Landscape context and long-term tree influences shape the dynamics of forest-meadow ecotones in mountain ecosystems

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Abstract. Forest-meadow ecotones are prominent and dynamic features of mountain ecosystems. Understanding how vegetation changes are shaped by long-term interactions with trees and are mediated by the physical environment is critical to predicting future trends in biological diversity across these landscapes. We examined 26 yr of vegetation change (1983–2009) across 20 forest-meadow ecotones spanning a range of landforms/hydrologies and elevations (montane and subalpine) in the Three Sisters Biosphere Reserve, Oregon (USA). We quantified changes in tree structure (cover, density, and basal area) and in the abundance and diversity of ground-layer vegetation based on species' habitat associations and growth forms. To explore the contributions of tree structure, landscape context, and initial vegetation to changes in ecotonal communities, we used a combination of NMDS, PCA, and multiple regression.

Despite a long history (50–100 yr) of tree invasion, ecotones were still dominated by meadow species in 1983. Ecotones exhibited significant but varying patterns of change over the study period while adjacent forest and meadow habitats remained stable. Despite a significant increase in summer temperature, we found little evidence of a direct influence of climate on ecotonal changes. Declines in total richness, and in the cover and richness of meadow species, were greater where soil moisture was seasonally limiting (montane mesic slopes and subalpine early snowmelt sites). Forest species showed much greater increases in montane than subalpine ecotones; limited colonization of the latter reflects the depauperate nature of subalpine forest understories in this region. Vegetation changes were related to initial tree structure but not to changes in structure over the study period. Past tree invasions, a legacy of both climate variation and disturbance history, continue to exert strong influences on ecotonal ground-layer communities. However, the consequences for local diversity vary across the landscape. Quantifying the nature of this variation through long-term observations is a critical step toward predicting future changes in the biological diversity of these and other mountain ecosystems.

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INTRODUCTION

Ecotones are ubiquitous features of most biomes (Gosz 1991) that regulate the movement of organisms, materials, and energy (Fagan et al. 2003, Yarrow and Marin 2007), and can have profound influences on the dynamics of populations and communities (Fagan et al. 1999). They are vegetation zones across which compositional or structural changes are steep relative to

neighboring communities (Lloyd et al. 2000), and can reflect underlying gradients or discontinuities in environmental factors, sharp contrasts in plant physiognomy (herbs vs. trees), or past disturbances (van der Maarel 1990, Wilson and Agnew 1992, Cadenasso et al. 2003). Ecotones are often viewed as "tension zones", sensitive to changes in climate or other extrinsic factors (van der Maarel 1990). Recent work has focused on detecting and characterizing the spatial structure of ecotones (Fagan et al. 2003, Strayer et al. 2003, Yarrow and Marin 2007). However, major challenges remain in understanding why and how ecotones change over time and what these changes imply for other ecological attributes or functions (e.g., Hufkens et al. 2009). Answers to these questions are fundamental to predicting future changes in vegetation at both local and landscape scales (Cadenasso et al. 2003, Strayer et al. 2003, Hufkens et al. 2009).

Among terrestrial systems, forest-grassland ecotones are among the most striking, dynamic, and widely studied (Archer 1995, Scholes and Archer 1997, Coop and Givnish 2008). Globally, grass- and forb-dominated ecosystems are experiencing encroachment by trees (Van Auken 2000, Bowman et al. 2001, Duarte et al. 2006), spurring concern over the loss of biological diversity and other ecosystem services. Given the time spans necessary to detect change, the ecological effects of encroachment are often inferred retrospectively (Jackson et al. 2002, Briggs et al. 2005, Haugo and Halpern 2007). Direct long-term observations that are critical to documenting and interpreting these changes are rare.

Climatically defined ecotones, where tree establishment or growth is controlled by temperature or precipitation (e.g., alpine/arctic or lower arid treelines), are a common research focus (Allen and Breshears 1998, Bond 2008, Batllori et al. 2009, Harsch et al. 2009, Virtanen et al. 2010). Many forest-grassland ecotones, however, are shaped by other factors such as landform, soils, hydrology, and disturbance (Franklin and Halpern 1999, Gibson 2009). In these contexts, tree establishment and growth are not climatically limited and ecotones can change rapidly. Within the Pacific Northwest, for example, many such ecotones in the montane and subalpine zones have shifted dramatically during the 20th centu-

ry (Miller and Halpern 1998). The patterns and causes of these changes have been characterized (Franklin et al. 1971, Rochefort et al. 1994, Woodward et al. 1995, Miller and Halpern 1998, Takaoka and Swanson 2008, Zald 2009), but few studies have addressed the community-level consequences of encroachment either at local (Magee and Antos 1992, Haugo and Halpern 2007, 2010) or landscape scales.

Tree establishment in herb-dominated systems can effect two types of compositional change: competitive exclusion of resident meadow species and facilitation of forest understory species (Duarte et al. 2006, 2007, Haugo and Halpern 2007, 2010). Both processes can be influenced by the structural characteristics of the ecotone (spatial distribution, density, and size of trees) and the rates at which these change. Patterns of species' loss and gain are also likely to vary with landscape context (Jones and Callaway 2007) in response to resource or environmental variation that can affect the outcomes of tree-herb interactions (Bertness and Callaway 1994), or to variation in the sizes or traits of species' pools. Understanding the role of landscape context is particularly important for predicting future responses to climate warming (Cannone et al. 2007, Damschen et al. 2010, Harrison et al. 2010, Virtanen et al. 2010), whether these are driven by direct effects on plant performance (De Valpine and Harte 2001, Morgan et al. 2007, Forrest et al. 2010) or indirect effects mediated by tree establishment and growth (Franklin et al. 1971, Miller and Halpern 1998, Batllori et al. 2009, Harrison et al. 2010).

In this paper, we explore long-term changes in the structure and composition of forest-meadow ecotones in the Three Sisters Biosphere Reserve, a largely undisturbed mountain landscape in the central Cascade Range of Oregon. Building on earlier studies in this landscape (Halpern et al. 1984, Miller and Halpern 1998), we analyze three decades of vegetation change (1983–2009) across ecotones representing diverse physical environments (both montane and subalpine), vegetation types, and tree invasion histories. We are unaware of similar studies of comparable duration, ecological breadth, or spatial extent.

We address the following questions: (1) How has vegetation (species composition, richness and abundance) changed across forest-meadow eco-

tones over the past 26 yr? (2) Do the magnitude and direction of change in vegetation differ among forest, ecotone, and meadow habitats? (3) How have richness and abundance changed for groups of species defined by habitat association (meadow vs. forest understory) or growth form (grasses, sedges/rushes, herbs, and shrubs)? (4) How are patterns within the ecotone related to landscape context, local tree influences, and initial vegetation?

METHODS

Study area

The Three Sisters Biosphere Reserve (TSBR) is a federal wilderness area of nearly 100,000 ha in the Cascade Range of central Oregon, USA. It encompasses two physiographic provinces, the Western and High Cascades. The former are older, more deeply dissected landforms, comprised of volcanic flows and pyroclastic deposits that originated during the Oligocene and Miocene epochs (Orr et al. 1992). Soils derive from basalts, andesites, and pyroclastic tuffs and breccias. Primary ridge crests approach 1500 m in elevation. The High Cascades province lies to the east at higher elevations, dominated by younger (Quaternary) shield and composite volcanoes. Topography is more gentle and rolling. Soils are deep and well drained, derived from recent deposits of pumice, ash, and cinders (Orr et al. 1992).

The climate is maritime, with cool, wet winters and warm, dry summers. Temperature and precipitation vary with elevation and topography, reflecting strong orographic effects. Within the study area, mean annual precipitation ranges from 1700 to 2700 mm and falls primarily as snow (Daly et al. 2008). However, depth and duration of snowpack—thus length of growing season—differ markedly in montane and subalpine environments. In the latter, snow can persist into late July or August in some years. Average maximum July temperature ranges from 19 to 23°C and minimum January temperature ranges from −9 to −4°C (Daly et al. 2008).

TSBR supports a broad range of forest, meadow, and ecotonal communities, whose structure and composition vary with elevation, topography, soils, and hydrology (Halpern et al. 1984). We consider those that are characteristic of montane and subalpine environments (Franklin and Dyrness 1988, Franklin and Halpern 1999; Appendix A), but not those of upper timberline or treeline environments. In the montane zone (<1600 m), forests are dominated by *Abies grandis, Pseudotsuga menziesii, A. amabilis*, and *Pinus contorta*, and graminoid-, herb- and shrub-dominated meadows occur on south-facing slopes, in hydric basins, and on poorly drained flats. In the subalpine zone (1600–2000 m), forests of *Tsuga mertensiana* and *A. lasiocarpa* are distributed among a mosaic of graminoid-, forb-, and heath-dominated meadows (Halpern et al. 1984, Franklin and Halpern 1999). Descriptions of the composition and environmental correlates of these forested and non-forested communities have been reported previously for TSBR (Halpern et al. 1984) and other mountain landscapes in western North America (Fonda and Bliss 1969, Brooke et al. 1970, Kuramoto and Bliss 1970, Douglas 1972, Henderson 1973, Hickman 1976, Franklin and Halpern 1999).

Fire, the primary disturbance agent in this system, occurs infrequently. Disturbance histories suggest fire-return intervals of 100–150 yr in the montane zone (Teensma 1987, Cissel et al. 1999), and many hundreds of years in the subalpine (Halpern et al. 1984). Although aboriginal burning of meadows likely occurred—primarily at lower elevations (Burke 1979, Boyd 1999)—direct evidence is lacking in TSBR. None of our study locations have experienced recent fire. Sheep grazing was common in TSBR from 1880–1910 (Rakestraw and Rakestraw 1991), as in most meadows of the Cascade Range, until deteriorating range conditions resulted in the closure of most grazing allotments between 1920 and 1938 (Rakestraw and Rakestraw 1991, Miller and Halpern 1998). Sheep last grazed in TSBR in 1947 (Johnson 1985).

Field measurements

In 1983, 21 transects were established across forest-meadow ecotones spanning a range of elevations, landforms, and vegetation types (Tables 1 and 2). Transects were 2 m wide and ranged in length from 50–220 m (Table 1, Fig. 1). Each originated in closed-canopy forest and extended into open meadow, beyond any tree invasion. In 1983 and 1993, all trees (>10 cm tall)

Table 1. Physical characteristics and transect length at each study site in the Three Sisters Biosphere Reserve, Oregon.

Study site	Site code	Elevation (m)	Slope (%)	Aspect	Hydrology†	Transect length (m)
Quaking Aspen 1	QA1	1280	5	NE	H	87
Quaking Aspen 2	QA2	1283	3	N	H	70
Cow Swamp	CS	1343	0	Flat	H	110
Corral Flat‡	CF	1386	0	Flat	H	58
Walker 1	W1	1498	50	SSE	M	65
Olallie Meadow‡	OM	1520	12	SSW	M	120
Walker 2	W2	1535	45	SSE	M	151
Yankee Mountain	YM	1555	70	SSE	M	68
Rebel Rock	RR	1597	25	W	M	82
Lowder Mountain 1	LW1	1668	5	NE	M	76
Lowder Mountain 2‡	LW2	1669	1	Flat	M	93
Separation Meadow	SM	1758	3	SSE	H	75
Linton Meadow 1	LM1	1828	58	SW	M	60
Obsidian Creek	OC	1830	22	S	M	90
James Creek	JC	1832	27	SW	M	98
Wickiup Plains‡	WP	1850	2	E	M	79
Linton Meadow 2‡	LM2	1852	32	W	M	60
Obsidian Flat	OF	1869	15	WSW	M	60
Racetrack Meadow	RM	1882	34	NE	M	100
Green Lake‡	GL	2000	0	Flat	H	220

†Hydrological condition: M = mesic upland, H = hydric (seasonally high water table).
‡Not sampled in 1993.

Table 2. Initial (1983) tree composition and structure (>10 cm tall) in the ecotone at each study site in the Three Sisters Biosphere Reserve, Oregon.

Study site	Site code	Primary tree species†	Density (no./ha)	Basal area (m²/ha)	Tree cover (%)	CV of tree cover
Quaking Aspen 1	QA1	Al, Pe, Tm	1033	3.9	32.2	1.2
Quaking Aspen 2	QA2	Al, Pe, Tm	2286	5.8	47.9	1.1
Cow Swamp	CS	Pc	132	1.4	11.7	2.5
Corral Flat	CF	Pe, Pc	467	33.7	72.1	0.8
Walker 1	W1	Ag	179	48.2	64.2	0.7
Olallie Meadow‡	OM	Ag, Pc	546	29.5	56.5	1.0
Walker 2	W2	Ag	148	32.8	38.9	1.5
Yankee Mountain	YM	Ag, Pm	250	1.5	14.7	2.1
Rebel Rock	RR	Tm, Ag, Al	928	12.6	44.5	1.2
Lowder Mountain 1	LW1	Tm, Al	765	6.3	53.5	0.9
Lowder Mountain 2‡	LW2	Tm, Al	608	15.7	37.9	1.2
Separation Meadow	SM	Tm, Al	426	9.4	15.3	2.3
Linton Meadow 1	LM1	Al	403	49.7	62.2	1.1
Obsidian Creek	OC	Al	3214	12.2	49.3	1.0
James Creek	JC	Tm, Al	917	19.3	41.3	1.0
Wickiup Plains‡	WP	Tm	357	32.4	31.4	1.1
Linton Meadow 2‡	LM2	Tm	56	0.1	0.3	2.9
Obsidian Flat	OF	Tm, Pa	286	0.8	14.0	1.7
Racetrack Meadow	RM	Tm	3784	0.3	19.7	1.2
Green Lake‡	GL	Pc, Tm	9	0.1	4.0	2.1

†Codes for tree species: Ag = *Abies grandis*, Al = *A. lasiocarpa*, Pa = *Pinus albicaulis*, Pc = *Pinus contorta*, Pe = *Picea engelmannii*, Pm = *Pseudotsuga menziesii*, Tm = *Tsuga mertensiana*
‡Not sampled in 1993.

and tree seedlings (≤10 cm tall) within each transect were spatially mapped, measured for diameter (basal or breast height, depending on size), and aged to enable reconstructions of tree invasion history (Miller and Halpern 1998). In addition, 1 × 1 m quadrats were established on alternating sides of each transect ($n = 39–108$ quadrats per transect). In each quadrat, the cover (%) of each vascular plant species was estimated visually. Cover of tree species was estimated
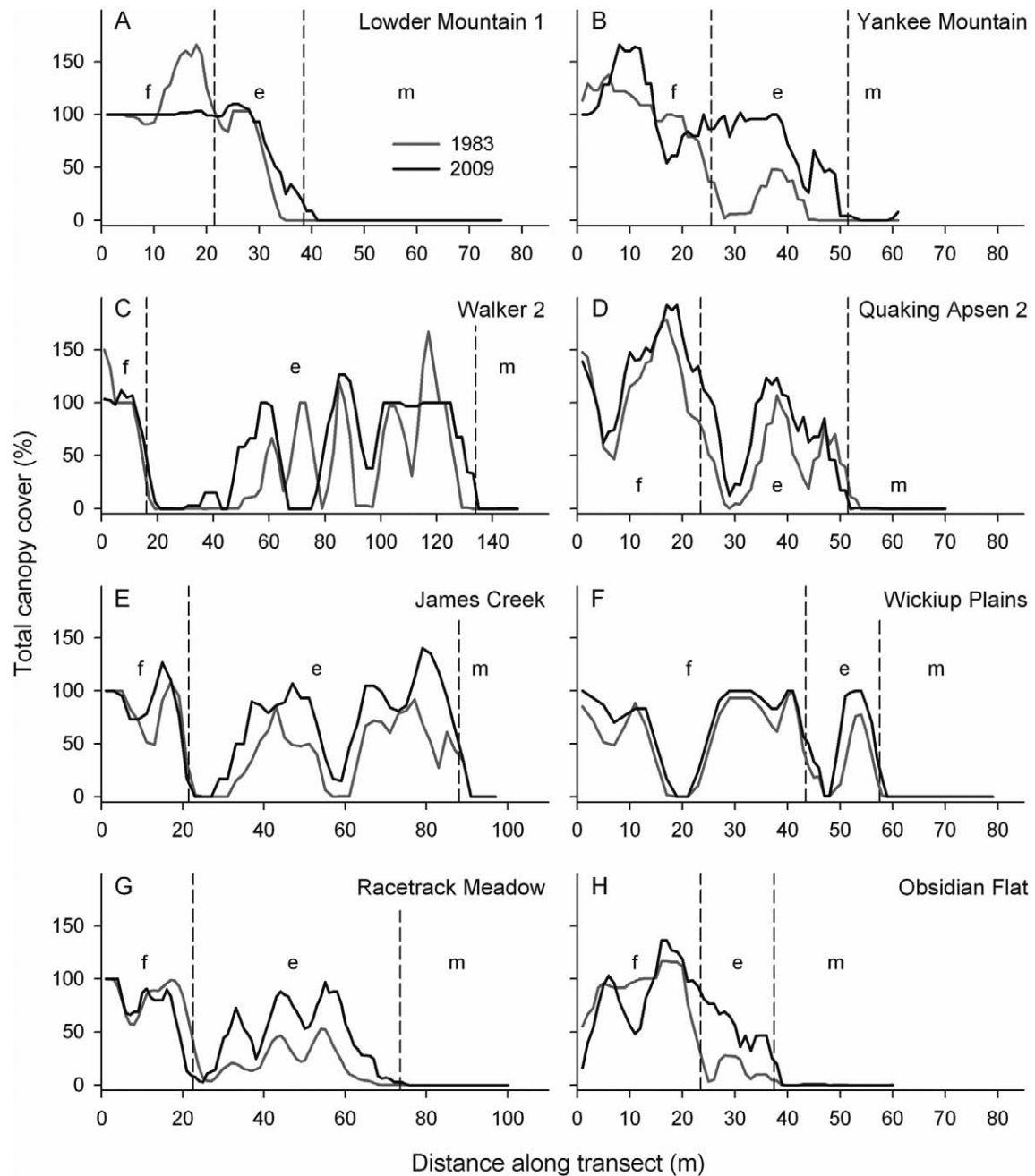
Fig. 1. Total canopy cover (summed cover of all tree species) in 1983 (gray) and 2009 (black) for select forest-meadow ecotones in the (A–D) montane and (E–H) subalpine zones of the Three Sisters Biosphere Reserve, Oregon. Values are 3-m running averages. Habitats are delineated by vertical dashed lines and coded as f = forest, e = ecotone, m = meadow.

separately for seedlings and trees. In 2009, 26 yr after establishment, we recensused tree populations and recorded post-1993 recruitment on each transect, and repeated cover estimates in each quadrat. Sixteen transects were resampled in 1993 and 20 transects in 2009.

Habitat definitions and species classification

We delineated three habitats along each transect—forest, ecotone, and meadow—based on the presence, cover, and ages of trees (Fig. 1). Forest was defined by the presence of trees that established prior to 1900 (typically much earlier; Miller and Halpern 1998) and by continuous (occasionally patchy) canopy cover at the initial measurement in 1983. Meadow was defined as the terminal portion of the transect in which trees were absent or present only as seedlings in 2009. At one site (Obsidian Creek), we removed from the analysis a 10-m section of transect where a small, isolated tree island, >30 m from the forest, interrupted otherwise contiguous open-meadow habitat. Ecotone was defined as the zone between forest and meadow, representing former meadow into which conifers had established during the 20th century. Differences in the timing, intensity, and spatial pattern of tree invasion (Miller and Halpern 1998) led to considerable variation in the cover, density, and spatial distribution of trees among ecotones (Fig. 1). Between 1983 and 2009, trees recruited past the endpoints of two transects (Rebel Rock and Olallie Meadow) resulting in complete loss of meadow habitat.

We classified all ground-layer taxa as characteristic of meadow ($n = 195$) or forest understory ($n = 73$) (Appendix B). Trees were not classified, nor were 23 other taxa (ruderal species and those identified only to genus). Assignments were based on regional floras (Hitchcock et al. 1969, Hitchcock and Cronquist 1973), phytosociological studies in TSBR (Halpern et al. 1984), and previous chronosequence-based studies of conifer encroachment (Haugo and Halpern 2007, 2010). Although this classification simplifies the distributions of some species (e.g., those tolerant of edge environments), it captures the distinct habitat associations of most. To assess physiognomic changes in the ground layer, we also classified species by growth form: grass, sedge/rush, herb (including ferns), and shrub (including sub-shrubs).

Climatic variation

To assess vegetation changes within the context of recent trends or inter-annual variation in climate, we examined climate records from 1940 to 2009. We examined four climatic variables known to influence plant phenology or productivity: mean summer (June–August) temperature, mean annual temperature, total summer precipitation, and spring snowpack (snow water equivalent [SWE] on 1 April, a proxy for soil moisture availability and length of growing season) (Walker et al. 1993). Temperature and precipitation data were taken from the closest meteorological station with long-term records (McKenzie Bridge, 450 m; U.S. Historical Climatological Network; ⟨http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html⟩). Although models such PRISM (Daly et al. 2008) can be used to estimate temperature and precipitation in complex mountainous terrain—including our sites, which occur at higher elevations—projections for the period of interest (1940–2009) are susceptible to inhomogeneities in temporal data (reflecting undocumented changes in climate stations or station locations; Luzio et al. 2008). Moreover, previous regional scale analyses of long-term climatic trends in the Pacific Northwest suggest strong coherency among climate stations at varying elevations (Mote 2003, 2004). Snowpack data were taken from the nearest SNOTEL site (McKenzie Pass, 1454 m; USDA Natural Resources Conservation Service; ⟨ftp://ftpfc.sc.egov.usda.gov/OR/snow/snowcourse/or_data⟩). For each climatic variable, we tested for significant linear relationships with time for the full record (1940–2009) and for the period of study (1983–2009).

Measures of vegetation structure and diversity

We computed several measures of tree structure and ground-layer diversity and abundance for each habitat (forest, ecotone, and meadow) × transect × measurement period. Measures of tree structure included mean tree density (>10 cm tall) and basal area (m²/ha) within the 2-m-wide belt transect. Tree cover (sum of individual tree species) and the coefficient of variation (CV) in tree cover were computed from quadrat values; the CV was included to characterize the patchy distribution of tree cover in many ecotones. Measures of ground-layer diversity and abundance included total species richness, richness and total cover of meadow and forest species, and total cover of each growth form. We do not report patterns of growth-form richness, which were dominated by herbaceous species at most sites.

Comparing rates of change between sampling intervals

Prior to more comprehensive analyses, we tested whether rates of vegetation change were similar between sampling intervals (1983–1993 vs. 1993–2009). Comparable rates would support simpler analyses of change over the full study period. For each response variable × habitat combination, we computed the annualized change for each sampling interval, then compared intervals using paired t-tests ($n = 16$). Intervals differed ($P < 0.05$) in only two of 38 tests (change in richness of forest species in ecotone and meadow habitats). Given the consistency between intervals, we based all further analyses of change on the 26-yr study period (1983–2009).

Temporal changes among forest, ecotone, and meadow habitats

To compare temporal changes in vegetation among habitats (questions 1–3), we employed repeated measures Permutational Analysis of Variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001). We used PERMANOVA because of heterogeneous variance among many of the response variables. Analyses used a blocked, split-plot design with transects as blocks, habitat (forest, ecotone, or meadow) as the main plot, and time (1983 or 2009) as the subplot. Models also included the time × transect and time × habitat interactions. For significant habitat effects or time × habitat interactions, post-hoc pairwise comparisons were made using Fisher's LSD (Zar 1999). Models were run using Euclidean distances with 9,999 permutations in the PERMANOVA+ (v.1.0.2) add-on for PRIMER 6.0 (Anderson et al. 2008).

To visualize temporal changes in species composition among habitats (questions 1 and 2), we used non-metric multidimensional scaling (NMDS; Kruskal 1964). Ordinations were based on the average species composition of each habitat × time, with rare species (present in <5% of habitat × time samples) removed and Bray-Curtis distance measures. To prevent floristic variation among the full set of transects from masking temporal trends, each of the four landscape contexts (see *Methods: Comparing changes among ecotones across the landscape*) was ordinated separately. Ordinations had two-di-

mensional solutions, were initiated from random starting configurations for a maximum of 400 iterations, and were rerun up to 40 times or until an instability criterion of 0.00001 was met. Final solutions were rotated with Principal Components Analysis (PCA; Hotelling 1933) to maximize the variation explained by the first axis. Final solutions had stress values of 4.7 to 19.3. Stress is rough measure of fit—dependent, in part, on sample size—with values <5 generally considered excellent and values <15, satisfactory (McCune and Grace 2002). NMDS was run using the *metaMDS* function of the V*egan v1.11-0* package in R v2.10.0 (R Development Core Team 2009).

Comparing changes among ecotones across the landscape

To assess how patterns of change within ecotones varied with landscape context (question 4), we qualitatively defined the environmental (landscape) context of each transect based on NMDS ordination of the composition of meadow habitats in 1983. Using this method of indirect ordination, relationships among transects are based on floristic dissimilarity. Environmental or landscape gradients are not defined a priori, but are inferred from the distributions of species in ordination space. We ran NMDS (as described above) with each transect represented by the average species composition of its meadow quadrats in 1983, thus minimizing effects of trees. For the two transects without meadow habitat in 2009 (see *Methods: Habitat definitions and species classification*, above), we used the average composition of ecotonal quadrats lacking tree cover in 1983 and 2009. The final two-dimensional solution had a stress value of 13.9. We subjectively assigned transects to four distinct "landscape contexts" (Fig. 2A) based on their positions in ordination space and our knowledge of the primary environmental gradients by which communities are structured in this system: elevation (montane vs. subalpine) and landform (affecting soil moisture availability) (Halpern et al. 1984, Franklin and Halpern 1999). The four landscape contexts are: (1) montane hydric basins: lower elevation basins with seasonally high water tables; (2) montane mesic slopes: lower elevation, south-facing slopes or benches; (3) subalpine early snowmelt sites: higher eleva-
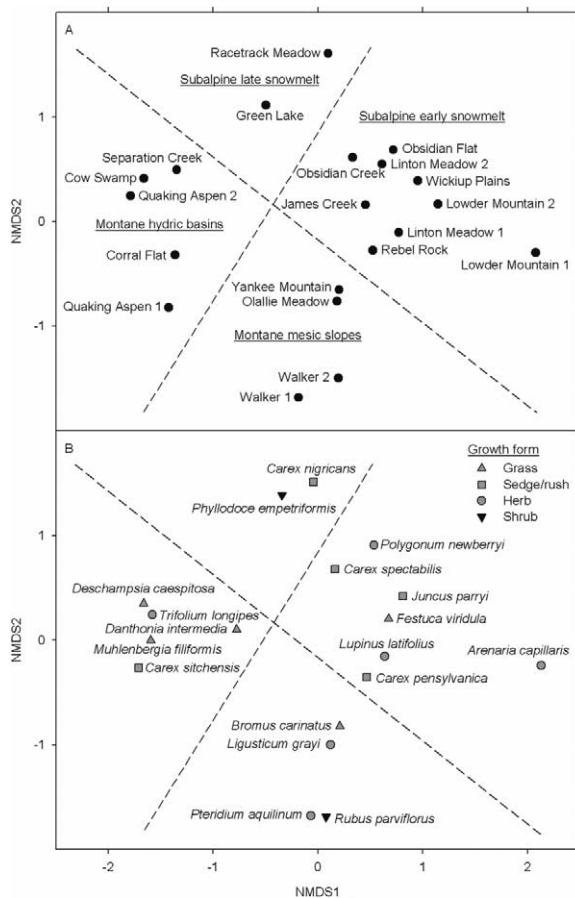
Fig. 2. NMDS ordination illustrating (A) the landscape context of each transect and (B) characteristic meadow species coded by growth form. Transect positions are based on the average species composition of meadow habitats in 1983. The dashed lines are included as interpretive guides distinguishing the four landscape contexts (also see Appendix A).

tion benches and south-facing slopes with longer growing seasons; and (4) subalpine late snowmelt sites: higher elevation basins and north-facing slopes with shorter growing seasons (Appendix A). Each supports a distinct flora (Fig. 2B; Halpern et al. 1984, Franklin and Halpern 1999).

Results of NMDS were used in two ways to explore the importance of landscape context for changes in the ecotone. First, positions in ordination space served as a template for comparing changes in tree structure and ground-layer vegetation over the study period. For each response variable, we produced a

"bubble plot" quantifying the direction (positive or negative) and magnitude of change at each site. Second, scores on NMDS1 and NMDS2 were used as surrogates for landscape context (landform/hydrology and elevational zone, respectively) in models of vegetation change (see *Methods: Modeling the importance of tree influence, landscape context, and initial vegetation*, below).

Modeling the importance of tree influence, landscape context, and initial vegetation

We used multiple regression models to assess the joint contributions of tree influence, landscape context (NMDS scores, as defined above), and initial vegetation to changes within ecotones from 1983–2009 (question 4). Tree influence was quantified by two types of variables. The first summarized initial (1983) tree structure: tree cover, CV of tree cover, tree density, and basal area. These served as measures of cumulative tree influence over the study period, with the expectation that vegetation responses would be greater where the initial (and thus cumulative) effects of tree structure were greater (e.g., Pugnaire et al. 1996, Haugo and Halpern 2010). The second represented changes in each structural measure over the study period (2009 minus 1983 values), with the expectation that vegetation responses would be greater where changes in tree structure were greater. We used PCA to reduce the dimensionality of these structural variables, using the function *prcomp* in R v2.10.0 (R Development Core Team 2009). The first principal component (PC1) explained 37% of the total variation and correlated positively with initial tree structure (tree cover, homogeneity of tree cover, and basal area) (Appendix C). PC2 explained 26% of the total variation and correlated negatively with measures of change in tree structure (change in density, basal area, and cover).

Predictors in regression models included scores on NMDS1 and NMDS2 (landscape context), scores on PC1 and PC2 (tree influence), and the initial (1983) value of each response variable. The latter was used to test whether the magnitude of change was correlated with the initial condition (e.g., if sites with greater richness experienced greater loss of species). For each measure of vegetation change, we started with a "full" model and removed predictors in reverse
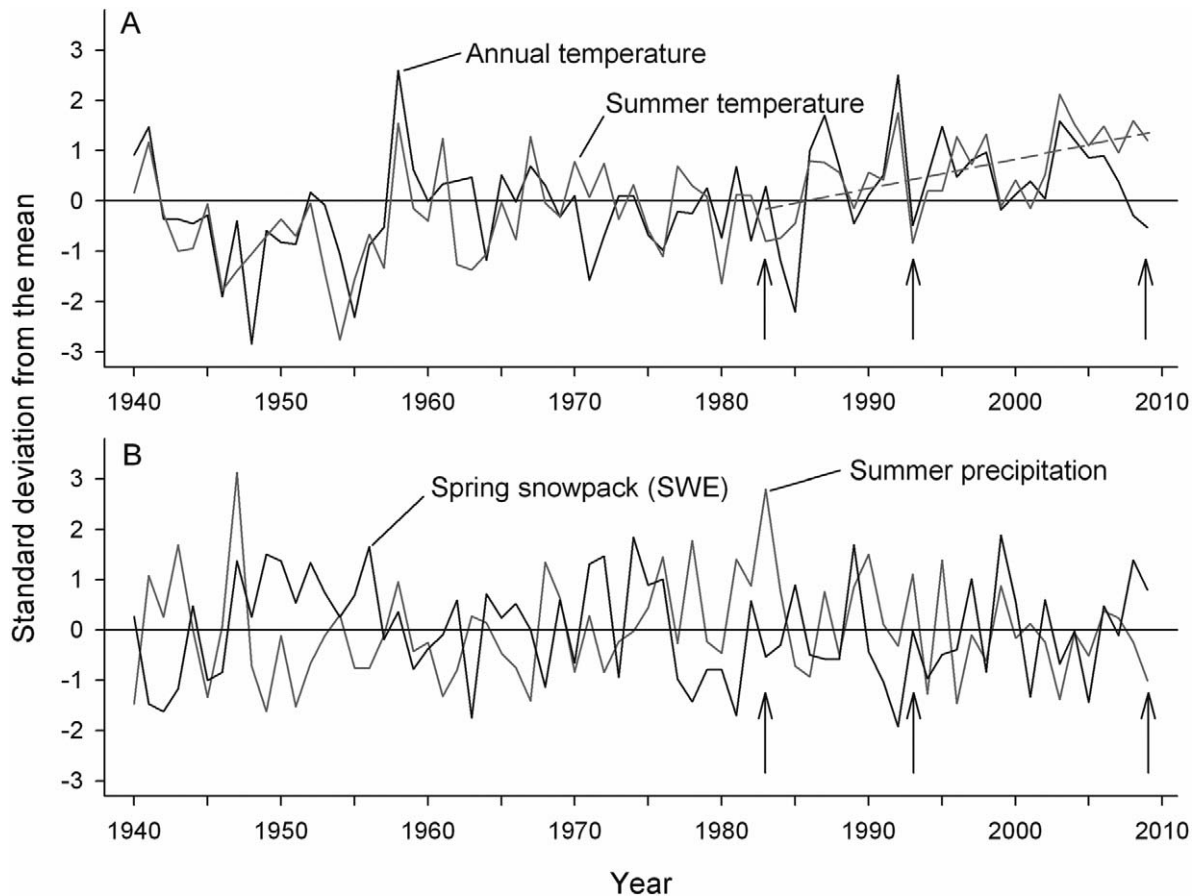
Fig. 3. Climatic variation between 1940 and 2009 (expressed as standard deviations from the 1940–2009 mean). (A) Temperature and (B) precipitation data are from McKenzie Bridge, Oregon (450 m elevation). Snowpack data are from McKenzie Pass, Oregon (1453 m), expressed as snow water equivalent (SWE) on 1 April. The summer period for temperature and precipitation is June through August. Vertical arrows denote sampling dates (1983, 1993, and 2009). The dashed regression line represents the significant increase in summer temperature during the period of study.

order of strength (sums of squares) to minimize the Akaike Information Criterion (AIC; Akaike 1974). We used standard diagnostics to confirm normality and homogeneity of variance (Zar 1999). Models were developed in SPSS 17.0 (SPSS 2008).

RESULTS

Climatic trends and inter-annual variation

In the long-term record (1940–2009), we detected small but statistically significant increases in mean annual temperature (0.01°C/yr; $R^2 = 0.105$, $P = 0.006$) and mean summer temperature (0.03°C/yr; $R^2 = 0.312$, $P < 0.001$) (Fig. 3A), but no

trends in summer precipitation or spring snowpack (Fig. 3B). During the period of study (1983–2009), we detected a significant increase in summer temperature (0.064°C/yr; $R^2 = 0.354$, $P = 0.001$; Fig. 3A), but no changes in mean annual temperature, precipitation, or spring snowpack. Among sampling years, 1983 and 1993 had relatively cool/wet summers, with average to below-average temperatures, above-average summer precipitation, and average spring snowpack (Fig. 3A, B). In contrast, 2009 had a warm, dry summer (Fig. 3A) but above-average spring snowpack (Fig. 3B).
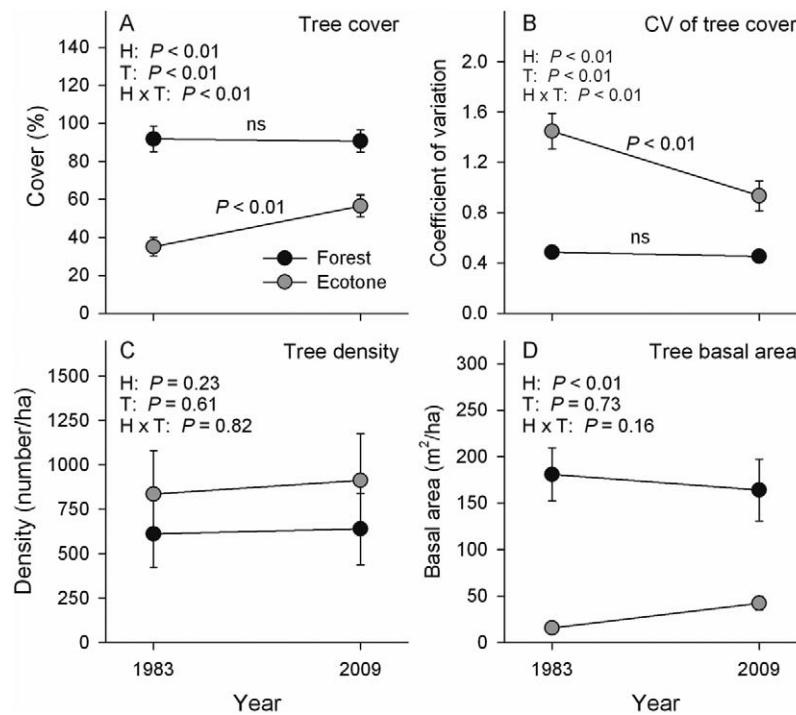
Fig. 4. Changes in tree structure (mean ±1 SE) over the study period for forest (black) and ecotone (gray) habitats. For each variable, *P*-values for the habitat (H), time (T), and habitat × time (H × T) terms are from a univariate repeated measures PERMANOVA. For significant habitat × time terms, the results of post-hoc comparisons using Fisher's LSD are shown between times for each habitat.

Temporal changes in vegetation among habitats

Vegetation changed to varying degrees among habitats (questions 1–3). All measures of tree structure were stable in forest habitats (Fig. 4). In contrast, tree cover increased and heterogeneity of cover decreased in ecotonal habitats (Fig. 4A, B), although tree density and basal area did not change significantly (Fig. 4C, D). Tree cover and basal area remained greater in the forest and heterogeneity of cover remained greater in the ecotone over the study period.

For most ground-layer variables, values in the ecotone were intermediate to those in the forest and meadow (Fig. 5). Exceptions included total richness (ecotone = meadow; Fig. 5A), sedge/rush cover (ecotone = forest; Fig. 5G), and shrub cover (similar in all habitats; Fig. 5I). Ecotones were more dynamic than adjacent forest and meadow habitats. In the ecotones, total richness (Fig. 5A), richness of meadow species (Fig. 5B), and cover of grasses (Fig. 5F) declined, whereas richness of forest species (Fig. 5D) increased. In contrast,

cover of shrubs did not differ among habitats, but increased over time (Fig. 5I).

Species composition in the ecotone was intermediate between forest and meadow (Fig. 6), except at Green Lake (Fig. 6D), where tree structure was minimal (Table 2). Over time, the composition of most ecotonal habitats trended toward adjacent forests. By comparison, compositional changes within meadows were small and non-directional.

Changes among ecotones across the landscape

Among ecotonal habitats, changes in vegetation varied with landscape context (question 4). Increases in tree structure (basal area, cover, and homogeneity of cover) were generally greater where soil moisture was more limiting—on mesic slopes in the montane zone and on early snowmelt sites in the subalpine zone (Fig. 7B–D). By comparison, tree density was generally stable (Fig. 7A). Landscape-scale variation in the ground-layer was more complex. With one
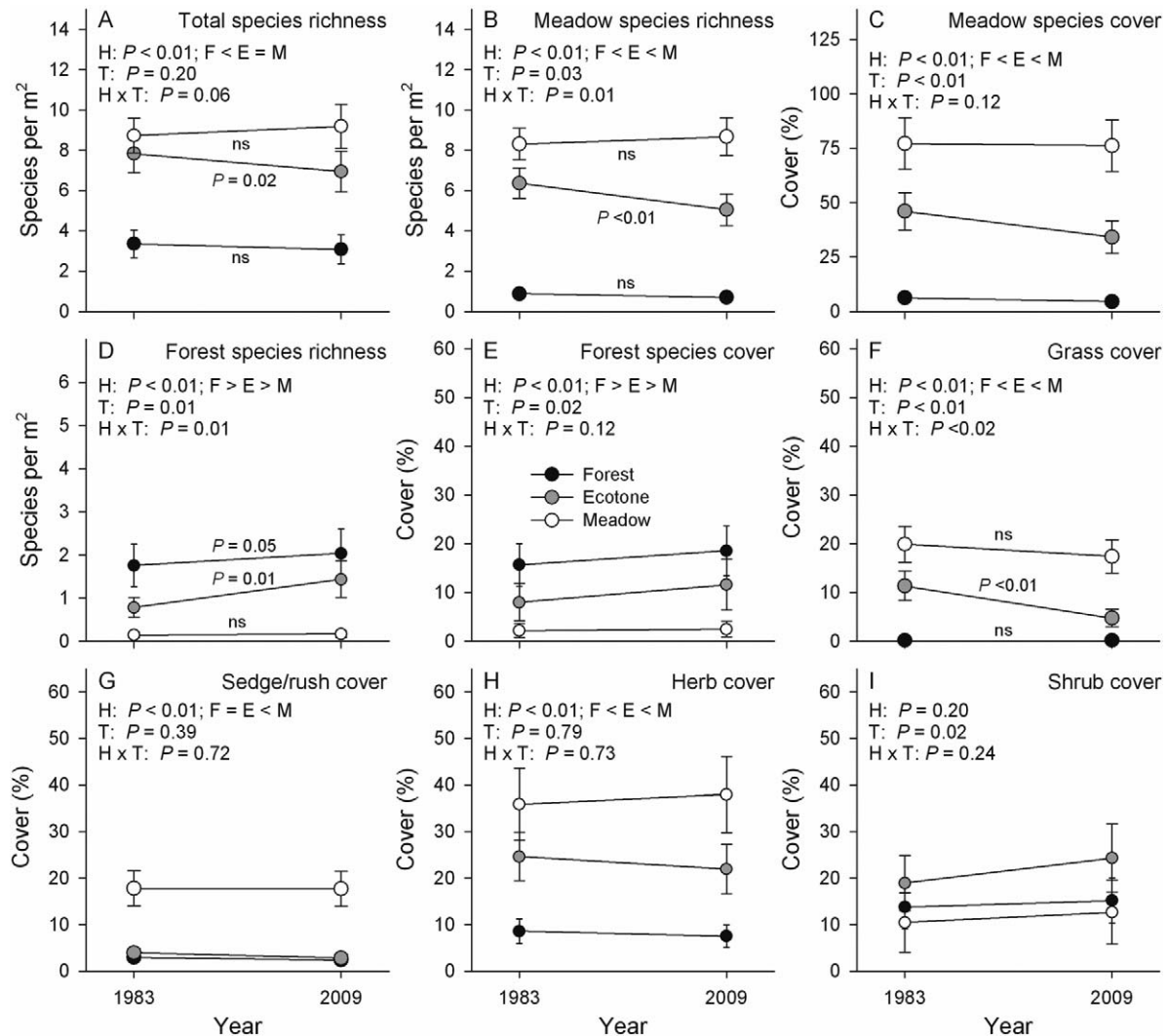
Fig. 5. Changes in ground-layer vegetation (mean ±1 SE) over the study period for forest (black), ecotone (gray), and meadow (white) habitats. For each variable, *P*-values for the habitat (H), time (T), and habitat × time (H × T) terms are from a univariate repeated measures PERMANOVA. For significant habitat terms, the results of post-hoc comparisons using Fisher's LSD are reported after the *P*-value.

exception (Corral Flat), declines in total richness were greatest in subalpine early snowmelt sites (Fig. 8A), reflecting similar declines in richness of meadow species (Fig. 8B). In contrast, increases in richness and cover of forest species were greater in montane than in subalpine sites (Fig. 8D, E). Among growth forms, grass cover declined in montane hydric basins (Fig. 8F) and shrub cover increased in all landscape contexts except subalpine early snowmelt sites (Fig. 8I). Changes in sedges/rushes and herbs were highly variable across the landscape (Fig. 8G, H).

Modeling the importance of tree influence, landscape context, and initial vegetation

Multiple regression models, incorporating tree influence, landscape context, and initial vegetation (question 4), explained significant variation in all measures of vegetation change in the ecotone (R^2 of 0.30–0.81, $P < 0.05$; Table 3). Change in tree structure (PC2) was not a significant predictor in any model. However,
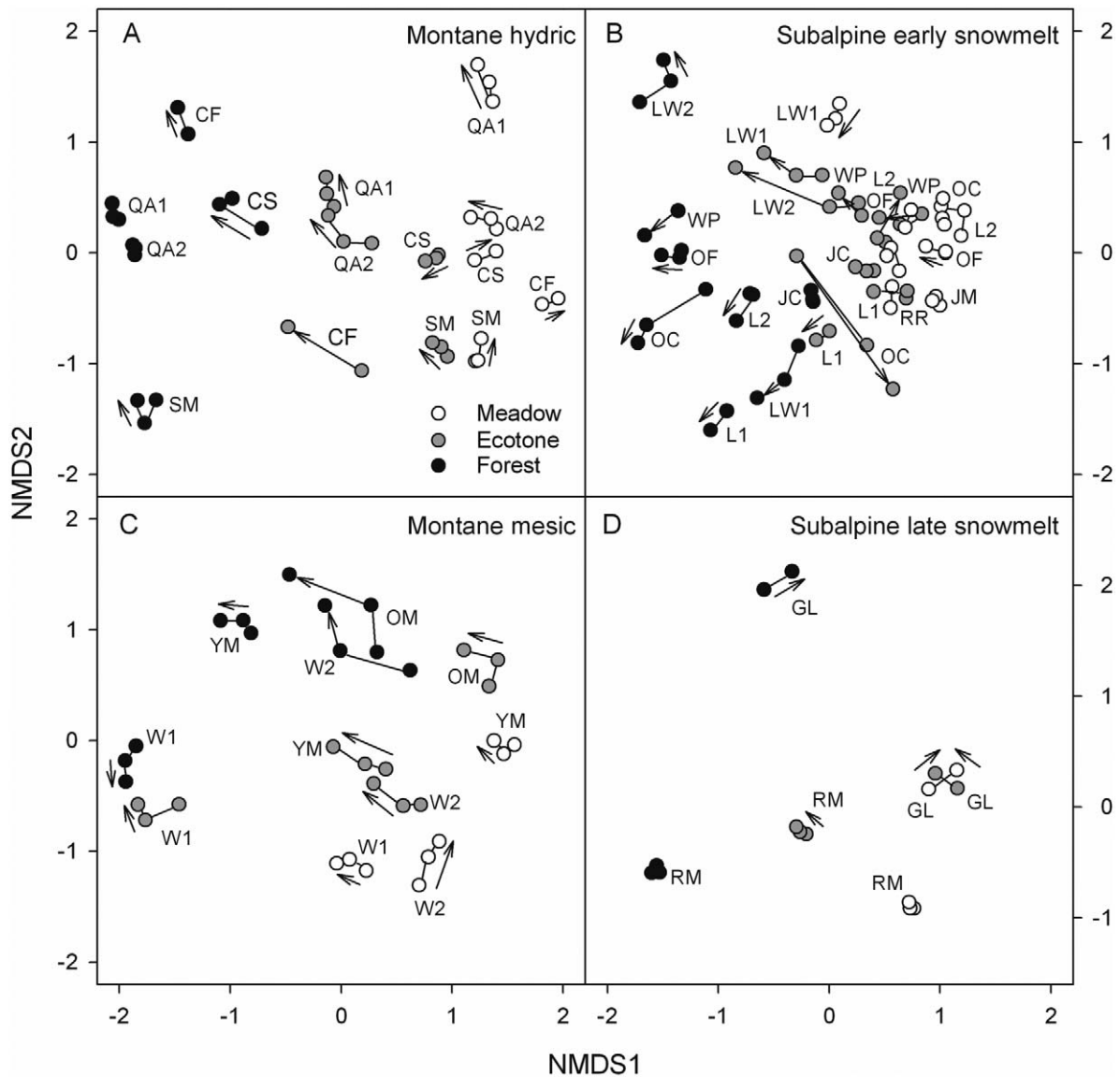
Fig. 6. Temporal changes in species composition in the forest, ecotone, and meadow habitat at each site, as portrayed in NMDS ordination space. A separate ordination was run for each landscape context (Fig. 2A) to avoid masking of temporal trends by floristic differences among sites. Samples represent the average species composition of each habitat × sampling date (1983, 1993, and 2009). Lines connect sampling dates; arrows indicate directions of change over time. Transect codes are defined in Table 1. CF, WP, LM2, OM, and GL were not sampled in 1993.

initial tree structure (PC1) was significant in four of nine models (Table 3). Sites with greater initial tree structure showed larger declines in cover and richness of meadow species, in total richness, and in herb cover.

Landscape context was significant in models of richness, but not of cover. Where moisture was more limiting (montane mesic slopes and subalpine early snowmelt sites; high scores on NMDS1), declines in meadow and total species richness were greater. At lower elevations (montane sites; low scores on NMDS2), meadow species experienced greater declines and forest species experienced greater increases in richness.
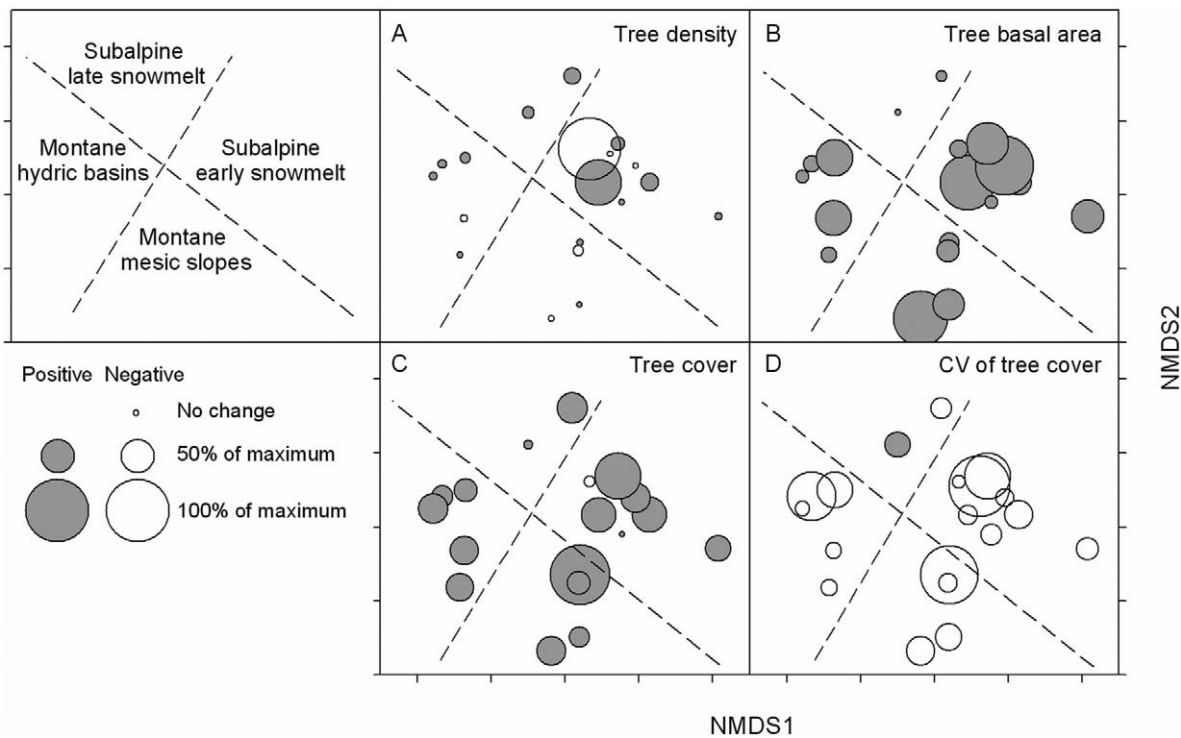
Fig. 7. Changes (1983–2009) in ecotone tree structure across the TSBR landscape, as portrayed in NMDS ordination space (see Fig. 2A). Gray and white circles represent positive and negative changes, respectively. Magnitude of change is proportional to symbol size, scaled to the maximum for each variable: (A) tree density = 3,000 trees/ha; (B) tree basal area = 70 m^2/ha; (C) tree cover = 60%; and (D) CV of tree cover = 1.4.

The initial value of each response variable was a significant predictor of change in all models (Table 3). Cover and richness of meadow species and cover of non-woody growth forms declined more where initial values were greater. In contrast, cover and richness of forest species and cover of shrubs increased more where initial values were greater.

DISCUSSION

Forest-meadow boundaries are prominent features of the montane and subalpine zones of this and other mountain landscapes. Conifer encroachment into meadows has occurred for over a century in TSBR (Miller and Halpern 1998), yet ecotonal habitats remain structurally distinct from adjacent forests and retain similarities to adjoining meadows. It is within these historical and ecological contexts that we explore the contributions of landscape context and tree influence to recent changes in ecotonal vegeta-

tion.

The dynamics of forest-meadow ecotones

The structure, composition, and diversity of ecotonal habitats changed significantly over 26 yr of study, whereas forest and meadow habitats remained stable. Climate warming has been implicated in compositional changes in other mountain ecosystems of North America and Europe (Damschen et al. 2010, Harrison et al. 2010, Lenoir et al. 2010), yet we saw little evidence of a direct effect of warming on ground-layer vegetation in this system. If warming was having a direct effect, it likely would not be limited to ecotonal habitats. Although tree canopies can buffer microclimatic changes in the forest (e.g., Damschen et al. 2010), changes in snowpack, timing of snowmelt, or summer drought stress should be as apparent in open meadow as in the ecotone. Alternatively, recent warming could have an indirect effect limited to ecotones if it were mediated by effects on tree
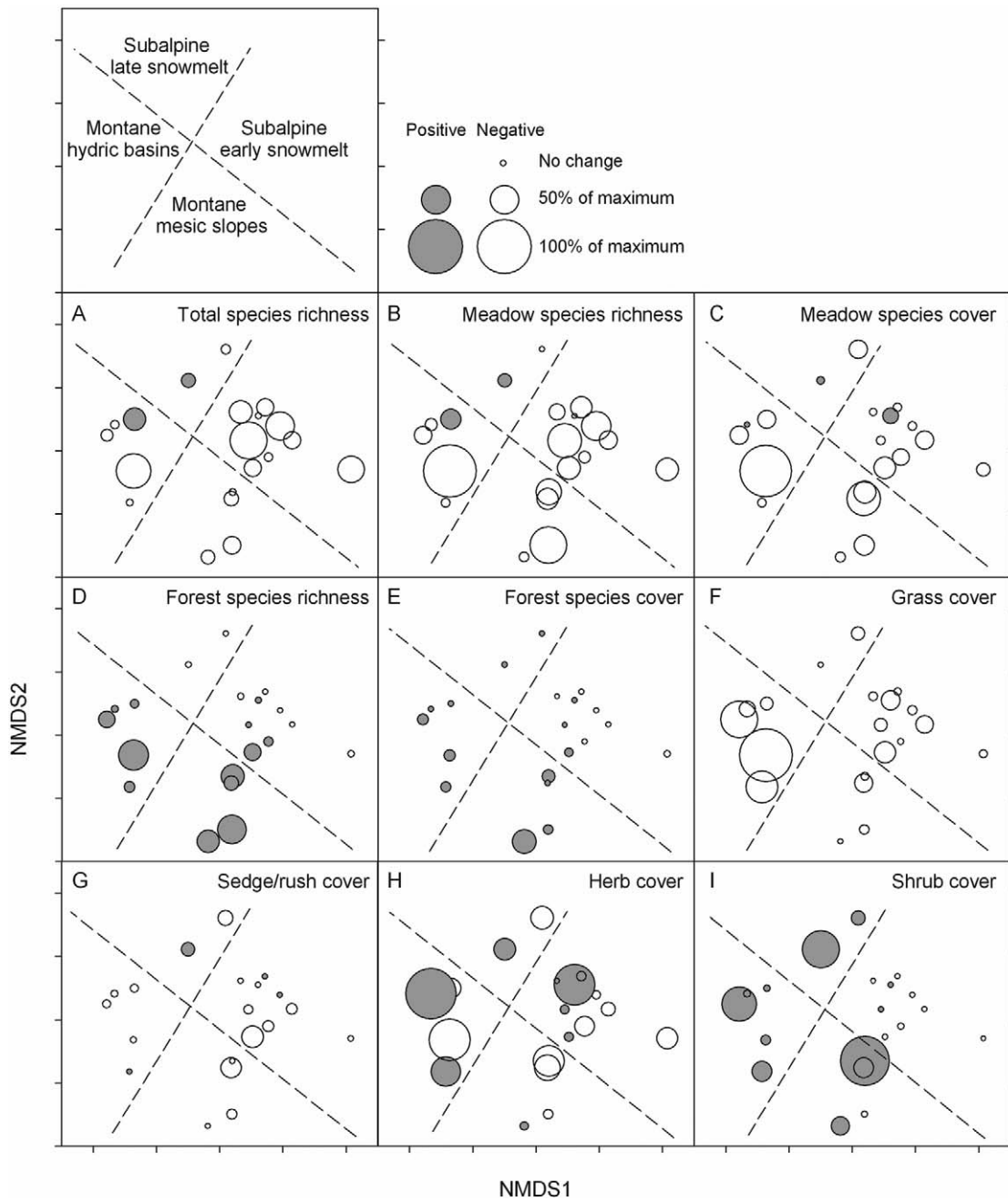
Fig. 8. Changes (1983–2009) in ecotone ground-layer vegetation across the TSBR landscape, as portrayed in NMDS ordination space (see Fig. 2A). Gray and white circles represent positive and negative changes, respectively. Magnitude of change is proportional to symbol size, scaled to the maximum for each variable: (A, B, and D) species richness = 5 species/m^2; and (C and E–I) cover = 60%.

growth. This also seems unlikely, as regression models consistently showed a lack of response to variation in tree growth (PC2; changes in cover,

homogeneity of cover, or basal area). However, climate variation during the 20th century has played a major role in initiating conifer invasions

Table 3. Results of multiple regression models explaining changes in species richness and cover in ecotonal habitats from 1983–2009.

Response variable	Final model Adj. R^2	Final model P	NMDS1 Coeff.	NMDS1 P	NMDS2 Coeff.	NMDS2 P	PC1 Coeff.	PC1 P	PC2 Coeff.	PC2 P	Initial value Coeff.	Initial value P
Total species richness	0.43	**0.007**	−0.89	**0.005**			−0.45	**0.023**			−0.75	**0.014**
Meadow species cover	0.46	**0.002**					−0.47	**0.012**			−0.55	**0.005**
Meadow species richness	0.53	**0.003**	−0.83	**0.004**	0.40	**0.037**	−0.49	**0.015**			−0.98	**0.002**
Forest species cover	0.81	**<0.001**			−0.22	0.090					0.77	**<0.001**
Forest species richness	0.61	**<0.001**			−0.53	**0.005**					0.41	**0.021**
Grass cover	0.63	**<0.001**					−0.28	0.068			−0.81	**<0.001**
Sedge/rush cover	0.41	**0.004**					−0.26	0.155			−0.64	**0.002**
Herb cover	0.35	**0.044**	−0.50	0.064	−0.36	0.149	−0.62	**0.012**	0.312	0.161	−0.68	**0.019**
Shrub cover	0.30	**0.019**					−0.28	0.166			0.54	**0.012**

Notes: Results include adjusted R^2 (variation explained) and level of significance (P) for the final model, and standardized coefficients (Coeff.) and significance (P) of predictors. Significant ($P < 0.05$) predictors are in bold font. Starting with a full model, final models were derived by sequential removal of predictors to minimize AIC. Predictors included two measures of landscape context (scores on NMDS1 and NMDS2; Fig. 2A); initial tree structure (PC1 score); change in tree structure over the study period (PC2 score); and the initial value of the response variable.

of these and similar meadows in both montane and subalpine settings throughout western North America (Brink 1959, Taylor 1995, Miller and Halpern 1998, Rochefort et al. 1994, Woodward et al. 1995). It is these legacies of past changes in climate that continue to exert their influences.

The role of landscape context

Understanding how landscape context affects the dynamics of species' interactions within ecotones is critical for predicting the broader ecological consequences of forest encroachment or expansion (Baker and Weisberg 1995, Jones and Callaway 2007, Harrison et al. 2010). Despite considerable variation among ecotones, two important patterns emerged across the landscape. First, declines in richness of meadow species were greater where soil moisture is seasonally limiting—on mesic slopes in the montane zone, and in early snowmelt sites in the subalpine. A similar relationship was not observed for cover, suggesting that declines reflect local extirpation of subordinate species. It is possible that under conditions of moisture stress, these subordinate taxa may be more susceptible to below-ground competition from trees. Where soil moisture is less limiting (hydric and late snowmelt sites), root competition may be less intense and declines are more likely to be driven by competition for light (Tilman 1988) and thus related to ecotone structure (tree influence) rather than landscape position.

Second, despite the expansion of trees in ecotonal habitats, increases in the richness and cover of forest herbs were largely limited to montane sites. Studies from old fields, secondary forests, and forest-grassland mosaics have demonstrated that dispersal opportunities largely determine the development of forest understory communities (Matlack 1994, Brunet and von Oheimb 1998, Verheyen and Hermy 2004, Duarte et al. 2007). Montane forests in this region support a rich diversity of shade-tolerant species (66 taxa among the nine montane transects in TSBR) that can readily disperse into the understories of invading forests (Haugo and Halpern 2007, 2010). Subalpine forests are depauperate in comparison: the 11 subalpine transects in TSBR supported only 37 forest species, and 22 of these were restricted to the Rebel Rock transect. Deep and persistent snow packs, short growing seasons, and young, infertile soils contribute to this floristic condition (Halpern et al. 1984, Franklin and Halpern 1999), which limits the potential for forest species to colonize newly forming forest habitats. Together, these two trends can have profound, local effects. Tree invasion into subalpine, early-snowmelt sites leads to loss of meadow species, but there are few forest species to colonize these newly forming habitats, leading to marked declines in plant diversity. In more general terms, our results illustrate the diverse ways in which landscape context can mediate compositional changes in structurally dynamic environments: environmental or resource variation can affect the outcomes of species' interactions (Bertness and Callaway 1994) or pose

constraints on the pool of available species (Taylor et al. 1990, Eriksson 1993).

The nature and strength of tree influences

Trees substantially alter their local environments, particularly in non-forest settings. They create shade, moderate air and soil temperatures, affect precipitation and snow accumulation, compete for soil resources, and alter litter inputs and nutrient cycles (Belsky et al. 1993, Scholes and Archer 1997, Coomes and Grubb 2000, Hibbard et al. 2001, Musselman et al. 2008). Thus, we were surprised to find that changes in the ground-layer vegetation were unrelated to changes in tree structure (PC2), but strongly related to initial structure (PC1). These seemingly contradictory results can be explained by considering the conditions and processes that lead to vegetation change in this system. First, despite decades of tree presence, ecotones were still dominated by meadow species when initially sampled in 1983 and thus had significant potential for change. Second, multiple decades of change in the ground layer reflect the cumulative effects of trees already present (Pugnaire et al. 1996, Haugo and Halpern 2010). Variation in initial structure was large among sites, reflecting diverse invasion histories (Miller and Halpern 1998). In comparison, changes in structure were small and less variable. Thus, ecotones with initially greater tree cover or basal area had the potential to effect larger changes in the ground layer. Interestingly, despite the significance of initial tree structure in these models, declines in the cover and richness of meadow species were also correlated with initial cover and richness. This relationship may reflect the statistical property that communities with greater richness or cover have "further to fall." However, it also reveals significant variation in the ground layer that was unrelated to initial tree structure, but indicative of the potential for change.

In contrast to meadow species, forest species did not respond to variation in tree structure. Although we anticipated greater colonization (change in richness) and growth (change in cover) of forest species in ecotones with greater initial tree structure or greater change in structure, neither predictor was significant in regression models. We attribute this general lack of response to patterns in the subalpine zone, where poorly developed understories result in limited potential for dispersal and colonization of the ecotone (e.g., Matlack 1994, Brunet and von Oheimb 1998). Similar constraints do not exist at lower elevations where forest herbs can disperse rapidly into ecotonal habitats formed by invading trees (Haugo and Halpern 2007, 2010).

Implications and future changes

Long-term observations of forest-meadow ecotones in TSBR allow us to place recent changes into the broader historical context of forest expansion, and to consider what these changes imply for the future. Despite nearly a century of forest encroachment, ecotones remain structurally distinct from adjacent forests and retain elements of the meadows from which they originate. Ecotone characteristics also vary across the landscape in response to past invasion patterns (Miller and Halpern 1998) and to underlying gradients in resource availability. Vegetation dynamics in ecotonal habitats are the cumulative effect of how these factors interact to cause species' losses and gains.

Our study was not designed to quantify the rate or extent of recent meadow loss, or the susceptibility to encroachment of meadows representing different landscape contexts—larger-scale questions that are being addressed through remote sensing and change-detection analysis (e.g., Takaoka and Swanson 2008, Zald 2009). However, we can describe the community-level consequences of encroachment where it does occur. In this sense, our work has important implications for the use of remote sensing to quantify landscape-scale changes in ecosystem state. First, even in the absence of detectable increases in forest extent, changes in the ground-layer along existing forest-meadow boundaries can be significant. Second, simple estimates of change in forest cover may not capture the variation in biological response (e.g., loss of meadow species or establishment by forest species) that occurs in different portions of the landscape. Integrating our results with remote sensing tools could provide a more complete understanding of the extent and ecological consequences of forest encroachment in this and similar landscapes.

Future changes in climate are likely to alter the dynamics of forest-meadow ecotones through effects on tree establishment or growth. Current predictions are for warmer drier summers, warmer wetter winters (Mote and Salathe 2009), and shifts in the form of precipitation (snow to rain; Elsner et al. 2009), suggesting the potential for increasing summer drought and longer growing seasons. These effects are likely to be manifested to varying degrees and in complex ways across the elevational, topographic, and edaphic gradients that define mountain landscapes (Daly et al. 2009). In the montane zone, for example, warmer drier summers may reduce rates of tree invasion and growth on mesic upland slopes, but enhance them in hydric basins, where waterlogged soils currently limit both the extent of tree establishment and associated changes in ground-layer vegetation (Miller and Halpern 1998). Similar "switches" may occur in early- vs. late-snowmelt sites in the subalpine zone in response to changing snowpack and growing-season length. Climate change also has the potential to elicit indirect or secondary effects in the form of increased frequency or intensity of insect outbreaks or wildfire (Littell et al. 2009), disturbances that can dramatically alter the characteristics of existing ecotones or create new boundaries. Where invading trees are killed, ecotonal areas are likely to revert quite rapidly to dominance by meadow species (C. B. Halpern, unpublished data).

To our knowledge, this analysis represents the first long-term, large-scale assessment of recent responses of mountain meadows to 20th-century forest expansion. Understanding how tree influence and landscape context shape the dynamics of forest-meadow boundaries represents a first critical step toward predicting future changes in the biological diversity of these and other mountain landscapes.

Acknowledgments

Literature Cited

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. Proceedings of the National Academy of Sciences of the United States of America 95:14839–14842.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 32–46.

Anderson, M. J., R. N. Gorley, and K. R. Clark. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth, UK.

Archer, S. 1995. Tree-grass dynamics in *Prosopis*–thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2:83–99.

Baker, W. L., and P. J. Weisberg. 1995. Landscape analysis of the forest-tundra ecotone in Rocky Mountain National Park, Colorado. Professional Geographer 47:361–375.

Batllori, E., J. J. Camarero, J. M. Ninot, and E. Gutierrez. 2009. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. Global Ecology and Biogeography 18:460–472.

Belsky, A. J., S. M. Mwonga, R. G. Amundson, J. M. Duxbury, and A. R. Ali. 1993. Comparative effects of isolated trees on their undercanopy environments in high-rainfall and low-rainfall savannas. Journal of Applied Ecology 30:143–155.

Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

Bond, W. J. 2008. What limits trees in C-4 grasslands and savannas? Annual Review of Ecology Evolution and Systematics 39:641–659.

Bowman, D., A. Walsh, and D. J. Milne. 2001. Forest expansion and grassland contraction within a

Eucalyptus savanna matrix between 1941 and 1994 at Litchfield National Park in the Australian monsoon tropics. Global Ecology and Biogeography 10:535–548.

Boyd, R., editor. 1999. Indians, fire and the land in the Pacific Northwest. Oregon State University, Corvallis, Oregon, USA.

Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition. Causes and consequences of the conversion of mesic grassland to shrubland. Bioscience 55:243–254.

Brink, V. C. 1959. A directional change in the subalpine forest-heath ecotone in Garibaldi Park, British Columbia. Ecology 40:10–16.

Brooke, R. C., E. B. Peterson, and V. J. Krajina. 1970. The subalpine mountain hemlock zone. Ecology of Western North America 2:147–349.

Brunet, J., and G. von Oheimb. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. Journal of Ecology 86:429–438.

Burke, C. J. 1979. Historic fires in the central western Cascades, Oregon. Oregon State University, Corvallis, Oregon, USA.

Cadenasso, M. L., S. T. A. Pickett, K. C. Weathers, S. S. Bell, T. L. Benning, M. M. Carreiro, and T. E. Dawson. 2003. An interdisciplinary and synthetic approach to ecological boundaries. Bioscience 53:717–722.

Cannone, N., S. Sgorbati, and M. Guglielmin. 2007. Unexpected impacts of climate change on alpine vegetation. Frontiers in Ecology and the Environment 5:360–364.

Cissel, J. H., F. J. Swanson, and P. J. Weisberg. 1999. Landscape management using historical fire regimes: Blue River, Oregon. Ecological Applications 9:1217–1231.

Coomes, D. A., and P. J. Grubb. 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. Ecological Monographs 70:171–207.

Coop, J. D., and T. J. Givnish. 2008. Constraints on tree seedling establishment in montane grasslands of the Valles Caldera, New Mexico. Ecology 89:1101–1111.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28:2031–2064.

Daly, C., D. R. Conklin, and M. H. Unsworth. 2009. Local atmospheric decoupling in complex topography alters climate change impacts. International Journal of Climatology 30:1857–1864.

Damschen, E. I., S. Harrison, and J. B. Grace. 2010. Climate change effects on an endemic-rich edaphic flora: resurveying Robert H. Whittaker's Siskiyou sites (Oregon, USA). Ecology 91:3609–3619.

De Valpine, P., and J. Harte. 2001. Plant responses to experimental warming in a montane meadow. Ecology 82:637–648.

Douglas, G. W. 1972. Subalpine plant communities of the western North Cascades, Washington. Arctic and Alpine Research 4:147–166.

Duarte, L. D., M. B. Carlucci, S. M. Hartz, and V. D. Pillar. 2007. Plant dispersal strategies and the colonization of *Araucaria* forest patches in a grassland-forest mosaic. Journal of Vegetation Science 18:847–858.

Duarte, L. D. S., R. E. Machado, S. M. Hartz, and V. D. Pillar. 2006. What saplings can tell us about forest expansion over natural grasslands. Journal of Vegetation Science 17:799–808.

Elsner, M. M., L. Cuo, N. Voisin, J. S. Deems, A. F. Hamlet, J. A. Vano, K. E. B. Mickelson, S. Y. Lee, and D. P. Lettenmaier. 2009. Implications of 21st century climate change for the hydrology of Washington State. The Washington climate change assessment: evaluating Washington's future in a changing climate. Climate Impacts Group, University of Washington, Seattle, Washington, USA.

Eriksson, O. 1993. The species pool hypothesis and plant community diversity. Oikos 68:371–374.

Fagan, W. F., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. American Naturalist 153:165–182.

Fagan, W. F., M. J. Fortin, and C. Soykan. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. Bioscience 53:730–738.

Fonda, R. W., and L. C. Bliss. 1969. Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. Ecological Monographs 39:271–301.

Forrest, J., D. W. Inouye, and J. D. Thomson. 2010. Flowering phenology in subalpine meadows: Does climate variation influence community co-flowering patterns? Ecology 91:431–440.

Franklin, J. F., W. H. Moir, G. W. Douglas, and C. Wiberg. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arctic and Alpine Research 3:215–224.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.

Franklin, J. F., and C. B. Halpern. 1999. Pacific Northwest forests. Pages 123–159 *in* M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, New York, New York, USA.

Gibson, D. J. 2009. Grasses and grassland ecology. Oxford University Press, Oxford, UK.

Gosz, J. R. 1991. Fundamental ecological characteristics

of landscape boundaries. Pages 8–30 *in* M. M. Holland, P. G. Risser, and R. J. Naiman, editors. Ecotones: the role of landscape boundaries in the management and restoration of changing environments. Chapman and Hall, New York, New York, USA.

Halpern, C. B., B. G. Smith, and J. F. Franklin. 1984. Composition, structure, and distribution of the ecosystems of the Three Sisters Biosphere Reserve/Wilderness Area. Final report to the USDA. Forestry Sciences Laboratory, Corvallis, Oregon, USA.

Harrison, S., E. I. Damschen, and J. B. Grace. 2010. Ecological contingency in the effects of climatic warming on forest herb communities. Proceedings of the National Academy of Sciences of the United States of America 107:19362–19367.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.

Haugo, R. D., and C. B. Halpern. 2007. Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. Canadian Journal of Botany 85:285–298.

Haugo, R. D., and C. B. Halpern. 2010. Tree age and tree species shape positive and negative interactions in a montane meadow. Botany 88:488–499.

Henderson, J. A. 1973. Composition, distribution, and succession of subalpine meadows in Mount Rainier National Park, Washington. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Hibbard, K. A., S. Archer, D. S. Schimel, and D. W. Valentine. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology 82:1999–2011.

Hickman, J. C. 1976. Non-forest vegetation of the central western Cascade Mountains of Oregon. Northwest Science 50:145–155.

Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1969. Vascular plants of the Pacific Northwest. University of Washington Press, Seattle, Washington, USA.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, Washington, USA.

Hotelling, H. 1933. Analysis of complex statistical variables in principle components. Journal of Experimental Psychology 24:417–441, 493–520.

Hufkens, K., P. Scheunders, and R. Ceulemans. 2009. Ecotones in vegetation ecology: methodologies and definitions revisited. Ecological Research 24:977–986.

Jackson, R. B., J. L. Banner, E. G. Jobbagy, W. T. Pockman, and D. H. Wall. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418:623–626.

Johnson, R. R. 1985. Historical records inventory for the Willamette National Forest: Forest grazing permits. Forest Service Warehouse, USDA Forest Service, Willamette National Forest, Eugene, Oregon, USA.

Jones, C. G., and R. M. Callaway. 2007. The third party. Journal of Vegetation Science 18:771–776.

Kruskal, J. B. 1964. Nonmeteric multidimensional scaling: a numerical method. Psychometrika 29:115–129.

Kuramoto, R. T., and L. C. Bliss. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. Ecological Monographs 40:317–347.

Lenoir, J., J. C. Gegout, J. L. Dupouey, D. Bert, and J.-C. Svenning. 2010. Forest plant community changes during 1989–2007 in response to climate warming in the Jura Mountains (France and Switzerland). Journal of Vegetation Science 21:946–964.

Littell, J. S., E. E. O'Neil, D. McKenzie, J. A. Hickie, J. A. Lutz, R. A. Norheim, and M. M. Elsner. 2009. Forest ecosystems, disturbance, and climatic change in Washington State, USA. The Washington climate change assessment: evaluating Washington's future in a changing climate. Climate Impacts Group, University of Washington, Seattle, Washington, USA.

Lloyd, K. M., A. A. M. McQueen, B. J. Lee, R. C. B. Wilson, S. Walker, and J. B. Wilson. 2000. Evidence on ecotone concepts from switch, environmental and anthropogenic ecotones. Journal of Vegetation Science 11:903–910.

Luzio, M. D., G. L. Johnson, C. Daly, J. K. Eischeid, and J. G. Arnold. 2008. Constructing retrospective gridded daily precipitation and temperature datasets for the conterminous United States. Journal of Applied Meteorology and Climatology 47:475–497.

Magee, T. K., and J. A. Antos. 1992. Tree invasion into a mountain-top meadow in the Oregon Coast Range, USA. Journal of Vegetation Science 3:485–494.

Matlack, G. R. 1994. Plant speicies migration in a mixed-history forest landscape in eastern North America. Ecology 75:1491–1502.

McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290–297.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MJM Software, Gleneden Beach, Oregon, USA.

Miller, E. A., and C. B. Halpern. 1998. Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. Journal of Vegetation Science 9:265–282.

Morgan, J. A., D. G. Milchunas, D. R. LeCain, M. West, and A. R. Mosier. 2007. Carbon dioxide enrichment alters plant community structure and accelerates

shrub growth in the shortgrass steppe. Proceedings of the National Academy of Sciences of the United States of America 104:14724–14729.

Mote, P. W. 2003. Trends in temperature and precipitation in the Pacific Northwest during the twentieth century. Northwest Science 77:271–282.

Mote, P. W. 2004. How and why is Northwest climate changing? Pages 11–22 *in* D. L. Peterson, J. L. Innes, and K. O'Biran, editors. Climate change, carbon, and forestry in northwestern North America: proceedings of a workshop, Orcas Island, Washington, November 14–15, 2001. PNW-GTR-614. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Mote, P. W., and E. P. Salathe. 2009. Future climate in the Pacific Northwest. The Washington climate change impacts assessment: evaluating Washington's future in a changing climate. Climate Impacts Group, University of Washington, Seattle, Washington, USA.

Musselman, K. N., N. P. Molotch, and P. D. Brooks. 2008. Effects of vegetation on snow accumulation and ablation in a mid-latitude sub-alpine forest. Hydrological Processes 22:2767–2776.

Orr, E. L., W. N. Orr, and E. M. Baldwin. 1992. Geology of Oregon. Kendall/Hunt Publishing Co, Dubuque, Iowa, USA.

Pugnaire, F. I., P. Haase, J. Puigdefabregas, M. Cueto, S. C. Clark, and L. D. Incoll. 1996. Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. Oikos 76:455–464.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rakestraw, L., and M. Rakestraw. 1991. History of the Willamette National Forest. USDA Forest Service, Willamette National Forest, Eugene, Oregon, USA.

Rochefort, R. M., R. L. Little, A. Woodward, and D. L. Peterson. 1994. Changes in the distribution of subalpine conifers in western North America: a review of climate and other factors. The Holocene 4:89–100.

Scholes, R. J. and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28:517–544.

SPSS. 2008. SPSS 17.0. SPSS Inc., Chicago, Illinois, USA.

Strayer, D. L., M. E. Power, W. F. Fagan, S. T. A. Pickett, and J. Belnap. 2003. A classification of ecological boundaries. Bioscience 53:723–729.

Takaoka, S. and F. J. Swanson. 2008. Change in extent of meadows and shrub fields in the central western Cascade Range, Oregon. Professional Geographer 60:527–540.

Taylor, A. H. 1995. Forest expansion and climate change in the Mountain Hemlock (*Tsuga mertensiana*) Zone, Lassen National Park, California, USA. Arctic and Alpine Research 27:207–216.

Taylor, D. R., L. W. Aarssen, and C. Loehle. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. Oikos 58:239–250.

Teensma, P. D. A. 1987. Fire history and fire regimes of the central western Cascades of Oregon. Dissertation. University of Oregon, Eugene, Oregon, USA.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31:197–215.

van der Maarel, E. 1990. Ecotones and ecoclines are different. Journal of Vegetation Science 1:135–138.

Verheyen, K., and M. Hermy. 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. Journal of Vegetation Science 15:125–134.

Virtanen, R., M. Luoto, T. Rama, K. Mikkola, J. Hjort, J. A. Grytnes, and H. J. B. Birks. 2010. Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. Global Ecology and Biogeography 19:810–821.

Walker, D. A., J. C. Halfpenny, M. D. Walker, and C. A. Wessman. 1993. Long-term studies of snow-vegetation interactions. Bioscience 43:287–301.

Wilson, J. B., and A. D. Q. Agnew. 1992. Positive-feedback switches in plant communities. Advances in Ecological Research 23:263–336.

Woodward, A., E. G. Schreiner, and D. G. Silsbee. 1995. Climate, geography, and tree establishment in sub-alpine meadows of the Olympic Mountains, Washington, USA. Arctic and Alpine Research 27:217–225.

Yarrow, M. M., and V. H. Marin. 2007. Toward conceptual cohesiveness: A historical analysis of the theory and utility of ecological boundaries and transition zones. Ecosystems 10:462–476.

Zald, H. S. J. 2009. Extent and spatial patterns of grass bald land cover change (1948–2000), Oregon Coast Range, USA. Plant Ecology 201:517–529.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.
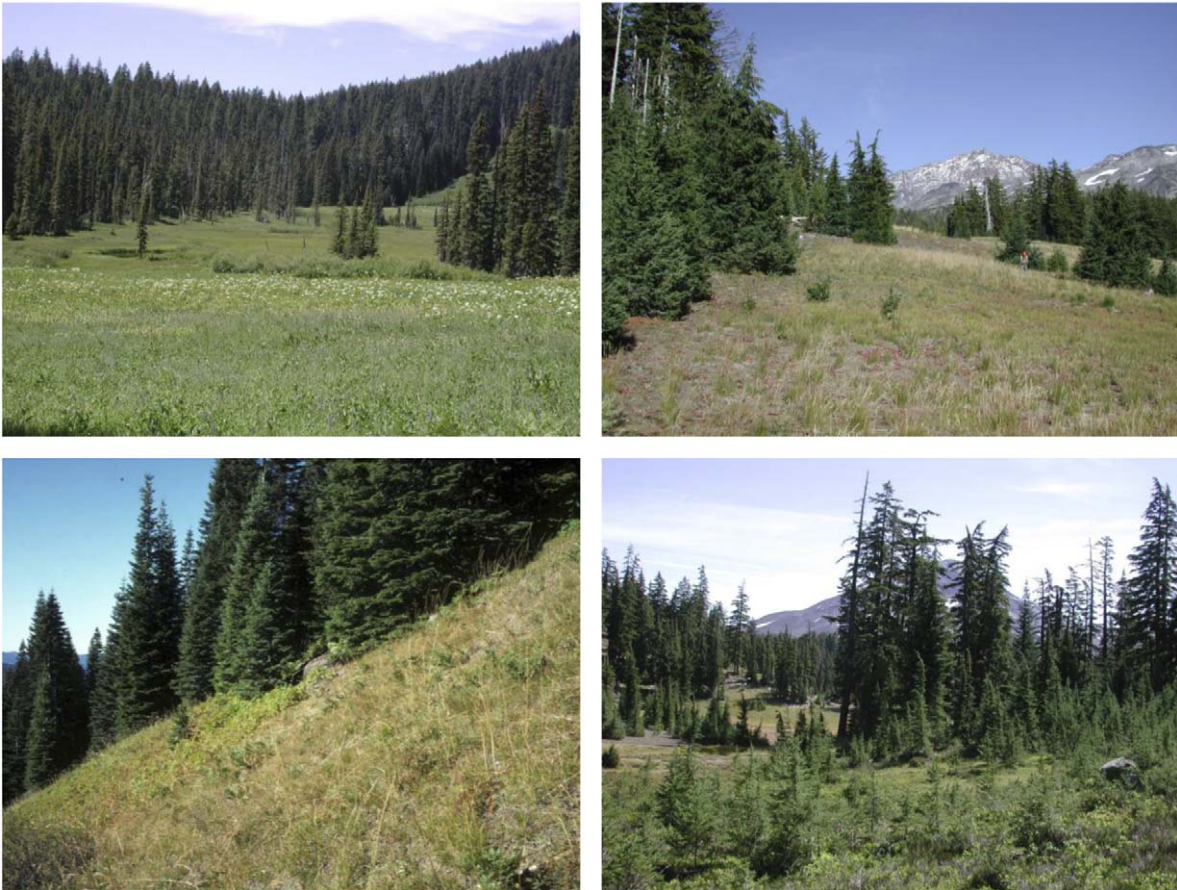
Appendix A

Fig. A1. Forest-meadow ecotones representing each of the four landscape contexts in the Three Sisters Biosphere Reserve, Oregon. Montane hydric (upper left), montane mesic (lower left), subalpine early snowmelt (upper right), subalpine late snowmelt (lower right).

APPENDIX B

Table B1. Species observed between 1983 and 2009 in forest-meadow ecotone transects in the Three Sisters Biosphere Reserve, Oregon. Species are grouped by habitat preference (forest, meadow, or unclassified) and growth form (grasses, sedges/rushes, herbs, and shrubs). Conifers are included, but not classified by habitat preference. Nomenclature follows Hitchcock and Cronquist (1973).

Forest species
  Grasses
    Bromus vulgaris
    Festuca occidentalis
    Melica subulata
    Trisetum canescens
    Trisetum cernuum
  Sedges/Rushes
    Luzula hitchcockii
    Luzula parviflora
  Herbs
    Achlys triphylla
    Actea rubra
    Adenocaulon bicolor
    Anemone deltoidea
    Anemone lyallii
    Anemone oregana
    Arenaria macrophylla
    Arnica latifolia
    Arnica mollis
    Asarum caudatum
    Blechnum spicant
    Campanula scouleri
    Circaea alpina
    Clintonia uniflora
    Corallorhiza species
    Disporum species
    Galium oreganum
    Galium triflorum
    Goodyera oblongifolia
    Habenaria unalascensis
    Hieracium albiflorum
    Hypopitys monotropa
    Lactuca muralis
    Linnaea borealis
    Listera caurina
    Listera cordata
    Mianthemum dilatatum
    Mitella breweri
    Mitella trifida
    Monotropa hypopitys
    Osmorhiza chilensis
    Osmorhiza occidentalis
    Pedicularis racemosa
    Polystichum munitum
    Pyrola picta
    Pyrola secunda
    Smilacina racemosa
    Smilacina stellata
    Tellima grandiflora
    Tiarella trifoliata
    Trientalis latifolia
    Trillium ovatum
    Viola glabella
    Viola orbiculata

Table B1. Continued.

    Xerophyllum tenax
  Shrubs
    Acer circinatum
    Berberis nervosa
    Chimaphila menziesii
    Chimaphila umbellata
    Cornus canadensis
    Cornus nuttallii
    Corylus cornuta
    Gaultheria ovatifolia
    Holodiscus discolor
    Pachistima myrsinites
    Rhododendron albiflorum
    Rhododendron macrophyllum
    Rosa gymnocarpa
    Rubus lasiococcus
    Rubus ursinus
    Symphoricarpos mollis
    Vaccinium alaskaense
    Vaccinium membranaceum
    Vaccinium scoparium
    Whipplea modesta
Meadow species
  Grasses
    Agrostis exarata
    Agrostis humilis
    Agrostis scabra
    Agrostis tenuis
    Agrostis thurberiana
    Agrostis variabilis
    Bromus carinatus
    Calamagrostis canadensis
    Calamagrostis inexpansa
    Cinna latifolia
    Danthonia californica
    Danthonia intermedia
    Deschampsia atropurpurea
    Deschampsia caespitosa
    Elymus glaucus
    Festuca idahoensis
    Festuca viridula
    Glyceria elata
    Hordeum brachyantherum
    Koeleria cristata
    Muhlenbergia filiformis
    Phleum alpinum
    Poa pratensis
    Sitanion hystrix
    Stipa occidentalis
    Tisetum spicatum
  Sedges/Rushes
    Carex breweri
    Carex buxbaumii
    Carex eurycarpa
    Carex halliana
    Carex hoodii
    Carex jonesii
    Carex lenticularis
    Carex limnophila
    Carex luzulina
    Carex mertensii
    Carex microptera
    Carex muricata
    Carex nigricans

Table B1. Continued.

Carex pachystachya
Carex pensylvanica
Carex praeceptorum
Carex rossii
Carex rostrata
Carex scopulorum
Carex sitchensis
Carex spectabilis
Eleocharis pauciflora
Juncus balticus
Juncus drummondii
Juncus mertensianus
Juncus parryi
Scirpus congdonii
Herbs
Achillea millefolium
Aconitum columbianum
Agoseris aurantiaca
Anaphalis margaritacea
Angelica arguta
Antennaria alpina
Antennaria umbrinella
Aquilegia formosa
Arabis drummondii
Arabis holboellii
Arenaria capillaris
Aspidotis densa
Aster alpigenus
Aster foliaceus
Aster ledophyllus
Aster occidentalis
Calochortus subalpinus
Caltha biflora
Castilleja arachnoidea
Castilleja hispida
Castilleja miniata
Cerastium vulgatum
Cheilanthes gracillima
Cirsium callilepes
Collinsia parviflora
Cryptantha affinis
Cuscuta species
Delphinium menziesii
Dicentra formosa
Dodecatheon jeffreyi
Drosera anglica
Drosera rotundifolia
Epilobium alpinum
Epilobium angustifolium
Epilobium glandulosum
Epilobium watsonii
Equisetum arvense
Erigeron aliceae
Eriogonum nudum
Eriogonum pyrolaefolium
Eriogonum umbellatum
Eriophyllum lanatum
Erysimum arenicola
Fragaria vesca/F. virginiana
Galium bifolium
Galium trifidum
Gentiana simplex
Geum macrophyllum
Gilia aggregata
Gilia capitata
Habenaria dilatata
Heracleum lanatum
Hieracium cynoglossoides

Table B1. Continued.

Hieracium gracile
Hieracium scouleri
Hydrophyllum capitatum
Hydrophyllum occidentale
Hypericum anagalloides
Iris chrysophylla
Lathyrus nevadensis
Lewisia pygmaea
Ligusticum grayi
Linanthus bicolor
Lomatium martindalei
Luetkea pectinata
Lupinus latifolius
Lupinus lepidus
Mertensia species
Microseris alpestris
Microseris boreale
Microseris nutans
Microsteris gracilis
Mimulus guttatus
Mimulus moschatus
Mimulus primuloides
Montia parvifolia
Montia sibirica
Montia spathulata
Myosotis laxa
Nemophila parviflora
Orogenia fusiformis
Orthocarpus imbricatus
Pedicularis attolens
Pedicularis bracteosa
Pedicularis groenlandica
Penstemon cardwellii
Penstemon procerus
Perideridia gairdneri
Phacelia heterophylla
Polemonium carneum
Polygonum bistortoides
Polygonum douglasii
Polygonum minimum
Polygonum newberryi
Polygonum phytolaccaefolium
Potentilla drummondii
Potentilla flabellifolia
Potentilla glandulosa
Prunella vulgaris
Pteridium aquilinum
Ranunculus alismaefolius
Ranunculus flammula
Ranunculus gormanii
Rudbeckia occidentalis
Sanicula graveolens
Sedum spathulifolium
Senecio cymbalarioides
Senecio triangularis
Sidalcea cusickii
Sisyrinchium douglasii
Spiranthes romanzoffiana
Spraguea umbellata
Stachys cooleyae
Stellaria crispa
Stellaria obtusa
Thalictrum occidentale
Tofieldia glutinosa
Trifolium longipes
Valeriana sitchensis
Veratrum californicum
Veratrum viride

Table B1. Continued.

    Veronica americana
    Veronica scutellata
    Veronica serpyllifolia
    Veronica wormskjoldii
    Vicia americana
    Viola macloskeyi
    Viola nuttallii
  Shrubs
    Arctostaphylos nevadensis
    Betula glandulosa
    Cassiope mertensiana
    Gaultheria humifusa
    Haplopappus greenei
    Kalmia microphylla
    Kalmia occidentalis
    Phyllodoce empetriformis
    Rosa pisocarpa
    Rubus parviflorus
    Salix commutata
    Spiraea densiflora
    Spiraea douglasi
    Vaccinium caespitosum
    Vaccinium occidentale
Unclassified species
  Sedges/Rushes
    Carex deweyana
    Luzula campestris
  Herbs
    Cystopteris fragilis
    Erythronium grandiflorum
    Lilium columbianum

    Lycopodium sitchense
    Polemonium pulcherrimum
    Rumex acetosella
    Taraxacum officinale
    Viola adunca
  Shrubs
    Acer glabrum
    Alnus sinuata
    Amelanchier alnifolia
    Castanopsis chrysophylla
    Crataegus douglasii
    Lonicera ciliosa
    Rhamnus purshiana
    Ribes lacustre
    Ribes lobbii
    Ribes sanguineum
    Ribes viscosissimum
    Sambucus racemosa
    Sorbus sitchensis
  Conifers
    Abies amabilis
    Abies grandis
    Abies lasiocarpa
    Calocedrus decurrens
    Picea engelmannii
    Pinus albicaulis
    Pinus contorta
    Pinus monticola
    Pseudotsuga menziesii
    Tsuga heterophylla
    Tsuga mertensiana

APPENDIX C

Table C1. Variable loadings from principal components analysis of tree structural characteristics within ecotone habitats (see *Methods: Modeling the importance of tree influence, landscape context, and initial vegetation*). Variables included measures of initial (1983) structure and changes in structure over the study period (1983–2009). The first two components were used as predictors in multiple regression models (see Table 2). The variation explained by PC1 = 0.37; by PC2 = 0.26.

Variable	Correlation PC1	PC2
Measures of initial structure		
Initial density	0.13	0.42
Initial basal area	0.44	−0.21
Initial cover	0.53	−0.04
Initial CV of cover	−0.54	0.04
Measures of change in structure		
Change in density	−0.13	−0.47
Change in basal area	0.24	−0.51
Change in cover	−0.11	−0.48
Change in CV of cover	0.35	0.26