

Vegetation responses to conifer encroachment in a dry, montane meadow:
a chronosequence approach

Ryan D. Haugo

A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington

2006

Program Authorized to Offer Degree:
Forest Resources

University of Washington
Graduate School

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Ryan D. Haugo

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Committee Members:

Charles B. Halpern

Joseph A. Antos

Donald McKenzie

Date: _____

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Abstract

Vegetation responses to conifer encroachment in a dry, montane meadow:
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Ryan D. Haugo

Chair of the Supervisory Committee:
Research Professor Charles B. Halpern
College of Forest Resources

Conifer encroachment into montane and subalpine meadows is widespread throughout much of western North America. Yet, little is known about consequences of encroachment for loss of meadow habitat and biological diversity. Bunchgrass Ridge, a dry, montane meadow in the western Cascade Range of Oregon has experienced encroachment of grand fir (*Abies grandis*) and lodgepole pine (*Pinus contorta*) for ca. 200 years. I used a chronosequence approach to reconstruct the temporal patterns of loss of meadow species and colonization of forest species. Additionally, I investigated how these changes in vegetation correlate to changes in light and forest structure.

Vegetation composition, tree size and age distributions, and light levels were determined for 356, 10 x 10 m subplots across a gradient from open meadow to old forest (>90 yr). NMS ordination revealed strong turnover in species composition from open meadow to old forest; NMS axes were highly correlated to light availability and changes in overstory structure (density and basal area of

Pinus and *Abies*). Meadow species declined steeply in cover once density of *Abies* reached a threshold; richness declined more gradually. Colonization by forest herbs was gradual and continuous. In multiple regression models, cover and richness of forest species displayed weaker relationships to changes in light and forest structure than did cover and richness of meadow species.

The meadow flora was highly sensitive to conifer encroachment — particularly to density of *Abies*. Colonization of forest herbs occurred within decades, but weak relationships to forest structure and light indicate that both environmental and dispersal limitation may be important. Dramatic changes in vegetation in fewer than 100 years suggest limited potential for restoration where conifers have become well established. Conservation of meadow communities may depend upon removing or killing established conifers before they cause declines in meadow vegetation.

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ACKNOWLEDGMENTS

First, I would like to express gratitude to my advisor and mentor, Charlie Halpern, who has been incredibly dedicated, supportive and helpful ever since he gave me the opportunity to be a part of the Bunchgrass project. My committee members, Joe Antos and Don McKenzie have been a source of valuable feedback throughout this process. Thanks to Nicole Lang, my Bunchgrass “twin”, both for putting up with and helping me in so many ways; Kyle Smith, James Freund, Jess Niederer, Janine Rice, Michael Frank, Markus Koch for field assistance; and Jim Lutz, Martin Dovciak and the rest of the Halpern lab group for advice, comments and critiques. Thanks also to Duane Lammers and Ted Dyrness for descriptions of soils; Shelley Evans for verifying species’ identifications; and staff of the USFS McKenzie River Ranger District and Willamette National Forest for facilitating field research at Bunchgrass Ridge.

I would also like to acknowledge and thank two outstanding teachers who played a vital role in shaping the course of my (some may say extended) formal educational experiences: Jim Papacek (Mr. P) who first drew out my love of the natural world and Charles Umbanhowar who taught me how exciting plants can be(!).

Finally, I am extremely grateful to my family and friends; my parents who have been tremendously supportive of all my endeavors; my close friends from Fargo and St. Olaf who help to make life rich and interesting; and Roo, for providing so much love and support.

Thank You!

Introduction

Encroachment of woody species threatens the biological diversity of grasslands and other non-forested ecosystems in many regions of the world (van Auken 2000). The causes of encroachment have been considered from many perspectives, including responses to changes in climate, land management, and natural disturbance regimes (e.g., Magee & Antos 1992; Knight et al. 1994; Miller & Halpern 1998; Bond & Midgley 2000; Sturm et al. 2005). The consequences can be far-reaching and potentially irreversible, affecting soil ecosystem properties (Prichard et al. 2000; Jackson et al. 2002; Haubensak & Parker 2004; Griffiths et al. 2005), vegetation structure and productivity (Hobbs & Mooney 1986; Archer 1990; Scholes & Archer 1997), and native plant diversity (Bakker & Berendse 1999; Moore & Huffman 2004).

Montane and subalpine meadows throughout western North America have experienced encroachment by conifers over the past century, resulting in conspicuous changes to landscape structure. In the Pacific Northwest, a region dominated by coniferous forest, loss of montane meadows to tree encroachment can greatly reduce the diversity of species and habitats. These natural openings serve as fire breaks, provide habitat for wildlife, and support distinctive communities of plants (Hickman 1968; Halpern et al. 1984; Franklin & Halpern 1999) and arthropods (e.g., Miller et al. 2003). Faced with gradual loss to forest expansion, public land management agencies are placing increasing emphasis on

their conservation and restoration (Wilson et al. 1999, Davis et al. 2005).

Considerable attention has been devoted to quantifying temporal patterns of conifer encroachment and to understanding the factors that have triggered or facilitated invasion. These include changes in climate (Jakubos & Romme 1993; Taylor 1995; Woodward et al. 1995; Rochefort & Peterson 1996; Miller & Halpern 1998) or grazing pressure (Dunwiddie 1977; Vale 1981; Miller & Halpern 1998), or long-term suppression of fire (Arno & Gruell 1986; Hadley 1999; Foster & Shaff 2003). In contrast, very little research has been devoted to the consequences of encroachment for loss of biological diversity. I address this gap in knowledge with a focus on the rates, patterns, and potential controls on vegetation change.

Two types of successional processes accompany the transformation of grass- or forb-dominated meadow ecosystems to those dominated by woody plants (trees in particular): loss of resident species adapted to open environments, and colonization of understory species adapted to shade. Displacement of the resident taxa can occur through reductions in light, physical effects of litter accumulation, or changes in the chemical or biological properties of soils (Scholes & Archer 1997; Lett & Knapp 2003, 2005; Siemann & Rogers 2003; Griffiths et al. 2005). Positive feedbacks may develop between shrubs or trees and soil processes, ultimately leading to an alternative stable state (e.g., Archer 1990; Lett & Knapp 2003, 2005). Given the strong controls of trees on light, soil resources, and

physical environment (Zinke 1962; Belsky et al. 1989; Amiotti et al. 2000), declines in the abundance and diversity of grassland or meadow species should be closely tied to the density and duration of tree cover.

In contrast, colonization of new forests by understory species requires not only suitable environmental conditions, but also successful dispersal (e.g., Brunet & von Oheimb 1998; Fuller & del Moral 2003). However, dispersal distances are short for many forest herbs (Bierzychudek 1982; Cain et al. 1998) potentially limiting rates of colonization and patterns of community assembly (Matlack 1994; Verheyen & Hermy 2004; Butaye et al. 2002; Verheyen et al. 2003; but see Vellend 2005). Subsequent development of the understory is influenced by many factors including changes in resource availability, competitive interactions, and potential for clonal spread (Tappeiner & Alaback 1989; Cain & Damman 1997; Lezberg et al. 1999, 2001). Thus, relative to declines in meadow taxa, patterns of colonization and growth of forest understory species are likely to be less predictable and to show poorer relationships with changes in light and forest structure.

Here, I use a chronosequence approach to describe patterns of vegetation change associated with encroachment of a dry montane meadow by *Pinus contorta* and *Abies grandis* in the western Cascade Range of Oregon. The study site, Bunchgrass Ridge, provides an ideal setting to reconstruct vegetation change: it supports a 100-ha mosaic of grass- and forb-dominated meadow with patches of

forests of varying age that have established over a period of nearly two centuries on similar soils and topography. My work has two objectives. The first is to document temporal changes in the abundance and richness of meadow and forest species during the transition from open meadow to old forest. The second is to identify the attributes of forest structure that are associated with these changes. To address the first objective, I ask three questions:

- (1) How does species composition change during the transition from open meadow to old forest?
- (2) How do the richness and abundance of meadow and forest species change during this transition?
- (3) Do species within these groups show parallel trends in abundance; if not, can their variation be explained by differences in growth form or life history (e.g., mode of dispersal)?

To address the second object, I ask three additional questions:

- (4) Are changes in species composition correlated with changes in light and/or forest structure (density and basal area of the primary tree species)?
- (5) Which attributes of forest structure show the strongest relationships with richness and abundance of meadow and forest species?
- (6) Are these relationships weaker for forest species than for meadow species?

Methods

Study area

Bunchgrass Ridge (henceforth Bunchgrass) lies in the Willamette National Forest of central western Oregon (44°17'N, 121°57'W). It forms a gently sloping plateau at the boundary between the older and steeply dissected western Cascade Range and the rolling terrain of the High Cascade province, which is characterized by more recent shield and composite volcanoes (Franklin & Dyrness 1988). Elevations at Bunchgrass range from ca. 1300 to 1375 m a.s.l.; slopes are generally <5% and face southward.

Bunchgrass supports a mosaic of dry meadow, areas of recent conifer encroachment (30-70 yr), and older forest (>100 yr). Meadows are dominated by graminoids (primarily *Festuca idahoensis* and *Carex pensylvanica*) and forbs (*Lupinus latifolius*, *Fragaria* spp., and *Erigeron aliceae*). Forests are dominated by *Abies grandis* both in the canopy and sub-canopy, but *Pinus contorta*, which is less tolerant of shade, commonly occurs as scattered individuals or cohorts that have invaded open meadow. Less common tree species include *Pseudotsuga menziesii*, *Abies procera*, *A. amabilis*, *Pinus monticola*, and *Tsuga mertensiana*. Understories in old forests are dominated by herbs typical of rich, mesic sites in this region (e.g., *Smilacina stellata*, *Achlys triphylla*, *Galium oreganum*, and *Anemone oregana*; Hemstrom et al. 1987). Bunchgrass is surrounded by mature and old-growth forests, except for some stands that were clearcut and replanted in

the 1970s and 1980s.

Soils are deep (>170 cm) fine to very-fine-sandy loams derived from andesitic basalt and tephra deposits and contain a large and highly variable component of glacially derived cobbles, stones, and boulders. They grade from Vitric Melanocryands in open meadow to Aquic Vitricryands in older forests (D. Lammers, unpubl. data). Soil profiles in areas of both open meadow and old forest suggest centuries of development beneath grassland vegetation (D. Lammers, pers. comm; soil scientist, US Forest Service, Feb. 2005).

At Santiam Pass (1,488 m a.s.l.), 17 km to the north (the closest appropriate climate station), annual precipitation averages ca. 216 cm with 7.5% falling from June through August; annual snowfall averages 1,152 cm. Average minimum and maximum temperatures are -6.9 and 0.7°C in January and 6.1 and 27.8°C in July (climate data for 1948-1985, the period of peak conifer encroachment; Western Regional Climate Center; <http://www.wrcc.dri.edu/summary/climsmor.html>).

Disturbance history

Site-specific information on fire and grazing history is lacking for Bunchgrass. Natural fire-return intervals for forests at this elevation are likely to be over 100 yr (Teensma 1987; Morrison & Swanson 1990) and episodic, driven by historical changes in climate and human activity (e.g., Weisberg & Swanson 2003). Native Americans are thought to have used fire to maintain open meadow habitats throughout the Pacific Northwest (Boyd 1999; but see Vale 2002).

However, there is no direct evidence of burning (e.g., fire scars) in adjacent forests at Bunchgrass, and archeological surveys have failed to produce artifacts from human use of the meadow prior to Euro-American settlement (E. Bergland pers. comm.; archaeologist, Willamette National Forest, April 2004). Grazing of sheep is likely to have occurred during the early part of the 20th century, synchronous with widespread grazing in the Cascade Mountains (Burke 1979; Johnson 1985; Rakestraw & Rakestraw 1991). However, archival records of the U.S. Forest Service lack sufficient detail to determine the timing or intensity of grazing at Bunchgrass (Johnson 1985; E. Bergland pers. comm.; archaeologist, Willamette National Forest, Jan. 2005).

Sampling methods

Comparisons of historical (1946, 1959) and more recent (1990, 1997) aerial photographs of Bunchgrass were used to delineate potential study areas that had pronounced conifer encroachment during the 20th century (Fig. 1). From these areas, four 1-ha (100 x 100 m) plots were selected that included open meadow, recent encroachment, and older forest. In July 2003, grid systems were surveyed at 10-m spacing to yield 100, 10 x 10 m subplots per plot, the sampling units of this study. An additional 23 subplots were established adjacent to two plots to ensure sufficient representation of open meadow.

Within each 1-ha plot, all live stems ≥ 1.4 m tall were tagged, identified to species, and measured for diameter at breast height (dbh). Snags ≥ 5 cm dbh were

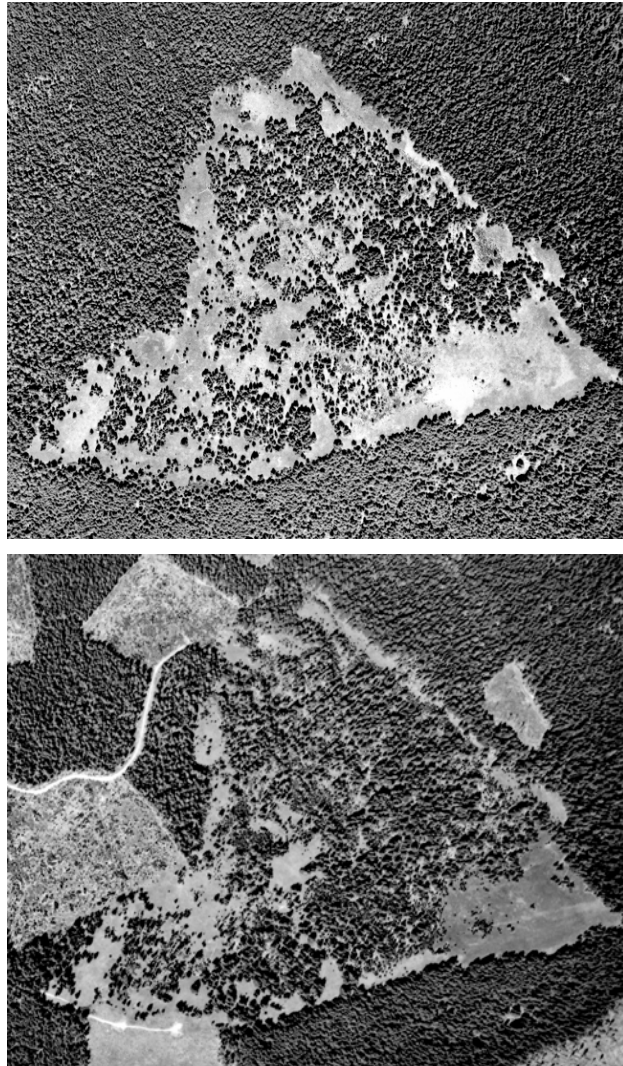


Figure 1. Aerial photographs of Bunchgrass Ridge from 1959 (top) and 1997 (bottom). Note the stable meadows in the SW and SE corners and the infilling of conifers in the central region. Portions of the surrounding landscape were clear cut in the 1970s and 1980s.

also identified to species and measured for dbh. Locations of all live stems and snags ($n = 6,872$) were mapped to the nearest 0.1 m. Ages of live stems ($n = 5,486$) were determined from increment cores or basal sections during July and August 2003 and 2004. Larger trees (greater than ca. 10 cm dbh; $n = 1,965$) were cored as close to the ground as possible and core height was recorded. Smaller trees ($n = 3,521$) were felled and a basal section was taken; height of the cut surface was also recorded. Cores were mounted and all samples were sanded following standard dendrochronological methods. Ring counts were made under 10-40x magnification. For cores lacking the pith, missing rings were estimated from a series of ring-pattern templates. Adjustments for age-to-sample height were based on age-height regressions developed from a destructive sample of 30-40 seedlings per species (C. Halpern, unpubl. data). For trees with rotten or incomplete cores ($n = 135$), age was estimated from diameter based on species-specific regression equations developed from the larger pool of aged cores and basal sections (C. Halpern, unpubl. data).

To estimate light availability, a digital hemispherical photograph was taken at the center of each 10 x 10 m subplot at a height of 1.65 m. Photographs were taken with a Nikon Coolpix 990 digital camera using a FC-E8 fisheye converter between 21 June and 4 August 2004, either before 08:00 or after 18:00 hr or on uniformly overcast days to avoid direct sunlight. Total transmitted light or photosynthetic photon flux density averaged over the year (PPFD, $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$),

was calculated with the software, Gap Light Analyzer 2.0 (Frazer et al. 1999), employing the standard overcast sky model.

Ground-layer vegetation (including trees <1.4 m tall) was sampled in a subset of the subplots ($n = 356$) between 5 July and 16 August 2004. Four 1-m² quadrats were established within the central 6 x 6 m area of each subplot, spaced 1 m apart along the NW-SE diagonal. Within each quadrat, I visually estimated the cover of each vascular plant species. Species within several taxa (*Corallorhiza*, *Disporum*, *Fragaria*, and *Listera*) were grouped at the generic level because species identification was difficult at the time of sampling. *Festuca viridula*, which was probably present in small amounts, was grouped with the dominant *F. idahoensis* because vegetative plants could not be distinguished to species.

Chronosequence development and forest structural variables

I used an agglomerative, hierarchical clustering technique (Wishart 1969) to classify subplots based on the age structure of trees (following the approach of Taylor & Skinner 2003). The classification served as the basis for analyzing and comparing changes in forest structure and ground-layer vegetation during the transition from open meadow to old forest. For each subplot, I tallied the number of conifers in each of eleven 20-yr age classes (i.e. the variables for the classification). I employed Ward's linkage method (Ward 1963) using relative Euclidean distance as the measure of dissimilarity (PC-ORD v. 4.0; McCune & Mefford 1999). Data were aggregated to the level of 75% of information

remaining, producing six “encroachment classes,” each characterized by a different age structure. Subplots without trees were omitted from the analysis, but were assigned to an additional class, Class 0, representing open meadow. The final classification, viewed as a chronosequence, revealed a gradual increase in the mode and range of tree ages from Class 0 (open meadow) to Class 6 (old forest with overstory trees >90 yr old) (see *Results: Conifer encroachment*). Evaluation of the full classification revealed that 34 of 356 subplots were misclassified (*sensu* McCune & Grace 2002); 19 subplots with only one or two trees were reassigned to Class 1; 15 subplots with three or more trees >90 yr old were reassigned to Class 6.

To quantify forest structure, subplots were characterized by basal area ($\text{m}^2 \cdot \text{ha}^{-1}$) and density ($\text{stems} \cdot \text{ha}^{-1}$) of both live and dead stems of the principal tree species, *Abies grandis* and *Pinus contorta*. Total basal area and total density of trees were not considered because they were highly correlated to values for *Abies*.

Classification of species

Species were grouped by habitat affinity (Table 1), and within these functional types, by growth form, based on previous studies (Halpern et al. 1984; Hemstrom et al. 1987) and regional floras (Hitchcock et al. 1969; Hitchcock 1973). Habitat groups included meadow ($n = 43$ species), forest understory ($n = 48$), or ruderal ($n = 7$). Understory trees ($n = 13$) and taxa that could not be assigned unambiguously to a group were not classified ($n = 6$). Growth forms

Table 1. Meadow, forest, and ruderal species at Bunchgrass Ridge. Potential for clonal growth (Clonal) and mode of dispersal (Dispersal) were determined for forest species only (see *Methods: Analysis: Classification of species*). Herbs include ferns, suffrutescent forbs, and sub-shrubs. Species with frequencies <1% are not listed.

Growth form / Species	Family	Origin	Clonal	Dispersal
Meadow species				
Sedges/rushes				
<i>Carex pachystachya</i>	Cyperaceae	native		
<i>Carex pensylvanica</i>	Cyperaceae	native		
Grasses				
<i>Agropyron repens</i>	Gramineae	exotic		
<i>Bromus carinatus</i>	Gramineae	native		
<i>Danthonia intermedia</i>	Gramineae	native		
<i>Elymus glaucus</i>	Gramineae	native		
<i>Festuca idahoensis</i> ^a	Gramineae	native		
<i>Poa pratensis</i>	Gramineae	exotic		
<i>Stipa occidentalis</i>	Gramineae	native		
Herbs				
<i>Achillea millefolium</i>	Compositae	native		
<i>Agoseris aurantiaca</i>	Compositae	native		
<i>Anaphalis margaritacea</i>	Compositae	native		
<i>Aster ledophyllus</i>	Compositae	native		
<i>Aster occidentalis</i>	Compositae	native		
<i>Aster radulinus</i>	Compositae	native		
<i>Calochortus subalpinus</i>	Liliaceae	native		
<i>Cirsium callilepis</i>	Compositae	native		
<i>Comandra umbellate</i>	Santalaceae	native		
<i>Erigeron aliciae</i>	Compositae	native		
<i>Fragaria vesca/virginiana</i>	Rosaceae	native		
<i>Hieracium gracile</i>	Compositae	native		
<i>Iris chrysophylla</i>	Iridaceae	native		
<i>Lathyrus nevadensis</i>	Leguminosae	native		
<i>Lupinus latifolius</i>	Leguminosae	Native		
<i>Microsteris gracilis</i>	Polemoniaceae	Native		
<i>Orthocarpus imbricatus</i>	Scrophulariaceae	native		
<i>Penstemon procerus</i>	Scrophulariaceae	native		
<i>Phlox diffusa</i>	Polemoniaceae	native		
<i>Polygonum douglasii</i>	Polygonaceae	native		
<i>Pteridium aquilinum</i>	Polypodiaceae	native		
<i>Vicia americana</i>	Leguminosae	native		
<i>Viola nuttallii</i>	Violaceae	native		

Table 1. Continued.

Growth form / Species	Family	Origin	Clonal	Dispersal
Forest species				
Grasses				
<i>Bromus vulgaris</i>	Gramineae	native	none	wind
<i>Melica subulata</i>	Gramineae	native	yes	wind
<i>Trisetum canescens</i>	Gramineae	native	yes	wind
Herbs				
<i>Actaea rubra</i>	Ranunculaceae	native	yes	ingested
<i>Achlys triphylla</i>	Berberidaceae	native	strong	ant
<i>Adenocaulon bicolor</i>	Compositae	native	none	wind
<i>Anemone deltoidea</i>	Ranunculaceae	native	strong	ant
<i>Anemone lyallii</i>	Ranunculaceae	native	yes	ant
<i>Anemone oregana</i>	Ranunculaceae	native	yes	ant
<i>Arenaria macrophylla</i>	Caryophyllaceae	native	strong	ant
<i>Asarum caudatum</i>	Aristolochiaceae	native	strong	ant
<i>Campanula scouleri</i>	Campanulaceae	native	yes	none
<i>Chimaphila menziesii</i>	Ericaceae	native	yes	none
<i>Chimaphila umbellata</i>	Ericaceae	native	yes	none
<i>Circaea alpina</i>	Onagraceae	native	yes	adhesive
<i>Clintonia uniflora</i>	Liliaceae	native	strong	ingested
<i>Cornus canadensis</i>	Cornaceae	native	strong	ingested
<i>Corallorhiza maculata</i>	Orchidaceae	native	yes	wind
<i>Disporum hookeri/smithii</i>	Liliaceae	native	yes	none
<i>Galium oreganum</i>	Rubiaceae	native	yes	adhesive
<i>Galium triflorum</i>	Rubiaceae	native	strong	adhesive
<i>Goodyera oblongifolia</i>	Orchidaceae	native	yes	none
<i>Hieracium albiflorum</i>	Compositae	native	none	wind
<i>Lactuca muralis</i>	Compositae	exotic	none	wind
<i>Linnaea borealis</i>	Caprifoliaceae	native	strong	none
<i>Listera caurina/cordata</i>	Orchidaceae	native	yes	none
<i>Osmorhiza chilensis</i>	Umbelliferae	native	none	adhesive
<i>Polystichum munitum</i>	Polypodiaceae	native		
<i>Pyrola picta</i>	Ericaceae	native	yes	none
<i>Pyrola secunda</i>	Ericaceae	native	strong	none
<i>Rubus lasiococcus</i>	Rosaceae	native	strong	ingested
<i>Rubus ursinus</i>	Rosaceae	native	strong	ingested
<i>Smilacina stellata</i>	Liliaceae	native	strong	none
<i>Tiarella trifoliata</i>	Saxifragaceae	native	yes	none
<i>Trientalis latifolia</i>	Primulaceae	native	yes	none
<i>Trillium ovatum</i>	Liliaceae	native	yes	ant
<i>Viola glabella</i>	Violaceae	native	yes	ballistic
<i>Viola orbiculata</i>	Violaceae	native	none	ballistic

Table 1. Continued.

Growth form / Species	Family	Origin	Clonal	Dispersal
Forest species (continued)				
Tall shrubs				
<i>Amelanchier alnifolia</i>	Rosaceae	native	yes	ingested
<i>Berberis aquifolium</i>	Berberidaceae	native	yes	ingested
<i>Berberis nervosa</i>	Berberidaceae	native	strong	ingested
<i>Rosa gymnocarpa</i>	Rosaceae	native	yes	ingested
<i>Symphoricarpos mollis</i>	Caprifoliaceae	native	yes	ingested
<i>Vaccinium membranaceum</i>	Ericaceae	native	yes	ingested
Ruderal species				
Sedges/rushes				
<i>Luzula campestris</i>	Juncaceae	native		
Herbs				
<i>Epilobium angustifolium</i>	Onagraceae	native		
<i>Epilobium watsonii</i>	Onagraceae	native		
<i>Montia sibirica</i>	Portulacaceae	native		
<i>Phacelia heterophylla</i>	Hydrophyllaceae	native		
<i>Rumex acetosella</i>	Polygonaceae	exotic		
Unclassified species				
Herbs				
<i>Lilium columbianum</i>	Liliaceae	native		
<i>Ranunculus uncinatus</i>	Ranunculaceae	native		
Understory hardwoods				
<i>Castanopsis chrysophylla</i>	Fagaceae	native		
<i>Rhamnus purshiana</i>	Rhamnaceae	native		
<i>Sorbus sitchensis</i>	Rosaceae	native		
Understory conifers				
<i>Abies grandis</i>	Pinaceae	native		
<i>Abies procera</i>	Pinaceae	native		
<i>Pinus contorta</i>	Pinaceae	native		
<i>Tsuga heterophylla</i>	Pinaceae	native		

^a Includes occasional *F. viridula*

included sedge/rush ($n = 3$ taxa), grass ($n = 11$), herb (fern, suffrutescent forb, and sub-shrub; $n = 68$), or tall shrub ($n = 9$). For forest species I also determined primary mode of dispersal and potential for clonal growth (Table 1). Modes of dispersal (*sensu* Matlack 1994) included wind (including fern spores, $n = 12$), ingested ($n = 13$), adhesive ($n = 4$), ant/ballistic ($n = 9$), or no obvious mechanism (none; $n = 10$). Potential for clonal growth was coded as “no,” “yes,” or “strong.”

Changes in species composition

Nonmetric multidimensional scaling (NMS; Kruskal 1964a, 1964b; Mather 1976) was used to portray changes in species composition across the chronosequence (Question 1). NMS was performed on the full matrix of 356 subplots and 117 species using Sørensen’s distance measure and the “slow and thorough” autopilot in PC-ORD v. 4.0 (McCune & Mefford 1999). The autopilot conducted 40 runs producing one- to six-dimensional solutions. Each run continued for a maximum of 400 iterations or until an instability threshold of 0.00001 was reached. I selected a final two-dimensional solution with a stress of 18.57 based on comparisons of final stress values for the best solutions at each dimensionality. To test whether the final stress was lower than expected by chance, stress for the final solution was compared to 50 runs of randomized data using a Monte Carlo test (McCune & Grace 2002). To simplify the graphical presentation of >350 data points, I computed a centroid (± 1 SE) for each

encroachment class based on subplot scores on NMS Axes 1 and 2. To identify environmental or structural correlates of compositional variation (Question 4), I computed Spearman rank correlations (Zar 1999) between subplot scores on NMS axes and measures of light availability (PPFD) and forest structure. Correlations were displayed as a biplot of structural vectors where $r_{\text{NMS1}} = \cos\theta$ and $r_{\text{NMS2}} = \sin\theta$.

I used multi-response permutation procedures (MRPP; Biondini et al. 1988) to test whether species composition differed among successive pairs of encroachment classes. MRPP is a non-parametric, Monte Carlo method that compares a weighted average within-group similarity to an expected average based on all possible partitions of the data for groups of the same size (McCune & Grace 2002). For consistency with NMS, I used a rank-transformed distance matrix based on Sørensen's distance (PC-ORD v. 4.0; McCune & Mefford 1999). Following an initial test that included all encroachment classes, separate comparisons were made between pairs of classes. To test whether composition of forest understory species converged along the chronosequence, I compared the mean similarity (1 - Sørensen's distance) of subplots among encroachment classes using only the pool of forest species.

Changes in cover and richness of meadow and forest species

For each subplot, I computed the total (summed) cover, richness, and Shannon's diversity index (Shannon & Weaver 1949) of forest and meadow

species, and of growth forms within each group. Averages were then computed for each encroachment class and compared graphically to illustrate changes in the abundance and diversity of functional types during the transition from open meadow to old forest (Question 2). Patterns of richness and diversity were similar, thus only the former are presented.

To examine how individual species contributed to these community trends (Question 3), I plotted the frequency (proportion of subplots) and average cover of common meadow and forest species. Species were plotted if present in >50% of subplots in Class 0 (meadow species) or Class 6 (forest species).

Relationships between forest structure/light and plant functional types

Multiple linear regression was used to explore relationships between forest structure and light and the richness or abundance of functional types (Questions 5 and 6). Potential predictors in these models included total transmitted light (PPFD) and the basal area and density of live and dead stems of *Abies* and *Pinus*. Models were created through stepwise addition and subtraction of predictors, with a probability of 0.05 to add and 0.10 to remove a variable (Neter et al. 1996). Model coefficients were standardized to allow direct comparison of the effects of predictors on response variables (Neter et al. 1996). Standard diagnostics were used to test the assumptions of normality and constant variance of residuals. As a result, PPFD, basal area, and density were square-root transformed. Regression analyses were conducted with SPSS 13.0 (2004).

Results

Conifer encroachment

Conifer recruitment occurred during two broad periods at Bunchgrass, with peaks in establishment in 1870-1890 and 1950-1970 (Fig. 2). *Abies grandis* dominated both periods ($n = 4,571$). Peak establishment of *Pinus* preceded that of *Abies*, although this was less apparent for the initial cohort of *Pinus* (see insert, Fig. 2) — most *Pinus* stems from the initial cohort had died by 2004 and were present only as snags ($n = 75$ snags of equal or larger diameter than live stems from the initial cohort).

Encroachment classes 0-5 displayed a clear progression of increasing mode and range of tree ages (Fig. 3). Class 6 displayed a bi-modal age structure (peaks at 140 and 60 yr), which contributed to stratification of the canopy into distinct overstory and understory layers. The transition from Class 5 to 6 represents passage of considerably more time than that between more recent encroachment classes (Fig. 3).

Light transmission and overstory structure changed markedly across the chronosequence. PPF_D dropped steeply with initial establishment of trees (Class 0 to 1; Fig. 4a). Subsequent forest development was characterized by rapid and abundant recruitment of *Abies* (Class 2; Fig. 4b) followed by a gradual reduction in density and an increase in basal area (Classes 2-5; Figs. 4b, c).

The transition from Class 5 to 6 included a three-fold increase in basal area of

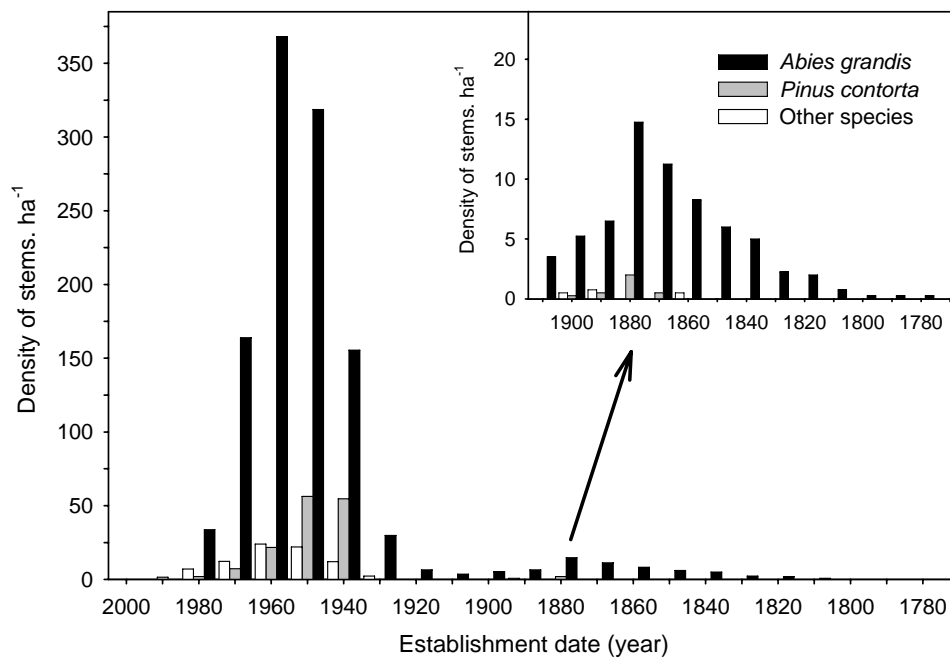


Figure 2. Age structure for all trees ≥ 1.4 m tall within the four 1-ha plots. Dates represent 20-yr age classes. The age structure for the earlier cohort is rescaled and enlarged for clarity.

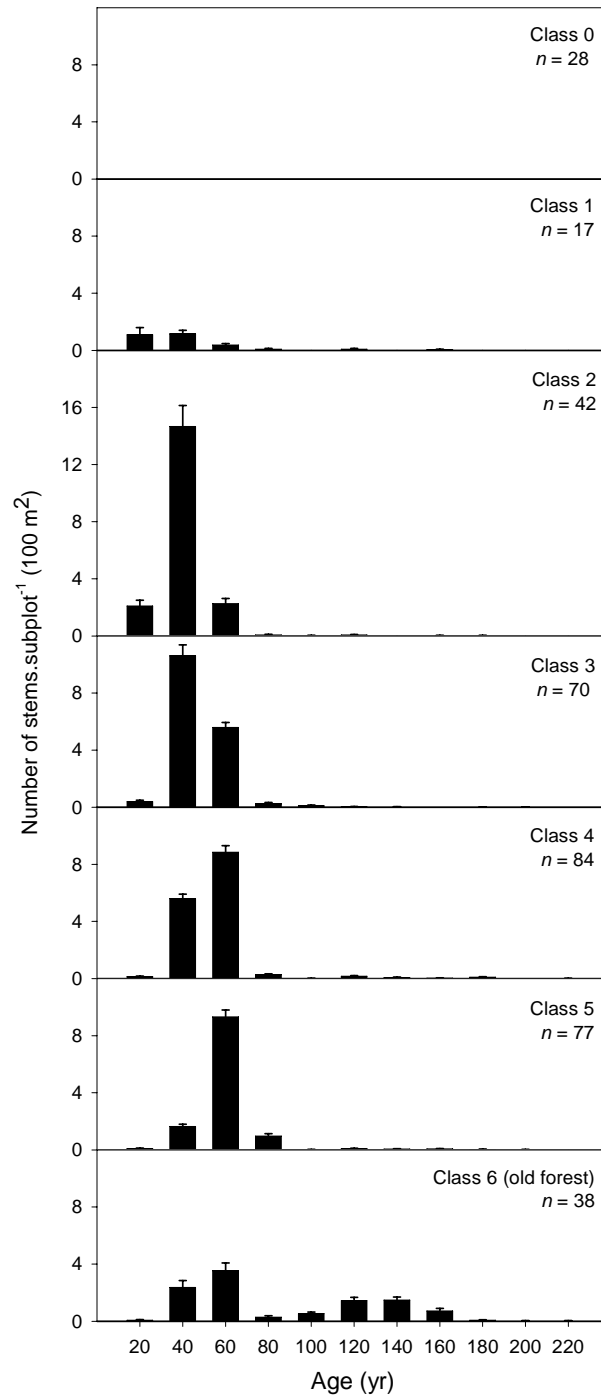


Figure 3. Age structures for all trees ≥ 1.4 m within each of the seven encroachment classes. Ages represent 20-yr age classes.

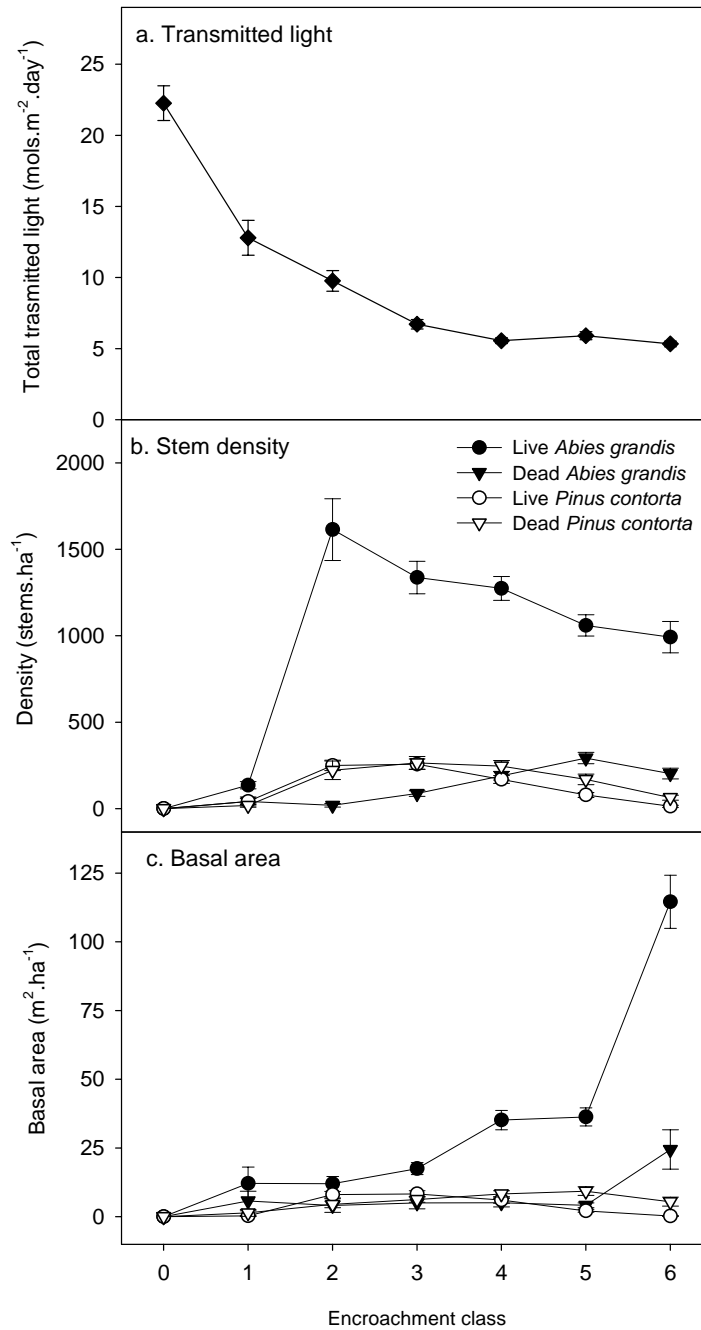


Figure 4. Changes in (a) transmitted light, (b) stem density, and (c) basal area among encroachment classes (0 = open meadow, 6 = old forest). Values are means \pm 1 SE.

Abies, reflecting the presence of large-diameter (70-130+ cm) trees. *Pinus* showed parallel trends in density and basal area, with maximum presence in Classes 2-4. PPFD had significant negative correlations with most measures of forest structure (Spearman r of -0.16 to -0.55; all $p < 0.001$); the strongest correlations were with density and basal area of live *Abies* (r of -0.55 and -0.49, respectively).

Changes in species composition

In total, 117 vascular taxa were identified from the 356 subplots; these represented 94 genera and 38 families (Table 1). Families with the greatest diversity of species included Compositae (14), Gramineae (11), and Rosaceae (8).

NMS ordination revealed a gradual shift in species composition from open meadow (Class 0; high scores on NMS 1; Fig. 5a) to old forest (Class 6; low scores on NMS 1). The meadow-dependent species, *Orthocarpus imbricatus* and *Penstemon procerus*, had the highest scores on NMS 1, and the clonal forest herbs, *Smilacina stellata* and *Achlys triphylla*, had the lowest scores (Fig. 5b). Ruderal species were uncommon (except for *Lactuca muralis* in Class 6), but widely distributed across NMS 1.

MRPP indicated highly significant ($A = 0.258$, $p < 0.0001$) differences in species composition among encroachment classes. Using the A-statistic as a measure of effect size (McCune & Grace 1999), pairwise comparisons between successive classes indicated a large compositional change between Classes 0

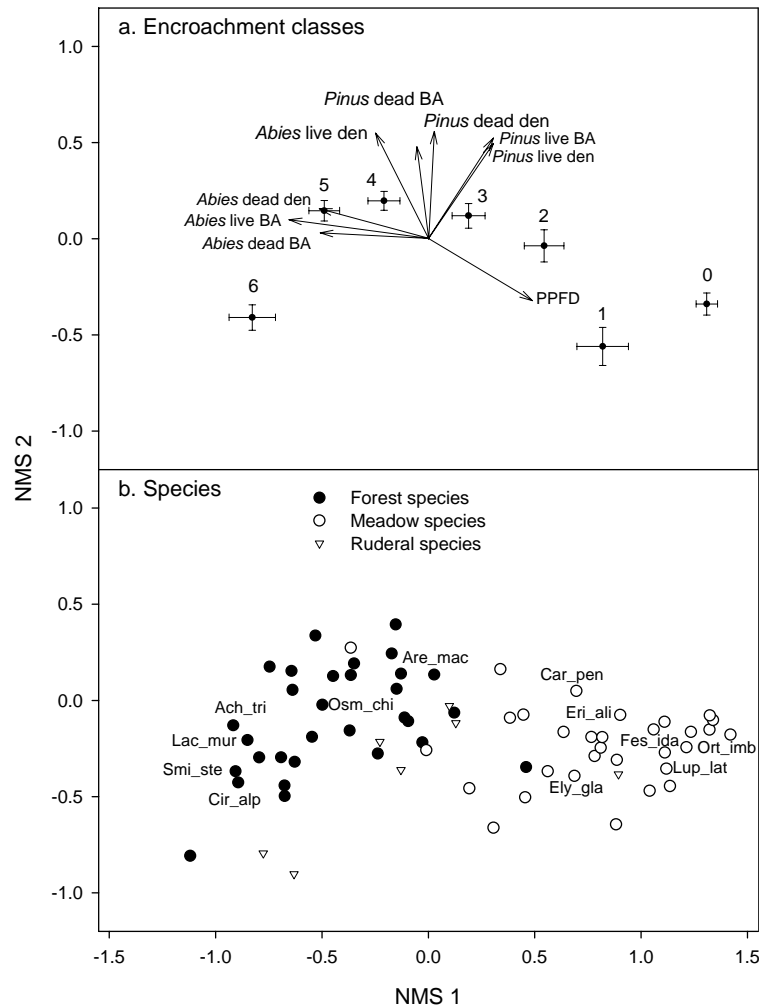


Figure 5. NMS ordination of (a) subplots, represented by encroachment class centroids (± 1 SE) and (b) species, coded by functional type. Vectors portray the direction and strength of Spearman-rank correlations between forest structural variables (basal and density of live or dead trees, or transmitted light [PPFD]) and ordination axes. Codes are shown for selected common forest and meadow species: Ort_imb = *Orthocarpus imbricatus*, Fes_ida = *Festuca idahoensis*, Lup_lat = *Lupinus latifolius*, Eri_ali = *Erigeron aliceae*, Car_pen = *Carex pennsylvanica*, Ely_gla = *Elymus glaucus*, Are_mac = *Arenaria macrophylla*, Osm_chi = *Osmorhiza chilensis*, Lac_mur = *Lactuca muralis*, Cir_alp = *Circaea alpine*, Ach_tri = *Achlys triphylla*, and Smi_ste = *Smilacina stellata*.

(open meadow) and 1 (initial recruitment) ($A = 0.104$) and between Classes 5 and 6 (old forest) ($A = 0.088$). Effect sizes were significant, but smaller for the remaining comparisons: 1 vs. 2 ($A = 0.055$), 3 vs. 4 ($A = 0.028$), 2 vs. 3 ($A = 0.024$), and 4 vs. 5 ($A = 0.012$). For forest understory species, compositional similarity among subplots increased progressively from 0.29 in Class 0 (open meadow) to 0.75 in Class 6 (old forest).

Changes in cover and richness of meadow and forest species

Meadow and forest species displayed contrasting trends in cover and richness (Figs. 6 and 7). Cover of meadow species changed little in response to initial establishment of trees (*cf.* Classes 0 and 1), and meadow grasses actually increased in abundance (reflecting a marked increase in *Elymus glaucus*, see below) (Fig. 6a). Cover declined sharply in Class 2 (peak density of *Abies*; Fig. 4b). Subsequent declines were more gradual, reflecting losses among all growth forms. Richness of meadow species declined more slowly than did cover; both grass and herbaceous species were lost (Fig. 7a).

Cover of forest species increased slowly across the chronosequence, surpassing that of meadow species in Class 4 and peaking at ca. 50% in Class 6 (Fig. 6b). In contrast, richness of forest species increased rapidly, surpassing that of meadow species in Class 3 and peaking in Class 5 (Fig. 7b). Increases in cover and richness of forest species were primarily attributable to herbaceous taxa.

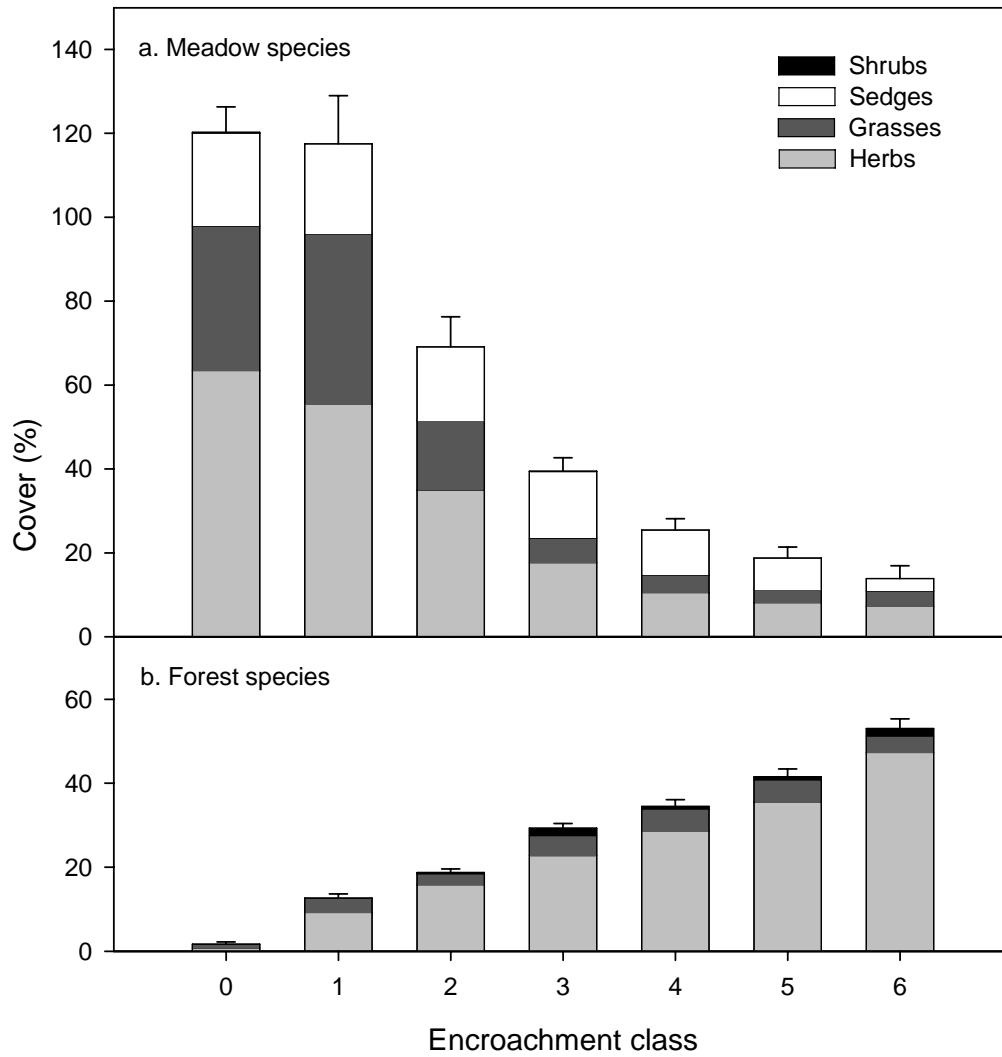


Figure 6. Changes in mean cover (+1 SE; %) of (a) meadow and (b) forest species by growth form among encroachment classes (0 = open meadow, 6 = old forest).

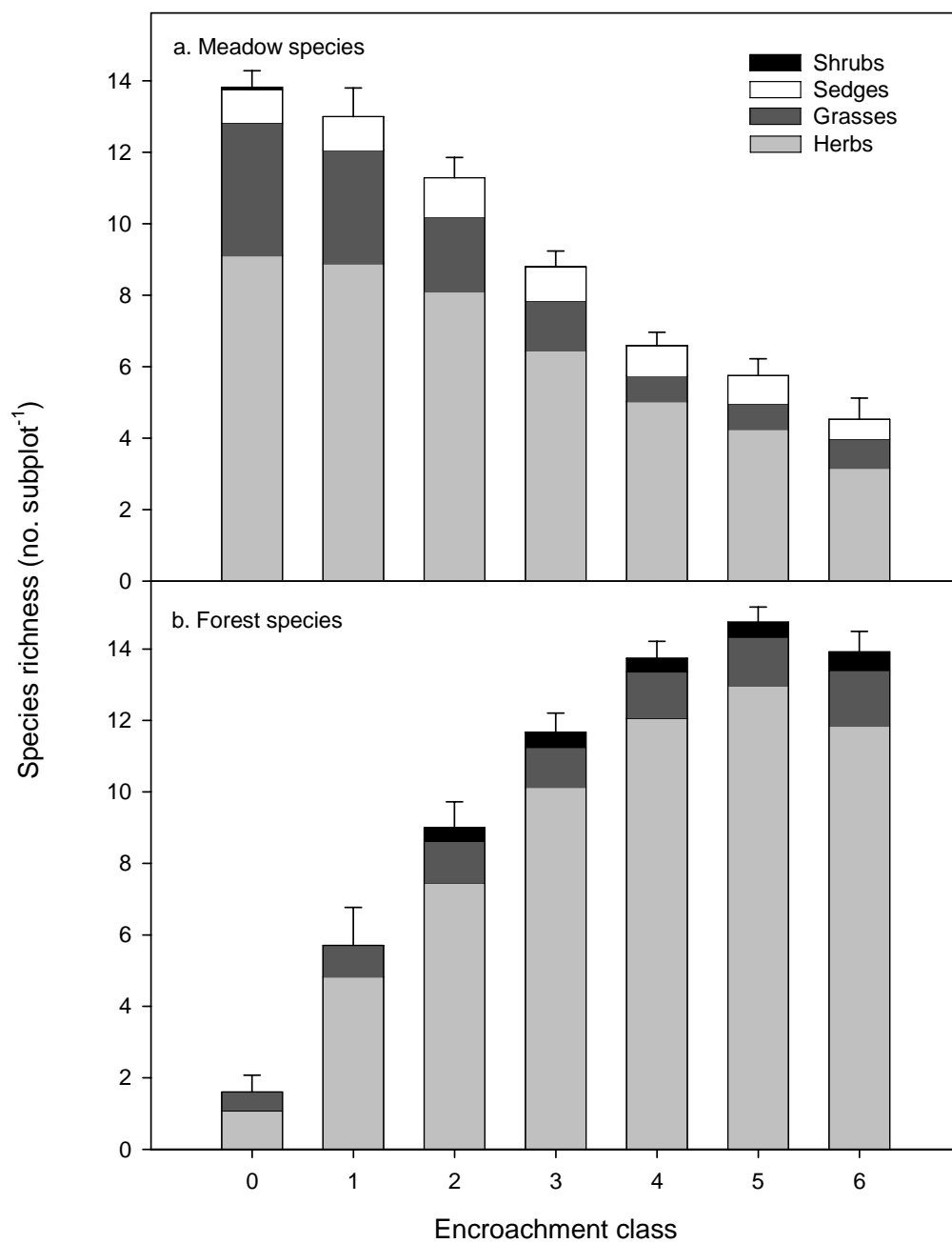


Figure 7. Changes in mean richness (+1 SE; species.subplot⁻¹) of (a) meadow and (b) forest species by growth form among encroachment classes (0 = open meadow, 6 = old forest).

Temporal trends in frequency and cover varied among the primary species contributing to functional group responses (Fig. 8). Two types of trends emerged among meadow species. Eight species peaked in cover in Class 0 (open meadow) then declined across the chronosequence, either gradually (e.g., *Carex pennsylvanica*, *Festuca idahoensis*, and *Erigeron aliceae*) or abruptly (e.g., *Lupinus latifolius* and *Orthocarpus imbricatus*). In contrast, four taxa peaked in Class 1 (or 2), then declined gradually (e.g., *Fragaria* spp.) or abruptly (e.g., *Elymus glaucus* and *Bromus carinatus*). Although all meadow species showed marked declines in frequency and cover, only *Orthocarpus* exhibited local extirpation (Fig. 8).

Forest species showed a diversity of abundance patterns, reflecting varying rates of colonization and growth (Fig. 9). By Class 1 some species had already recruited into 80% of subplots (*Viola glabella* and *Arenaria macrophylla*). Others established more slowly, achieving similar frequency in Class 3 or 4 (*Bromus vulgaris*, *Galium triflorum*, *Anemone deltoidea*, and *Osmorhiza chilensis*), or as late as Class 6 (*Smilacina stellata*, *Achlys triphylla*, *Lactuca muralis*, and *Circaea alpina*). Trends in cover varied from unimodal to irregular. For several species, cover increased gradually to a peak in Class 5 (*Arenaria macrophylla*, *Bromus vulgaris*, and *Anemone deltoidea*). For others, cover remained low in young forest (Classes 2-5), but showed a distinctive increase in old forest (*Smilacina stellata*, *Achlys triphylla*, *Circaea alpina*, *Lactuca muralis*, and *Galium triflorum*).

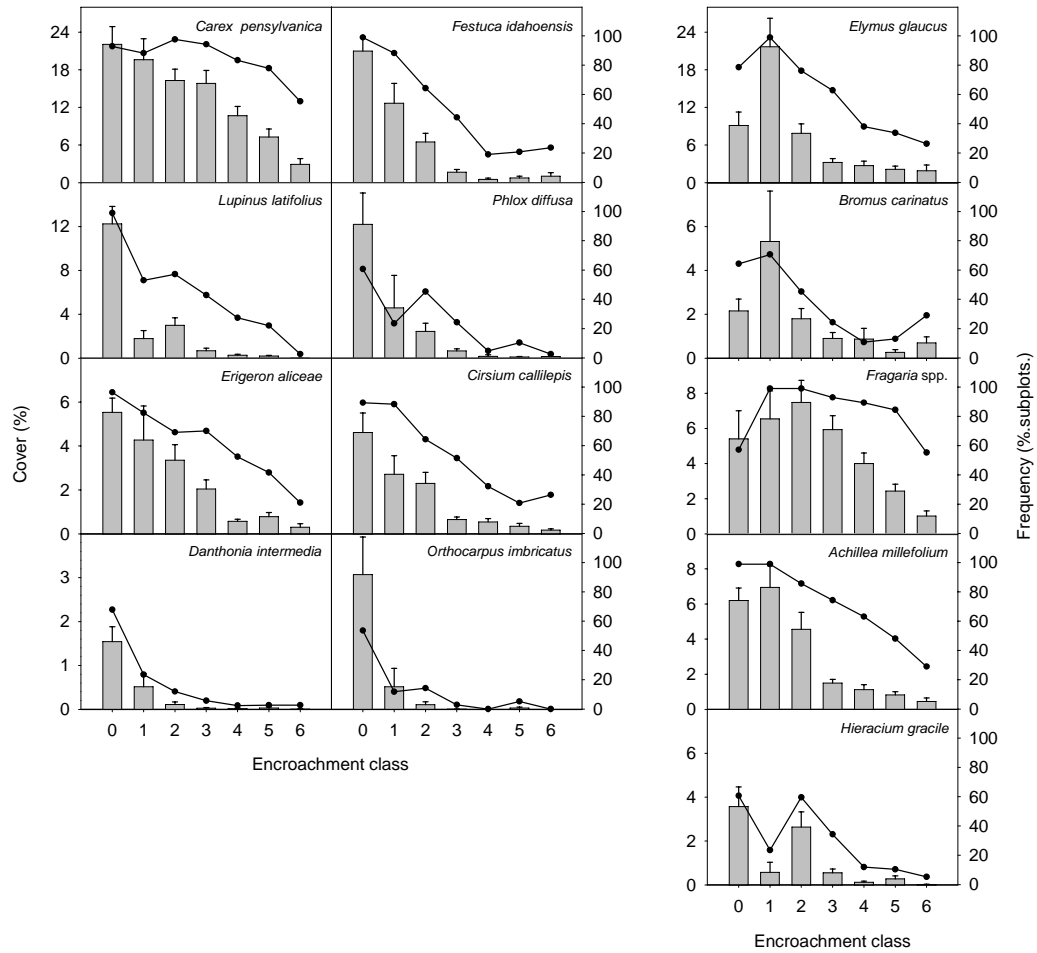


Figure 8. Changes in mean cover (+1 SE) (bars; left axes) and frequency (lines; right axes) among encroachment classes for common meadow taxa (present in $\geq 50\%$ of open meadow [Class 0] subplots). Note that scales on the cover axes vary.

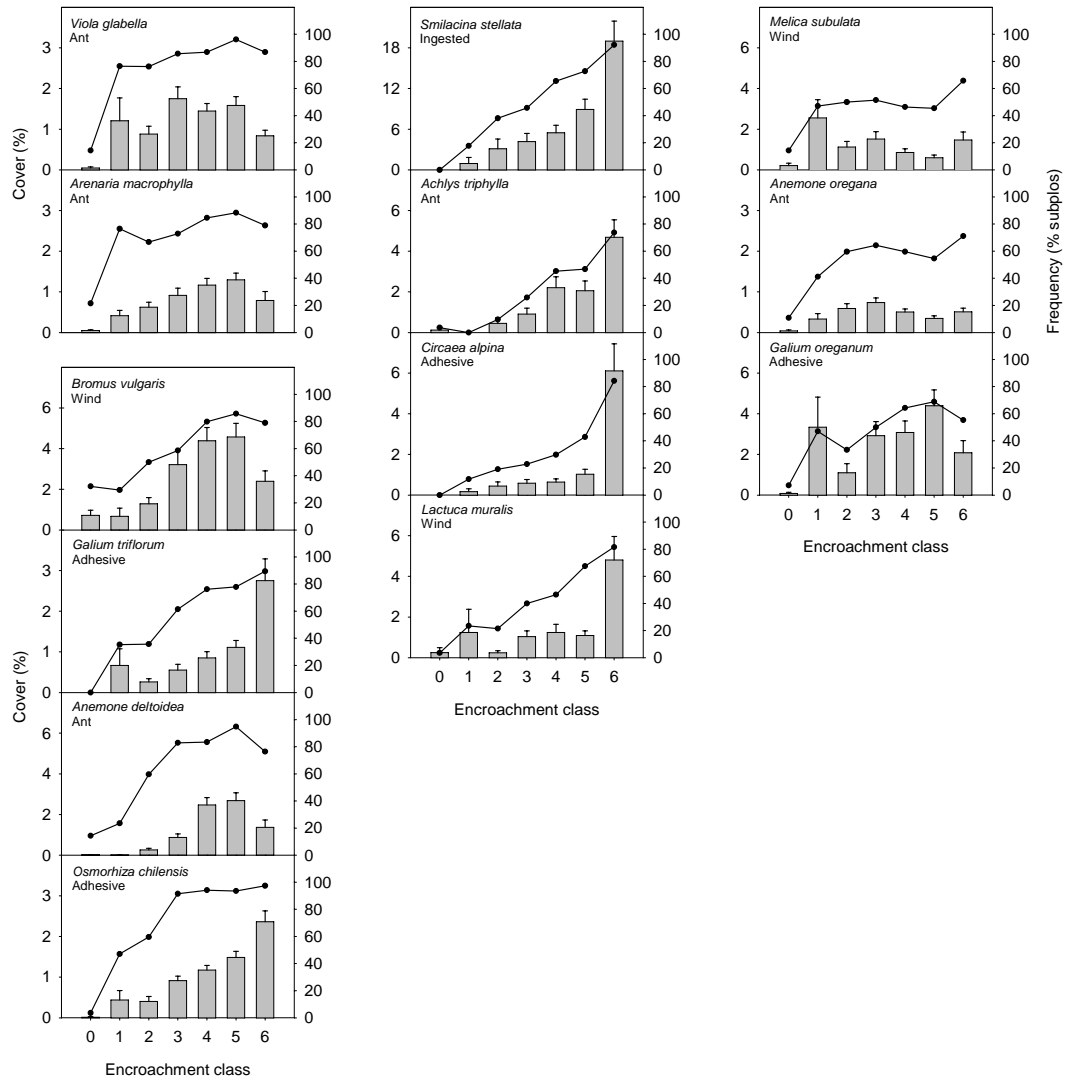


Figure 9. Changes in mean cover (+1 SE) (bars; left axes) and frequency (lines; right axes) among encroachment classes for common forest understory taxa (present in $\geq 50\%$ of old forest [Class 6] subplots). Primary mode of dispersal is listed below the name of each species. Note that scales on the cover axes vary.

Still others showed no strong temporal trend in cover (e.g., *Viola glabella*, *Melica subulata*, *Anemone oregana*, and *Galium oreganum*). There was little correspondence between trends in frequency and dispersal mechanism: species with similar trends in frequency often had different modes of dispersal, and species with similar modes of dispersal often had distinctly different trends in frequency (Fig. 9).

Relationships between ground-layer vegetation, light, and forest structure

NMS axes showed strong correlations with light availability and overstory structure (Fig. 5b). NMS 1 was highly correlated with PPF (Spearman $r = 0.49$), basal area of live and dead *Abies* ($r = -0.66$ and -0.51 , respectively), and density of dead *Abies* ($r = -0.51$) (all $p < 0.001$). NMS 2 was highly correlated with density of dead *Pinus* ($r = 0.56$), basal area of live *Pinus* ($r = 0.52$), and density of live *Abies* ($r = 0.55$) (all $p < 0.001$). Structural vectors in ordination space (Fig. 5b) illustrate the gradual replacement of *Pinus* by *Abies* (first in density, then in basal area; see also Fig. 4), closely tracking the temporal progression of encroachment classes.

Multiple regression models suggest a stronger influence of forest structure on loss of meadow species than on colonization and growth of forest understory plants. Models of cover and richness were stronger for meadow ($R^2 = 0.54$ and 0.48) than for forest species ($R^2 = 0.34$ and 0.42) (all $p < 0.001$; Table 2).

Table 2. Standardized coefficients and *p* values of significant predictors in stepwise multiple regression models of richness and cover of meadow and forest species. Regression models are based on all vegetation subplots (*n* = 356). Light availability (PPFD) and all density and basal area (BA) variables were square-root transformed. All variance inflation factors (VIF) were <3.5 except where noted.

Model	Adjusted R ²	PPFD	<i>Abies, live</i>		<i>Abies, dead</i>		<i>Pinus, live</i>		<i>Pinus, dead</i>	
		(mols. m ⁻² . day ⁻¹)	Density (stems. ha ⁻¹)	BA (m ² . ha ⁻¹)	Density (stems. ha ⁻¹)	BA (m ² . ha ⁻¹)	Density (stems. ha ⁻¹)	BA (m ² . ha ⁻¹)	Density (stems. ha ⁻¹)	BA (m ² . ha ⁻¹)
Meadow species										
Richness	0.48	0.263		-0.298	-0.307		0.152		-0.320 ^a	0.191
<i>p</i>	<0.001	<0.001		<0.001	<0.001		0.005		<0.001	0.007
Cover	0.54	0.470		-0.267	-0.184					
<i>p</i>	<0.001	<0.001		<0.001	<0.001					
Forest species										
Richness	0.42	-0.445	0.144		0.160		-0.317			
<i>p</i>	<0.001	<0.001	0.010		0.001		<0.001			
Cover	0.34	-0.331		0.211			-0.326			-0.129
<i>p</i>	<0.001	<0.001		<0.001			<0.001			0.008

^a Variance inflation factor (VIF) = 4.3

Transmitted light (PPFD) was a strong predictor in all models (positive for meadow and negative for forest species). Three additional predictors were highly significant in meadow models: basal area of live *Abies* and density of dead *Abies* (negative correlations) in both models, and density of dead *Pinus* (negative correlation) in the richness model. Models for forest species shared only one structural variable in common — basal area of live *Pinus* (negative correlations; Table 2); additional variables proved significant, but were weaker predictors.

Discussion

My detailed reconstruction of tree establishment patterns suggests a fairly simple model of conifer invasion and forest development. *Pinus* typically initiates invasion of open meadow at low densities, although *Abies* can also recruit into open meadow. Over a period of two to four decades, *Abies* seedlings establish in great abundance beneath or in association with the initial recruitment of *Pinus* or *Abies*. Subsequent stand development is characterized by a gradual increase in the basal area of *Abies* and a marked reduction in density. Basal area of *Pinus* peaks well before that of *Abies*, then declines, reflecting its intolerance of shade (Minore 1979) and relatively short life span (maximum age of 137 yr in the current study). After more than a century of development, forests are composed of large-diameter *Abies*, which also dominates the sub-canopy.

Decline of meadow vegetation

Meadow vegetation was highly sensitive to conifer establishment. Significant changes in composition were observed at the earliest stage of encroachment, reflecting declines among meadow dominants (e.g., *Festuca idahoensis*, *Lupinus latifolius*, and *Phlox diffusa*) and less frequent but characteristic species (e.g., *Danthonia intermedia*, *Cirsium callilepis*, and *Orthocarpus imbricatus*). These changes were consistent with the responses of other temperate grasslands to woody plant invasions (Hobbs & Mooney 1986;

Davies & Waite 1998; Briggs et al. 2002a). Declines in cover were particularly dramatic when *Abies* reached peak density (Class 2). However, not all meadow taxa showed an initial negative response to encroachment. Between Class 0 (open meadow) and Class 1, *Elymus glaucus* and *Bromus carinatus* doubled in abundance, replacing *Festuca* as the principal grass species and contributing to an overall increase in cover of meadow grasses. *Fragaria* spp. also showed a notable increase in cover through Class 2. Clearly, the temporal trends of meadow species as a group hinge on the classification of individual species. Although most meadow taxa showed greatest abundance in open meadow subplots, some did not and may be more accurately described as “transitional” or “ecotonal”.

Despite large and progressive declines in cover and richness, some meadow species persisted in the forest understory; 24 of 43 meadow taxa were recorded in old forest (Class 6) and contributed an average of more than four species per subplot. Although most species were greatly reduced or absent from particular forest patches, larger scale extirpations were rare (limited to *Orthocarpus imbricatus*). Moreover, several taxa, including the dominant sedge, *Carex pensylvanica*, and *Fragaria* spp., were present in ca. 50% of old forest subplots. Persistence of these open-habitat species may reflect the patchy nature of forest development at Bunchgrass, which has occurred through a process of nucleation

and expansion of tree islands, often leaving small patches of remnant meadow within larger blocks of forest (Fig. 1).

Several processes associated with tree establishment may contribute to loss of meadow vegetation. Woody plants strongly reduce light availability in grasslands (Scholes & Archer 1997; Lett & Knapp 2003, 2005; Siemann & Rogers 2003), and light is likely to be a primary resource limiting the persistence of meadow vegetation at Bunchgrass. PPFD declined steeply with initial establishment of conifers (ca. 22 to 13 $\text{mols.m}^{-2}.\text{day}^{-1}$ from Class 0 to 1), then more gradually to ca. 5 $\text{mols.m}^{-2}.\text{day}^{-1}$ in older forests. The initial reduction in light was synchronous with a large compositional change and with the transition in dominance from needle-leaved (*Festuca*) to broad-leaved grasses (*Elymus* and *Bromus*). This shift in plant form is consistent with the general observation that plants in shaded environments exhibit a lower leaf mass to area ratio (Givnish 1988). Light was also a highly significant predictor in multiple regression models for meadow species, particularly for total cover (Table 2).

However, it is unlikely that shading is the sole mechanism by which establishment of conifers affects meadow composition and diversity. Although regression models revealed strong positive relationships with light availability, similarly strong relationships were observed for other measures of forest structure (basal area of live and density of dead *Abies*) and may be indicative of changes in below-ground resources and environment. At nearby sites on Bunchgrass Ridge,

Griffiths et al. (2005) found strong gradients from open meadow to old forest in litter depth, soil moisture, nitrogen availability, microbial activity, and the presence of ectomycorrhizal mats associated with tree roots. For many of these variables, transitional areas were more similar to old forest than to meadow. Declines in meadow species may be driven by these changes in litter or soil properties (e.g., Belsky et al. 1989; Facelli & Pickett 1991) or by competition for soil resources with the newly established trees or forest understory plants (Callaway et al. 1991; Davies et al. 1998). Perhaps of most importance is the potential for positive feedbacks to develop between trees and soils, accelerating tree establishment and hastening the decline of meadow species (e.g., Li & Wilson 1998). The dramatic loss of cover of meadow species in Class 2 subplots may illustrate this phenomenon: declines were relatively small at the onset of invasion when tree densities were low (Class 1), but were very large when *Abies* recruited *enmasse* several decades later beneath the initial cohorts of *Pinus* and *Abies*.

Colonization of forest understory plants

Colonization of forest understory species occurred synchronously with loss of the meadow flora. Increases in total cover and richness began early in the encroachment process (prior to the massive establishment of *Abies* in Class 2), and were continuous over most of the chronosequence. Within 60-80 yr of tree establishment, understory communities were dominated in both richness and

cover by forest species. However, the final transition from Class 5 (the oldest patches of young forest) to Class 6 (old forest initiated almost a century earlier) was distinctive in the decline in richness of forest species and the marked increases in cover of *Achlys triphylla*, *Circaea alpina*, *Galium triflorum*, and *Smilacina stellata*. It is likely that these changes are related: reductions in local diversity may reflect the competitive effects of *Smilacina* and *Achlys*, two strongly clonal herbs (Antos & Zobel 1984; Antos 1988) that can form large contiguous patches in mature and late-seral forests, often to the exclusion of other species. Concomitant reductions in the abundance of a number of smaller-statured herbs and the gradual increase in the homogeneity of species composition among subplots suggest that competitive interactions become increasingly important in structuring these forest communities.

Abundance of forest understory species was related to both the available light and forest structure. PPFD was the strongest predictor, showing a negative correlation with the cover and richness of forest plants. The primary tree species, *Abies* and *Pinus*, had very different effects on forest understory plants. In regression models, richness and cover of forest species were positively correlated with *Abies* density or basal area, and in the ordination, *Abies* structural variables were highly correlated with NMS 1 (representing a gradient from open meadow to old forest). In contrast, richness and cover of forest species were negatively correlated to *Pinus* abundance and *Pinus* structural variables were uncorrelated to

NMS 1. Thus, *Pinus* appears to influence forest understory assembly in only an indirect fashion, by facilitating recruitment of *Abies* that ultimately leads to development of dense forest.

Although significant, light (PPFD) and forest structural variables explained only 34-42% of the variation in richness and cover of forest plants — consistently less than that explained for meadow species. Some of the residual variation may be explained by un-measured environmental variables (e.g., litter depth or soil resource availability). However, increases in local richness and cover of forest species are also subject to the vagaries of dispersal and establishment, processes that can be highly stochastic. In contrast, loss of meadow species is a more deterministic result of environmental changes that affect existing individuals.

Succession in response to conifer encroachment differs from that initiated by stand-replacing disturbance, where community development is driven by vegetative recovery of a largely persistent flora (e.g., Antos & Zobel 1984; Haeussler & Coates 1986; Halpern 1989; Antos & Halpern 1997). To a large degree, species' presence and abundance in secondary forests are shaped by initial composition, disturbance intensity, and rates of canopy closure (Halpern 1988; Halpern & Franklin 1990; Halpern & Spies 1995). With conifer encroachment, however, tree establishment precedes recruitment of forest herbs and community assembly is shaped by the regional species pool, dispersal traits, distances to seed sources, and the degree to which new environments are suitable for germination

(e.g., Butaye et al. 2002; Ozinga et al. 2005). The process thus resembles assembly of forest understory communities during succession of abandoned fields to secondary forests. Evidence from these systems suggests that dispersal limitation is the principal factor structuring community assembly (Brunet et al. 2000; Ehrlén & Eriksson 2000; Verheyen et al. 2003) rather than environmental conditions (Brunet & von Oheimb 1998; Bossuyt et al. 1999; but see Velland 2005).

Here I could not distinguish dispersal from environmental limitation: species may be infrequent early in the encroachment process for both reasons. However, temporal trends in frequency suggest that for at least some forest herbs (e.g., *Arenaria macrophylla* and *Viola glabella*), dispersal is not limiting: species were as frequent in newly established forest (Class 1) as in old forest (Class 6), the latter being the likely source of propagules. Interestingly, seeds of *Arenaria* and *Viola* are ant (or ballistically) dispersed, thus movement should be fairly limited (Andersen 1988; Matlack 1994). For other species, the slow increase in frequency with forest age could be indicative of dispersal limitation or environmental constraints. Slow rates of increase, however, were not associated with slower dispersal types. Instead, such species represented a wide range of seed dispersal mechanisms including ant (*Achlys triphylla*), adhesive (*Circaea alpina* and *Galium triflorum*), ingested (*Smilacina stellata*), and wind (*Lactuca muralis*). This differs from the strong correspondence between rates of movement

and dispersal mechanism for forest herbs in agricultural landscapes (e.g, Matlack 1994; Brunet & von Oheimb 1998). At Bunchgrass the proximity of old forest patches to areas of recent encroachment may be sufficient to ensure abundant and rapid dispersal of most forest species. The prediction that several centuries may be needed to “reconstitute” the forest flora following abandonment of agricultural fields (Matlack 1994) contrasts sharply with the relatively short time spans over which forest understories can assemble in these montane meadow mosaics.

Implications for management

Conversion from meadow to forest has been rapid at Bunchgrass, characterized by large changes in community structure and composition. It is unclear whether the shift from meadow to forest species represents a transient departure triggered by a change in climate or disturbance regime, or whether it suggests movement to an alternative stable state (e.g., Archer 1990; Petraitis & Latham 1999), reinforced by positive feedbacks between trees and soil properties. In other grassland ecosystems that have been transformed to shrub or woodland, reintroducing fire to restore grass or forb dominance is often unsuccessful (e.g., Laycock 1991; Heisler et al. 2004). Even with mechanical removal of woody species, residual effects on soils may retard recovery of grassland communities (Lett & Knap 2003, 2005). At Bunchgrass, chemical and biological properties of soils differ between open meadow and areas of recent conifer encroachment (Griffiths et al. 2005). In particular, bacterial activity and nitrogen availability

decline in these transitional areas and ectomycorrhizal fungi become abundant, potentially enhancing survival and early growth of conifer seedlings (Amaranthus & Perry 1989; Steinfeld et al. 2003). In the absence of disturbance, these positive feedbacks can favor persistence and further expansion of forest.

Even with removal of trees the potential for meadow restoration may be constrained. There is limited capacity for vegetative recovery of the flora given the dramatic reductions in species frequency, cover, and diversity. Moreover, the vast majority of meadow species do not maintain viable seeds in the soil, thus precluding the potential for restoration from a seed bank (Lang 2006). Instead, seed banks in both meadow and forest soils are dominated by early successional species; exposure or disturbance of mineral soils by restoration activities (tree removal or prescribed burning) could facilitate development of weedy species that compete with species targeted for restoration. Moreover, some clonal shrubs and vines (e.g., *Symphoricarpos mollis* and *Rubus ursinus*) can show vigorous release following overstory removal (e.g., Halpern 1989; Hauessler et al. 1990), further limiting the potential for establishment of meadow species. Although fire is likely to have played a role in the origin or maintenance of dry montane meadows in this region, its reintroduction in the form of prescribed burning may have limited value. Exposure of mineral soils may not only foster development of ruderals from the seed bank, but also provide ideal sites for conifer germination. Experimental burns conducted among tree islands in this and nearby meadow

ecosystems have been followed by dense recruitment of tree seedlings (C. Halpern, pers. comm.) suggesting strong legacy effects of canopy trees. In combination, these observations suggest large barriers to restoration where conifers have become well established. A more effective strategy for the conservation and maintenance of these systems is to remove or kill trees early before positive feedbacks lead to a potentially irreversible change in community state.

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