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Monitoring shifts in plant diversity in response to climate change: a method for landscapes

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Abstract. Improved sampling designs are needed to detect, monitor, and predict plant migrations and plant diversity changes caused by climate change and other human activities. We propose a methodology based on multi-scale vegetation plots established across forest ecotones which provide baseline data on patterns of plant diversity, invasions of exotic plant species, and plant migrations at landscape scales in Rocky Mountain National Park, Colorado, USA. We established forty two 1000-m^2 plots in relatively homogeneous forest types and the ecotones between them on 14 vegetation transects. We found that 64% of the variance in understory species distributions at landscape scales were described generally by gradients of elevation and under-canopy solar radiation. Superimposed on broad-scale climatic gradients are small-scale gradients characterized by patches of light, pockets of fertile soil, and zones of high soil moisture. Eighteen of the 42 plots contained at least one exotic species; monitoring exotic plant invasions provides a means to assess changes in native plant diversity and plant migrations. Plant species showed weak affinities to overstory vegetation types, with 43% of the plant species found in three or more vegetation types. Replicate transects along several environmental gradients may provide the means to monitor plant diversity and species migrations at landscape scales because: (1) ecotones may play crucial roles in expanding the geophysiological ranges of many plant species; (2) low affinities of understory species to overstory forest types may predispose vegetation types to be resilient to rapid environmental change; and (3) ecotones may help buffer plant species from extirpation and extinction.

Key words: exotic species, multi-scale vegetation sampling, plant diversity, species-environment relationships, vegetation ecotones

Introduction

Paleoecological evidence clearly shows that plant species migrate long distances in response to climate change (Woods and Davis 1989; Sykes and Prentice 1996; Kullman 1996). What surprises many plant ecologists are the modeled rates of migration, with the pollen record of some tree species presumably migrating up to a kilometer per year coinciding with climate warming in the Holocene (Pitelka et al. 1997). In recent decades, emphasis on plant migrations has shifted to the rate of spread of exotic invasive plant species. Eurasian cheatgrass (*Bromus tectorum* L.), for example, spread over 200,000 km^2 in about 40 years (Mack 1986; Pitelka et al. 1997). Even more rapid plant migrations may be likely in the near future in response to accelerated climate change (Foley et al. 1996; Grabherr et al. 1994) and land-use change (Stohlgren et al. 1998c).

Managers of national parks and other natural areas are justly concerned about rapid plant migrations. First, plant species could migrate from designated 'protected' areas in preserves to less protected areas outside preserves (Peters and Darling 1985). Second, some plant species may be squeezed into smaller or fewer habitats, such as high elevation or wetland sites (Whitlock 1993). Third, more sedentary species could be out-competed by rapidly invading species, such as exotic plants. Vegetation monitoring in nature preserves must be capable of detecting, monitoring, and predicting changes in species composition and plant migrations caused by factors such as the ubiquitous threats of habitat destruction, altered disturbance regimes, climate change, and nitrogen deposition from air pollution.

Many vegetation sampling programs may be poorly designed to detect change. Vegetation plots have often been too small (commonly < 3 m^2; Kareiva and Anderson 1985), easily missing most plant species at each sampling site (Stohlgren et al. 1998b). Equally stifling, since Clements (1916), many plant ecologists have been preoccupied with delineating, classifying, and monitoring 'homogeneous plant communities' (Daubenmire 1968; Mueller-Dombois and Ellenberg 1974; Barbour et al. 1987) rather than developing an understanding of species-specific migrations and the disassociation of plant communities in time and space (Gleason 1926). Oddly, many ecologists interested in 'gradient analysis' subjectively placed vegetation plots in more homogeneous areas (Whittaker 1967; Peet 1981; Allen et al. 1991), avoiding local environmental gradients between homogeneous and heterogeneous or peripheral areas of a vegetation type (Stohlgren and Bachand 1997). However, peripheral (marginal) areas of a population and mixed-species stands may have different patterns of establishment, growth, and survival than homogeneous (or core) areas of a population (Neilson 1991; Stohlgren 1992, 1993). Placing vegetation plots only in homogeneous areas may: (1) exaggerate the differences between plant communities (Stohlgren and Bachand 1997; Stohlgren et al. 1998a); and (2) reduce our ability to monitor and predict plant species migrations, which are more likely to occur first at the geophysiological boundaries of the species.

To understand plant species distributions, migrations, and changes in plant diversity at landscape-scales, ecologists are now focusing more attention on ecotones (Gillison 1970; Wiens et al. 1985; Holland et al. 1991; Cornelius and Reynolds 1991; Hansen and di Castri 1992; Risser 1993; Gosz 1993; Rusek 1993; Weisberg and Baker 1995). In 1995, Risser argued that we must understand the steepness of environmental gradients between homogeneous vegetation associations before we can understand the dynamic nature of landscapes. Little progress had been made since a similar call to action by Wiens et al. (1985) ten years earlier.

Most ecotone studies were not designed to directly answer questions about plant migrations or plant diversity patterns at landscape scales. Usually only one transect or ecotone was measured (e.g., Montaña et al. 1990; Wesser and Armbruster 1991; Martinez and Fuentes 1993; Giesler et al. 1998; Kieft et al. 1998). In other studies with replicate transects, emphasis was placed on the boundaries of a few dominant plant species (Rusek 1993; Puyravaud et al. 1994; Stohlgren and Bachand 1997; Stohlgren et al. 1998a). One study assessed α and β diversity of plants relative to water recession on the shores of one reservoir (i.e., one ecotone) in central Tanzania (Backéus 1993). We found no studies that were designed to monitor species richness patterns, exotic species invasions, and the direction and magnitude of species migrations with replicate ecotones in a landscape.

Our goal was to design a long-term vegetation monitoring program to: (1) assess changes in plant diversity at landscape scales; (2) detect species migrations in response to rapid environmental change; and (3) monitor the invasion of exotic plant species in the forests of Rocky Mountain National Park, Colorado, USA.

Study area

The Colorado Front Range in the southern Rocky Mountains spans an elevation range from 1600 to over 4300 m. This mountain region embraces a wide array of vegetation, including shortgrass steppe, shrub-steppe, montane pine and fir forests, subalpine coniferous forests, and alpine tundra. Since the origination of the present forest stands, these areas have remained relatively undisturbed. Latitudinal and elevational arrangements of plant species distributions have been attributed to temperature and precipitation, as typically influenced by elevation and topographic position (Peet 1981, 1988; Allen et al. 1991). Common tree species of Rocky Mountain National Park include: ponderosa pine (*Pinus ponderosa* P. and C. Lawson; 2320–3170 m), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco; 2370–3213 m), lodgepole pine (*Pinus contorta* Doug. ex. Loud; 2380–3480 m), aspen *(Populus tremuloides* Mich; 2350–3500 m), Engelmann spruce (*Picea Engelmannii* Perry ex. Engel.; 2530–3710 m), subalpine fir (*Abies lasiocarpa* (Hook) Nutt.; 2530–3710 m), and limber pine (*Pinus flexilis* James; 2620–3560 m). Paleoecological evidence suggests that forest ecotones in the Rocky Mountains of Colorado may be sensitive indicators of climate change, since the distributions of tree species probably changed faster than soil development in many areas (Madole 1976; Markgraf and Scott 1981; Stohlgren and Bachand 1997).

Methods

Vegetation sampling and environmental measurements

Fourteen transects (120–480 m long, 20 m wide) consisting of one hundred and forty-six 20 m × 20 m forest plots were established between 1992 and 1995 in Rocky

Mountain National Park, to assess tree species distributions (Table 1; Stohlgren and Bachand 1997; Stohlgren et al. 1998a). Two replicate ecotone transects were placed from lodgepole pine to spruce/fir, and three replicate transects each from lodgepole pine to limber pine, Douglas-fir to lodgepole pine, ponderosa pine to lodgepole pine, and ponderosa pine to Douglas-fir. Twelve of the fourteen transects were located in an unbiased manner using a stratified random sampling design based on the vegetation cover type map of the Park and a geographic information system (GIS; see Stohlgren and Bachand 1997 for details). Two of the transect starting points (Bear Lake and Hitchen's Gulch) were selected subjectively, closer to roads and trails, to more easily test field sampling techniques (because lodgepole to spruce/fir ecotones were difficult to identify from the vegetation map based on a minimum mapping unit size of 2 ha), and to facilitate educational use. In each case, no prior information was available regarding the density or basal area of tree species, understory vegetation, or environmental characteristics (i.e., soil depth, surface rockiness, under-canopy light), so we are confident that selecting the starting locations for these transects did not strongly bias results.

At each study site, the transects were established across major environmental gradients (i.e., elevation or aspect; Table 1) such that both terminal sections of each transect were in homogeneous stands of their respective forest types, with 70% of the basal area in the dominant tree species (Figure 1). Thus, we define the ecotone as the transition zone between the two relatively homogeneous forest types. Environmental factors that were measured along these ecotone transects in our previous study (Stohlgren et al. 1998a) included: (1) average soil depth from 144 sites in each 20 m × 20 m forest plot; (2) average surface rockiness (i.e., the percent of soil depth measurements

Table 1. Ecotone transects in Rocky Mountain National Park, Colorado, USA.

Transect name	From veg. type	To veg. type	UTM E	UTM N	Elevation (m)	Slope (%)	Aspect (°)	Est. age
Aspenglen	*Pin pon*	*Pin con*	449475	4471602	2530–2610	4.0–9.0	135	180
Deer Ridge	*Pin pon*	*Pin con*	447399	4470812	2740–2800	5.0–8.0	90	130
Upr. Beaver	*Pin pon*	*Pin con*	449361	4468475	2530–2550	6.0–7.0	360	130
Bear Lake	*Pin con*	*Picea-Abies*	445000	4462297	2870	9.0–14.0	0–22	90
Hitchen's	*Pin con*	*Picea-Abies*	426802	4475867	2960–2990	7.0–14.0	90	110
Lawn Lake	*Pin con*	*Pin fle*	446227	4475343	3020–3080	5.0–7.0	270	130
Meeker Dr.	*Pin con*	*Pin fle*	451653	4455112	3000–3050	5.0–7.0	90	100
Wild Basin	*Pin con*	*Pin fle*	452459	4451880	2980–3080	4.0–7.0	180	120
South Lt.	*Pin pon*	*Pse men*	448690	4046592	2614–2628	2.0–20.0	360	90
Eagle Cliff	*Pin pon*	*Pse men*	451110	4467540	2471–2540	4.0–27.0	20	70
High Drive	*Pin pon*	*Pse men*	450672	4469798	2926–2942	26.0–35.0	90	240
Aspen Brook	*Pse men*	*Pin con*	453824	4461062	2727–2764	6.0–29.0	270	110
Emld Mtn.	*Pse men*	*Pin con*	450227	4464606	2746–2762	5.0–16.0	360	110
Thunder Mtn.	*Pse men*	*Pin con*	450310	4464500	2620–2630	6.0–24.0	90	95

Pin pon = Pinus ponderosa; Pin con = Pinus contorta; Pse men = Pseudotsuga menzesii; Picea-Abies = spruce/fir; *Pin fle = Pinus flexilis.*

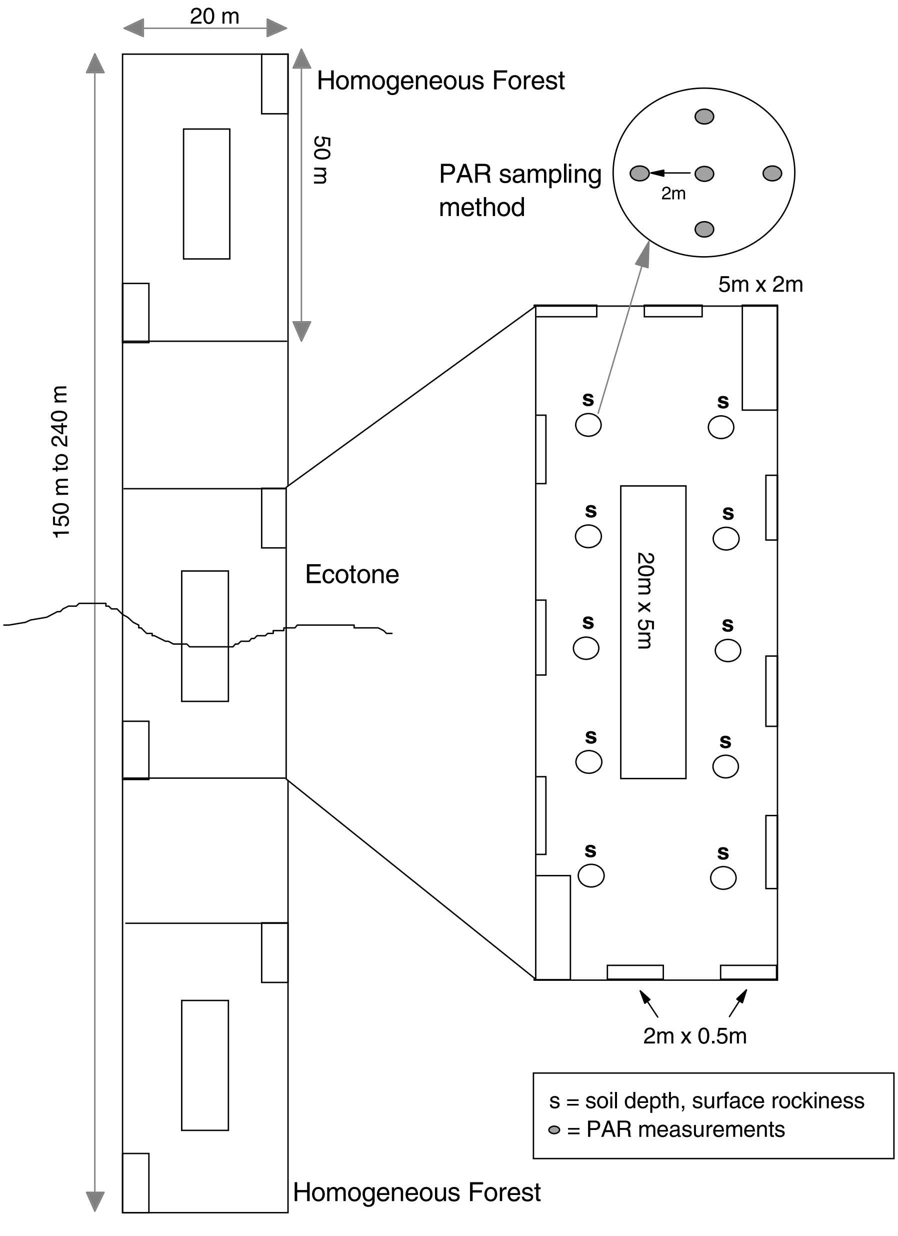

Figure 1. Diagram of transect, plot layout, and methods.

that were impenetrable due to surface rock); and (3) average photosynthetically active radiation (PAR; 400–700 nm, in micromoles m^{-2} s^{-1}; Decagon Sunfleck Ceptometer Model SF-80) beneath the forest canopy between 10 a.m. and 2 p.m. on cloud-free days in late June or early July. The ceptometer was held horizontally 1 m above ground level, and five readings (80 sensors per reading) were taken at four cardinal directions in each quadrant and the centers of each 20 m × 20 m plot, then averaged for each plot (Figure 1). Measurements also were taken in canopy openings to calculate a PAR index (average plot reading divided by the maximum open-canopy reading for the day), interpreted as the measure of light available to understory vegetation.

At the terminal ends (comparatively homogeneous forest stands) and center (ecotone) of the 14 transects, a 20 m × 50 m Modified-Whittaker nested vegetation sampling plot was established (Stohlgren et al. 1995). The Modified-Whittaker plot design, in this case, had the ten 0.5 m × 2 m (1 m^2) subplots arranged systematically inside and adjacent to the plot perimeter. Percent cover by species and average height by species were recorded in the 1-m^2 subplots. Total species were recorded in the ten 1-m^2 subplots, the two 10-m^2 subplots, the 100-m^2 subplot, and the remaining unsampled areas of the 1000-m^2 plot (Figure 1). Sampling was conducted at peak phenology (flowering) for most perennial plant species (mid-June to mid-August, from low to high elevations). Each transect was located with a precise global positioning system with base station post processing, with three labeled, copper-top stainless steel survey stakes at the beginning, middle and end of each transect. Thus, the precise locations of the plots and subplots can be relocated and re-measured in the future.

Statistical analysis

We used Jaccard's Coefficient to quantify plant species overlap between vegetation types (Krebs 1989). Jaccard's Coefficient (J) is defined as:

$$J = A/(A + B + C)$$

where A = the number of species found in both vegetation types, B = species in vegetation type 1 but not in vegetation type 2, and C = species in vegetation type 2 but not in vegetation type 1. In other words, Jaccard's Coefficient is the proportion of combined diversity shared between two plots. Complete overlap (i.e., identical species lists) between two plots is indicated when $J = 1.0$, while $J = 0.0$ indicates no overlap.

We used canonical correspondence analysis (CCA; CANOCO software version 3.12; ter Braak 1987b, 1991) to characterize the relationship between understory composition (cover of the dominant five species) and environmental measurements (e.g., slope, aspect, elevation, PAR index, soil depth, surface rockiness). CCA is a direct gradient analysis technique that constrains the extracted pattern of vegetation to a linear combination of the measured environmental variables (ter Braak 1986, 1987a), and it is a proven, robust method for describing species-environment relationships (see Palmer 1993 for a complete review; Reed et al. 1993). All the default options were selected in the CCA (i.e., no special weighting of species or environmental factors, no samples were excluded from the analysis). Aspect was converted to a linear scalar as the absolute value of 180° minus the azimuth reading such that values ranged from 0° (due south) to 180° (due north). We assessed all environmental variables for multicollinearity problems and none were found. Monte Carlo permutation tests (99 random permutations) were performed to test the significance of the first canonical axis (ter Braak 1991).

We used stepwise forward multiple regressions (SYSTAT 7.0) to assess the ability of environmental factors to predict native, exotic, and total species richness. Environmental factors included slope, aspect, elevation, PAR index, surface rockiness, and soil depth. The forward linear regression models included only variables meeting the $P < 0.15$ criterion (Neter et al. 1990). Data were assessed for normality prior to analysis (Zar 1974), and only exotic species richness required a $\log_{10}$ transformation. Finally, we used distance-weighted, least squares models (SYSTAT 7.0) to create three-dimensional displays of native and exotic species richness in relation to elevation and PAR.

Results

Species richness patterns in homogenous forest plots and ecotone plots

Native and exotic species richness varied greatly by ecotone type and vegetation type (Table 2). Mean native species richness in 1000-m^2 plots ranged from 15.3 (+2.6) species/plot in homogeneous, high-elevation lodgepole pine plots to 47.7 (+2.3) species/plot in homogeneous, low-elevation ponderosa pine plots. Likewise, higher elevation plots in ecotones generally had fewer species than lower-elevation ecotone plots (Table 2).

Mean exotic species richness in the 1000-m^2 plots was highest in low-elevation vegetation types, ranging from 0 species/plot in Douglas-fir to lodgepole pine transects, to 2.3 (+0.7) species/plot in homogeneous and ecotone plots in ponderosa pine to Douglas-fir transects (Table 2). For all ecotone plots combined, mean exotic species richness was 10% greater than in homogeneous forest types combined, but this difference was not significant. Total species richness patterns mimicked native species richness patterns due to the low numbers of exotic species (Table 2). Higher mean richness of native, exotic, and total species coincided with higher ($P < 0.1$) mean PAR values in ecotone plots (Table 2).

Species overlap between vegetation types

Plant species overlap between pairs of 1000-m^2 plots along all ecotone types was high (Figure 2). Ponderosa pine plots shared 65% of the plant species found in the ecotone plots on the ponderosa pine to Douglas-fir transects. Mean species overlap between ecotone plots and the homogeneous forest types was almost as high, ranging

Table 2. Mean number of native, exotic, total, and unique plant species in 1000-m^2 plots in various ecotone and forest types. Mean under-canopy photosynthetically active radiation (PAR) index by ecotone and forest type.

Ecotone type/ vegetation type	No. plots	No. native spp. Mean (SE)	No. exotic spp. Mean (SE)	No. total spp. Mean (SE)	No. unique spp. Mean (SE)	PAR Mean (SE)
P. ponderosa to *P. menziesii*						
P. ponderosa	3	47.7 (2.3)	2.3 (0.7)	50.0 (2.9)	1.0 (0.6)	0.55 (0.11)
P. menziesii	3	36.7 (7.2)	1.7 (0.7)	38.3 (7.8)	0.3 (0.3)	0.61 (0.12)
Ecotone	3	41.7 (3.8)	2.3 (0.7)	44.0 (4.5)	0.7 (0.3)	0.76 (0.13)
P. ponderosa to *P. contorta*						
P. ponderosa	3	40.3 (10.5)	2.0 (1.0)	42.3 (11.4)	3.7 (2.2)	0.56 (0.12)
P. contorta	3	31.0 (8.1)	0.7 (0.7)	31.7 (8.4)	0.7 (0.3)	0.31 (0.06)
Ecotone	3	43.7 (9.9)	2.0 (1.5)	45.7 (10.8)	3.0 (1.7)	0.56 (0.13)
P. menziesii to *P. contorta*						
P. menziesii	3	35.0 (4.4)	0.0 (0.0)	35.0 (4.4)	1.0 (0.0)	0.28 (0.12)
P. contorta	3	21.0 (1.2)	0.0 (0.0)	21.0 (1.2)	0.0 (0.0)	0.43 (0.08)
Ecotone	3	30.0 (3.6)	0.0 (0.0)	30.0 (3.6)	0.7 (0.7)	0.54 (0.14)
P. contorta to *Picea-Abies*						
P. contorta	2	27.5 (3.5)	1.0 (1.0)	28.5 (4.5)	1.5 (0.5)	0.44 (0.16)
Picea-Abies	2	26.0 (0.0)	0.5 (0.5)	26.5 (0.5)	2.0 (0.0)	0.31 (0.04)
Ecotone	2	19.5 (3.5)	0.0 (0.0)	19.5 (3.5)	0.5 (0.5)	0.34 (0.01)
P. contorta to *P. flexilis*						
P. contorta	3	15.3 (2.6)	0.0 (0.0)	15.3 (2.6)	0.0 (0.0)	0.35 (0.07)
P. flexilis	3	25.7 (7.2)	0.3 (0.3)	26.0 (7.6)	0.3 (0.3)	0.60 (0.06)
Ecotone	3	25.0 (6.1)	0.3 (0.3)	25.3 (6.4)	1.3 (0.7)	0.54 (0.08)
All types to ecotone						
All types	28	30.9 (2.4)	0.9 (0.2)	31.8 (2.6)	1.0 (0.3)	0.45 (0.04)
Ecotones	14	32.9 (3.4)	1.0 (0.4)	33.9 (3.8)	1.3 (0.4)	0.56 (0.04)

from 44% to 61%. Species overlap between pairs of homogeneous forest plots on the transects ranged from 35% to 56% (Figure 2).

Low-elevation forest types shared a high percentage of plant species, while high-elevation types shared a lower percentage of plant species (Table 3). Combining the species lists for the homogeneous plots by forest type revealed that 59% of the species found in the ponderosa pine type were also found in the Douglas-fir type. The lodgepole pine type shared almost half the species found in the ponderosa pine and Douglas-fir types, but shared less than one-third of its species with the high-elevation limber pine type (Table 3).

Species affinities to individual vegetation types

Plant species showed weak affinities to overstory vegetation types (Figure 3). Only 49 (27.8%) of the 176 plant species encountered had strong affinities to individual

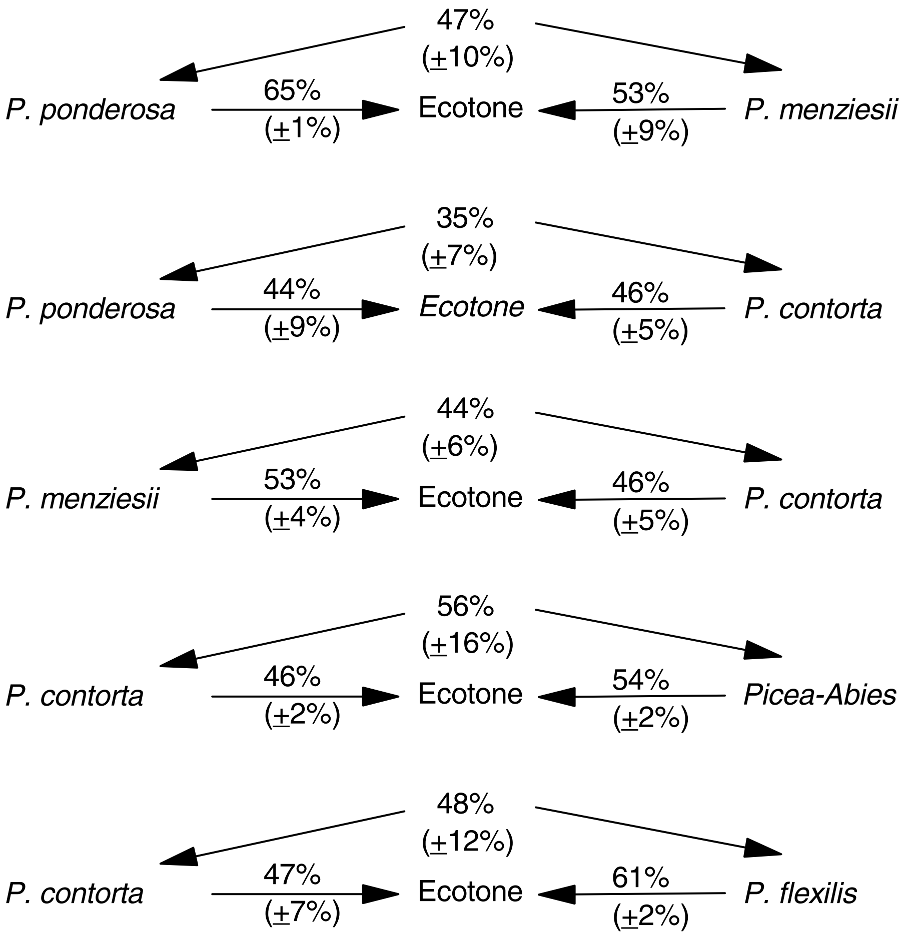

Figure 2. Mean species overlap in ecotone transects.

vegetation types. Of these 49 plant species, 48 were locally rare species found in only one plot while sampling, 23 of which were unique to the low-elevation ponderosa pine plots. Fifty-two species were found in two vegetation types, with 24 species shared between low-elevation ponderosa pine and Douglas-fir plots. Over 72% of the plant

Table 3. Species overlap between vegetation types based on combined species lists from replicate plots.

	P. menziesii (%)	*P. contorta* (%)	*Picea-Abies* (%)	*P. flexilis* (%)
P. menziesii	59	47	22	24
P. contorta		48	27	27
Picea-Abies			43	32
P. flexilis				24

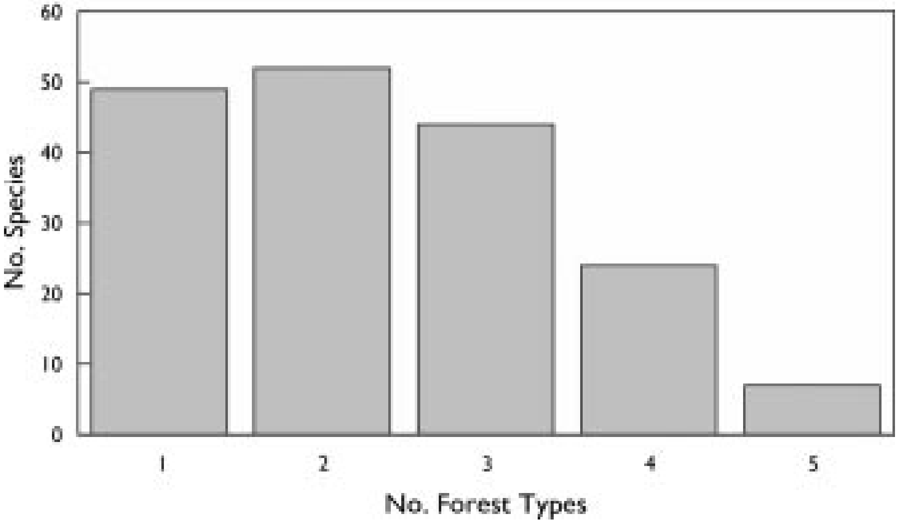

Figure 3. Species affinities to individual vegetation types.

species were found in two or more vegetation types, with 43% of the plant species found in three or more vegetation types (Figure 3).

Canonical correspondence analysis of ecotones

Based on canonical correspondence analysis of the 14 vegetation transects, we found that dominant understory species distributions at landscape-scales were described generally by gradients of elevation and available light (under-canopy PAR). The first two ordination axes explained 64% of the variance in vegetation patterns. Environmental factors that correlated significantly ($P < 0.001$) to the first ordination axis included: elevation ($r = -0.94$) and PAR ($r = 0.64$). Environmental factors that significantly correlated to the second ordination axis included: aspect (degrees from due south; $r = -0.60$; $P < 0.001$) and slope ($r = 0.46$; $P < 0.002$). The correlation matrix showed that elevation was significantly correlated to aspect ($r = -0.51$; $P < 0.001$). Monte Carlo permutation tests showed that the first canonical axis was highly significant (eigenvalue = 0.84; F-ratio = 3.4; $P < 0.01$).

We mapped the domain of understory species associated with the particular overstory tree species by connecting perimeter plots from the same vegetation type on the CCA plot. Connecting the perimeter plots from only the homogeneous plots (Figure 4, top) resulted in small domains for the five dominant understory species associated with the spruce-fir and limber pine vegetation types. The domain of understory species associated with lodgepole pine is fairly large, as is the domain for the understory species of Douglas-fir and ponderosa pine. However, when the ecotone plots are included, the potential domain of dominant understory species is greatly

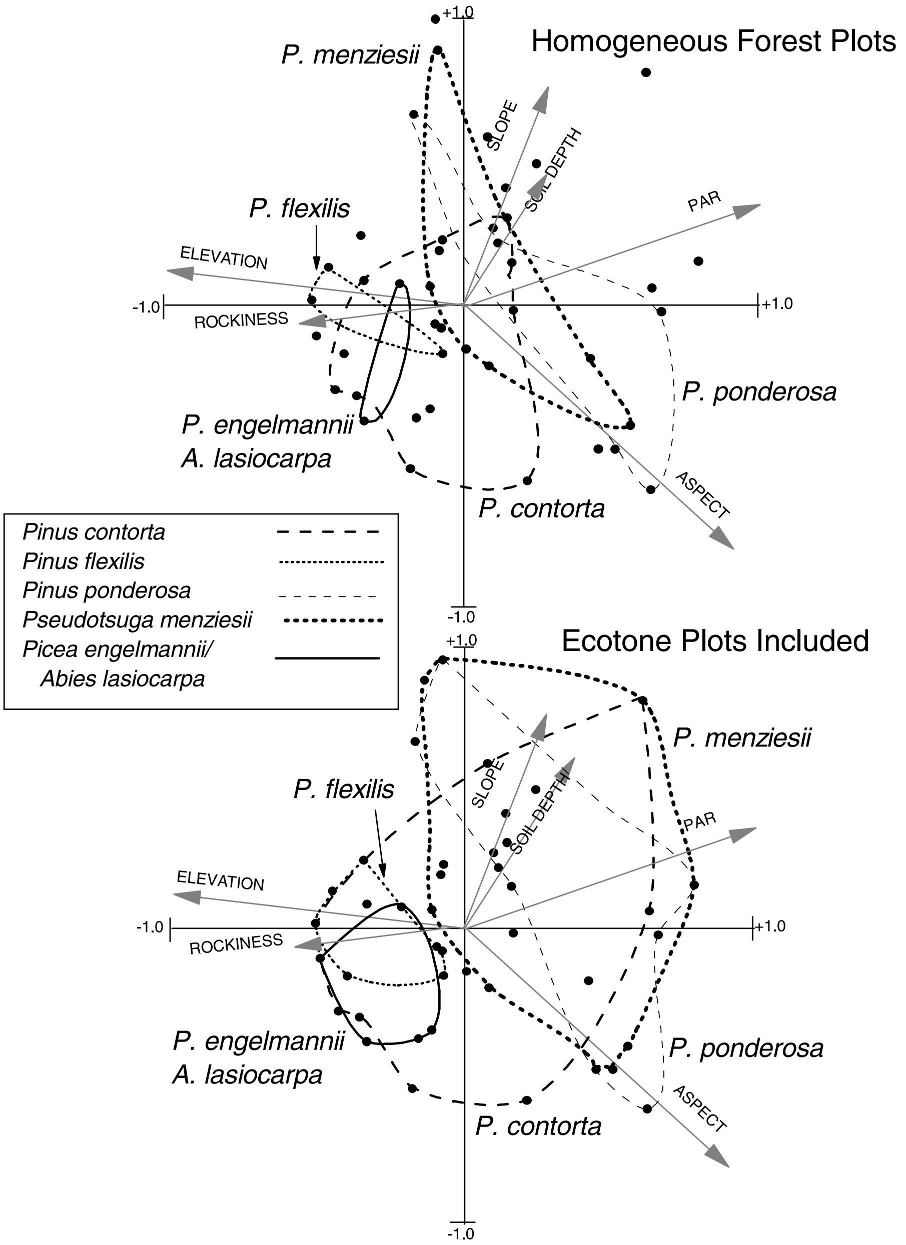

Figure 4. Canonical Correspondence Analysis ordination. Top diagram shows the domain of the dominant five understory species per plot excluding the ecotone plots, while the bottom diagram includes the ecotone plots.

expanded for all forest types (Figure 4, bottom). The domain of the dominant understory plants associated with Douglas-fir more than doubled on the CCA plot.

Predictors of species richness at landscape scales

Multiple regression analysis showed that most of the environmental factors we measured were important predictors of native species richness and total species richness in 1000-m^2 plots spread across the landscape (Table 4). For example, 59% and 60% of the variance in native and exotic plant species richness, respectively, could be explained by aspect, slope, elevation, PAR, and soil depth. Elevation was the only negatively correlated variable in both cases. Almost 66% of the variance in exotic species richness (log$_{10}$ transformed data) could be explained by positive relationships with PAR and the number of native species (Table 4). The t- and P-values showed that all individual variables used in the regressions were significant.

Frequencies of plant species in 1000-m^2 plots

We found a steeply declining curve of plant species frequencies in 1000-m^2 plots. Forty-eight of the 176 species encountered were not found in multiple plots (Figure 5). Common juniper (*Juniperus communis* L.) was found in 36 of 42 plots. Douglas-fir was found in 30 of the 42 plots, despite the fact that only 6 of the 14 transects were anchored in Douglas-fir communities.Seedlings of limber pine, a species usually considered to be found in high-elevation areas, were found in 57% of the

Table 4. Multiple regression results for the 42 plots combined.

Dependent variable/ predictors	Coefficient	t	P	Model F, R^2, P
No. native species				
Constant	91.211	4.42	0.001	$F = 10.54$
Aspect	0.080	2.61	0.013	$R^2 = 0.594$
Slope	0.481	2.68	0.011	$P < 0.001$
Elevation	−0.034	−4.76	0.001	
PAR	23.246	3.26	0.002	
Soil depth	0.580	2.81	0.008	
No. exotic species (log$_{10}$)				
Constant	−0.379	−5.16	0.001	$F = 37.53$
PAR	0.289	2.16	0.032	$R^2 = 0.658$
No. native species	0.014	6.59	0.001	$P < 0.001$
Total no. species				
Constant	95.816	4.34	0.001	$F = 10.89$
Aspect	0.089	2.72	0.010	$R^2 = 0.602$
Slope	0.500	2.60	0.013	$P < 0.001$
Elevation	−0.037	−4.76	0.001	
PAR	25.788	3.37	0.002	
Soil depth	0.626	2.84	0.007	

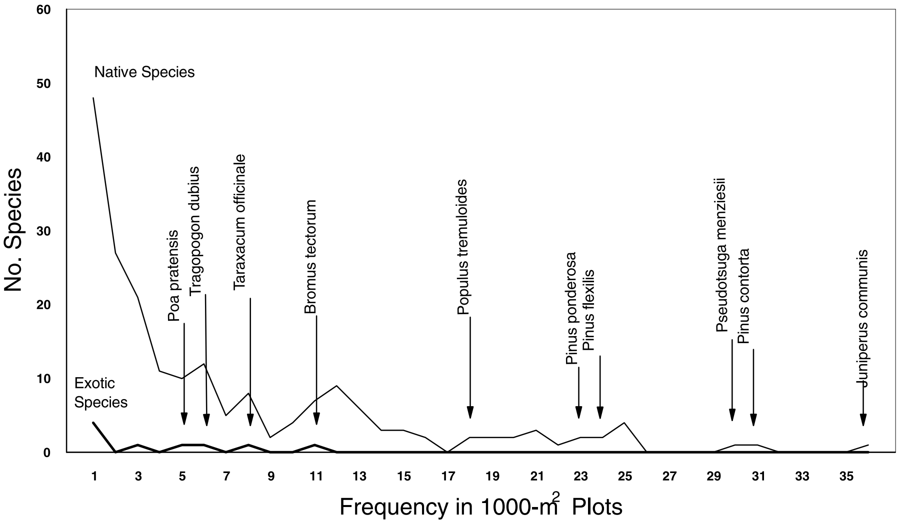

Figure 5. Frequencies of plant species in 1000-m^2 plots with selected species shown.

plots, while aspen was found in 43% of the plots. The exotic species *Bromus tectorum* L., was found in 11 plots, and 18 plots contained at least one exotic species (Figure 5).

Patterns of native and exotic species richness at landscape scales

The distance-weighted least square (three dimensional) models showed important differences in the distributions of native and exotic species at landscape scales (Figure 6). Elevation and available light (PAR) were significant ($P < 0.001$) predictors of both native and exotic species richness ($R^2 = 0.40$ and $R^2 = 0.33$, respectively). Native species richness remained high at high elevations as long as there was adequate light (Figure 6, top), whereas exotic species richness sharply declined with increasing elevation, regardless of the available light (Figure 6, bottom).

Discussion

Baseline data for monitoring changes in plant diversity at landscape-scales

Monitoring changes in plant diversity at landscape scales will not be easy because: (1) patterns of species richness and cover are determined by multiple environmental factors; (2) plant species have low affinities to overstory vegetation types; and (3) understanding and predicting species-specific responses to environmental change and multiple stresses may seem hopelessly complex. Still, this series of ecotone transects, initially established for the analysis of tree distribution changes (Stohlgren et al.

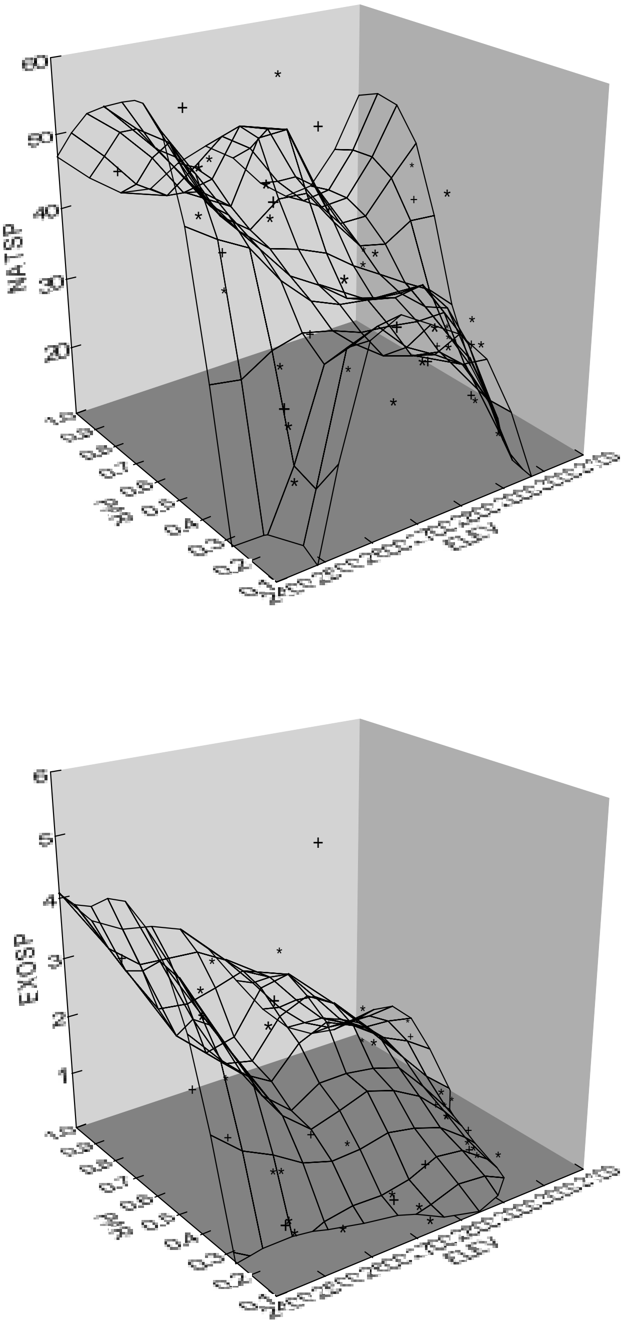

Figure 6. Patterns of native (NATSP) and exotic (EXOSP) species richness in 1000-m^2 plots with respect to elevation and PAR, using a distance-weighted least squares model. A plus sign (+) indicates an ecotone plot, and asterisks ($*$) indicates a homogeneous forest plot.

1998a), may be ideally suited to monitor long-term changes in plant diversity as illustrated below.

There is little doubt that patterns of plant species richness are determined by many environmental factors. Climate is likely a driving force for overstory species at large spatial scales (Table 3, Figure 6), as evidenced by broad responses of species to elevation, which is correlated to temperature, slope, and aspect (which are correlated to soil moisture; Peet 1981; Stohlgren and Bachand 1997). However, superimposed on broad-scale climatic gradients are small-scale gradients characterized by patches of light (Table 2), pockets of fertile soil (Stohlgren et al. 1997b), and zones of high soil moisture (Stohlgren et al. 1997c). Disturbances, such as fire and insect outbreaks, which occur at multiple scales, influence local and landscape-scale patterns of diversity (Stohlgren et al. 1997b,c). Monitoring plant species richness along major environmental gradients, along with a series of monitoring plots in disturbed areas, can provide the baseline data necessary to isolate the effects of climate change from successional change.

No vegetation monitoring system of plots and transects will be able to capture all aspects of plant diversity change. The species we encountered were about 80% perennials, 14% annuals, and 6% biennials, so temporal variation in species richness in groups of large plots (0.1 ha) may not be as great as spatial variation. Even so, annual variation in species richness, cover, and frequency at one or a few sites could be substantial. Successive years of sampling several plots is needed to determine the optimum frequency and intensity needed to meet specific management objectives such as early detection of invasive exotic species or shifts in certain species distributions due to climate change.

Keystone species such as aspen are captured surprisingly well in the forty two 1000-m^2 plots in randomly placed transects. Aspen have been thought to be relatively rare on the landscape, representing $<$2% of the forest cover on broad-scale vegetation maps (Stohlgren et al. 1997a). Aspen stands provide critical habitat for many species of plants, butterflies, and birds. Of major concern to resource managers was one recent study that showed virtually no aspen regeneration in large stands in the Estes Valley due to excessive browsing by large populations of elk in Rocky Mountain National Park (Baker et al. 1997). A broader study showed that many other large aspen stands in the Park and surrounding forests had more aspen regeneration (Suzuki 1997), but little is known about the contribution of small stands and scattered aspen trees to the persistence of aspen. We found that 43% of the plots surveyed contained aspen trees or saplings (Figure 5). These broadly distributed trees and saplings may serve as a vast reservoir of potentially large clones after a fire or insect outbreak (Hadley and Veblen 1993). Long-term monitoring of aspen in these randomly located plots will provide a landscape perspective of the persistence of aspen and associated plants and animals.

This study also aids the selection of 'indicator species' to assess environmental change. It is rather obvious that common juniper, found in 71% of the plots and in five vegetation types, may be less sensitive to environmental change than a narrowly distributed plant species such as the western yellow paintbrush (*Castilleja occidentalis* Torr.), which occurred primarily in the limber pine type. Distributional changes of the latter species along elevation and moisture gradients in the limber pine transects may be a sensitive indicator of climate change, and therefore, a good species to monitor. Changes in the distribution frequency of several species (Figure 5) linked to environmental data (e.g., soil characteristics, PAR, topography) may help ecologists select appropriate indicators for specific, anticipated environmental changes.

Another unexpected finding was that limber pine was found in 57% of the plots and in all five vegetation types. Limber pine, generally considered a high elevation species in the Colorado Rockies, was presumably more common in the low elevations of the Park in the early Holocene (Markgraf and Scott 1981). Low-elevation populations still persist on rocky cliffs in the nearby plains, and our finding of limber pine throughout the elevation range attests to its broad environmental and physiological range. Monitoring the establishment and growth of limber pine into higher elevation tundra sites may indicate a response to long-term annual warmer and wetter conditions (Baker and Weisberg 1997), while expanding limber pine populations in lower elevation habitats may indicate local cooler and wetter summer conditions in response to land-use change (Stohlgren et al. 1999b).

Detecting, monitoring, and predicting the migrations of most species will not be easy. It is becoming increasingly clear that modeling vegetation change must consider distribution shifts of individual species (Woodward 1993; Bartlein et al. 1997). Simple vegetation-change models based on homogeneous plant communities (e.g., Peters and Darling 1985; Romme and Turner 1991) and biomes (Crumley 1993; Neilson 1995) may poorly reflect potential changes in plant diversity. The broad distributions of overstory species in the Front Range (Peet 1981; Stohlgren and Bachand 1997; Stohlgren et al. 1998a) and understory species (Peet 1981; this study Figures 2–4) suggests that plant species respond to the range and variation of microsite conditions more than 'average' precipitation, temperature, and potential evapotranspiration (assumed in most vegetation change models). The low affinity of understory to overstory vegetation (Figure 5) further suggests that: (1) any perceived 'plant communities' are loosely organized around a few dominant species or small segments of multiple environmental gradients (Figure 4, top); (2) the majority of the landscape is a mix of transient, locally rare, understory species and mixed-species overstory stands (Stohlgren et al. 1998a, 1999a); and (3) individualistic responses to environmental change likely have dominated the landscape in the past and will likely dominate in the future (Davis 1991; Bazzaz 1996). Identifying broad suites of indicator species will require additional research and experimentation, but a mix of species with broad and narrow ranges may be useful in quantifying local and landscape-scale changes.

Monitoring the invasion of exotic plant species

Monitoring exotic plant invasions provides a means to assess changes in native plant diversity and plant migrations. For example, 43% of the plots contained at least one exotic species (Figure 5). Elevation and PAR were strong predictors of exotic species richness at landscape scales (Figure 6). They are currently confined to low-elevation sites with fairly high light levels in the understory (Figure 6, bottom), but that could change. However, exotic species declined rapidly with increasing elevation even when light was available, suggesting that temperature may control the distributions of many exotic species in these mountains. Increasing temperatures in the high elevations could facilitate the spread of mid- and lower-elevation plant species from Mediterranean areas throughout the world (Vitousek et al. 1996).

Several invasive plants are particularly worthy of future monitoring. Cheatgrass was found in 26% of the plots and is known to spread excessively after fire. After decades of fire suppression and fuel build-up in the forests, fires and the continued spread of cheatgrass are inevitable. Common dandelion (*Taraxacum officinale* Wiggers) has already spread from low-elevation ponderosa pine stands to high-elevation limber pine stands. Changes in the frequency and cover of other exotic plant species will be easy to detect with this system of long-term, multi-scale monitoring plots.

Implications to theorists and land managers

Theorists are making important inroads in models of ecotone structure (Milne et al. 1996) and edge detection (Fortin 1994). Our work adds a significant challenge to theorists to model changes in both overstory structure and understory species diversity at the same sites. Phase transition theory must be expanded to include more than simple ‘forest to grassland ecotones’ and two-dimensional transition zones. Multiple environmental gradients (Table 3) and non-linear responses to them (Figures 4 and 6) may have to be addressed with a combination of statistical models (e.g., Fortin 1994; Milne et al. 1996) and ecosystem process models (e.g., Coughenour 1993). New structural equation modeling techniques (e.g., Grace and Pugesek 1997) appear well suited for these complex systems. The spatial processes of seed dispersal and herbivory are equally complex for modelers. Current multivariate techniques, such as canonical correspondence analysis and multiple regression, are hard-pressed to describe patterns of plant diversity at multiple spatial scales. Developing accurate spatial and temporal models of changes in plant species diversity will be a significant endeavor.

Because ecotones and heterogeneous forests can occupy large proportions of many landscapes, we propose that monitoring ecotones may significantly contribute to our understanding of landscape-scale patterns of plant diversity in three ways. First, ecotones may play crucial roles in expanding the geophysiological range of many plant species (Figure 4, bottom) and fostering species composition overlap among communities (Figure 2, Table 4). Bazzaz (1996) fully recognized that different genotypes could be found in ‘patches differing in levels of environmental resources due to their different tolerances of those resources’ (page 228) and that the spatial distributions of genotypes profoundly affects the way ‘communities as a whole’ respond to environmental change. By exploiting ecotones, plant species can greatly expand their domain (Figure 4, bottom) and extend the physiological tolerance of certain genotypes. This process may be especially important if the landscape contains large heterogeneous areas relative to the amount of core, homogeneous forest stands (Stohlgren and Bachand 1997; Stohlgren et al. 1998a).

Second, high species overlap among ecotones and donor communities (Figure 2), and low affinities of understory species to overstory forest types (Figure 3), may predispose vegetation types (and biomes) to rapidly respond to environmental change. Questions arise whether species will be able to readily adapt to climate change (Bartlein et al. 1997). The ability of a plant species to migrate following climate change is determined by dispersal modes, recruitment and growth patterns, competitive relationships, and general trends in environmental factors (Bazzaz 1996). In our study area, ponderosa pine, a superior invading species over the past 6000 years, was found in 75% of the ecotone plots, and 50% of the homogeneous forest plots. Invasive exotic grasses and forbs also established more frequently in ecotone plots (Table 2). Ecotones and heterogeneous sites may be the breeding grounds for successful migrators.

Third, the same ecotone characteristics that expand the physiological ranges of many plant species may also: (1) foster species composition overlap among communities; (2) improve the ability of plant species to migrate in response to rapid environmental change; and (3) help buffer plant species from extirpation and extinction. For example, limber pine, which was more common in the early Holocene (Markgraf and Scott 1981) and is now a predominantly high-elevation species with low-elevation refugia, was found in 67% of the ecotone plots and 57% of the homogeneous forest plots. Thus, ecotones and heterogeneous sites may serve as refugia for genotypes that were common under previous climate scenarios. We propose that ecotones play important roles in maintaining plant diversity at landscape scales and prolonging species persistence in rapidly changing environments.

Monitoring changes in plant diversity requires monitoring of many individual species. Gleason (1926) was right! The fact that understory species had very low affinity to overstory types (Figures 2 and 3), with over 72% of the plant species found in two or more vegetation types, soundly supports Gleason’s individualistic concept. Previous research in the study area showed that seedlings, saplings, and trees of all the dominant conifer species were found throughout the forests, and that large, single-species stands were rare at landscape scales (Stohlgren et al. 1998a).

Replicate transects along several environmental gradients may provide the means to monitor plant diversity and species migrations at landscape scales (Figures 2 and 4). Additional research is needed to link landscape-scale monitoring in a regional-scale, hierarchical sampling framework to monitor shifts in plant diversity in response to climate and land-use changes.

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References

Allen RB, Peet RK and Baker WL (1991) Gradient analysis of latitudinal variation in southern Rocky Mountain forests. Journal of Biogeography 18: 123–139

Backéus I (1993) Ecotone versus ecocline: vegetation zonation and dynamics around a small reservoir in Tanzania. Journal of Biogeography 20: 209–218

Baker WL and Weisberg PJ (1997) Using GIS to model tree population parameters in the Rocky Mountain National Park forest-tundra ecotone. Journal of Biogeography 24: 513–526

Baker WL, Munroe JA and Hessl AE (1997) The effect of elk on aspen population in the winter range of Rocky Mountain National Park, Colorado, USA. Ecography 20: 155–165

Barbour MG, Burk JH and Pitts WD (1987) Terrestrial Plant Ecology, 2nd edn. Benjamin/Cummings, Menlo Park, California

Bartlein PJ, Whitlock C and Shafer SL (1997) Future change in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology 11: 782–792

Bazzaz FA (1996) Plants in Changing Environments. Cambridge University Press, New York

Clements FE (1916) Plant Succession: An Analysis of the Development of Vegetation. Publication 242. Carnegie Institution of Washington, Washington, DC

Coughenour MB (1993) Savanna – Landscape and Regional Ecosystem Model: Documentation. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado

Cornelius JM and Reynolds JF (1991) On determining the statistical significance of discontinuities within ordered ecological data. Ecology 72: 2057–2070

Crumley CL (1993) Analyzing historic ecotonal shifts. Ecological Applications 3: 377–384

Daubenmire RF (1968) Plant Communities: A Textbook of Plant Synecology. Harper and Row, New York

Davis MB (1991) Insights from paleoecology on global change. Ecol. Soc. Am. Bull. 70: 222–228

Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, Sitch S and Haxeltine A (1996) An integrated biosphere model of land surface processes, terrestrial carbon balance and vegetation dynamics. Global Biogeoch. Cycles 10: 603–628

Fortin M (1994) Edge detection algorithms for two-dimensional ecological data. Ecology 75: 956–965

Giesler R, Högberg M and Högberg P (1998) Soil chemistry and plants in Fennoscandian boreal forest as exemplified by a local gradient. Ecology 79: 119–137

Gillison AN (1970) Structural and floristics of a montane grassland/forest transition, Doma Peaks Region, Papua. Blumea 18: 71–86

Gleason HA (1926) The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53: 1–20

Gosz JR (1993) Ecotone hierarchies. Ecological Applications 3: 369–376

Grabherr G, Gottfried M and Pauli H (1994) Climate effects on mountain plants. Nature 369: 448

Grace JB and Pugesek BH (1997) A structural equation model of plant species richness and its application to a coastal wetland. The American Naturalist 149: 436–460

Hadley KS and Veblen TT (1993) Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. Canadian Journal of Forest Research 23: 479–491

Hansen AJ and di Castri F (eds) (1992) Landscape Boundaries: Consequences for Biotic Diversity and Landscape Flows. Ecological Studies 92. Springer-Verlag, New York

Holland MM, Risser PG and Naiman RJ (eds) (1991) Ecotones. Chapman & Hall, New York

Kareiva PM and Anderson M (1988) Spatial aspects of species interactions: The wedding of models and experiments. In: Hastings A (ed) Community Ecology, pp 35–50. Lecture Notes in Biomathematics 77. Springer-Verlag, Berlin

Kieft TL, White CS, Loftin SR, Aguilar R, Craig JA and Skaar DA (1998) Temporal dynamics in soil carbon and nitrogen resources at a grassland-shrubland ecotone. Ecology 79: 671–683

Krebs CJ (1989) Ecological Methodology. Harper and Row, New York

Kullman L (1996) Norway spruce present in the Scandes Mountains, Sweden, at 8000 BP: new light on Holocene tree spread. Global Ecology and Biogeog. Letters 5: 94–101

Mack RN (1986) Alien plant invasion into the Intermountain West: A case history. In: Mooney HA and Drake JA (eds) Ecology of Biological Invasions of North America and Hawaii, pp 191–212. Springer-Verlag, New York

Madole RF (1976) Glacial geology of the Front Range, Colorado. In: Mahaney WC (ed) Quaternary Stratigraphy of North America, pp 319–351. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania

Markgraf V and Scott L (1981) Lower timberline in central Colorado during the past 15,000 yr. Geology 9: 231–234

Martinez E and Fuentes E (1993) Can we extrapolate the California model of grassland-shrubland ecotone? Ecological Applications 3: 417–423

Milne BT, Johnson AR, Keith TH, Hatfield CA, David J and Hraber PT (1996) Detection of critical densities associated with piñyon-juniper woodland ecotones. Ecology 77: 805–821

Montaña C, Lopez-Portillo J and Mauchamp A (1990) The response of two woody species to the conditions created by a shifting ecotone in an arid ecosystem. Journal of Ecology 78: 789–798

Mueller-Dombois D and Ellenberg H (1974) Aims and Methods of Vegetation Ecology. Wiley, New York

Neilson RP (1991) Climatic constraints and issues of scale controlling regional biomes. In: Holland MM, Naiman RJ, and Risser PG (eds) Role of Landscape Boundaries in the Management and Restoration of Changing Environments, pp 31–51. Chapman & Hall, New York

Neilson RP (1995) A model for predicting continental-scale vegetation distribution and water balance. Ecological Applications 5: 362–385

Neter J, Wasserman W and Kutner MH (1990) Applied Linear Statistical Models: Regression, Analysis of Variance, and Experimental Designs, 3rd edn. Irwin, Homewood, Illinois

Palmer MW (1993) Putting things in even better order: The advantages of canonical correspondence analysis. Ecology 74: 2215–2230

Peet RK (1981) Forest vegetation of the Colorado Front Range. Vegetatio 45: 3–75

Peet RK (1988) Forests of the Rocky Mountains. In: Barbour MG and Billings WD (eds) North American Terrestrial Vegetation, pp 63–101. Cambridge University Press, New York

Peters RL and Darling JD (1985) The greenhouse effect and nature reserves. BioScience 35: 707–717

Pitelka LF and the Plant Migration Workshop Group (1997) Plant migration and climate change. American Scientist 85: 464–473

Puyravaud J, Pascal J and Dufour C (1994) Ecotone structure as an indicator of changing forest-savanna boundaries (Linganamakki Region, southern India). Journal of Biogeography 21: 581–593

Reed RA, Peet RK, Palmer MW and White PS (1993) Scale dependence of vegetation-environment correlations: A case study of a North Carolina piedmont woodland. Journal of Vegetation Science 4: 329–340

Risser PG (1993) Ecotones: Ecotones at local to regional scales from around the world. Ecological Applications 3: 367–368

Risser PG (1995) The status of the science of examining ecotones. BioScience 45: 318–325

Romme WH and Turner MG (1991) Implications of global change for biogeographic patterns in the Greater Yellowstone Ecosystem. Conservation Biology 5: 373–386

Rusek J (1993) Air-pollution-mediated changes in alpine ecosystems and ecotones. Ecological Applications 3: 406–416

Stohlgren TJ (1992) Resilience of a heavily logged grove of giant sequoia (*Sequoiadendron giganteum*) in Kings Canyon National Park, California. Forest Ecology and Management 54: 115–140

Stohlgren TJ (1993) Spatial patterns of giant sequoia (*Sequoiadendron giganteum*) in two sequoia groves in Sequoia Canyon National Park, California. Canadian Journal of Forest Research 23: 120–132

Stohlgren TJ, Falkner MB and Schell LD (1995) A modified-Whittaker nested vegetation sampling method. Vegetatio 117: 113–121

Stohlgren TJ and Bachand RR (1997) Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, USA. Ecology 78: 623–641

Stohlgren TJ, Chong GW, Kalkhan MA and Schell LD (1997a) Multi-scale sampling of plant diversity: effects of the minimum mapping unit. Ecological Applications 7: 1064–1074

Stohlgren TJ, Chong GW, Kalkhan MA and Schell LD (1997b) Rapid assessment of plant diversity patterns: a methodology for landscapes. Env. Monit. Assessment 48: 25–43

Stohlgren TJ, Coughenour MB, Chong GW, Binkley D, Kalkhan MA, Schell LD, Buckley DJ and Berry JK (1997c) Landscape analysis of plant diversity. Landscape Ecology 12: 155–170

Stohlgren TJ, Bachand RR, Onami Y and Binkley D (1998a) Species-environment relationships and vegetation patterns: effects of scale and tree life-stage. Plant Ecology 135: 215–228

Stohlgren TJ, Bull KA and Otsuki, Y (1998b) Comparison of rangeland sampling techniques in the Central Grasslands. Journal of Range Management 51: 164–172

Stohlgren TJ, Chase TN, Pielke RA Sr, Kittel TGF, and Baron JS (1998c) Evidence that local land use practices influence regional climate, vegetation, and stream flow patterns in adjacent natural areas. Global Change Biology 4: 495–504

Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Bashkin M and Son Y (1999a) Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25–46

Stohlgren TJ, Schell LD and Vanden Heuvel B (1999b) How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9: 45–64

Suzuki K (1997) Aspen regeneration in the elk winter range of Rocky Mountain National Park. Masters thesis. Colorado State University, Fort Collins, Colorado

Sykes MT and Prentice IC (1996) Climate change, tree species distributions and forest dynamics: A case study in the mixed conifer/hardwoods zone of northern Europe. Climatic Change 34: 161–177

ter Braak CJF (1986) Canonical correspondence analysis: a new eigen vector technique for multivariate direct gradient analysis. Ecology 67: 1167–1179

ter Braak CJF (1987a) The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69: 69–77

ter Braak CJF (1987b) CANOCO-a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1) Wageningen, The Netherlands: TNO Institute of Applied Computer Science

ter Braak CJF (1991) CANOCO version 3.12. Agricultural Mathematics Group, Wageningen, The Netherlands

Vitousek PM, D’Antonio CM, Loope LL and Westbrooks R (1996) Biological invasions as global environmental change. American Scientist 84: 468–478

Weisberg PJ and Baker WL (1995) Spatial variation in tree regeneration in the forest-tundra ecotone, Rocky Mountain National Park, Colorado. Canadian Journal of Forest Research 25: 1326–1339

Wesser SD and Armbruster WS (1991) Species distribution controls across a forest-steppe transition: a causal model and experimental test. Ecological Monographs 61: 323–342

Whitlock C (1993) Post-glacial vegetation and climate of Grand Teton and southern Yellowstone national parks. Ecological Monographs 63: 173–198

Whittaker RH (1967) Gradient analysis of vegetation. Biol. Rev. 42: 207–264

Wiens JA, Crawford CS and Gosz JR (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45: 421–427

Woods KD and Davis MB (1989) Paleoecology of range limits: Beech in the Upper Peninsula of Michigan. Ecology 70: 681–696

Woodward FI (1993) The lowland-to-upland transition – modeling plant responses to environmental change. Ecological Applications 3: 404–408

Zar JH (1974) Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey