Ryan Haugo Ph.D. Dissertation: Chapter 4

Landscape context and tree influences shape the long-term dynamics of forest-meadow ecotones in the central Cascade Range, Oregon

Abstract

Questions: How have vegetation structure, composition, and diversity changed over 26 yr across forest-meadow boundaries in a diverse mountain landscape? To what extent are changes in ground-layer vegetation (herbs and shrubs) shaped by landscape context and the dynamics of tree invasion?

Location: Three Sisters Biosphere Reserve (1280-2000 m a.s.l), Cascade Range, Oregon, U.S.A.

Methods: Species abundance and tree structure were sampled in permanent transects across 20 forest-meadow boundaries in 1983, 1993, and 2009. I delineated forest, ecotone, and meadow habitats along each transect and examined changes in tree structure and ground-layer vegetation. I used NMDS, PCA, and multiple-regression models to elucidate the importance of initial tree structure, changes in tree structure, landscape context, and initial vegetation characteristics for changes in ground-layer vegetation in the ecotone.

Results: I observed significant (though variable) changes in structure, diversity, and composition in the ecotone, but little change in adjacent forest or meadow. I found no evidence that changes in ecotone ground-layer vegetation were driven by the direct effects of climate variation. Species diversity in the ecotones was not greater than in adjacent habitats, and declined over time as losses of meadow species exceeded gains in forest species. Declines were greater where soil moisture was seasonally limiting (montane slopes and subalpine early-snow melt sites). Forest understory species increased in montane sites but not in subalpine sites with typically depauperate forest understories. Changes in richness and cover of each plant group were related to its initial value and to initial, but not changes in, tree structure.

Conclusions: Tree influence in the ecotone has been highly variable. Future changes in vegetation are likely to be greatest where past tree invasion has progressed the furthest—where tree cover and continuity of cover are greatest. However, tree effects are context dependent, mediated by underlying gradients in resource availability and the landscape-scale patterns of species distribution. Some portions of the landscape are resistant to change (montane hydric meadows); others are more susceptible (subalpine, early-snowmelt sites). Understanding the nature of biotic interactions and the importance of environmental controls is critical to predicting future vegetation changes.

Introduction

Ecotones, the zones of transition between communities or ecosystems, are ubiquitous features of most biomes (Gosz 1991). They are critical landscape components that regulate the movements of organisms, materials, and energy (Fagan et al. 2003, Yarrow and Marin 2007), and can have profound influences on population and community dynamics (Fagan et al. 1999). Ecotones can be defined as vegetation zones across which compositional or structural change is abrupt relative to neighboring communities (Lloyd et al. 2000). They can reflect underlying gradients in environment, sharp contrasts in plant physiognomy (woody vs. herbaceous dominance), or disturbances that create edges (van der Maarel 1990, Wilson and Agnew 1992, Cadenasso et al. 2003). Ecotones are viewed as "tension zones", sensitive to changes in climate or other extrinsic factors (van der Maarel 1990). Recent advances have been made in 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., Fagan et al. 2003, 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 woodlands and forests (Van Auken 2000, Bowman et al. 2001, Norman and Taylor 2005, Coop and Givnish 2007), prompting concerns over the loss of biological diversity and ecosystem services (Van Auken 2000, Hoekstra et al. 2005). Given the time spans necessary to detect change, the ecological effects of encroachment are often inferred retrospectively (Jackson et al. 2002, Lett and Knapp 2003, Briggs et al. 2005, Haugo and Halpern 2007). Direct observations of these processes are rare.

Emphasis is often placed on the dynamics of ecotones where tree growth is limited by temperature (alpine or arctic treelines) or precipitation (lower arid treelines) (Scholes and Archer 1997, Allen and Breshears 1998, Danby and Hik 2007, Bond 2008, Batllori et al. 2009, Harsch et al. 2009). In the Pacific Northwest and other topographically complex mountain landscapes, however, natural boundaries between forest and grassland (or meadow) are shaped by a range of physical and historical factors—landform, soils, hydrology, and disturbance—in addition to climatic controls (Kuramoto and Bliss 1970, Franklin and Halpern 1999, Halpern et al. 2010). These ecotones could potentially undergo rapid change given the limited climatic constraint on tree development, and indeed, dramatic shifts in the boundaries between forests and meadows have occurred throughout the Pacific Northwest during the 20th century. Many studies have examined the patterns and causes of encroachment in this region (Franklin et al. 1971, Vale 1981, Woodward et al. 1995, Miller and Halpern 1998, Hadley 1999, Takaoka and Swanson 2008, Zald 2009). However, few studies explore community-level consequences of encroachment or how these changes are manifested across the landscape (but see Magee and Antos 1992, Haugo and Halpern 2007, Takaoka and Swanson 2008, Haugo and Halpern 2010).

Ecotones are often described as regions of elevated diversity arising from the blending of neighboring species' pools and unique environmental conditions (Ries et al. 2004, Camarero et al. 2006, Peterson and Reich 2008). Although theory predicts that ecotones should have greater species diversity than neighboring communities (Gosz 1991, Ries et al. 2004), this pattern is not always observed (Luczaj and Sadowska 1997, Lloyd et al. 2000). Where trees invade grasslands or meadows, several patterns of diversity are possible. If tree influences are moderate or spatially heterogeneous (partial or patchy shade), species with differing light requirements may coexist (meadow species adapted to full sun and forest species to deep shade; Haugo and Halpern 2007, Haugo and Halpern 2010). However, coexistence either requires stability of ecotone structure or periodic disturbance to reset the encroachment process. In the absence of stability or disturbance, strong asymmetric competition between trees and herbs (Peltzer and Kochy 2001) may cause extirpation of meadow species. Depending on the rate or density at which trees establish and the abilities of forest herbs to disperse to the ecotone, diversity may decrease if meadow species are lost faster than forest species can colonize.

The net effect of extirpation of meadow species and colonization by forest species may depend on factors such as: (1) the structural characteristics of the ecotone (i.e., spatial distribution, density, and sizes of trees); (2) the magnitude or rate of structural change within the ecotone; (3) the pool of available species (and their physiological and reproductive traits) in adjoining habitats; and (4) the ways in which each of these factors is shaped by landscape context. In the Pacific Northwest, context dependency (Jones and Callaway 2007) is likely to play a critical role in the outcomes of tree-herb interactions through the direct or indirect influences of physical factors that vary widely across the landscape (e.g., temperature, snowpack, hydrology, soil depth). Moreover, changes to the physical environment (e.g. climate warming) may alter species’ interactions. Climate warming is anticipated to have particularly strong effects on the distribution and diversity of species in mountain environments (Cannone et al. 2007, Gonzalez et al. 2010, Lenoir et al. 2010). The ability to anticipate, adapt to, or manage for changes in biological diversity arising from gradual shifts in ecosystem state from meadow to forest requires an understanding of where on the landscape structural changes are most likely to occur or to have the greatest effect.

In this paper, I analyze long-term patterns of vegetation change across forest-meadow boundaries in the Three Sisters Biosphere Reserve/Wilderness Area (TSBR), a largely undisturbed mountain landscape in the central Cascade Range of Oregon. Data on vegetation structure and composition were collected over a 26-yr period (1983 – 2009) at 20 locations representing a diversity of physical environments and vegetation types. This is one of the longest and most extensive studies of vegetation change across forest-meadow boundaries in western North America. I address the following sets of questions, which explore patterns and correlates of vegetation change at a range of spatial scales.

1. How have vegetation structure, diversity, and composition changed across forest-meadow boundaries over 26 yr? Do the magnitude and direction of changes differ among forest, ecotone, and meadow habitats? How have the diversity and abundance of species with differing habitat preferences (meadow vs. forest understory species) and growth forms changed?
2. How are changes in the structure, diversity, and composition of ecotones related to landscape context?
3. To what extent are changes in the ground-layer vegetation driven by the dynamics of tree invasion? Do these relationships vary across the landscape?

Methods

Study area

The Three Sisters Biosphere Reserve is a federal wilderness area of nearly 100,000 ha in the Cascade Range of central Oregon, USA (Fig. 1). 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. The primary ridge crests average ~1500 m a.s.l. The High Cascades province lies to the east at higher elevations, dominated by younger (Quaternary) shield and composite volcanoes. Topography is comparatively 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). Average maximum July temperature ranges from 19.4 to 22.8^{o}C and minimum January temperature ranges from -9.2 to -3.6^{o}C (Table 1; Daly et al. 2008).

TSBR has a diverse array of forested and non-forested communities whose structure and composition vary with elevation, topography, soils, and hydrology (Halpern et al. 1984). In the montane zone (typically <1600 m a.s.l.) forests are dominated by *Abies grandis*, *Pseudotsuga menziesii*, *Abies amabilis*, and *Pinus contorta*. 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 a.s.l.) forests dominated by *Tsuga mertensiana* and *Abies lasiocarpa* are distributed among a mosaic of forb-, graminoid- and heath-dominated meadows (Halpern et al. 1984).

Fire is the primary agent of natural disturbance in this system, but is infrequent. Reconstructions of disturbance history suggest fire-return intervals of 100-150 yr in the montane zone (Teensma 1987, Cissel et al. 1999) but many hundreds of years in the subalpine (Halpern et al. 1984). Although aboriginal burning of meadows is likely to have occurred, primarily at lower elevations (Burke 1979, Boyd 1999), direct evidence is lacking in TSBR. None of the study locations has experienced recent fire. Sheep grazing was common in TSBR (and throughout the Cascade Range) between 1880 and 1910 (Rakestraw and Rakestraw 1991), and deteriorating range conditions resulted in closure of many areas 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 (Table 1, Fig. 1). These contributed to a broader study of the composition, environmental controls, and dynamics of major forest and meadow ecosystems in TSBR (Halpern et al. 1984, 1991). Transects are 2 m wide and range in length from 50 to 220 m (Table 1, Appendix A). Each originated in closed-canopy forest and extended into open meadow, beyond any tree invasion, in 1983. In 1983 and 1993, all trees (>10 cm tall) and tree seedlings ($\leq$ 10 cm tall) were spatially mapped, measured for diameter (basal or breast height, depending on tree size), and aged using increment core samples or bud scar counts, facilitating reconstructions of tree invasion history (Miller and Halpern 1998). Canopy cover (%) of conifers > 10 cm tall (henceforth tree cover) and cover of each vascular plant species (including conifers $\leq$ 10 cm tall) were estimated in 1-m^2 quadrats placed on alternating sides of each transect (n = 39-108 quadrats per transect). In 2009, 26 yr after establishment, I recensused tree populations, recorded new tree recruitment (post-1993), and repeated all cover estimates. Of the original 21 transects, 16 were resampled in 1993 and 20 in 2009.

Habitat definitions

I delineated three habitats along each transect—forest, ecotone, and meadow—based on the presence, cover, and ages of trees (Appendix A). Forest was defined by the presence of trees that had established prior to 1900 (typically much earlier; Miller and Halpern 1998) and by continuous (occasionally patchy) canopy cover at initial measurement (1983). Meadow was defined as the terminal transect section where trees were either absent or present only as seedlings in 2009. In one instance (Obsidian Creek), I removed from the analysis a 10-m section of meadow habitat where a single, isolated tree island (>30m from the forest) interrupted otherwise contiguous open meadow habitat. Ecotone was defined as the intervening zone, comprised of 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) have led to considerable variation in the cover, density, and distribution of trees (Appendix A). Between 1983 and 2009, trees recruited past the endpoints of two transects (Rebel Rock and Ollalie Meadow) resulting in complete loss of meadow habitat.

Species classification

To facilitate analyses of community patterns among sites with distinctly different floras, I classified all species (excluding conifers) as associated with meadow (*n* = 197) or forest understory (*n* = 72). Assignments were based on previous phytosociological studies in TSBR (Halpern et al. 1984), regional floras (Hitchcock et al. 1969, Hitchcock and Cronquist 1973), and recent retrospective studies (Haugo and Halpern 2007, 2010). Although this approach simplifies the distributions of some species, it captures the distinct habitat associations of most. Conifers and other species which could not be classified as either meadow or forest (*n* = 23) were also included in analyses of species composition and total richness (see *Measures of Community Structure and Diversity* below). I also classified species by growth form according to the long-term protocols for these transects: grasses, sedges/rushes, herbs (including ferns), and shrubs (including sub-shrubs).

Climatic variation

To assess the potential influence of long-term trends or inter-annual variation in climate on vegetation change I examined climate records extending back to 1940. I selected four variables that affect plant phenology or productivity: mean annual and mean summer (June-August) temperature, total summer precipitation, and spring snowpack (snow water equivalent [SWE] on 1 April, a proxy for soil moisture availability early in the growing season). Temperature and precipitation data were from the closest meteorological station with long-term records (McKenzie Bridge, 450 m a.s.l.;

U.S. Historical Climatological Network; http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html). Snowpack data were from the nearest SNOTEL site (McKenzie Pass, 1454 m a.s.l.; USDA Natural Resources Conservation Service; ftp://ftp-fc.sc.egov.usda.gov/OR/snow/snowcourse/or_data). For each variable I tested for a significant linear relationship with time for the full record (1940-2009) and for the period of study (1983-2009).

Measures of community structure and diversity

I computed average measures of community structure and diversity for each habitat (forest, ecotone, meadow) at each transect and measurement period based on the quadrat-scale data. I focused on data at the quadrat scale (1 m^2) because the number of quadrats varied substantially among habitats and transects (Appendix A). Measures of tree structure included average conifer density (live stems >10 cm in height), basal area (m^2/ha), cover (summation of all tree species >10cm tall), and the coefficient of variation (CV) in tree cover among quadrats. The CV of tree cover was included to characterize the patchy nature of many ecotones. Tree variables were used as predictors in models of ground-layer vegetation change. For the ground-layer vegetation, response variables included total species richness (number of species per quadrat), richness and cover of meadow and forest species, cover of each growth form, and heterogeneity of species composition. Heterogeneity was expressed as the mean Bray-Curtis distance of all pairwise comparisons of species composition among quadrats within a habitat for each transect.

Comparing rates of change between sampling intervals

Prior to more comprehensive analyses of vegetation patterns, I 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 using a larger sample size (20 transects, only 16 were sampled in 1993; Table 1). For each response variable x habitat combination, I computed an annualized change for each sampling interval (excluding compositional heterogeneity). I compared rates of change using paired *t*-tests ($n = 16$). Of 38 tests, I detected a significant difference ($P < 0.05$) in only two (change in richness of forest species in ecotone and in meadow habitats). Given the consistency of these results, I based all further analyses on changes over the 26-yr study period (1983-2009).

Temporal changes among forest, ecotone, and meadow habitats

To compare temporal changes in tree structure and ground-layer vegetation among habitats (question 1), I employed repeated measures Permutational Analysis of Variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001). I used PERMANOVA rather than ANOVA because the assumption of homogeneity of variance required for the latter was violated for many response variables. In PERMANOVA, significance tests are based on a "pseudo-*F* statistic" derived from permutations of randomized real data. 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 x transect and time x habitat interactions. For significant habitat effects or time x habitat interactions, post-hoc pairwise comparisons were made using Fisher's LSD (Zar 1999). Models were run with 9,999 iterations in the PERMANOVA+ (v.1.0.2) add-on for PRIMER 6.0 (Anderson et al. 2008).

To compare temporal changes in species composition among habitats (question 1), I used non-metric multidimensional scaling (NMDS; Kruskal 1964). Ordinations were based on the average species composition of each habitat at each sampling date, with rare species (those present in <5% of transects) removed and Bray-Curtis as the distance measure. Removing rare species minimizes the effect of different sample sizes among transects and habitats (e.g. species-area relationships). Large floristic differences among transects and habitats also reduces the effect of variable sample sizes. To prevent floristic differences among sites from masking temporal trends, sites (transects) were delineated into four landscape contexts (see below), which were analyzed separately using all transects and years for each context. To facilitate comparisons, I specified a two-dimensional solution for each ordination. Ordinations were initiated from random starting configurations for a maximum of 400 iterations and were rerun for a maximum of 40 times or until an instability criterion of 0.00001 was met (McCune and Grace 2002). 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 ranging from 4.7 to 19.3. NMDS was implemented in R using the *metaMDS* function of the V*egan v1.11-0* package in R (version 2.10.0, R Development Core Team 2009).

Comparing changes among ecotones across the landscape

I developed a novel approach to compare patterns of change among ecotones across the landscape (questions 2 and 3). To define the environmental context of each site (transect), I conducted an ordination using the floristic data. This provided an indirect method of integrating the influences of multiple (and often complex) gradients in environment across the landscape. I ran NMDS (as described above) with each transect represented by the average species composition of its meadow habitat at initial sampling (thus minimizing effects of trees). For the two transects lacking meadow habitat (see *Habitat definitions*, above), I used the average composition of ecotone quadrats that lacked tree cover during the entire study period. The final two-dimensional solution had a stress value of 13.9. Based on qualitative comparisons, the first axis (NMDS 1) was primarily related to landform and hydrology and the second axis (NMDS 2) was primarily related to elevation (Fig 2).

To facilitate comparisons, results of NMDS were used to assign transects to one of four “landscape contexts” (Fig. 2a), which reflected differences in elevation, landform/topography, and hydrology, and were consistent with previous phytosociological studies in TSBR (Halpern et al. 1984). They were: (1) montane hydric basins: lower elevation basins supporting seasonally high water tables; (2) montane mesic slopes: lower elevation, south-facing slopes or benches; (3) subalpine early snowmelt: higher elevation benches and south-facing slopes with longer growing seasons; and (4) subalpine late snowmelt: higher elevation basins and north-facing slopes with shorter growing seasons. Each landscape context supported a distinct meadow flora (Fig. 2b).

The ordination scores were used in two ways to explore the importance of landscape context for changes in the ecotone (question 2). First, positions in ordination space served as a template for comparing changes in tree structure and ground-layer vegetation over the study period (1983 to 2009). For each response variable I produced a "bubble plot" quantifying the direction (positive or negative) and magnitude of change (1983-2009) at each site. Second, scores on NMDS1 and NMDS2 were used as explanatory variables quantifying the contributions of physical environment for regression models (see below).

Modeling the importance of landscape context and tree influence

I used multiple regression models to assess the relative contributions of landscape context (NMDS scores) and tree influence on changes in the ground-layer vegetation within ecotone habitats over the 26-yr study period (questions 2 and 3).

Tree influence was quantified by two types of variables. The first represented ecotone tree structure at the initial (1983) sampling: tree cover, CV of tree cover, tree density, and basal area. Because responses of ground-layer vegetation reflect the cumulative influences of trees over the study period (e.g., Pugnaire et al. 1996, Haugo and Halpern 2010), effects should be greater where tree cover, density, or basal area were initially greater. The second type of variable represented changes in tree structure (1983-2009): change in tree cover, change in CV of tree cover, change in tree density, and change in basal area. Effects should be greater where changes in structure are greater. To reduce the dimensionality of these eight structural variables I first ran a principal components analysis (PCA) using the function *prcomp* in R (version 2.10.0; 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; Table 2). PC2 explained 26% of the total variation and correlated negatively with measures of change in tree structure (change in density, change in basal area, and change in cover; Table 2).

I built multiple regression models for each measure of ground-layer vegetation change in the ecotone. Potential predictor variables were the scores on NMDS1 and NMDS2, the scores on PC1 and PC2, and the initial (1983) value of each vegetation response variable (initial vegetation). The latter were used to test whether the magnitude of change was correlated with the initial condition (e.g., if sites with greater richness declined more in richness). For each variable, I started with a “full” model; predictors were then removed in reverse order of strength (sums of squares) to minimize the Akaike Information Criterion (AIC; Akaike 1974). I 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) I detected small but significant increases in mean annual temperature (0.01 ^{o}C/yr; $R^2 = 0.105$, $p = 0.006$) and mean summer temperature (0.03 ^{o}C/yr; $R^2 = 0.312$, $p < 0.001$) (Fig. 3a), but no significant trends in summer precipitation or spring snowpack (SWE) (Fig. 3b). During the period of study (1983-2009), I detected a significant increase in summer temperature (0.064 ^{o}C/yr; $R^2 =$

0.354, $p = 0.001$), 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 snowpack (Fig. 3b).

Temporal changes in tree structure

In forest habitats, tree structure was stable over the study period (Fig. 4). In contrast, tree cover increased and heterogeneity of cover decreased within ecotones habitats (Fig. 4a, b), but tree density and basal area did not change (Fig. 4c, d). Cover and basal area remained greater in the forest whereas heterogeneity of cover remained greater in the ecotone over the entire study period.

Temporal changes in ground-layer vegetation among forest, ecotone, and meadow habitats

For most measures of vegetation structure and diversity, values in the ecotone were intermediate to those in the forest and meadow (Fig. 5). Exceptions included total richness (ecotone = meadow; Fig. 5a), compositional heterogeneity (ecotone = forest; Fig. 5b), sedge/rush cover (ecotone = forest; Fig. 5h), and shrub cover (similar in all habitats; Fig. 5j). Ecotones were also more dynamic than adjacent forests or meadows, which remained stable for most community attributes. In ecotones, total richness (Fig. 5a), richness of meadow species (Fig. 5c), and cover of grasses (Fig. 5g) declined, whereas richness of forest species (Fig. 5e) increased. Despite decreased heterogeneity of tree cover, heterogeneity of species composition remained unchanged in the ecotone (Fig. 5b).

Species composition in the ecotone was intermediate between forest and meadow at all sites (Fig. 6) except Green Lake (Fig. 6d), where tree structure was minimal in the ecotone (Table 1, Appendix A). Over time, ecotone composition trended toward forest, and forest composition diverged from ecotone and meadow. At some sites, compositional change was as large or larger in the forest than in the ecotone. In contrast, changes in meadows were consistently small and non-directional.

Changes among ecotones across the landscape

Increases in most measures of 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 earlier snowmelt sites in the subalpine zone (Fig. 7b-d). By comparison, tree density was generally stable (Fig. 7a). Landscape-scale trends in the ground-layer were more complex. With one exception (Corral Flat), declines in total richness were greatest in subalpine early snowmelt sites (Fig. 7e), which resulted from declines in the richness of meadow species (Fig. 7g). In contrast, increases in richness and cover of forest species were greater in montane than in subalpine sites (Fig. 7i, j). Changes in the heterogeneity of species composition were not related to landscape context. All growth-forms had highly variable changes in cover across the landscape except for grasses, which showed large declines in montane hydric basins (Fig. 7k).

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

Multiple regression models explained significant variation in nearly all (9 of 10) measures of vegetation change in the ecotones (R^2 of 0.30-0.81 for all plant groups; Table 3). Measures of landscape context were of varying importance in models of meadow and forest species response. NMDS1 (related to landform and hydrology) was a significant predictor of change in richness of meadow species and total species richness (Table 3). Declines were greater where moisture was more limiting (montane mesic slopes and subalpine early snowmelt sites). NMDS2 (related to elevation) significantly predicted greater declines in meadow species and increases in forest species at lower elevations (montane sites).

Initial tree structure (PC1) was significant (in 4 of 10 models, Table 3): sites with initially greater/more complete tree cover and basal area had larger declines in the cover and richness of meadow species (and thus total richness), and in the cover of most growth forms. In contrast, amount of change in tree structure over the study period (PC2) was not significant in any model.

Initial vegetation values were significant predictors of change in all regression models except compositional heterogeneity (Table 3). Cover or richness of meadow species and cover of non-woody growth forms declined more where initial values were greater. In contrast, cover or richness of forest species and cover of shrubs increased more where initial values were greater.

Discussion

Forests have expanded into mountain meadows of the Pacific Northwest throughout most of the 20th century. In TSBR, patterns of conifer invasion have varied in time and space (Miller and Halpern 1998), giving rise to forest-meadow ecotones of diverse age, structure, and species composition. Despite this long history of tree invasion, however, these transitional zones remain structurally distinct from adjacent forests and dominated by a meadow flora. It is within these historical and structural contexts that I evaluate vegetation changes over the last quarter century.

The dynamics of forest-meadow ecotones

Ecotones are widely recognized as dynamic elements of the landscape, yet long-term measurements of vegetation change in them are rare (Cadenasso et al. 2003, Strayer et al. 2003, Hufkens et al. 2009). Using data collected from permanent transects over 26 years in TSBR I found significant changes in tree structure and shifts in the diversity and abundance of meadow and forest species. In contrast to earlier stages of invasion (Miller and Halpern 1998), recent changes in structure reflect the growth and canopy spread of established trees, not ongoing recruitment. During the same period, the structure, diversity and composition of adjacent forests and meadows remained stable. This contrast suggests a process of change in the ecotone (formerly meadow) driven by the cumulative influence of encroaching trees. It also provides evidence that climatic trends or inter-annual variation in climate were not directly responsible for these changes; direct effects of climate in the ecotone would also have been observed in the forest and meadow. Climate could have an indirect effect on ecotones manifested through tree growth. Any such effect, however, is subsumed in my assessment of tree influences (see below).

Patterns of species richness in the ecotone were counter to theoretical expectations of elevated species diversity within ecotones (Gosz 1991, Ries et al. 2004). Despite "blending" of species' pools from adjacent habitats, species richness was not elevated in the ecotone at the spatial scale of the sampling units (1 m^2 quadrats). At most sites, ecotones were dominated (in number and abundance) by meadow species and colonization of forest herbs was balanced, or outweighed, by concomitant loss of meadow taxa. However, trees may impose variation in microclimate or soils at larger spatial scales ($>1m^2$). For example, ecotones exhibited greater heterogeneity in species composition than meadows did, and this pattern persisted over the study period. This heterogeneity illustrates the potential for trees to enhance habitat diversity in these transitional zones (Peterson and Reich 2008).

The role of landscape context

It is important, but challenging, to identify the role of landscape context in shaping the dynamics of ecotones (Question 2). Most measures of community response varied considerably within and among landscape contexts (Fig. 7), and the proxies for landscape position were rarely significant predictors of vegetation change (Table 3). However, two important trends emerged. First, declines in meadow species (and overall richness) were greater in habitats with seasonally limiting soil moisture: montane mesic slopes and subalpine early snowmelt sites. The simplest explanation for this pattern may relate to how meadow species respond to differences in resource supply (in this case, soil moisture) under conditions of highly asymmetric competition with trees. Where soils are seasonally droughty, trees are at a competitive advantage due to greater lateral spread or depth of their root systems (Scholes and Archer 1997). Where soil moisture is not seasonally limiting (due to basin hydrology or late snowpack), competition for soil water is less relevant. Declines are more likely driven by competition for light (Tilman 1988) and thus be related to the structural characteristics of ecotones, not to landscape position.

Variation in the responses of forest herbs comprised the second important landscape trend: increases in richness and cover were largely limited to montane sites. This relationship to elevation reflects a simple, but striking aspect of the regional flora. Montane forests support a rich diversity of shade-tolerant species (total of 66 taxa, Appendix C) that can readily disperse into the ecotone (Haugo and Halpern 2007, 2010). Subalpine forests are depauperate by comparison. Only 37 forest understory species were identified in subalpine transects, and 22 of these taxa were found only at Rebel Rock (Appendix C). Deep and persistent snow packs, short growing seasons, and young, infertile soils contribute to poorly developed understories (Halpern et al. 1984, Franklin and Halpern 1999) and thus a limited source of plants that could colonize ecotones. When viewed in combination, these landscape-scale effects can lead to very low diversity in high-elevation, early-snowmelt sites.

The nature and strength of tree influences

I sought to examine the extent to which changes in ground-layer vegetation were driven by the recent dynamics of tree invasion (Question 3). Trees substantially alter their under canopy and near canopy environments—they create shade, moderate air and soil temperatures, affect 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). However, changes in tree structure (expressed by PC2 scores in my regression models) were not significant in any model of vegetation change. Instead, initial structure (expressed by PC1 scores) was a significant predictor in models for meadow species, with declines were more pronounced in ecotones in which tree structure was more developed at the time of initial sampling.

Several factors contribute to the limited importance of recent change in tree structure in models of vegetation response. First, these ecotones were still dominated by meadow vegetation at the beginning of the observations, indicating the potential for large vegetation changes due to tree influences. Second, vegetation responses to tree structure are cumulative, time-dependent processes (Pugnaire et al. 1996, Haugo and Halpern 2010). Thus, the magnitude of vegetation changes is the product of: (a) initial tree structure, (b) change in tree structure, and (c) the length of time over which tree influence is observed. Structural changes in these ecotones during the past 26 yr were small compared to initial conditions as trees have been present in these ecotones for as many as 50-100 yr prior to this study (Fig. 4). By comparison, the range of initial tree structure was large among sites (Table 1), reflecting diverse histories and intensities of invasion (Miller and Halpern 1998). As a result, vegetation change over the past three decades was more responsive to initial structure than to changes in structure.

Interestingly, initial cover and richness significantly predicted declines in meadow species that were proportional to their initial cover or richness, despite the presence of initial tree structure in these models. These relationships may reflect the simple statistical property that communities with greater richness or cover have “further to fall.” However, they also highlight the presence of significant variation in the ecotone that is unrelated to tree structure, but critical for predicting future change.

In contrast to meadow species, forest species were not responsive to variation in tree structure. Although I anticipated greater dispersal and growth of forest species (increases in richness and cover) in ecotones with greater or more rapidly changing tree structure, neither predictor was significant. I attribute this lack of response to constraints on colonization in the subalpine zone. The abundance and diversity of herbs in these forests are low, limiting the potential for successful dispersal into the ecotone. Similar constraints do not exist in the montane zone where the dispersal of forest herbs can be very rapid following invasion (Haugo and Halpern 2007, 2010).

Conclusions

Long-term observations of forest-meadow ecotones in TSBR allow me to place recent changes into the broader historical context of forest expansion, and to consider what they imply for the future. Despite nearly a century of tree encroachment in this landscape (Miller and Halpern 1998), ecotones remain structurally distinct from adjacent forests and retain many elements of the meadow flora. Tree influences in the ecotone are highly variable across the landscape—legacies of historical invasion patterns (Miller and Halpern 1998) that continue to exert important controls on ground-layer vegetation. In contrast, recent changes in tree structure have been small and have played a comparatively minor role in shaping vegetation change. My analyses also highlight the importance of landscape context in mediating the outcomes of tree-herb interactions (both negative and positive), and the broader consequences of these interactions for biological diversity across the landscape. They indicate that some habitats are more resistant to change (e.g., montane hydric systems), and others are more susceptible (subalpine, early snowmelt sites).

This study has simple, but important, implications for the use of remote sensing in quantifying the extent or rate of forest expansion at landscape scales (e.g., Takaoka and Swanson 2008, Zald 2009). First, even in the absence of detectable changes in forest extent, changes in ground-layer vegetation within the ecotone can be significant. Second, estimates of the magnitude of change in forest extent may not capture important differences in biological responses that are contingent on landscape context. However, the combined application of remote sensing with ground-based statistical or qualitative models could provide a powerful tool for quantifying or predicting the community-level consequences of encroachment.

Future climate change may alter vegetation dynamics by influencing rates or patterns of tree establishment or growth in the ecotone. Predictions of warmer drier summers, warmer wetter winters (Mote and Salathe 2009), and shifts in the form of precipitation (snow to rain; Elsner et al. 2009), suggest 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). For example, in the montane zone, 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 invasion 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 completely reset or reposition forest-meadow boundaries. Where invading trees are killed, ecotonal areas are likely to revert quite rapidly to dominance by meadow species.

To my knowledge, the permanent study sites in TSBR provide the first and only direct long-term measurements of recent vegetation response to 20th-century forest expansion in western North American meadows. Understanding the role of landscape context and the nature and diversity of tree influences within these transitional zones is a critical, yet challenging goal as we seek to anticipate or predict future changes in these and other mountain landscapes.

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Table 1. Landscape/environmental characteristics, transect length, and initial (1983) tree composition and structure in the ecotone at each transect in the Three Sisters Biosphere Reserve, Oregon. Temperature and precipitation are interpolated using Daly et al. (2008).

Physiographic province/Site	Site code	Annual precip. (mm)	July max. temp. (°C)	Jan min. temp. (°C)	Elev. (m)	Slope (%)	Aspect	Hyd.[a]	Trans. length (m)	Primary tree species[b]	Tree density (no./ha)	Tree basal area (m^2/ha)	Tree cover (%)	CV of tree cover (%)
Western Cascades														
Lowder Mountain 1	LW1	2154	21.0	-5.1	1668	5	Flat	M	76	Tm, Al	765	6.3	53.5	0.9
Lowder Mountain 2	LW2	2154	21.0	-5.1	1669	1	Flat	M	93	Tm, Al	608	15.7	37.9	1.2
Yankee Mountain	YM	2164	21.7	-4.2	1555	70	SSE	M	68	Ag, Pm	250	1.5	14.7	2.1
Olallie Meadow[c]	OM	2027	21.2	-4.6	1520	12	SSW	M	120	Ag, Pc	546	29.5	56.5	1.0
Walker 1	W1	2076	21.8	-3.9	1498	50	SSE	M	65	Ag	179	48.2	64.2	0.7
Walker 2	W2	2098	22.0	-3.7	1535	45	SSE	M	151	Ag	148	32.8	38.9	1.5
Rebel Rock	RR	1806	21.0	-4.1	1597	25	W	M	82	Tm, Ag, Al	928	12.6	44.5	1.2
Quaking Aspen 1	QA1	2029	22.3	-3.6	1280	5	NE	H	87	Al, Pe, Tm	1033	3.9	32.2	1.2
Quaking Aspen 2	QA2	2029	22.3	-3.6	1283	3	N	H	70	Al, Pe, Tm	2286	5.8	47.9	1.1
High Cascades														
Corral Flat[c]	CF	1735	22.2	-5.0	1386	0	Flat	H	58	Pe, Pc	467	33.7	72.1	0.8
Cow Swamp	CS	1723	22.0	-4.8	1343	0	Flat	H	110	Pc	132	1.4	11.7	2.5
James Creek	JC	2683	21.0	-7.7	1832	27	SW	M	98	Tm, Al	917	19.3	41.3	1.0
Separation Creek	SC	2647	21.0	-6.9	1758	3	SE	H	75	Al	426	9.4	15.3	2.3
Wickiup Plains[c]	WP	2670	20.7	-7.9	1850	2	E	M	79	Tm	357	32.4	31.4	1.1
Green Lake[c]	GL	2544	19.5	-9.2	2000	0	Flat	H	220	Pc, Tm	9	0.0	4.0	2.1
Linton Meadow 1	LM1	2723	21.1	-7.0	1828	58	SW	M	60	Al	403	49.7	62.2	1.1
Linton Meadow 2[c]	LM2	2709	20.5	-7.3	1852	32	W	M	60	Tm	56	0.0	0.3	2.9
Racetrack Meadow	RM	2720	20.9	-7.0	1882	34	NE	M	100	Tm	3784	0.3	19.7	1.2
Obsidian Flat	OF	2696	20.8	-7.0	1869	15	WSW	M	60	Tm, Pa	286	0.8	14.0	1.7
Obsidian Creek	OC	2719	20.7	-7.0	1830	22	S	M	90	Al	3214	12.2	49.3	1.0

[a] Hydrological condition: M = mesic upland, H = hydric (seasonally high water table)

[b] 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*

[c] Not sampled in 1993

Table 2. Variation explained and variable loadings from principal components analysis (PCA) of tree structural characteristics within ecotone habitats. 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 3).

	PC1	PC2
Variation explained:	0.37	0.26
Variable	Correlation	
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

Table 3. Results of multiple regression models explaining changes in ground-layer vegetation within ecotones from 1983-2009. Results for each response variable 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 ($P<0.05$) and marginally significant ($0.05<P<0.1$) 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. 2); initial tree structure (PC1 score; Table 2); change in tree structure over the study period (PC2 score; Table 2); and the value of the response variable at the initial sampling in 1983.

			NMDS1		NMDS2		PC1		PC2		Initial value	
Response variable	Adj. R^2	*P*	Coeff.	*P*	Coeff.	*P*	Coeff.	*P*	Coeff.	*P*	Coeff.	*P*
Compositional heterogeneity	0.14	0.108							-0.37	0.108		
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**
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**
Richness	0.61	<0.001			-0.53	**0.005**					0.41	**0.021**
Growth forms												
Grass cover	0.63	<0.001					-0.28	0.068			-0.81	**<0.001**
Sedge 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**

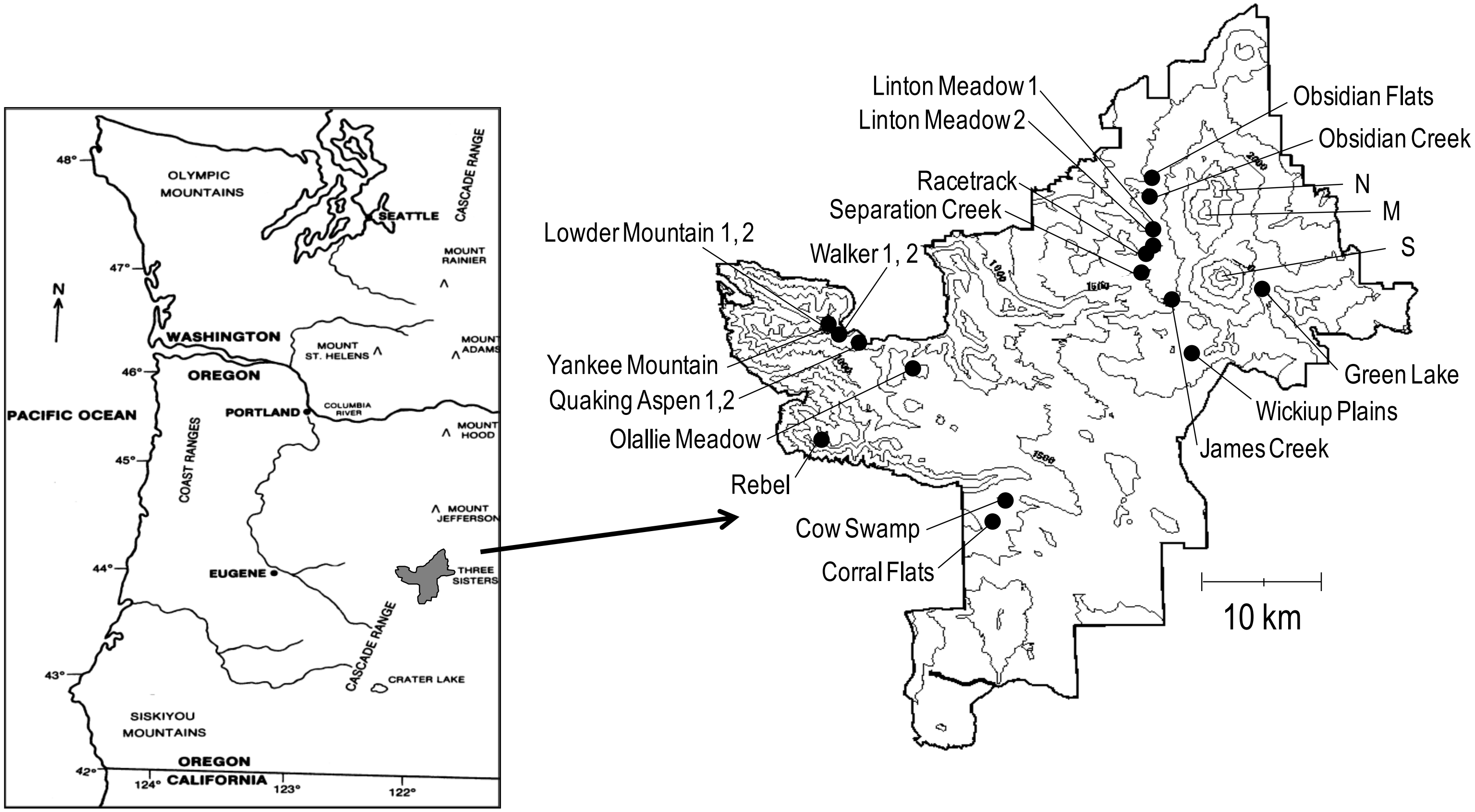


Fig 1. Location of permanent forest – meadow ecotone transects in the Three Sisters Biosphere Reserve. N, M, and S are the North, Middle and South Sisters respectively (~3,000 m volcanoes). Figure adopted from Miller and Halpern 1998.

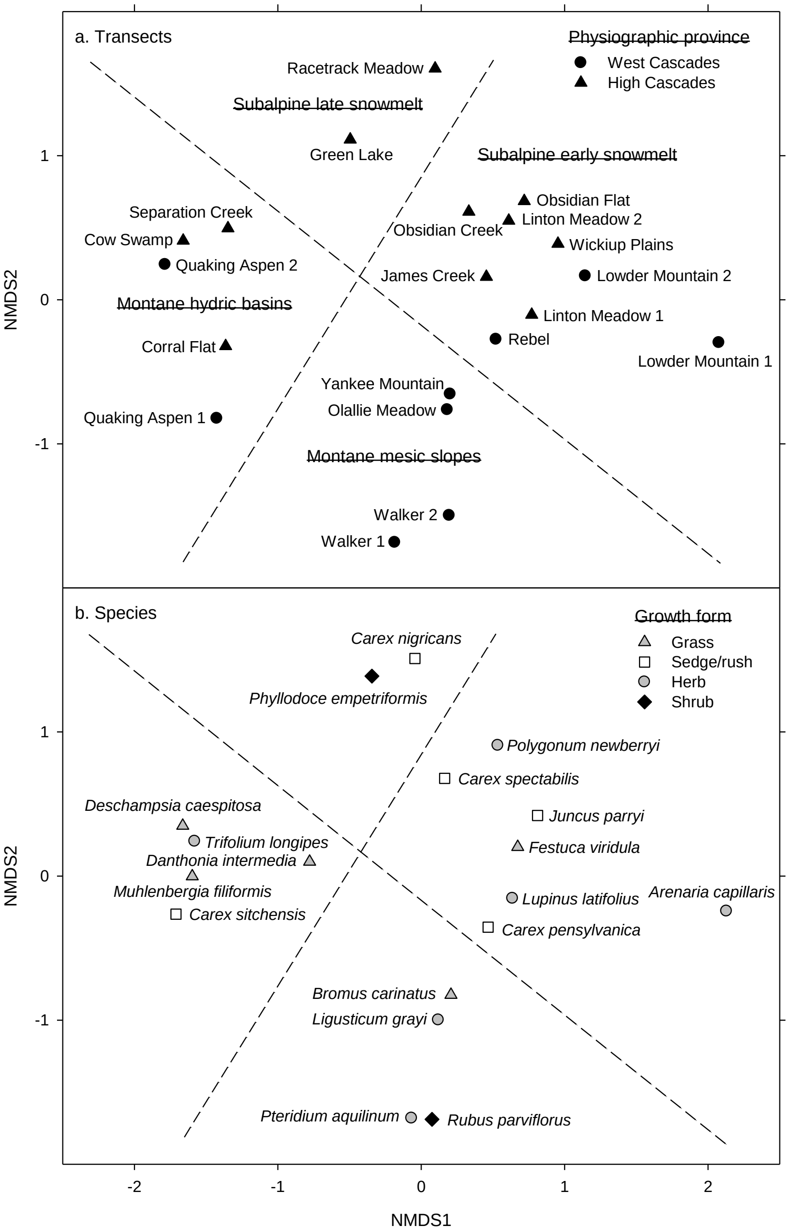


Fig. 2. NMDS ordination illustrating (a) the landscape context of each transect and (b) characteristic meadow species coded by growth form. Transect values represent the average species composition of meadow habitats at initial sampling (1983) (see *Methods: Comparing changes among ecotones across the landscape*). The dashed lines separate the four landscape contexts delineated for subsequent analyses. Species selected based on average cover and frequency within each landscape context. See Table 1 for other site descriptors.

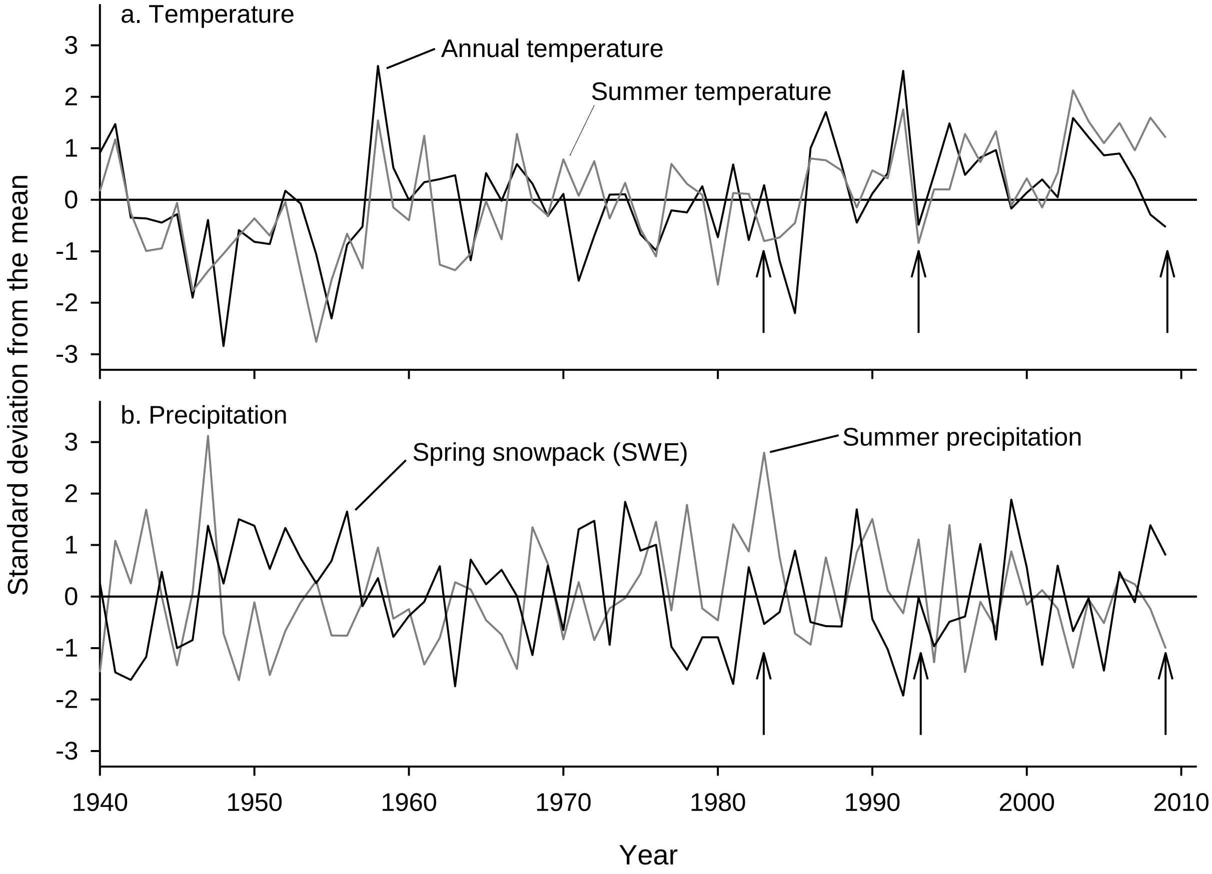


Fig. 3. Climatic variation between 1940 and 2009 (expressed as standard deviations from the 1940 – 2009 mean). Temperature and summer precipitation data are from McKenzie Bridge, Oregon (450 m a.s.l.). Spring snowpack data are from McKenzie Pass, Oregon (1453 m a.s.l), expressed as snow water equivalent (SWE) on 1 April. The summer period for temperature and precipitation is June through August. Vertical arrows denote the vegetation sampling dates in 1983, 1993 and 2009.

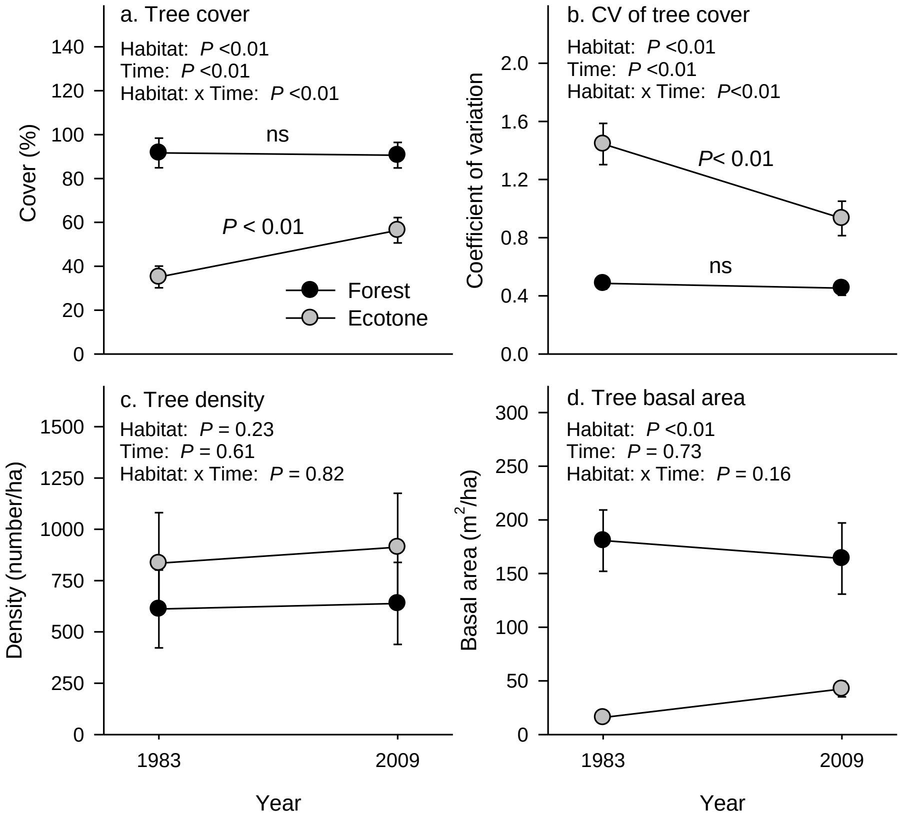


Fig. 4. Changes in tree structure (mean ±1 SE) over the study period for forest and ecotone habitats. Statistical significance (*P*-values) for habitat, time, and habitat x time terms are from univariate repeated measures PERMANOVA models. For habitat x time interactions, post-hoc comparisons within each habitat were made using Fisher's LSD.

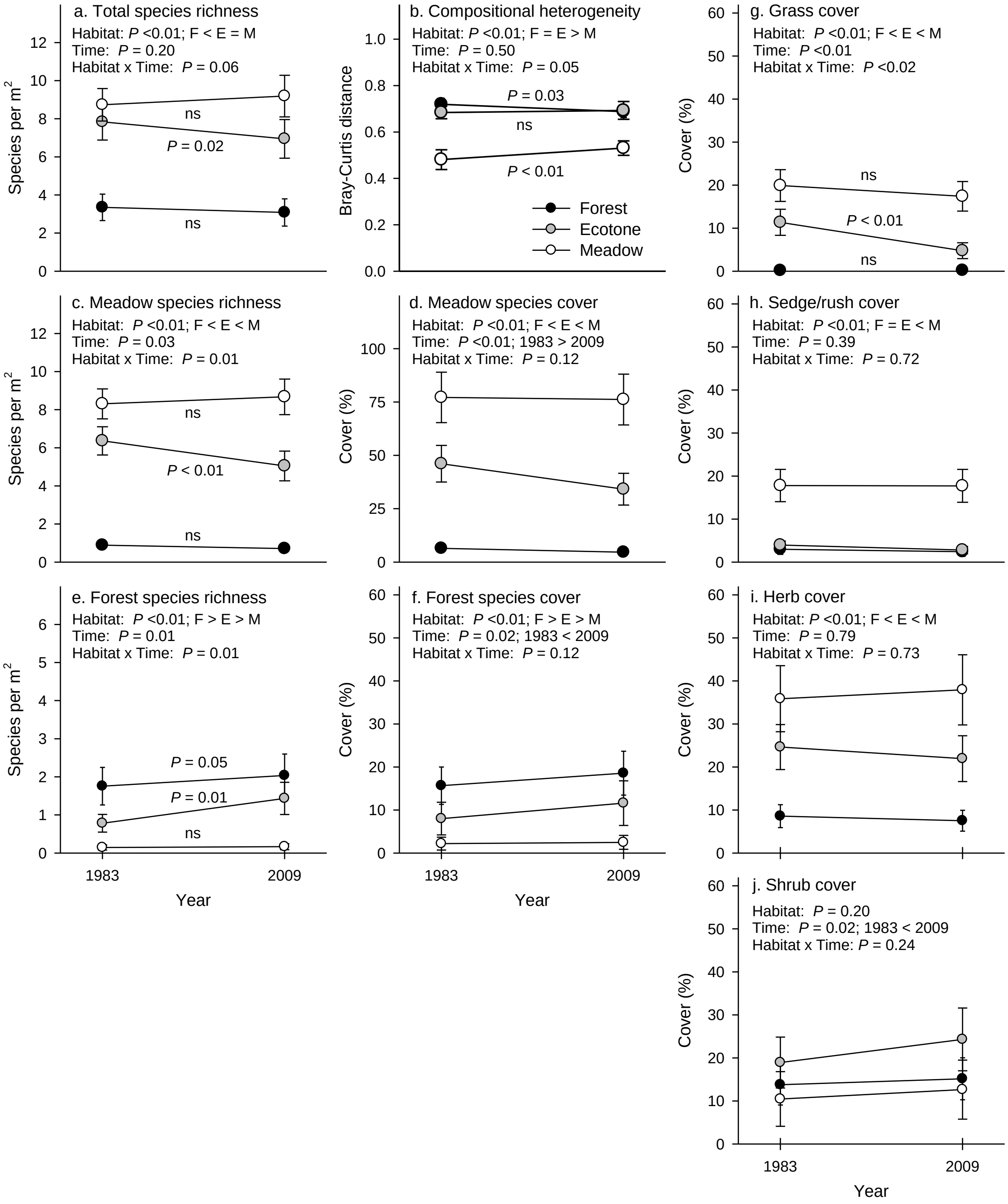


Fig. 5. Changes in ground-layer vegetation (mean ±1 SE) over the study period for forest (F), ecotone (E), and meadow (M) habitats. Statistical significance (*P*-values) for habitat, time, and habitat x time terms are from univariate repeated measures PERMANOVA models. For main effects and significant habitat x time interactions, post-hoc comparisons within each habitat were made using Fisher's LSD.

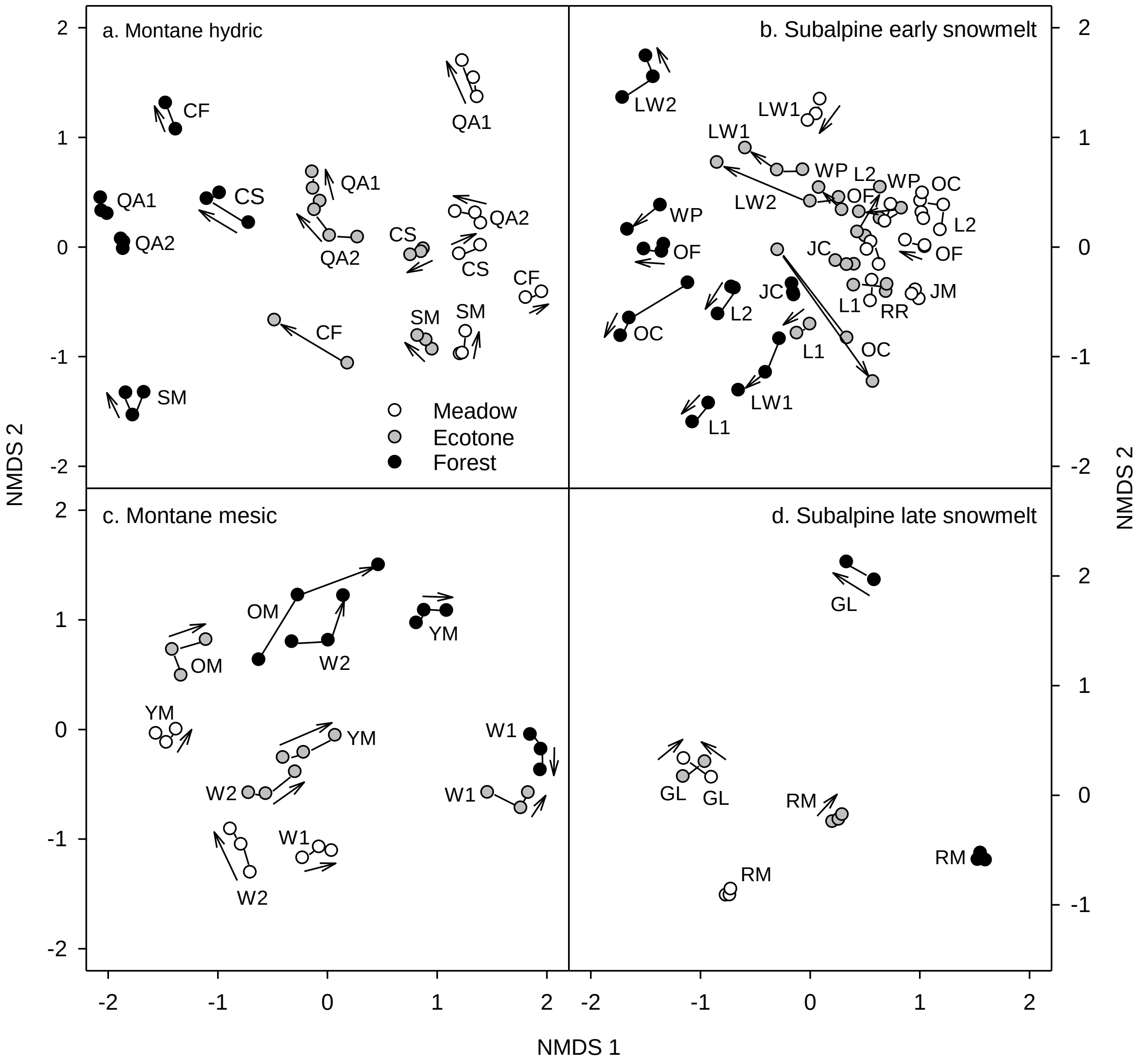


Fig. 6. Temporal changes in species composition in forest, ecotone, and meadow habitats at each site as portrayed in NMDS space. Separate ordinations were run for each landscape context (Fig. 2a; see *Methods: Temporal changes among forest, ecotone, and meadow habitats*). Samples represent the average species composition of each habitat at each sampling date (1983, 1993, and 2009). Lines connect sampling dates and arrows indicate directions of change over time. Transect abbreviations are defined in Table 1. Note: CF, WP, LM2, OM, and GL do not have data from 1993.

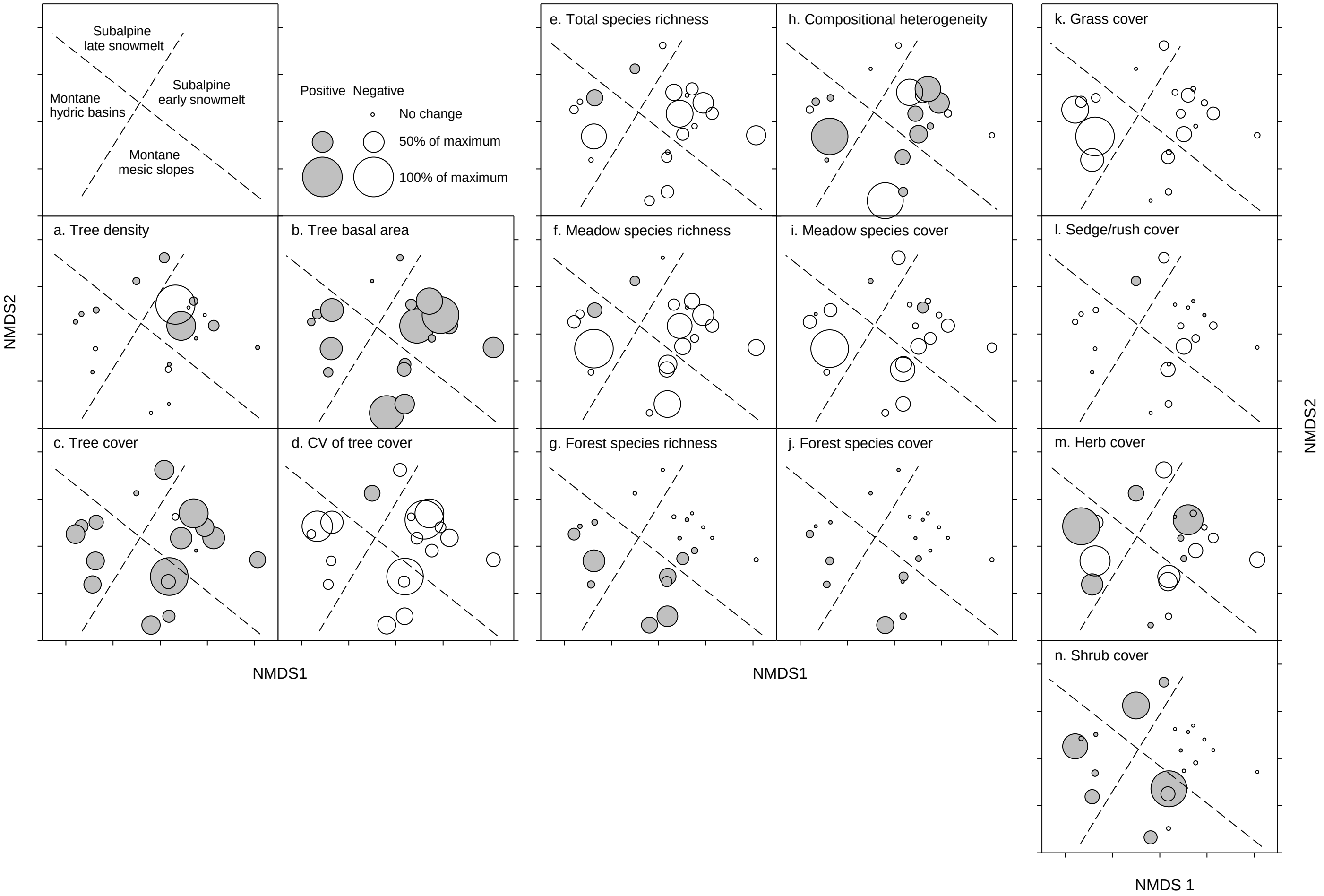
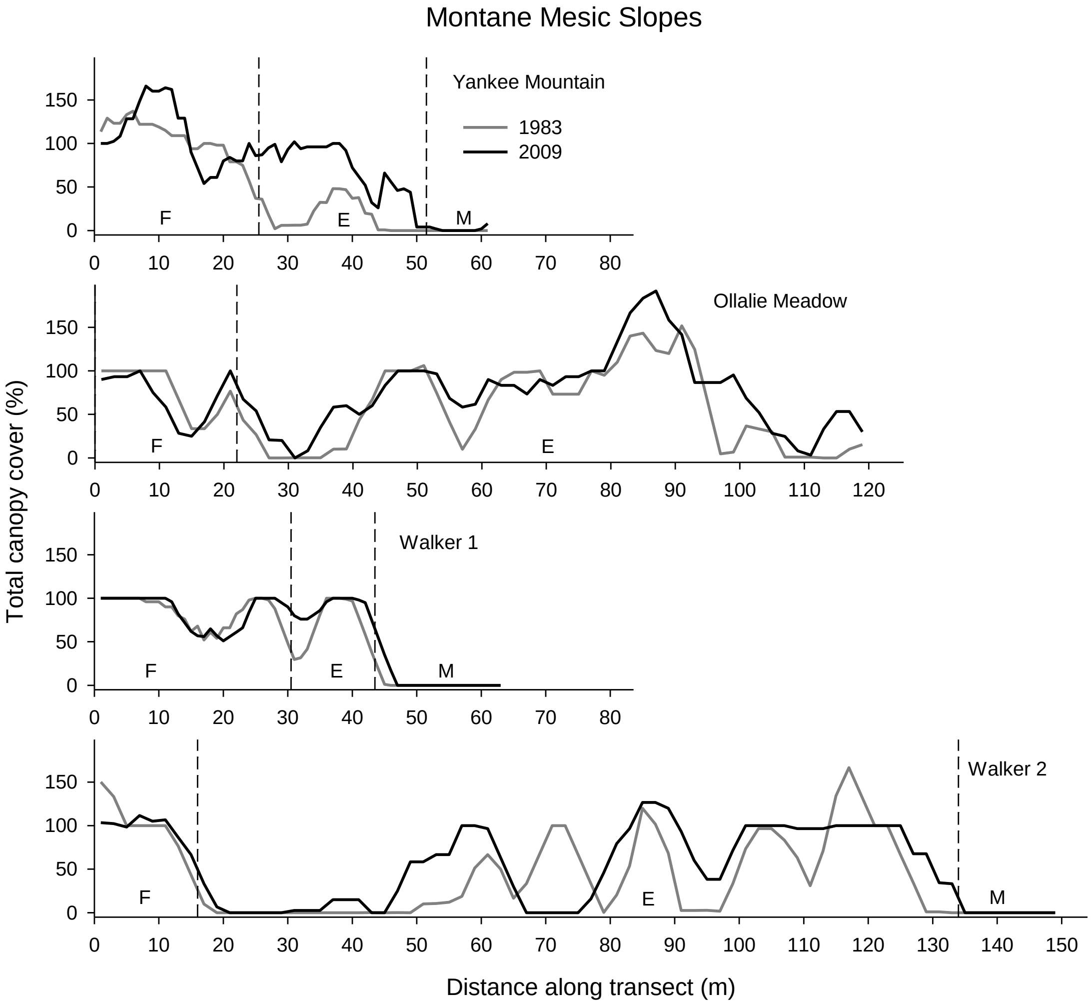


Fig. 7. Changes (1983-2009) in ecotone tree structure and ground-layer vegetation across the TSBR landscape as portrayed in NMDS space (see Fig. 2). Direction of change is coded as gray = positive and white = negative; magnitude of change is coded by symbol size, scaled to the maximum value of each variable. Maximum values are: (a) tree density = 3,000 trees/ ha, (b) tree basal area = 70 m^2/ha, (c, i-n) all cover variables = 60%, (d) CV of tree cover = 1.4, (h) compositional heterogeneity = 30% dissimilarity, and (e-g) all measures of species richness = 5 species/m^2.

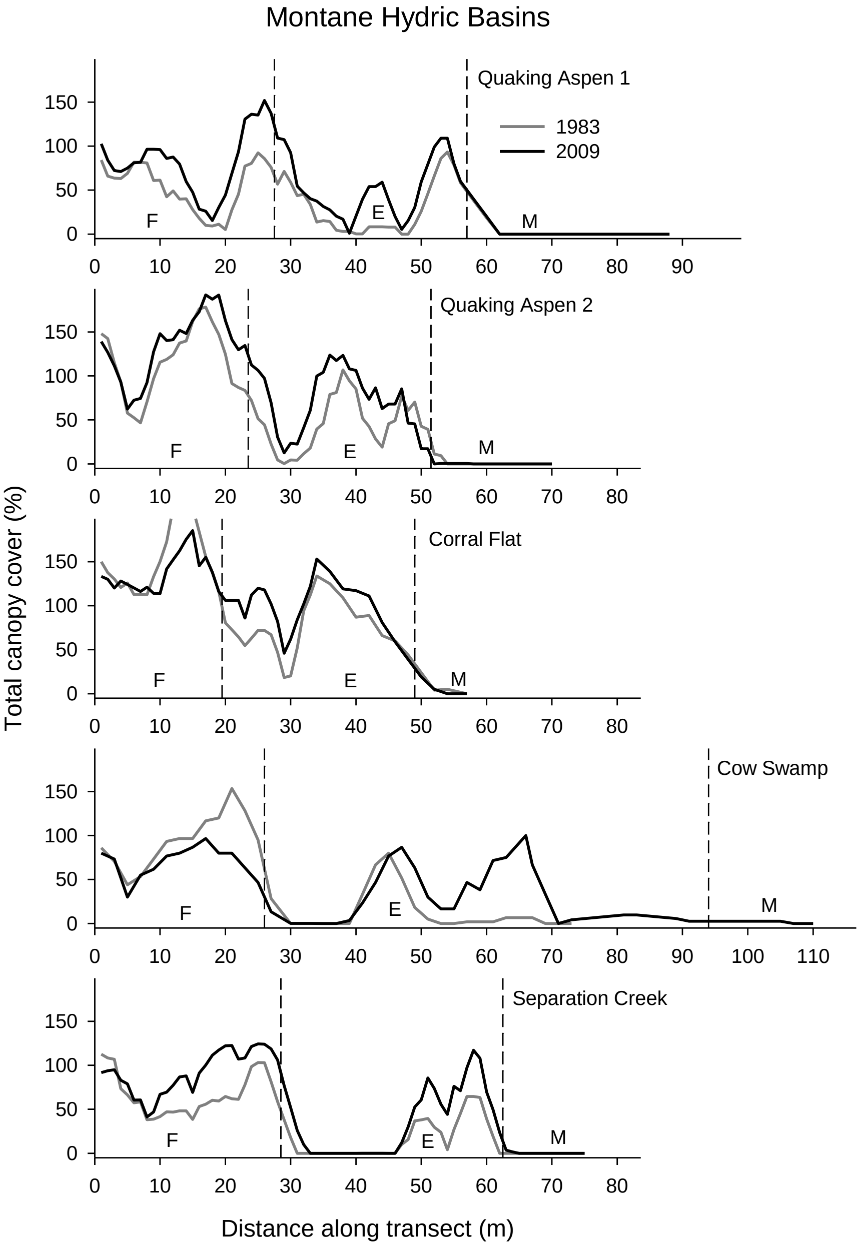
Appendix B

Tree canopy cover along TSBR forest-meadow ecotones

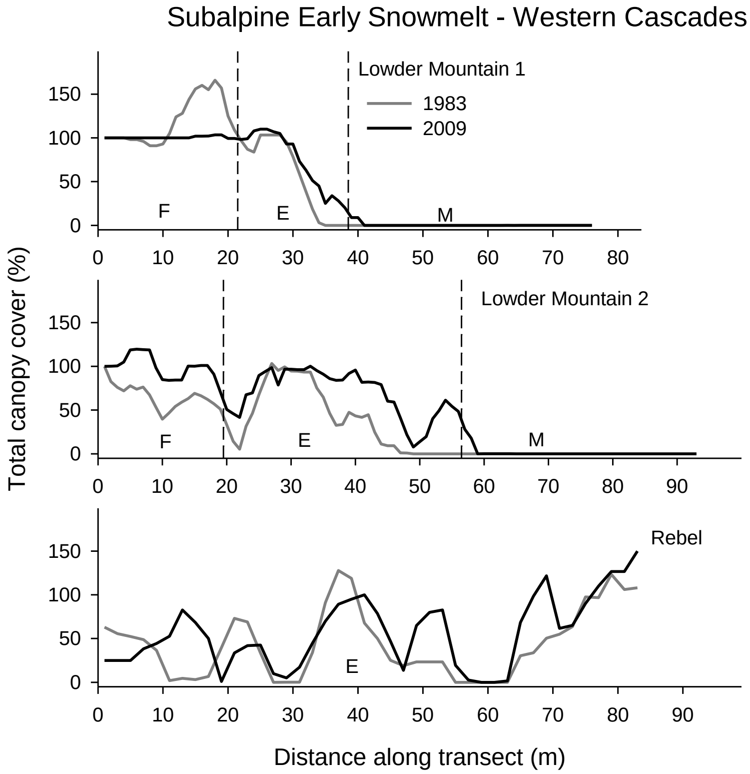
Changes in total canopy cover (summed cover of all conifer species) over the study period (1983-2009) for forest-meadow ecotone transects in the Three Sisters Biosphere Reserve (TSBR), Oregon. Values were smoothed as 3-m running averages. Gray lines represent 1983 values and black lines 2009 values. Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow. See *Chapter 4, Methods: Habitat definitions.*



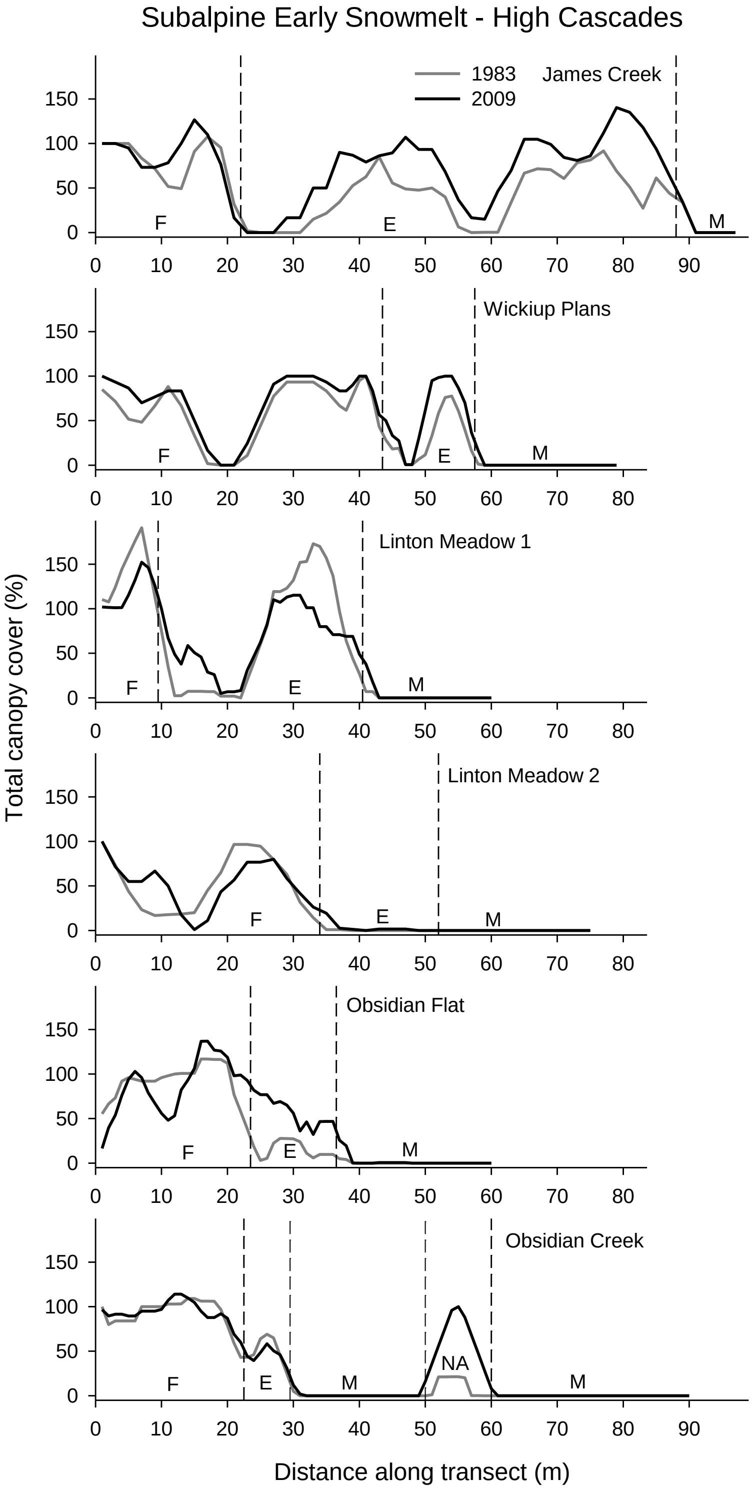
Appendix B.1. Changes in total canopy cover for transects located on montane mesic slopes (Western Cascades). Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow. Note: Ollalie Meadow did not contain meadow habitat as defined in this study (see *Methods: Habitat definitions*).



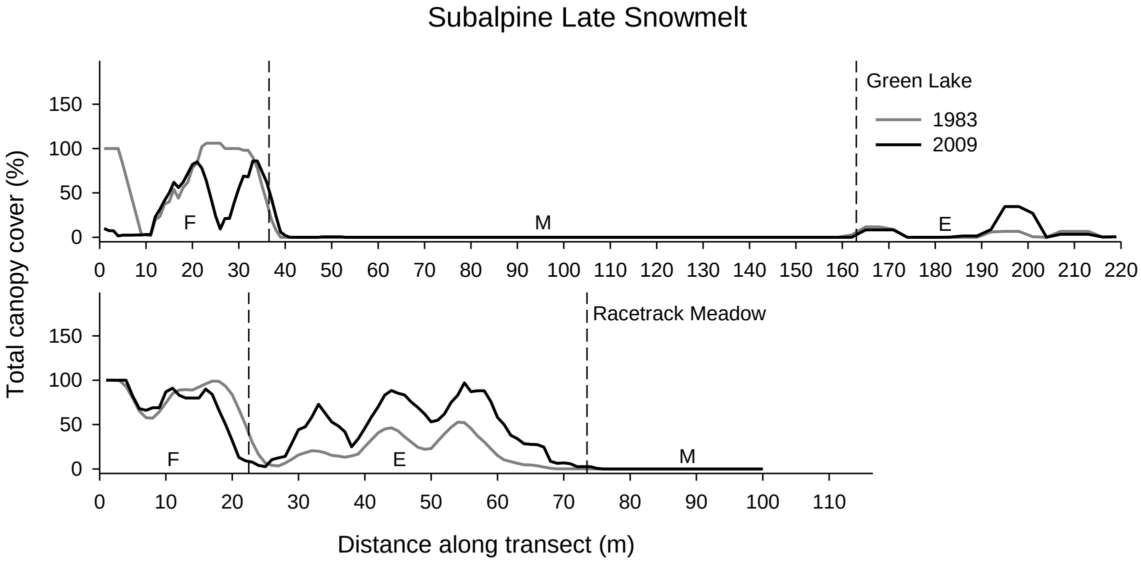
Appendix B.2. Changes in total canopy cover for transects located in montane hydric basins. Quaking Aspen 1 and 2 are in the Western Cascades; Separation Creek, Corral Flat, and Cow Swamp are in the High Cascades. Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow.



Appendix B.3. Changes in total canopy cover for transects located in subalpine sites with early snowmelt (Western Cascade sites). Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow. Note: Rebel did not contain forest or meadow habitat as defined in this study (see *Methods: Habitat definitions*).



Appendix B.4. Changes in total canopy cover for transects located in subalpine sites with early snowmelt (High Cascade sites). Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow. Note: At Obsidian Creek (d), the NA (not analyzed) denotes a 10-m section of the transect where a single isolated tree island (>30m from forest) interrupted otherwise contiguous open meadow habitat. .

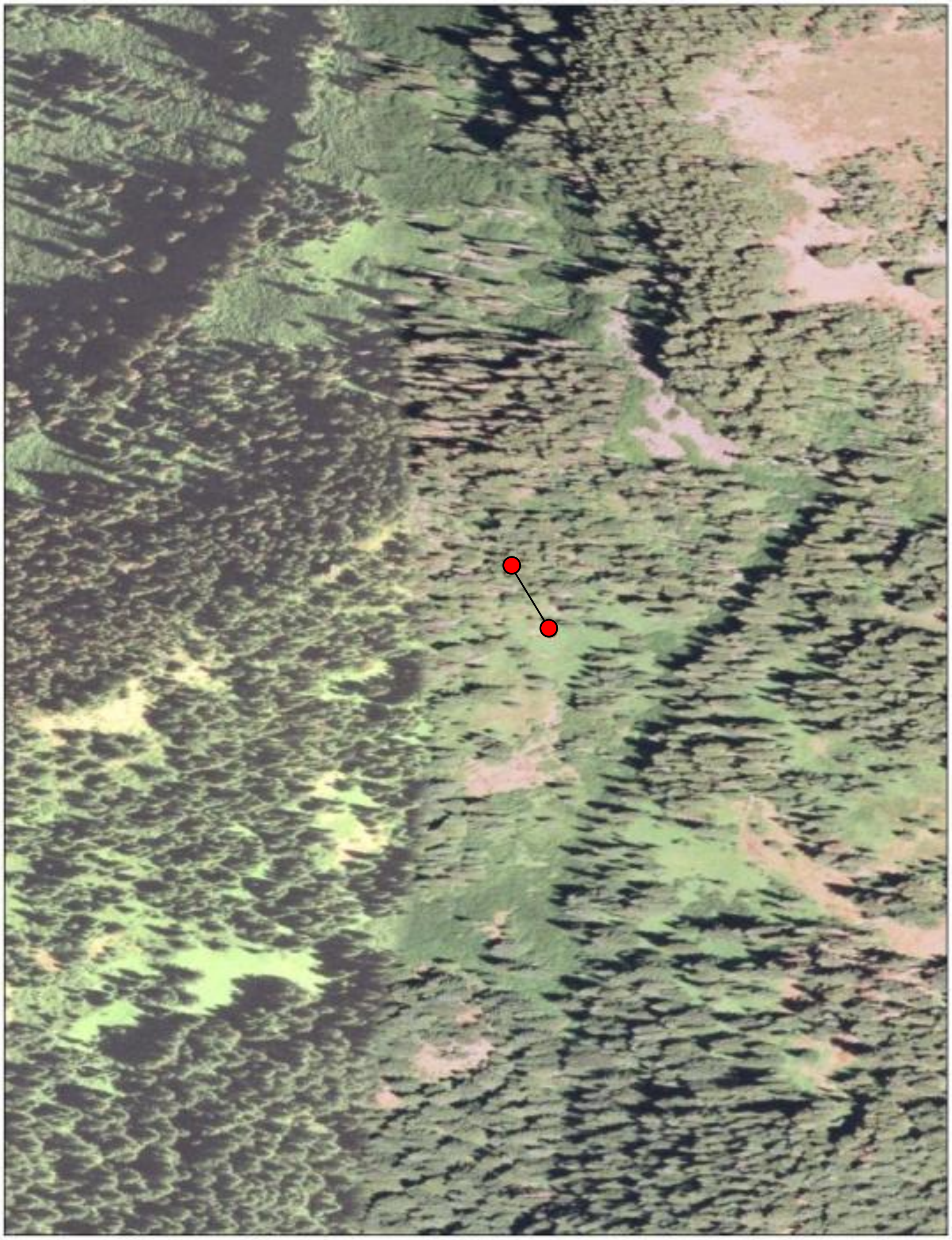


Appendix B.5. Changes in total canopy cover for transects located in subalpine sites with late snowmelt (High Cascades). Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow. Note: Reversed order of ecotone and meadow habitat at Green Lake represents an expanding patch of conifers in open meadow.

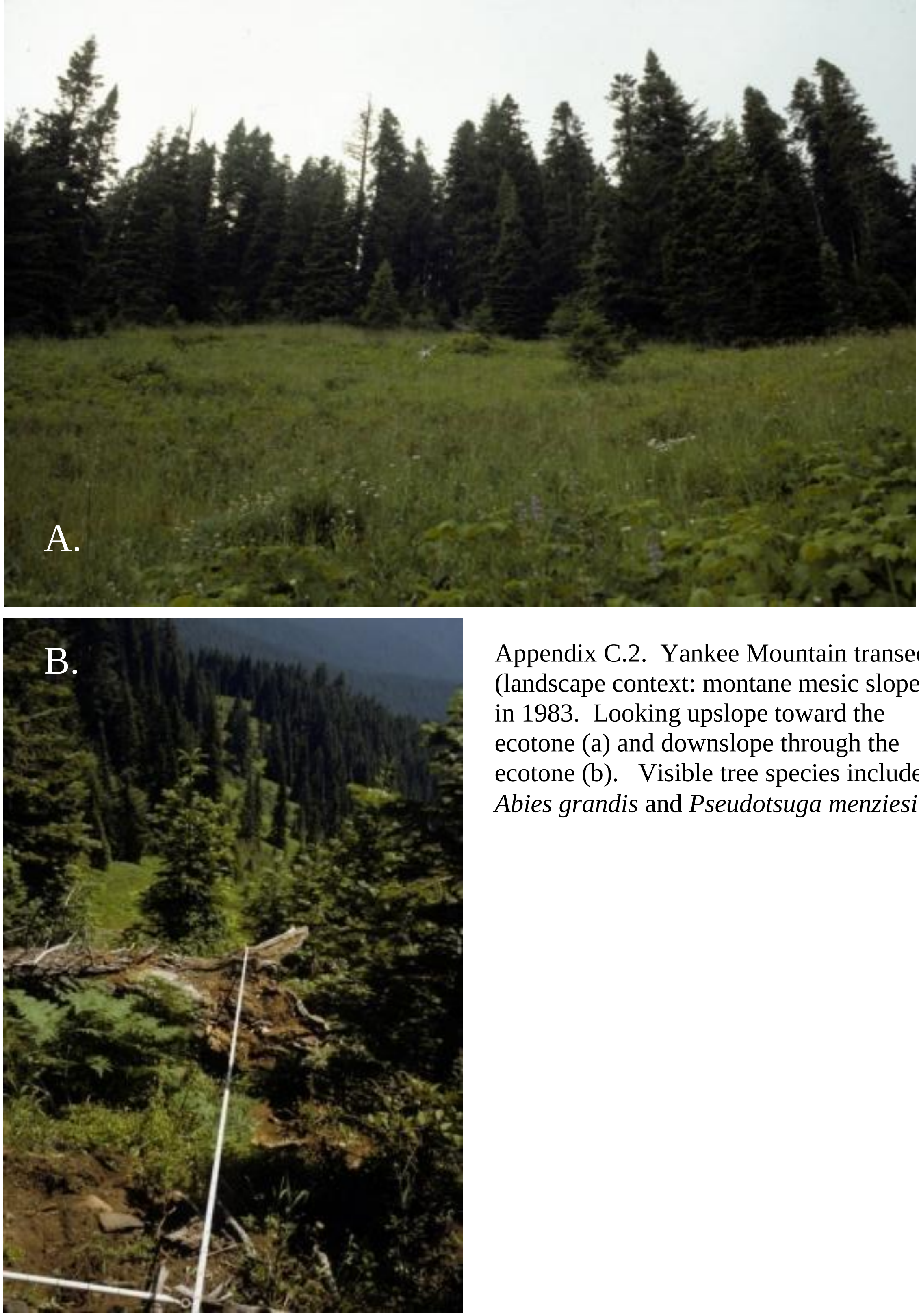
Appendix C

Photographs of TSBR forest-meadow ecotones

Aerial and ground-based photographs of the forest-meadow ecotone transects in the Three Sisters Biosphere Reserve (TSBR), Oregon. Aerial photographs (scale: 1:3500) were taken in 2006. Photographs are oriented N (top) to S (bottom). Transect end-points are indicated by red circles. Most ground-based photographs are from 1983 (as available) to illustrate ecotone structure at the beginning of the study. These are supplemented by more recent photographs (1993 and 2009).



Appendix C.1. Aerial photograph of the Yankee Mountain transect (landscape context: montane mesic slope) in 2006. The transect (68 m long) begins near a ridge top and extends downslope (upper left to lower right) through an ecotone with *Abies grandis* and *Pseudotsuga menziesii*.

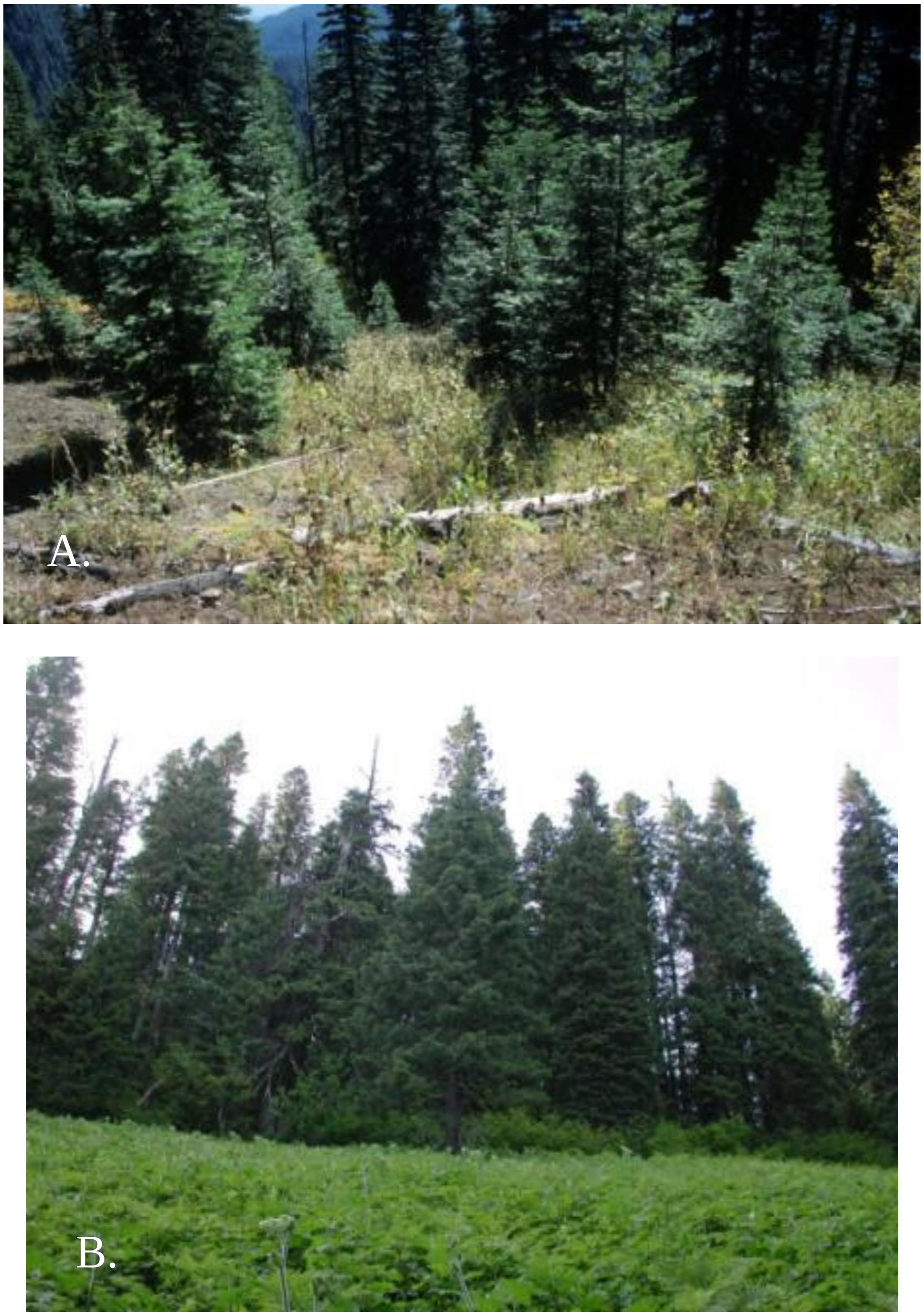


Appendix C.2. Yankee Mountain transect (landscape context: montane mesic slope) in 1983. Looking upslope toward the ecotone (a) and downslope through the ecotone (b). Visible tree species include *Abies grandis* and *Pseudotsuga menziesii*.

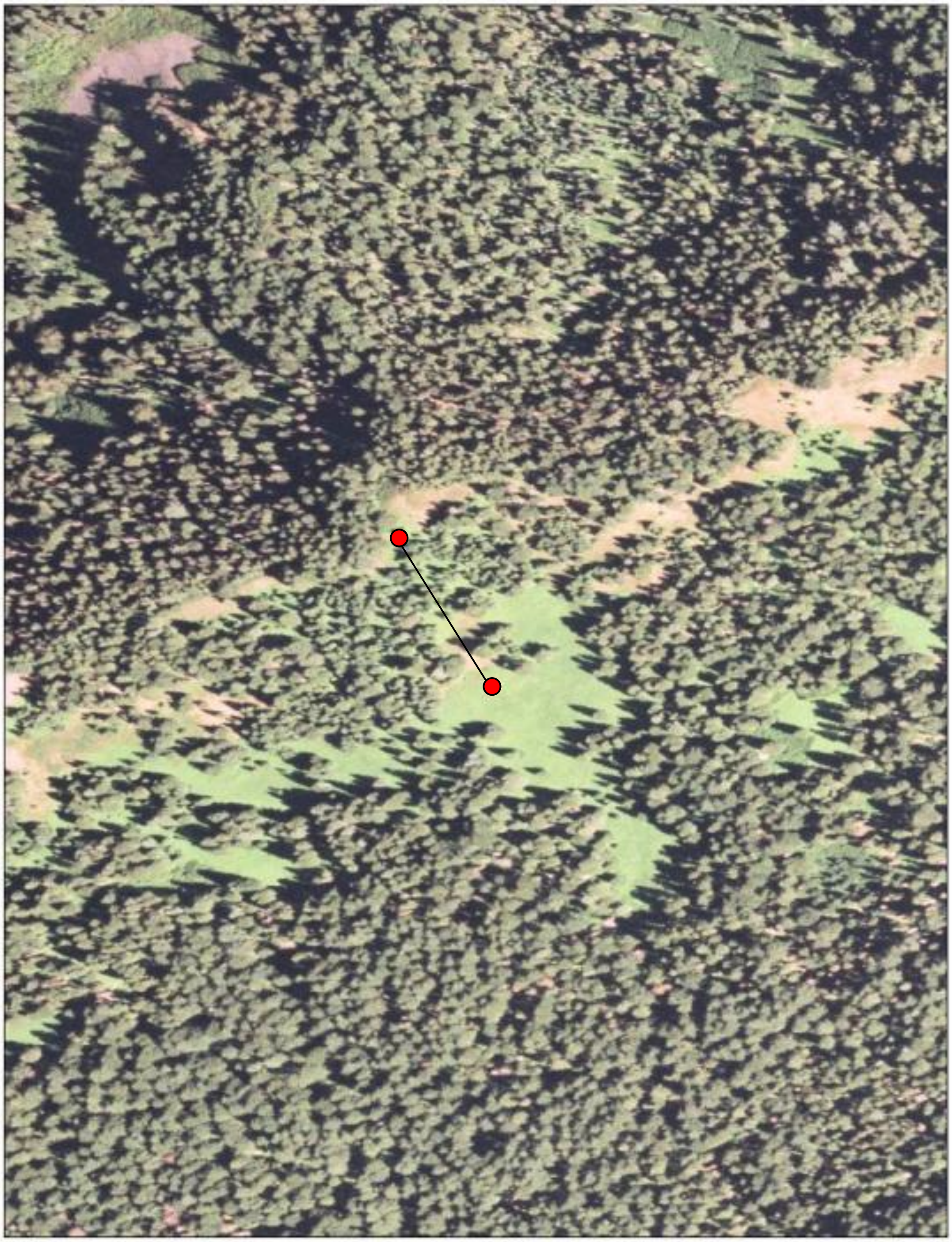
Appendix C.3. Aerial photograph of the Ollalie Meadow transect (landscape context: montane mesic slope) in 2006. The transect passes (120 m long; left to right) on level terrain from *Abies grandis* forest into dense ecotone with *Pinus contorta*, *Pseudotsuga menziesii*, and *Abies grandis*.

Appendix C.4. Ollalie Meadow transect (landscape context: montane mesic slope) in 1983. Looking along the ecotone to the forest. Visible tree species include *Pinus contorta* and *Pseudotsuga menziesii* (background) and *Abies grandis* (foreground); ground vegetation includes *Haplopappus greenei*, *Bromus carinatus*, and *Carex pensylvanica*.

Appendix C.5. Aerial photograph of the Walker 1 transect (landscape context: montane mesic slope) in 2006. The transect (65 m long) begins near a ridge top and extends downslope (upper left to lower right) through an ecotone with *Abies grandis* into *Rubus parviflorus-Pteridium aquilinum* meadow.



Appendix C.6. Walker 1 transect (landscape context: montane mesic slope). (a) Looking downslope along transect within the ecotone in 1993 (note tape running next to young *Abies grandis*). (b) Looking upslope toward the ecotone in 2009. Visible tree species include *Abies grandis* and *Pseudotsuga menziesii*. *Acer circinatum* is at the forest-meadow boundary; *Rubus parviflorus* and *Pteridium aquilinum* dominate the ground vegetation..

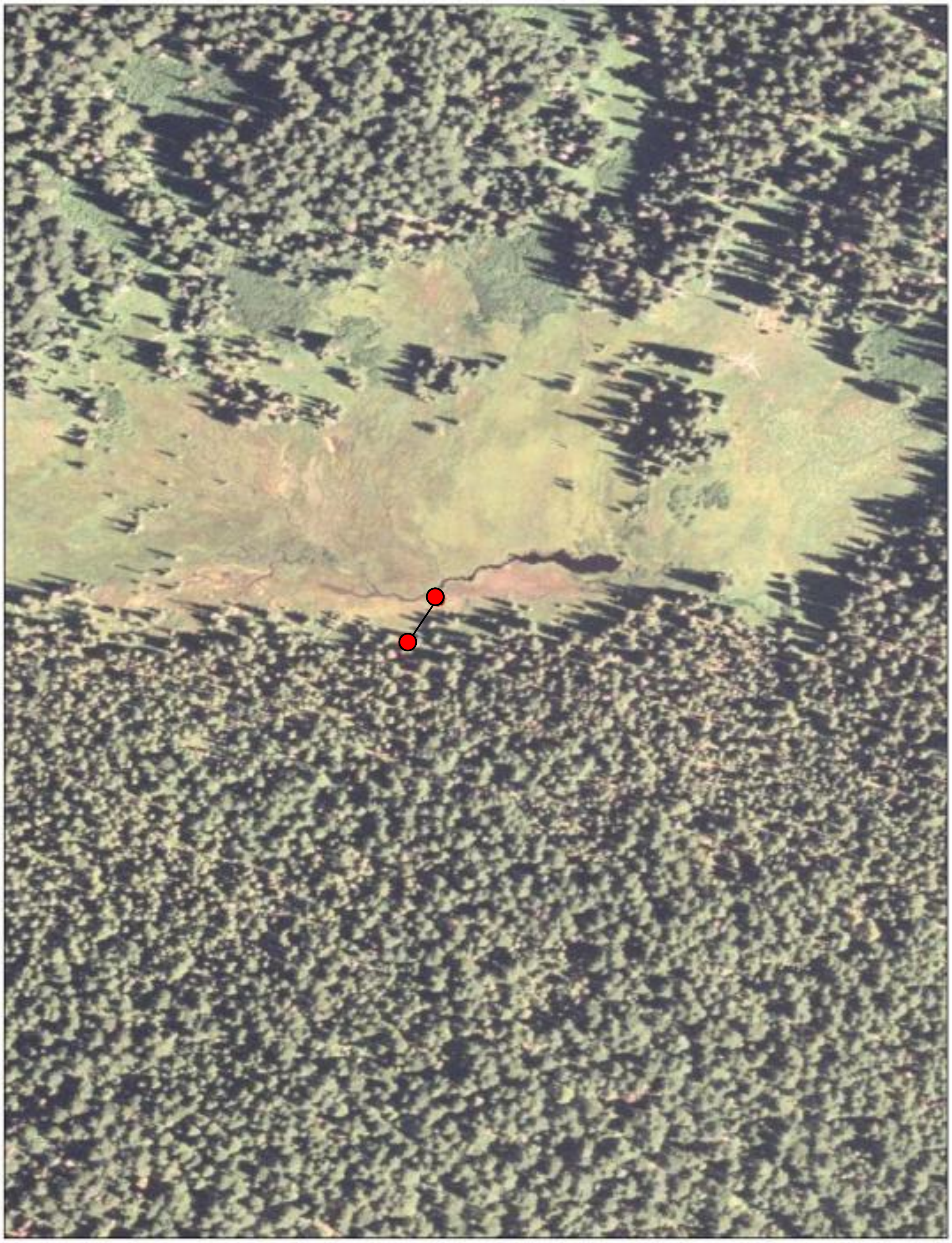


Appendix C.7. Aerial photograph of the Walker 2 transect (landscape context: montane mesic slope) in 2006. The transect (151 m long) begins near a ridge top and extends downslope (upper left to lower right) through a patchy ecotone with *Abies grandis* and *Pseudotsuga menziesii*.

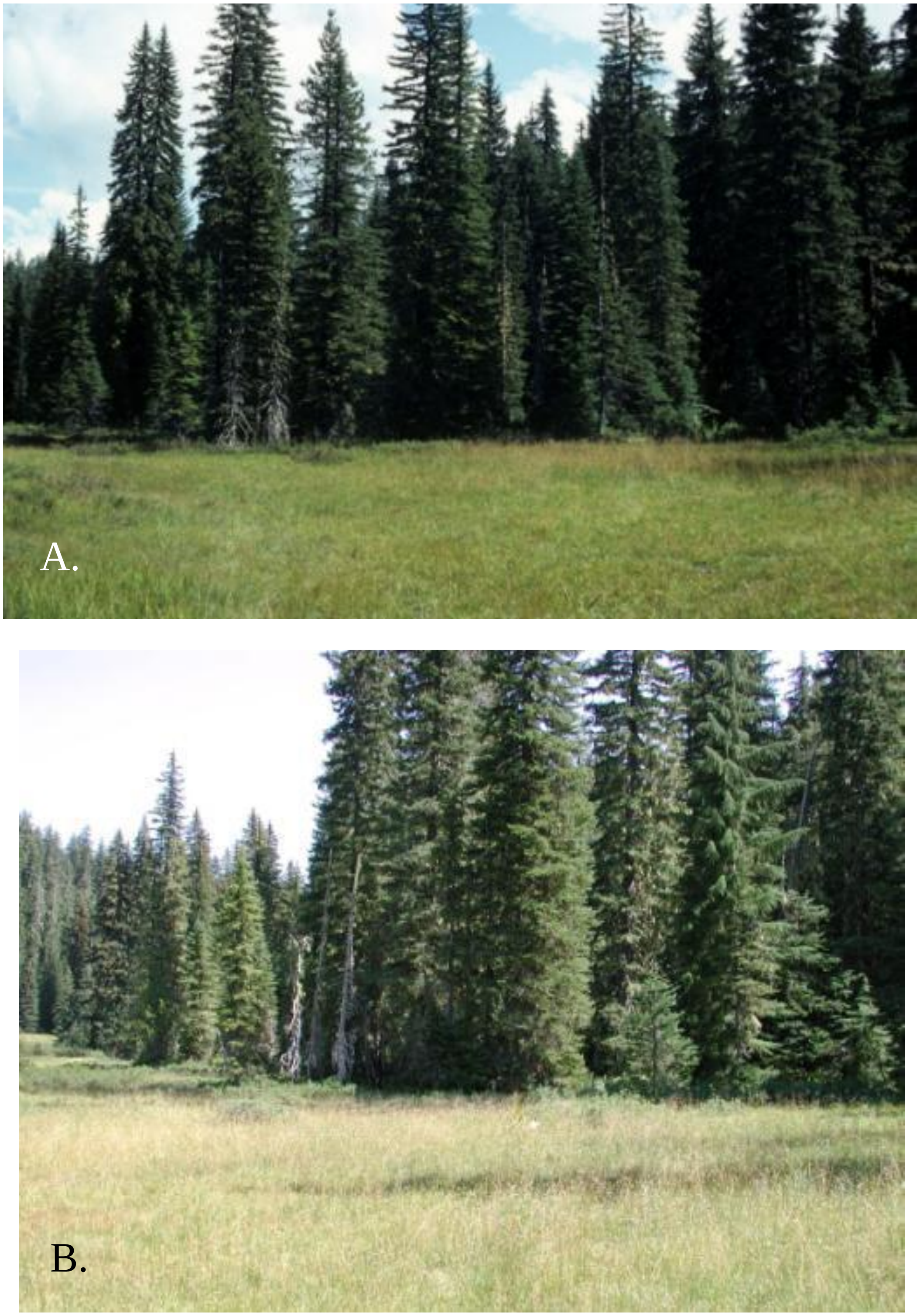
Appendix C.8. Walker 2 transect (landscape context: montane mesic slope). Looking upslope to the ecotone and forest in 1983 (a) and 2009 (b). Visible tree species include *Abies grandis* and *Pseudotsuga menziesii*.

Appendix C.9. Aerial photograph of the Quaking Aspen 1 transect (landscape context: montane hydric basin) in 2006. The transect (87 m long) begins in mixed forest of *Tsuga mertensiana*, *Abies amabilis*, *A. lasiocarpa*, and *Picea engelmannii* and extends across a sharp ecotone into hydric meadow.

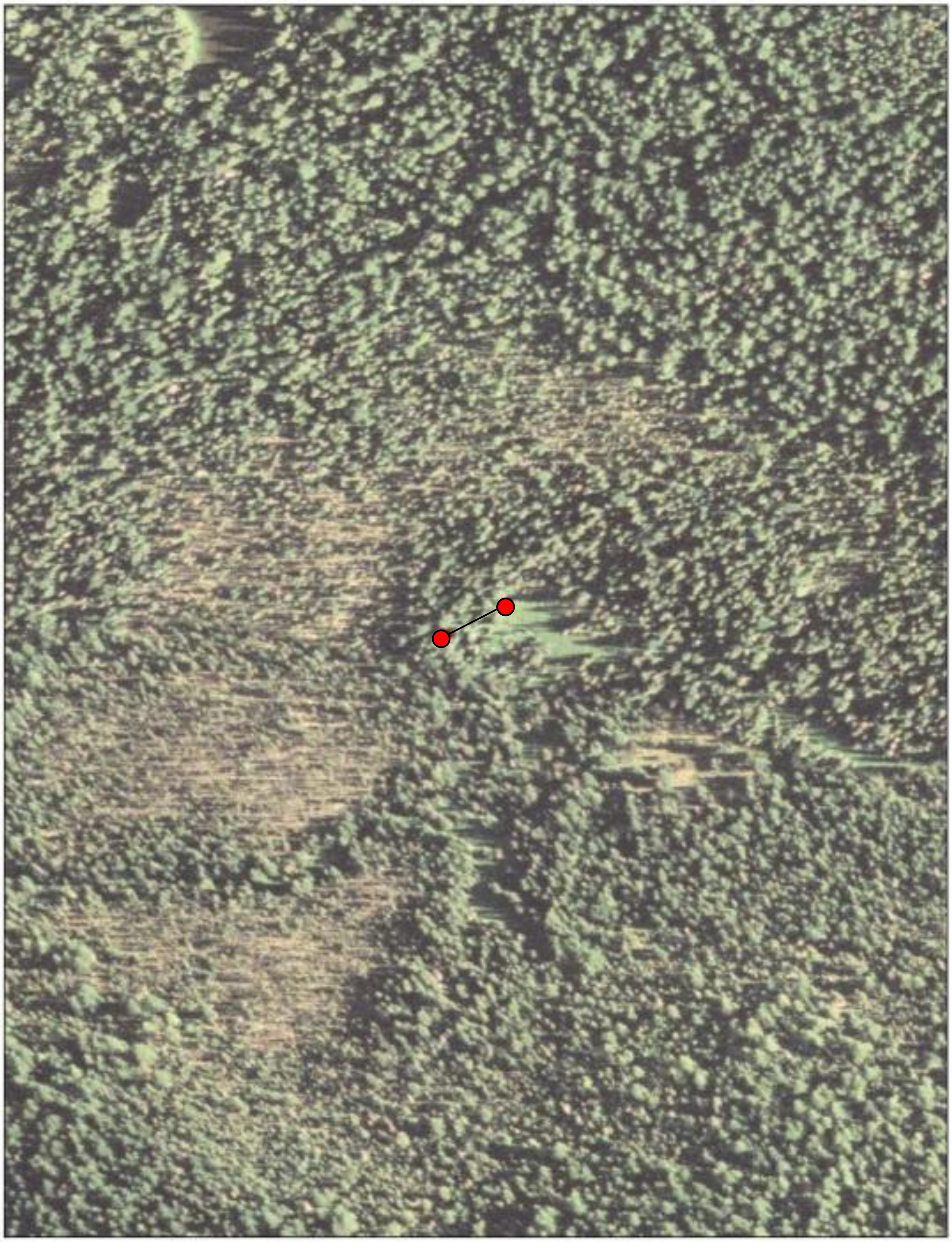
Appendix C.10. Quaking Aspen 1 (landscape context: montane hydric basin). Looking across the meadow to the ecotone and forest in (a) 1983 and (b) 2009. Visible tree species include *Abies lasiocarpa, Tsuga mertensiana,* and *Picea engelmannii*.



Appendix C.11. Aerial photograph of the Quaking Aspen 2 transect (landscape context: montane hydric basin) in 2006. The transect (70 m long) begins in mixed forest of *Tsuga mertensiana*, *Abies amabilis*, *A. lasiocarpa*, and *Picea engelmannii* and extends across a sharp ecotone into hydric meadow.

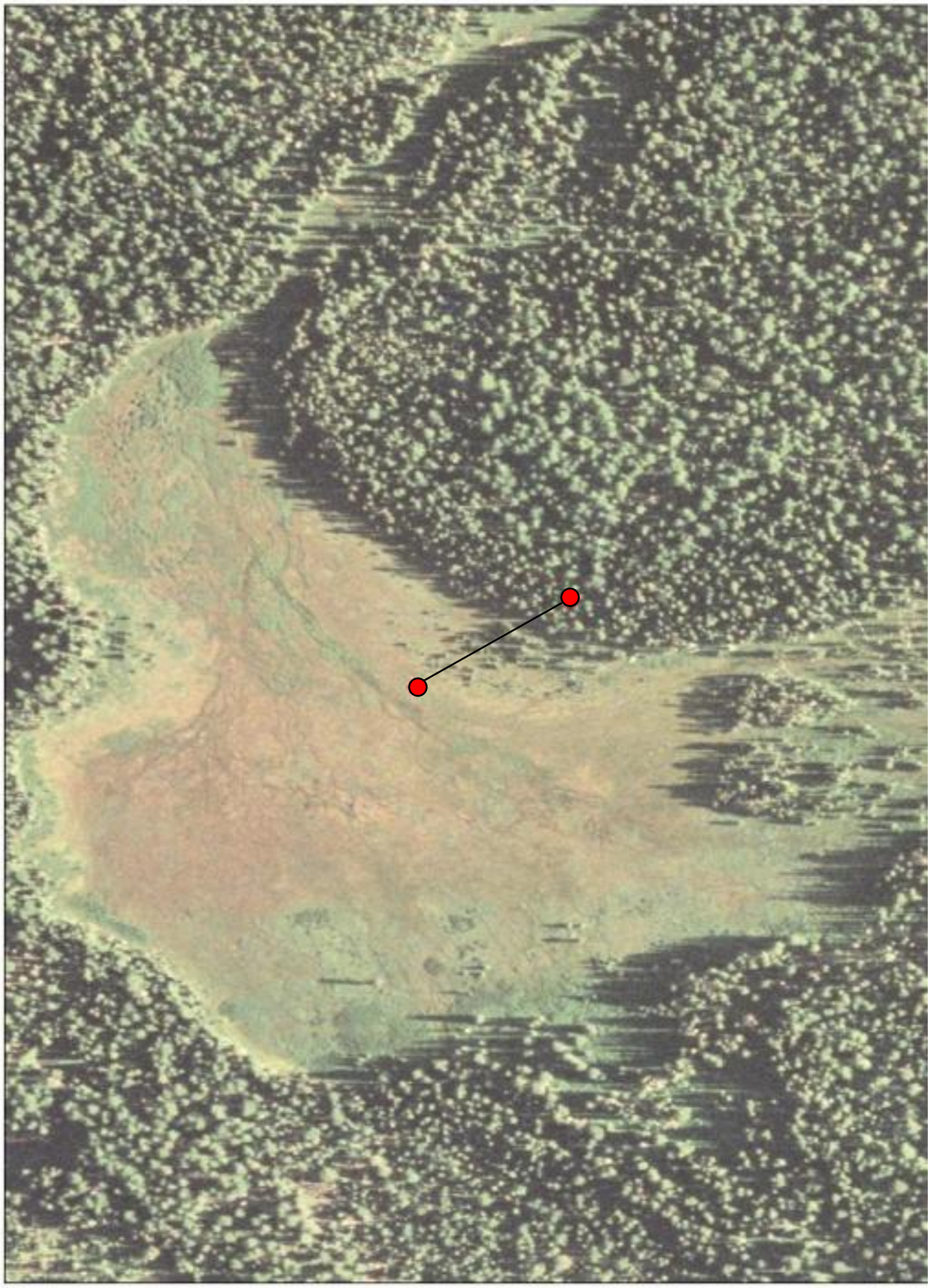


Appendix C.12. Quaking Aspen 2 (landscape context: montane hydric basin). Looking across the meadow to the ecotone and forest in (a) 1983 and (b) 2009. Visible tree species include *Abies lasiocarpa*, *Tsuga mertensiana*, and *Picea engelmannii*.



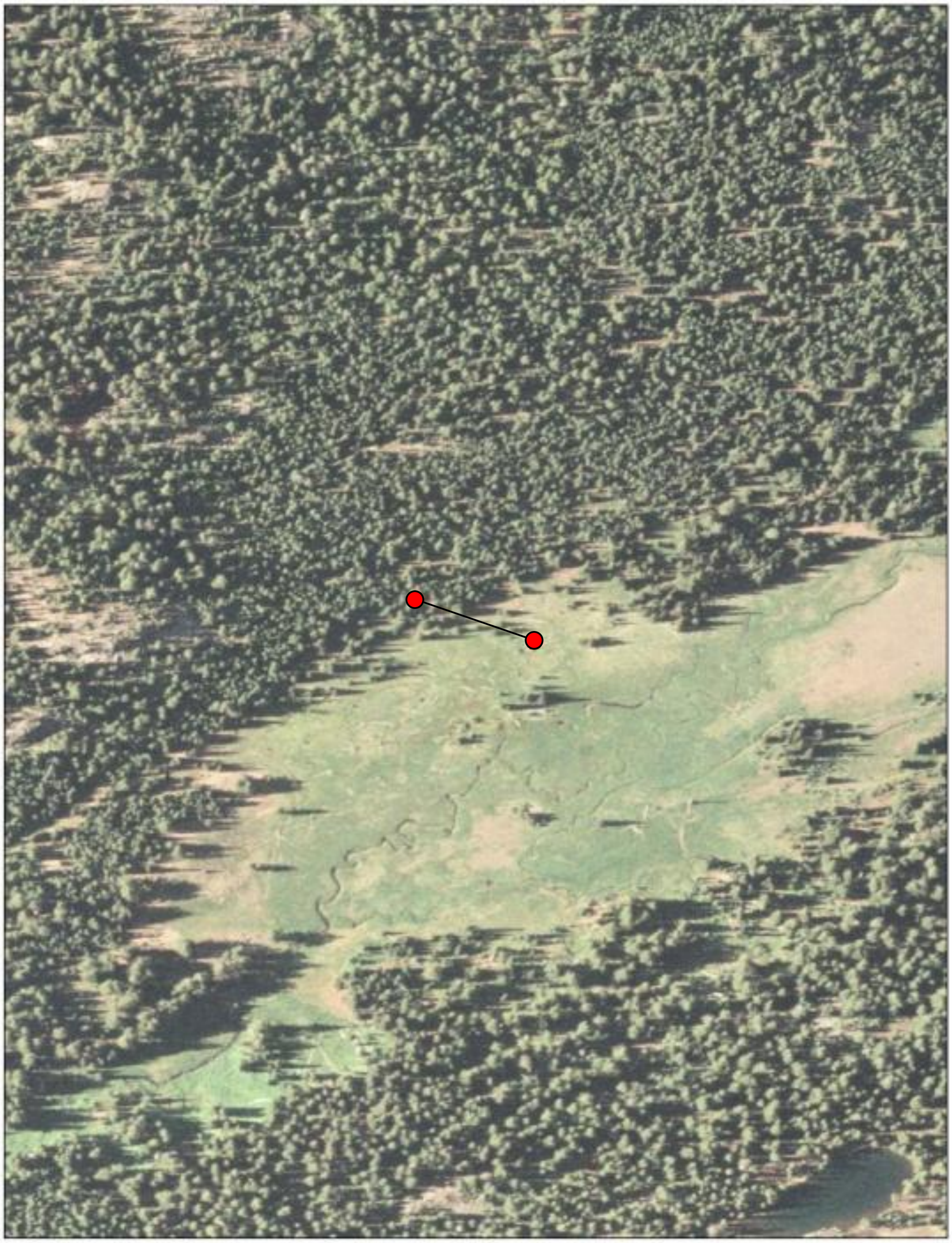
Appendix C.13. Aerial photograph of the Corral Flat transect (landscape context: montane hydric basin) in 2006. The transect (58 m long) begins in diverse forest of *Tsuga mertensiana*, *Picea engelmannii, Pseudotsuga menziesii, Abies lasiocarpa*, and *A. procera*, and extends (left to right) into hydric meadow invaded by *Picea engelmannii* and *Pinus contorta*.

Appendix C.14. Corral Flat transect (landscape context: montane hydric basin) in 1983. Looking from the transect end point in the meadow to the forest. Visible tree species include *Picea engelmannii* and *Pinus contorta* (ecotone and forest). Ground vegetation includes a diversity of graminoids and hydric-meadow forbs.



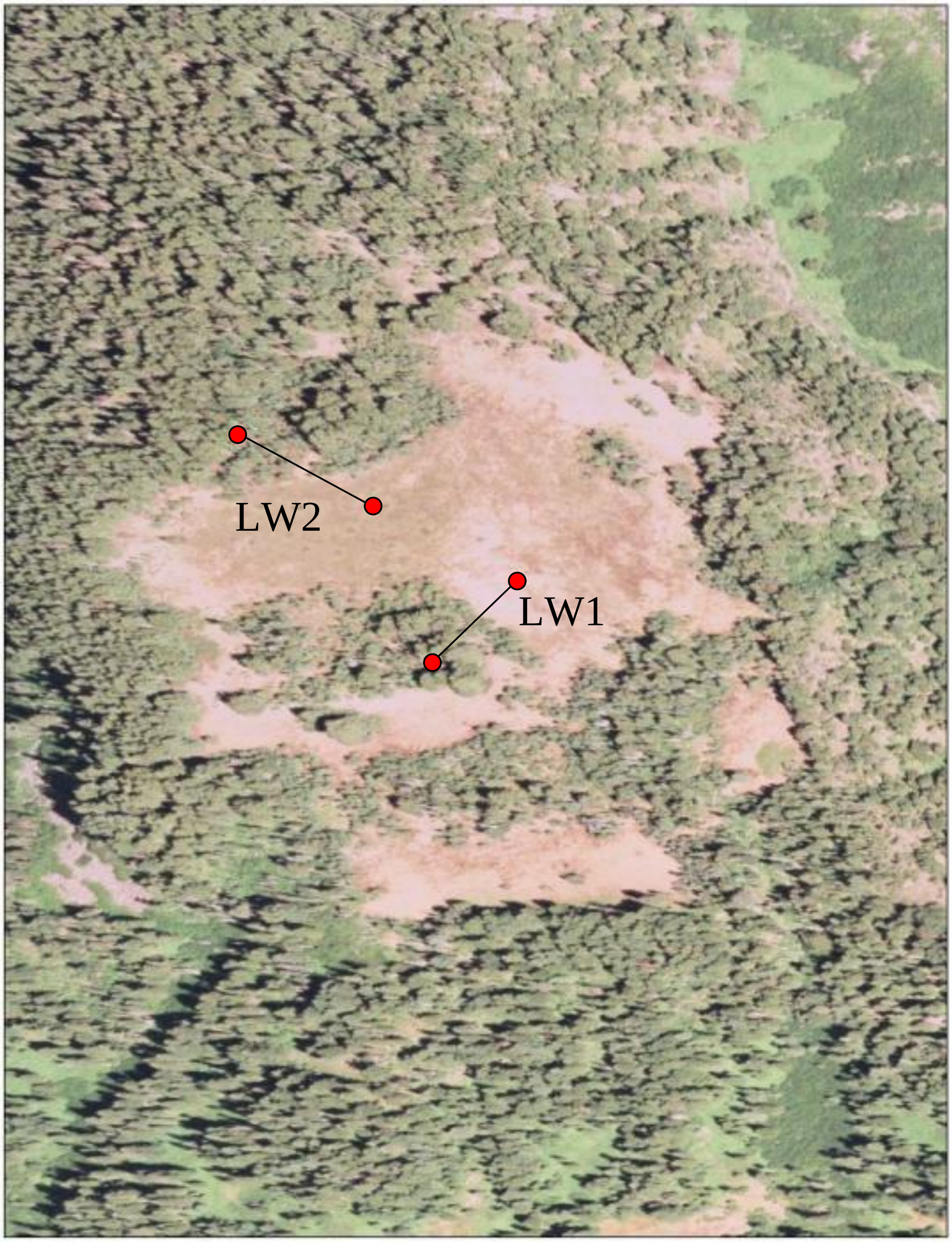
Appendix C.15. Aerial photograph of the Cow Swamp transect (landscape context: montane hydric basin) in 2006. The transect (110 m long) begins in mixed forest of *Picea engelmannii*, *Abies amabilis*, and *Pinus contorta* and extends across ecotone with *Pinus contorta* into hydric meadow.

Appendix C.16. Cow Swamp transect (landscape context: montane hydric basin) in 1983. Looking across the meadow to the ecotone and forest (note transect tape running through image). Visible tree species include *Picea engelmannii* (forest) and *Pinus contorta* (ecotone); ground vegetation is dominated by *Deschampsia caespitosa* and other hydric-meadow graminoids and forbs.



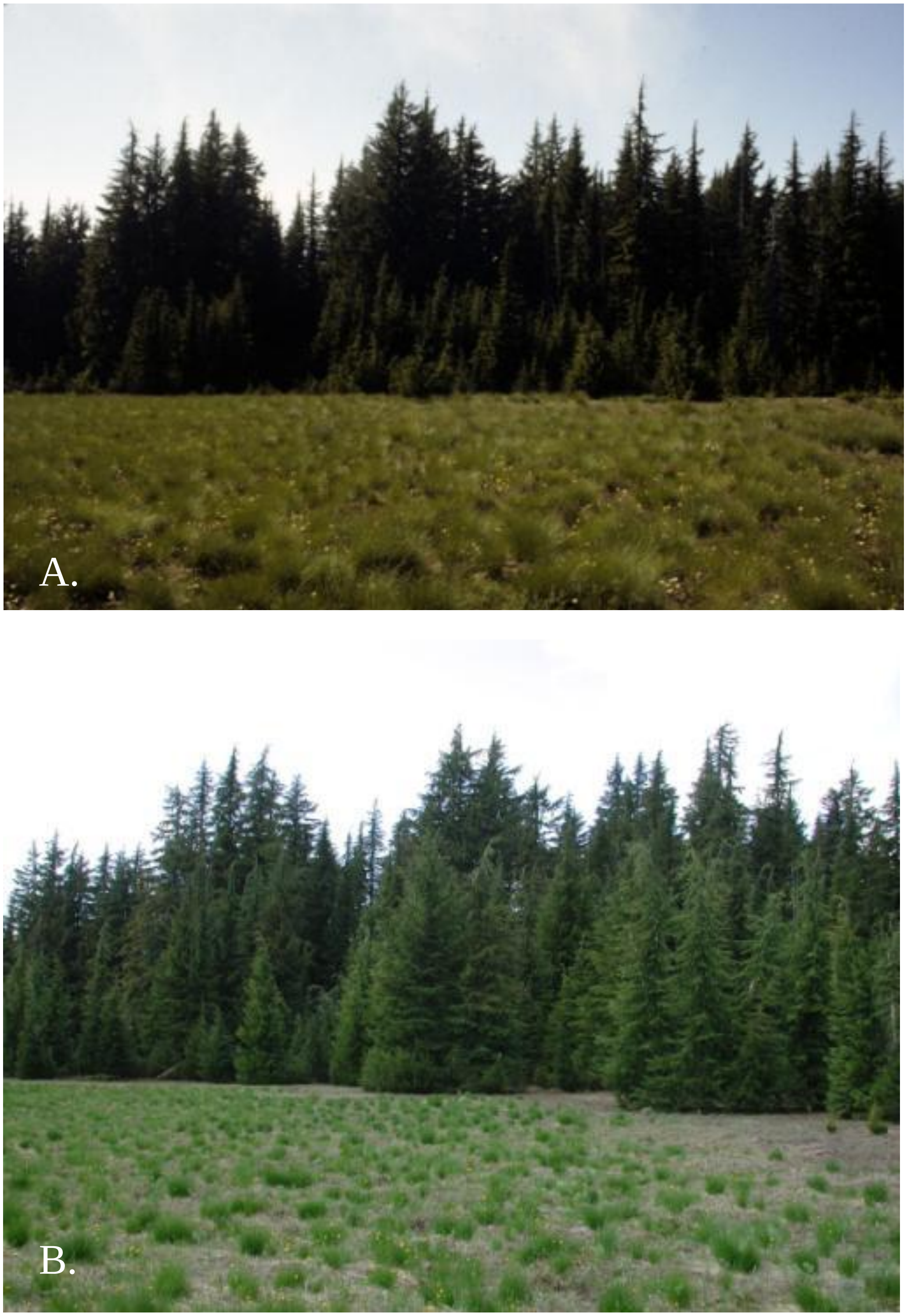
Appendix C.17. Aerial photograph of the Separation Creek transect (landscape context: montane hydric basin) in 2006. The transect (75 m long) begins in forest of *Tsuga mertensiana* and *Abies lasiocarpa* and extends across patchy ecotone into hydric meadow.

Appendix C.18. Separation Creek transect (landscape context: montane hydric basin). Looking across the meadow to the ecotone in (a) 1983 (note transect tape running across image) and (b) 2009. Visible tree species include *Abies lasiocarpa* and *Tsuga mertensiana*. Ground vegetation is dominated by *Deschampsia caespitosa*.



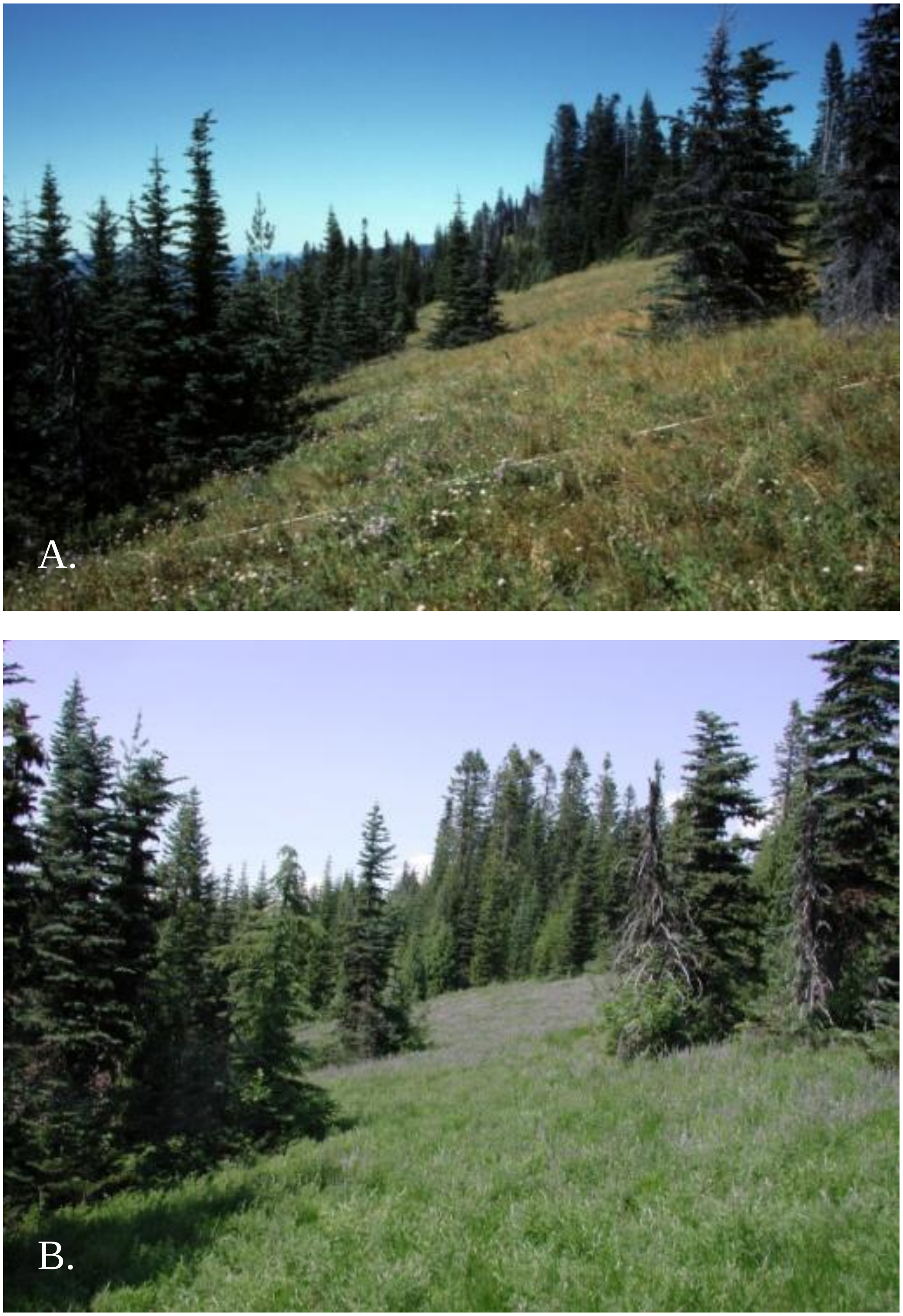
Appendix C.19. Aerial photograph of the Lowder Mountain 1 (LW1; 76 m long) and Lowder Mountain 2 (LW2; 93 m long) transects (landscape context: subalpine early snowmelt) in 2006. Transects begin in forests of *Tsuga mertensiana* and *Abies lasiocarpa* and extend across dense ecotones into meadows dominated by *Festuca viridula* (tan color at LW2) or *Arenaria capillaris* (lighter color at LW1).

Appendix C.20. Lowder Mountain 1 transect (landscape context: subalpine early snowmelt). Looking from the meadow to the ecotone and forest in (a) 1983 and (b) 2009. Note the sparse meadow vegetation in both transects. Visible tree species include *Tsuga mertensiana* in the forest (background) and *Tsuga mertensiana* and *Abies lasiocarpa* in the ecotone..



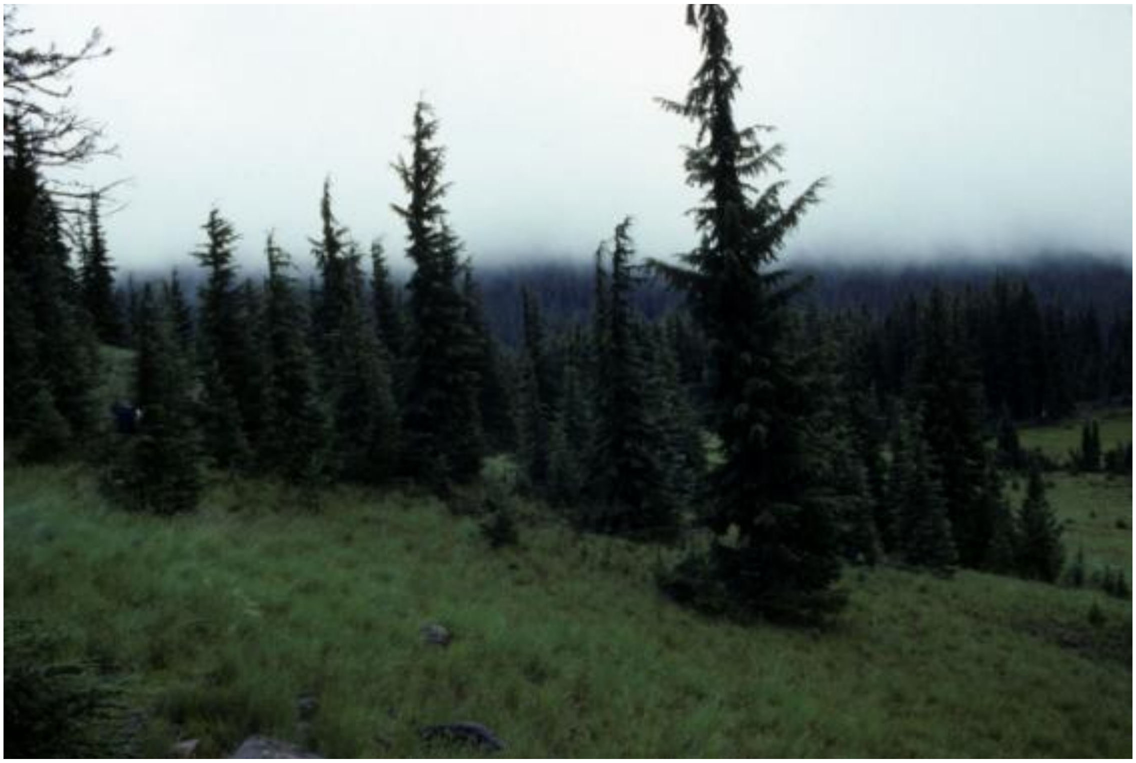
Appendix C.21. Lowder Mountain 2 transect (landscape context: subalpine early snowmelt). Looking from the meadow to the ecotone and forest in (a) 1983 and (b) 2009. *Tsuga mertensiana* dominates the forest (background) and ecotone. The principal meadow species is *Festuca viridula*. .

Appendix C.22. Aerial photograph of the Rebel Rock transect (landscape context: subalpine early snowmelt) in 2006. The transect (82 m long) extends (right to left) from a ridge top through a patchy ecotone dominated by *Tsuga mertensiana*, *Abies grandis*, and *A. lasiocarpa*.



Appendix C.23. Rebel transect (landscape context: subalpine early snowmelt). Looking across the ecotone in (a) 1993 and (b) 2009. Visible tree species (both up and downslope) include *Tsuga mertensiana*, *Abies grandis*, and *Abies lasiocarpa*; vsible meadow species include *Festuca viridula* and *Lupinus latifolius* (in flower in 2009).

Appendix C.24. Aerial photograph of the James Creek transect (landscape context: subalpine early snowmelt) in 2006. The transect (98 m long) extends (upper right to lower left) from open forest of *Tsuga mertensiana* downslope across a patchy ecotone with *Tsuga mertensiana* and *Abies lasiocarpa.*



Appendix C.25. James Creek (landscape context: subalpine early snowmelt) in 1983 looking across the ecotone. Visible tree species include *Tsuga mertensiana* and *Abies lasiocarpa*. The principal meadow species is *Festuca viridula*.

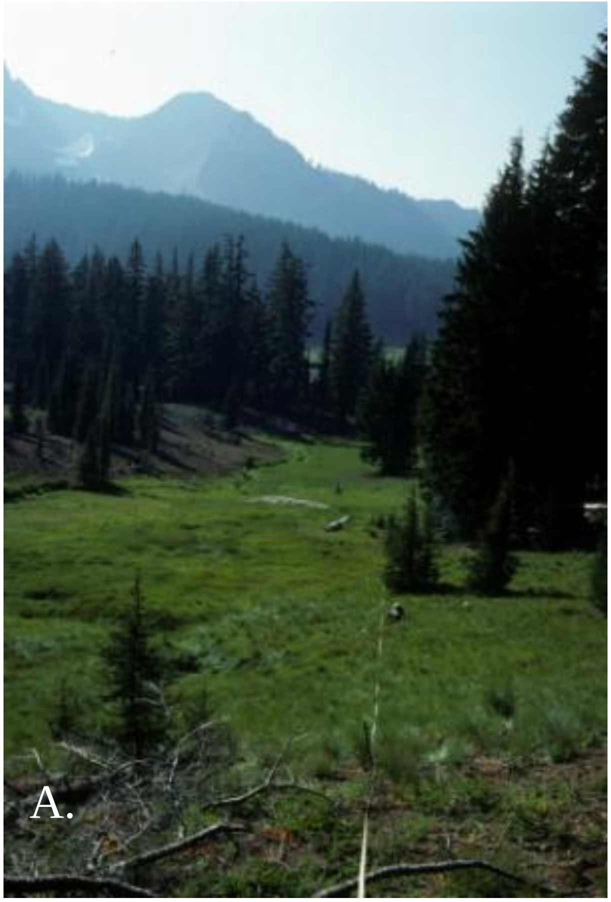
Appendix C.26. Aerial photograph of the Wickiup Plains transect (landscape context: subalpine early snowmelt) in 2006. The transect (79 m) begins in *Tsuga mertensiana* forest and extends across ecotone into dry, graminoid-dominated meadow and pumice flat.

Appendix C.27. Wickiup Plains (landscape context: subalpine early snowmelt) in 1983 looking from the ecotone to meadow. Visible tree species in the ecotone is *Tsuga mertensiana*; graminoids including *Festuca viridula, Sitanion hystrix, Stipa occidentalis, and Juncus paryii*, dominate the ground vegetation.

Appendix C.28. Aerial photograph of the Linton Meadow 1 transect (landscape context: subalpine early snowmelt) in 2006. The transect (60 m long) runs downslope (upper right to lower left) from forest of *Tsuga mertensiana* and *Abies lasiocarpa* into meadow dominated by *Festuca viridula*.

Appendix C.29. Linton Meadow 1 transect (landscape context: subalpine early snowmelt). Looking upslope to the meadow, ecotone, and forest in (a) 1983 and (b) 2009. Visible tree species are *Tsuga mertensiana* and *Abies lasiocarpa*. Meadow is dominated by *Festuca viridula*. Transect passes beneath recently dead *A. lasiocarpa* (2009 photograph).

Appendix C.30. Aerial photograph of the Linton Meadow 2 transect (landscape context: subalpine early snowmelt) in 2006. The transect (60 m long) extends downslope (right to left) from open *Tsuga mertensiana* forest across a sharp ecotone into meadow dominated by *Festuca viridula* and *Carex spectabilis*.



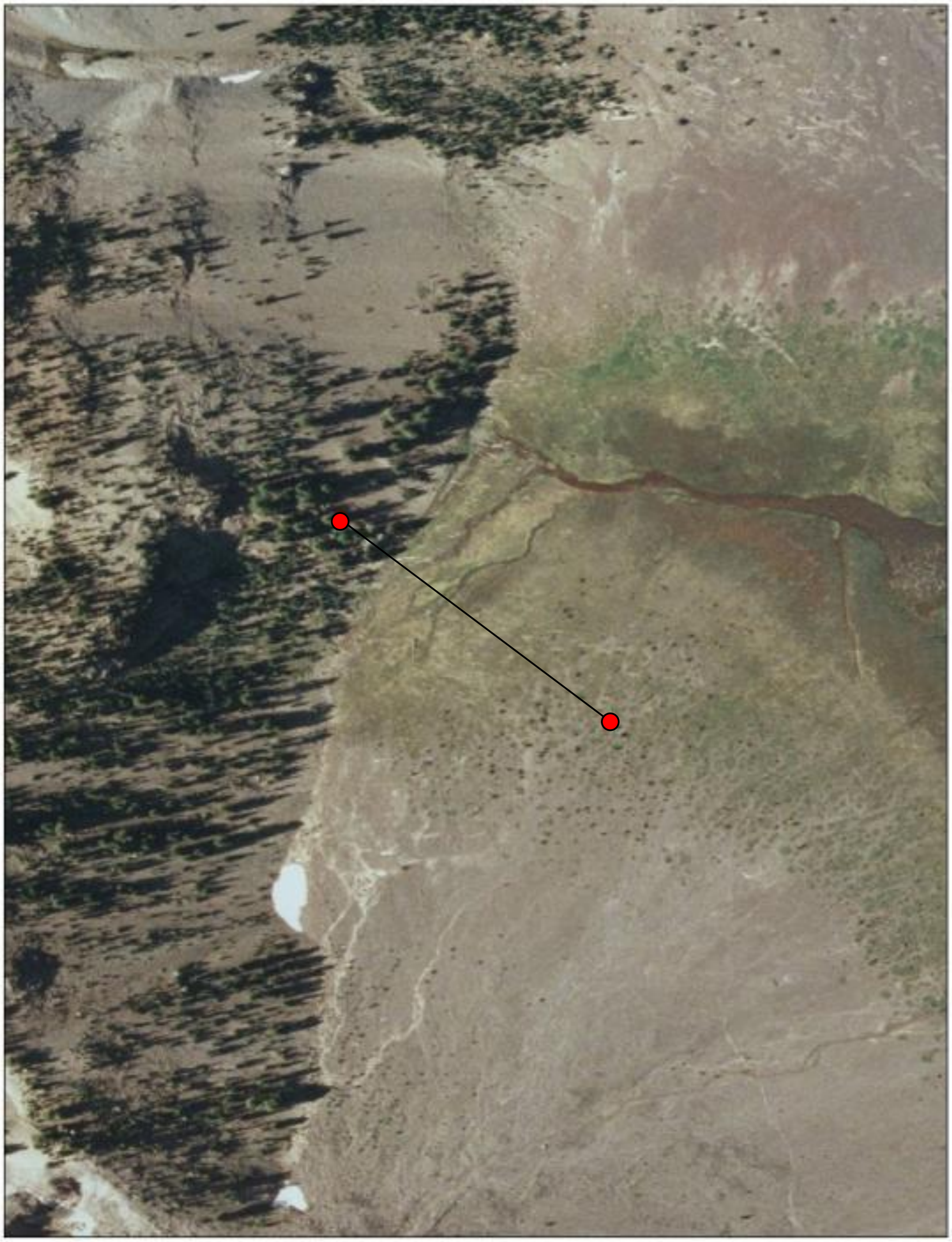
Appendix C.31. Linton Meadow 2 transect (landscape context: subalpine early snowmelt). (a) Looking downslope from the ecotone to the meadow in 1983. (b) Looking across the ecotone in 2009. Visible tree species is *Tsuga mertensiana* (forest and ecotone); ground vegetation is dominated by *Festuca viridula* and *Carex spectabliis* (lower on the slope).

Appendix C.32. Aerial photograph of the Obsidian Flat transect (landscape context: subalpine early snowmelt) in 2006. The transect (60 m long) extends (right to left) from open *Tsuga mertensiana* forest downslope into meadow dominated by *Festuca viridula*.

Appendix C.33. Obsidian Flat transect (landscape context: subalpine early snowmelt) in 2009. Looking from the meadow to ecotone and forest (note transect tape running across image). Visible tree species include *Tsuga mertensiana* (ecotone and forest); dead *T. mertensiana* and *Pinus albicaulis* are visible in the forest (center and right, respectively). Ground vegetation is dominated by *Festuca viridula*.

Appendix C.34. Aerial photograph of the Obsidian Creek transect (landscape context: subalpine early snowmelt) in 2006. The transect (90 m long) runs from hilltop forest of *Tsuga mertensiana* and *Abies lasiocarpa* downslope onto a graminoid-dominated flat.

Appendix C.35. Obsidian Creek transect (landscape context: subalpine early snowmelt) in 2009. Looking across the ecotone. Visible tree species include *Tsuga mertensiana* and *Abies lasiocarpa*. Ground vegetation is dominated by *Festuca viridula* and *Carex spectabilis* (lower on the flat).



Appendix C.36. Aerial photograph of the Green Lake transect (landscape context: subalpine late snowmelt) in 2006. The transect (220 m long) runs from open *Pinus albicaulis* forest on the slope onto a broad meadow flat.

Appendix C.37. Green Lake transect (landscape context: subalpine late snowmelt) in 1983. Looking down the transect across the meadow; small *Pinus contorta* are scattered in the background.

Appendix C.38. Aerial photograph of the Racetrack transect (landscape context: subalpine late snowmelt) in 2006. The transect (100 m long) runs downslope (left to right) from *Tsuga mertensiana* forest into a heath-dominated and sedge-dominated late snowlie basin.

Appendix C.39. Image of Racetrack (landscape context: subalpine late snowmelt). (a) Looking through dense establishment of *Tsuga mertensiana* in the ecotone in 1993. (b) Looking upslope at ecotone and forest from the meadow in 2009. Visible tree species is *Tsuga mertensiana* (forest and ecotone). Bare pumice soils are visible in the foreground. A dense carpet of *Carex nigricans* extends to the base of the slope giving way to a heath-dominated (*Phyllodoce empetriformis*) community within which invasion is most dense.

Appendix D

Species along TSBR forest-meadow ecotones

Species observed within permanent forest-meadow transects in the Three Sisters Biosphere Reserve (TSBR), Oregon during 1983, 1993, and/or 2009. Nomenclature follows Hitchcock and Cronquist (1973).

Appendix D.1. Species observed in montane forest-meadow ecotone transects in the Three Sisters Biosphere Reserve, Oregon. Species are grouped by habitat preference (meadow, forest, and unclassified) and growth form (grasses, sedges/rushes, herbs, and shrubs). Tree species were not classified. "X" indicates presence in a transect at one or more sampling dates (1983, 1993, or 2009). Asterisks denote non-native species. YM = Yankee Mountain, OM = Ollalie Meadow, W1 = Walker 1, W2 = Walker 2, QA1 = Quaking Aspen 1, QA2 = Quaking Apen 2, CF = Corral Flat, CS = Cow Swamp, SC = Separation Creek. See Chapter 3, Table 1 for more details.

	Mesic Slopes				**Hydric Basins**				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Forest Species									
Grasses									
Bromus vulgaris	X	X	X	X				X	
Festuca occidentalis	X			X		X	X		
Melica subulata	X		X	X			X		
Trisetum canescens	X	X							
Trisetum cernuum	X				X	X	X		
Sedges / Rushes									
Luzula hitchcockii									X
Luzula parviflora	X	X							
Herbs									
Achlys triphylla		X	X	X			X	X	
Actea rubra		X	X						
Adenocaulon bicolor			X	X					
Anemone deltoidea	X	X	X	X	X	X	X	X	
Anemone lyallii	X		X	X			X	X	
Anemone oregana		X							
Arenaria macrophylla	X	X	X	X		X			
Arnica mollis						X			
Asarum caudatum			X						
Blechnum spicant					X				
Campanula scouleri	X		X	X			X		
Circaea alpina		X							
Clintonia uniflora				X	X	X	X	X	
Disporum species		X	X	X	X	X			

Appendix D.1. Continued.

	Mesic Slopes				**Hydric Basins**				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Forest Species									
Herbs									
Galium oreganum	X	X		X					
Galium triflorum	X	X	X	X		X			
Goodyera oblongifolia		X	X	X					
Habenaria unalascensis	X								
Hieracium albiflorum	X	X		X		X	X	X	
*Lactuca muralis**		X	X	X					
Linnaea borealis							X		
Listera caurina		X					X	X	
Listera cordata						X			
Mianthemum dilatatum		X							
Mitella breweri		X			X	X			X
Mitella trifida	X	X	X	X					
Osmorhiza chilensis	X	X	X	X		X	X	X	
Osmorhiza occidentalis	X	X	X	X					
Pedicularis racemosa						X	X	X	X
Polystichum munitum	X			X					
Pyrola picta	X	X	X	X					
Pyrola secunda				X	X	X	X	X	X
Smilacina racemosa	X	X	X						
Smilacina stellata	X	X	X	X	X	X	X	X	
Tellima grandiflora	X								
Tiarella trifoliata							X	X	
Trientalis latifolia			X	X				X	
Trillium ovatum	X		X	X			X	X	
Viola glabella		X		X	X	X	X	X	
Viola orbiculata					X	X	X	X	X

Appendix D.1. Continued.

	Mesic Slopes				**Hydric Basins**				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Forest Species									
Herbs									
Xerophyllum tenax				X	X	X	X	X	
Shrubs									
Acer circinatum	X		X						
Berberis nervosa								X	
Chimaphila menziesii	X	X	X	X			X		
Chimaphila umbellata		X					X		
Cornus canadensis					X	X	X	X	
Cornus nuttallii								X	
Corylus cornuta	X								
Gaultheria ovatifolia					X	X		X	
Holodiscus discolor	X								
Pachistima myrsinites	X	X							
Rhododendron albiflorum					X				
Rhododendron macrophyllum					X				
Rosa gymnocarpa	X			X					
Rubus lasiococcus	X	X			X	X	X	X	X
Rubus ursinus						X			
Symphoricarpos mollis	X			X					
Vaccinium alaskaense / V. ovalifolium		X			X	X		X	
Vaccinium membranaceum	X	X		X	X	X	X	X	X
Vaccinium scoparium								X	X
Whipplea modesta						X			
Meadow Species									
Grasses									
Agrostis exarata					X				
Agrostis scabra	X					X	X	X	
Agrostis tenuis							X		

Appendix D.1. Continued.

	Mesic Slopes				**Hydric Basins**				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Grasses									
Agrostis thurberiana									X
Agrostis variabilis									X
Bromus carinatus	X	X	X	X		X	X		
Calamagrostis canadensis					X	X			
Calamagrostis inexpansa						X		X	X
Cinna latifolia					X				
Danthonia californica		X				X		X	
Danthonia intermedia		X				X	X	X	X
Deschampsia atropurpurea					X	X			X
Deschampsia caespitosa					X	X	X	X	X
Elymus glaucus	X	X	X	X	X	X	X	X	
Festuca idahoensis				X					
Festuca viridula	X	X		X					
Glyceria elata					X				
Hordeum brachyantherum							X		
Koeleria cristata									X
Muhlenbergia filiformis						X	X	X	X
*Poa pratensis**							X		
Stipa occidentalis	X	X		X					
Trisetum spicatum									X
Sedges / Rushes									
Carex buxbaumii								X	
Carex eurycarpa								X	
Carex halliana									X
Carex hoodii		X	X	X					
Carex jonesii							X		
Carex lenticularis					X				

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Sedges / Rushes									
Carex limnophila							X		
Carex luzulina					X	X	X	X	
Carex mertensii					X				
Carex microptera									X
Carex muricata						X			
Carex nigricans									X
Carex pachystachya		X			X				
Carex pensylvanica	X	X	X	X			X		X
Carex rossii						X			
Carex rostrata						X			
Carex sitchensis					X	X		X	
Carex spectabilis									X
Eleocharis pauciflora						X		X	
Juncus balticus						X		X	
Juncus mertensianus							X		X
Juncus parryi									X
Scirpus congdonii					X	X	X	X	
Herbs									
Achillea millefolium	X						X		
Aconitum columbianum					X				
Agoseris aurantiaca		X		X			X		
Anaphalis margaritacea	X	X							
Angelica arguta	X	X	X		X				
Antennaria umbrinella									X
Aquilegia formosa	X			X			X		
Aspidotis densa	X								
Aster alpigenus						X		X	X

Appendix D.1. Continued.

	Mesic Slopes				**Hydric Basins**				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Herbs									
Aster foliaceus	X	X			X	X	X	X	
Aster ledophyllus	X	X		X					
Aster occidentalis		X						X	
Calochortus subalpinus		X		X					
Caltha biflora					X	X		X	
Castilleja hispida	X								
Castilleja miniata							X	X	
Cerastium vulgatum							X		
Cheilanthes gracillima	X								
Cirsium callilepes	X	X	X	X					
Collinsia parviflora	X								
Cryptantha affinis				X					
Cuscuta species								X	
Delphinium menziesii		X		X					
Dodecatheon jeffreyi					X	X	X	X	
Drosera anglica						X			
Drosera rotundifolia						X			
Epilobium alpinum						X	X		X
Epilobium glandulosum					X	X			X
Epilobium species	X			X	X	X			X
Epilobium watsonii					X	X			
Equisetum arvense					X				
Erigeron aliceae	X	X	X	X		X			
Eriogonum nudum	X			X					
Eriophyllum lanatum	X								
Erysimum arenicola	X			X					
Fragaria species		X		X	X	X	X	X	

Appendix D.1. Continued.

	Mesic Slopes				**Hydric Basins**				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Herbs									
Galium bifolium	X		X	X					
Galium trifidum					X	X	X	X	
Gentiana simplex							X		
Geum macrophyllum					X		X		
Gilia aggregata	X	X		X					
Gilia capitata	X								
Habenaria dilatata					X	X			
Heracleum lanatum					X				
Hieracium gracile	X	X							X
Hieracium scouleri	X	X		X					
Hydrophyllum capitatum	X								
Hydrophyllum occidentale			X	X					
Hypericum anagalloides					X	X	X	X	X
Iris chrysophylla	X			X					
Lathyrus nevadensis	X	X	X	X			X	X	
Ligusticum grayi	X	X	X	X	X	X	X	X	X
Linanthus bicolor	X			X					
Luetkea pectinata									X
Lupinus latifolius		X		X					X
Mertensia species					X				
Microseris alpestris		X							
Microseris boreale					X	X		X	
Microseris nutans	X								
Microsteris gracilis	X	X		X					
Mimulus guttatus					X		X		
Mimulus moschatus	X		X	X			X		X
Mimulus primuloides						X			

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Herbs									
Montia parvifolia	X								
Montia sibirica	X	X	X	X					
Montia spathulata									X
Myosotis laxa			X						
Nemophila parviflora	X								
Orthocarpus imbricatus	X	X		X					
Pedicularis bracteosa					X	X			
Pedicularis groenlandica								X	
Penstemon procerus									X
Perideridia gairdneri							X		
Phacelia heterophylla	X	X	X	X					
Polemonium carneum	X	X							
Polygonum bistortoides					X		X		
Polygonum douglasii	X	X	X	X					
Polygonum minimum	X	X		X					
Polygonum phytolaccaefolium	X		X						
Potentilla drummondii	X		X		X	X	X	X	
Potentilla flabellifolia									X
Potentilla glandulosa	X	X		X		X			
Prunella vulgaris							X		
Pteridium aquilinum	X		X	X					
Ranunculus alismaefolius									X
Ranunculus flammula								X	
Ranunculus gormanii					X	X	X	X	
Rudbeckia occidentalis		X	X	X	X	X			
Sanicula graveolens	X			X					
Sedum spathulifolium	X								

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Herbs									
Senecio triangularis					X	X	X	X	X
Sidalcea cusickii							X		
Sisyrinchium douglasii						X	X		
Spiranthes romanzoffiana						X	X	X	X
Spraguea umbellata									X
Stachys cooleyae		X	X	X	X				
Stellaria crispa		X			X				
Thalictrum occidentale	X				X				
Tofieldia glutinosa					X	X		X	
Trifolium longipes						X	X	X	X
Valeriana sitchensis					X	X	X		
Veratrum viride					X				X
Veronica americana					X				
Veronica scutellata							X	X	
Veronica serpyllifolia							X		X
Veronica wormskjoldii					X	X	X		X
Vicia americana	X	X	X	X			X	X	
Viola macloskeyi					X	X		X	X
Viola nuttallii		X					X		
Shrubs									
Betula glandulosa								X	
Haplopappus greenei		X							
Kalmia microphylla						X			
Kalmia occidentalis					X	X		X	
Phyllodoce empetriformis					X	X			
Rosa pisocarpa								X	
Rubus parviflorus	X		X	X					

Appendix D.1. Continued.

	Mesic Slopes				**Hydric Basins**				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Shrubs									
Spiraea densiflora					X	X		X	
Spiraea douglasii					X	X		X	
Vaccinium caespitosum					X	X		X	X
Vaccinium occidentale					X	X		X	
Unclassified species									
Sedges / Rushes									
Carex deweyana			X						
Luzula campestris	X	X			X	X	X		
Herbs									
Cystopteris fragilis	X								
Lilium columbianum	X		X						
Lycopodium sitchense					X				
*Rumex acetosella**	X	X		X					
*Taraxacum officinale**							X		
Viola adunca						X	X		
Shrubs									
Acer glabrum	X		X	X					
Alnus sinuata					X				
Amelanchier alnifolia	X	X					X	X	
Castanopsis chrysophylla						X			
Crataegus douglasii					X				
Lonicera ciliosa						X		X	
Rhanmnus purshiana	X			X		X			
Ribes lacustre				X					
Ribes lobbii	X	X		X					
Ribes sanguineum	X			X					
Ribes viscosissimum	X			X					

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Unclassified species									
Shrubs									
Sambucus racemosa	X								
Sorbus sitchensis	X	X		X		X	X		
Trees Species									
Abies amabilis	X				X	X	X	X	X
Abies grandis	X	X	X	X		X	X		
Abies lasiocarpa	X	X			X	X	X		X
Abies procera							X		
Calocedrus decurrens		X							
Picea engelmannii		X			X	X	X	X	X
Pinus contorta		X					X	X	
Pinus monticola						X	X		X
Prunus emarginata						X			
Pseudotsuga menziesii	X	X		X			X		
Tsuga heterophylla						X	X		
Tsuga mertensiana					X	X	X		X

* exotic species

Appendix D.2. Species observed in subalpine forest-meadow ecotone transects in the Three Sisters Biosphere Reserve, Oregon. Species are grouped by habitat preference (meadow, forest, and unclassified) and growth form (grasses, sedges/rushes, herbs, and shrubs). Tree species were not classified. "X" indicates presence in a transect at one or more sampling dates (1983, 1993, or 2009). Asterisks denote non-native species. LW1 = Lowder Mountain 1, LW2 = Lowder Mountain 2, RR = Rebel, JC = James Creek, WP = Wickiup Plain, LM1 = Linton Meadow 1, LM2 = Linton Meadow 2, OF = Obsidian Flat, OC = Obsidian Creek, GL = Green Lake, RM = Racetrack Meadow. See Chapter 3, Table 1 for more details.

	Early Snowmelt									**Late Snowmelt**	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Forest Species											
Grasses											
Festuca occidentalis			X								
Trisetum canescens			X								
Trisetum cernuum			X								
Sedges / Rushes											
Luzula hitchcockii	X			X	X	X	X	X	X	X	X
Luzula parviflora	X									X	X
Herbs											
Anemone deltoidea			X								
Anemone oregana			X								
Arenaria macrophylla			X								
Arnica latifolia			X								
Arnica mollis										X	
Campanula scouleri			X								
Circaea alpina			X								
Corallorhiza species			X								
Galium oreganum			X								
Galium triflorum			X								
Goodyera oblongifolia			X								
Hieracium albiflorum	X		X			X					
Hypopitys monotropa	X										X
Listera caurina			X				X				X

Appendix D.2. Continued.

	Early Snowmelt									Late Snowmelt	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Forest Species											
Herbs											
Mitella breweri							X				X
Mitella trifida			X								
Monotropa hypopitys											X
Osmorhiza chilensis			X								
Osmorhiza occidentalis							X				
Pedicularis racemosa	X		X			X					
Pyrola picta			X								
Pyrola secunda						X	X				
Senecio cymbalarioides										X	
Smilacina racemosa			X								
Smilacina stellata			X								
Trillium ovatum			X								
Viola glabella			X								
Viola orbiculata	X										
Xerophyllum tenax			X								
Chimaphila umbellata			X								
Rubus lasiococcus	X		X	X		X	X		X		X
Vaccinium membranaceum			X			X	X		X		X
Vaccinium scoparium				X						X	X
Meadow Species											
Grasses											
Agrostis humilis				X							
Agrostis variabilis				X	X					X	X
Bromus carinatus			X								
Danthonia intermedia		X	X	X				X	X		
Deschampsia atropurpurea										X	X

Appendix D.2. Continued.

	Early Snowmelt									Late Snowmelt	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Meadow Species											
Deschampsia caespitosa									X	X	
Elymus glaucus			X			X					
Festuca viridula	X	X	X	X	X	X	X	X	X		
Phleum alpinum										X	
Sitanion hystrix				X	X	X		X	X	X	
Stipa occidentalis	X	X	X	X	X	X	X	X	X	X	
Sedges / Rushes											
Carex breweri					X						
Carex luzulina										X	
Carex microptera				X						X	
Carex nigricans							X		X	X	X
Carex pachystachya					X				X		
Carex pensylvanica	X	X	X	X		X		X	X		
Carex praeceptorum										X	
Carex rossii					X			X	X	X	
Carex scopulorum										X	
Carex spectabilis							X		X	X	X
Eleocharis pauciflora										X	
Juncus drummondii									X		
Juncus mertensianus										X	
Juncus parryi	X	X		X	X			X		X	X
Herbs											
Agoseris aurantiaca			X			X				X	X
Antennaria alpina										X	
Antennaria umbrinella								X			X
Arabis drummondii					X						

Appendix D.2. Continued.

	Early Snowmelt									**Late Snowmelt**	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Meadow Species											
Herbs											
Arabis holboellii			X								
Arenaria capillaris	X	X									
Aster alpigenus								X		X	X
Aster foliaceus			X	X		X	X	X		X	
Aster ledophyllus	X		X	X		X	X	X	X	X	
Calochortus subalpinus	X	X	X	X		X	X	X	X		
Castilleja arachnoidea					X			X	X		
Castilleja miniata											X
Cirsium callilepes			X								
Delphinium menziesii			X								
Dicentra formosa			X								
Epilobium alpinum										X	
Epilobium angustifolium			X			X					
Epilobium species					X		X				X
Epilobium watsonii			X				X				
Erigeron aliceae			X								
Eriogonum pyrolaefolium								X	X		X
Eriogonum umbellatum				X	X	X	X	X	X	X	
Erysimum arenicola			X								
Hieracium cynoglossoides			X								
Hieracium gracile				X	X		X	X	X	X	X
Lewisia pygmaea										X	
Ligusticum grayi	X		X							X	X
Lomatium martindalei				X		X				X	
Luetkea pectinata					X					X	X
Lupinus latifolius	X	X	X	X	X	X	X	X	X		X

Appendix D.2. Continued.

	Early Snowmelt									Late Snowmelt	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Meadow Species											
Herbs											
Lupinus lepidus										X	
Microseris alpestris	X	X		X	X	X	X	X	X		X
Microseris nutans			X								
Microsteris gracilis			X								
Montia sibirica			X								
Nemophila parviflora			X								
Orogenia fusiformis			X								
Pedicularis attolens										X	
Penstemon cardwellii			X								
Penstemon procerus					X					X	
Phacelia heterophylla			X								
Polygonum douglasii			X								
Polygonum minimum			X								
Polygonum newberryi				X	X	X	X	X	X	X	X
Polygonum phytolaccaefolium			X								
Potentilla flabellifolia											X
Pteridium aquilinum						X					
Ranunculus alismaefolius									X		
Senecio triangularis							X			X	
Spraguea umbellata	X			X	X		X	X	X	X	X
Stellaria obtusa										X	
Tofieldia glutinosa										X	
Valeriana sitchensis			X				X				
Veratrum californicum	X		X						X		
Veronica wormskjoldii										X	
Viola nuttallii			X	X		X		X			

Appendix D.2. Continued.

	Early Snowmelt									**Late Snowmelt**	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Meadow Species											
Shrubs											
Arctostaphylos nevadensis										X	
Cassiope mertensiana										X	X
Gaultheria humifusa										X	
Kalmia microphylla										X	
Phyllodoce empetriformis										X	X
Salix commutata										X	
Vaccinium caespitosum											X
Vaccinium occidentale										X	
Unclassified Species											
Sedges / Rushes											
Carex deweyana							X				
Luzula campestris	X	X									X
Herbs											
Erythronium grandiflorum		X	X								
Lycopodium sitchense										X	
Polemonium pulcherrimum						X					
Rumex acetosella	X										
Shrubs											
Acer glabrum			X								
Amelanchier alnifolia		X									
Ribes viscosissimum			X								
Sambucus racemosa			X				X				
Sorbus sitchensis	X		X			X				X	X

Appendix D.2. Continued.

	Early Snowmelt									**Late Snowmelt**	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Unclassified Species											
Shrubs											
Trees Species											
Abies amabilis	X	X	X				X	X			X
Abies grandis			X								
Abies lasiocarpa	X	X	X	X	X	X		X	X		
Abies procera			X								
Pinus albicaulis						X		X		X	
Pinus contorta				X						X	
Pinus monticola			X								
Pseudotsuga menziesii			X								
Tsuga mertensiana	X	X	X	X	X	X	X	X	X	X	X