02008.
- Manley, W.F., E.G. Parrish, and L.R. Lestak. 2009. *High-resolution orthorectified imagery and digital elevation models for study of environmental change at Niwot Ridge and Green Lakes Valley, Colorado: Niwot Ridge LTER*. Boulder: INSTAAR, University of Colorado at Boulder, digital media.
- Marr, J.W. 1961. *Ecosystems of the east slope of the Front Range in Colorado*. University of Colorado studies, series 8 in biology, 134 pp. Boulder: University of Colorado.
- Olofsson, J., L. Oksanen, T. Callaghan, P.E. Hulme, T. Oksanen, and O. Suominen. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* 15: 2681–2693.
- Pauli, H., M. Gottfried, and G. Grabherr. 1999. Vascular plant distribution patterns at the low temperature limits of life—the alpine-nival ecotone of Mount Schrankogel (Tyrol, Austria). *Phytocoenologia* 29: 297–325.
- Pauli, H., M. Gottfried, K. Reiter, C. Klettnner, and G. Grabherr. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: Observations (1994–2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology* 13: 147–156.
- Scherrer, D., and C. Körner. 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology* 16: 2602–2613.
- Scherrer, D., and C. Körner. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography* 38: 406–416.
- Schob, C., P.M. Kammer, P. Choler, and H. Velt. 2009. Small-scale plant species distribution in snowbeds and its sensitivity to climate change. *Polar Biology* 200: 91–104.
- Schultz, E.D., and H.A. Mooney. 1993. *Biodiversity and ecosystem function*. Berlin: Springer.
- Servilla, M., D. Costa, C. Laney, I. San Gil, and J. Brunt. 2008. *The EcoTrends Web Portal: An architecture for data discovery and exploitation*. Albuquerque: Environmental Information Management, University of New Mexico.
- Sherrod, S.K., T.R. Seastedt, and M.D. Walker. 2005. Northern pocket gopher (*Thomomys talpoides*) control of alpine plant community structure. *Arctic, Antarctic, and Alpine Research* 37: 585–590.
- Suding, K.N., A.E. Miller, H. Bechtold, and W.D. Bowman. 2006. The consequences of species loss on ecosystem nitrogen cycling depends on community compensation. *Oecologia* 149: 141–149.
- Tieszen, L.L. 1978. *Vegetation and production ecology of an Alaskan arctic tundra*. New York: Springer.
- Van Bogaert, R., K. Haneca, J. Hoogesteger, C. Jonasson, M.D. Dapper, and T.V. Callaghan. 2011. A century of tree line changes in sub-arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography* 38: 907–921.
- Voinov, A., C. Fitz, R. Boumans, and R. Costanza. 2004. Modular ecosystem modeling. *Environmental Modeling and Software* 19: 285–304.
- Volk, M., D. Obrist, K. Novak, R. Giger, S. Bassin, and J. Fuhrer. 2011. Subalpine grassland carbon dioxide fluxes indicate substantial carbon losses under increased nitrogen deposition, but not at elevated ozone concentrations. *Global Change Biology* 17: 366–376.
- Walker, M.D., C.H. Wahren, R.D. Hollister, G.H.R. Henry, L.E. Ahlquist, J.M. Alatalo, M.S. Bret-Harte, et al. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* 103: 1342–1346.
- Walker, M.D., D.A. Walker, T.A. Theodose, and P.J. Webber. 2001. The vegetation: hierarchical species–environment relationships. In *Structure and function of an alpine ecosystem*, ed. W.D. Bowman, and T.R. Seastedt, 99–127. New York: Oxford University Press.
- Walker, M.D., P.J. Webber, E.H. Arnold, and D. Ebert-May. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology* 76: 1067–1083.
- Webber, P.J. 1971. Gradient analysis of the vegetation around the Lewis Valle North-Central Baffin Island, Northwest Territories, Canada. PhD Thesis, Queen's University, Kingston, Canada.
- Webber, P.J., J.E. Emerick, D.C. Ebert May, and V. Komárková. 1976. Impacts of increased snowfall on alpine vegetation. In *Ecological impacts of snowpack augmentation in the San Juan Mountains Colorado*, ed. H.W. Steinhoff, and J.D. Ives, 201–264. Final report, San Juan Ecological Project, Colorado State University, Fort Collins.
- Williams, M.W., P.D. Brooks, and T. Seastedt. 1998. Nitrogen and carbon soil dynamics in response to climate change in a high-elevation ecosystem in the Rocky Mountains, U.S.A. *Arctic and Alpine Research* 30: 26–30.
- Wipf, S., and C. Rixen. 2010. A review of snow manipulation experiments in arctic and alpine tundra ecosystems. *Polar Research* 29: 95–109.
- Wipf, S., V. Stoeckli, and P. Bebi. 2009. Winter climate change in alpine tundra: Plant responses to changes in snow depth and snowmelt timing. *Climatic Change* 94: 105–121.
- Woodward, F.I., and M.R. Lomas. 2004. *Vegetation dynamics: Simulating responses to climatic change*. Cambridge: Cambridge University Press.
- Wookey, P.A., R. Aerts, R.D. Bardgett, F. Baptist, K.A. Brathen, J.H.C. Cornelissen, L. Gough, I.P. Hartley, et al. 2009. Ecosystem feedbacks and cascade processes: Understanding their role in the responses of arctic and alpine ecosystems to environmental change. *Global Change Biology* 15: 1153–1172.

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