

# Assessing the relationships between stand development and understory vegetation using a 420-year chronosequence

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## Abstract

The large-scale conversion of old forests to tree plantations has made it increasingly important to understand how understory vegetation responds to such landscape changes. For instance, in some forest types a reduction in understory richness and cover is thought to result from the development of canopy closure in plantations, although there is a paucity of empirical data demonstrating this relationship. We used a 420-year forest chronosequence as a case study to assess the relationship between stand age, tree canopy cover and understory vascular plant richness and composition in the Siskiyou Mountains of Oregon. The chronosequence consisted of six young managed (age 7–44) and nine older unmanaged (age 90–427) stands. All stands were similar in underlying geology, slope, elevation, and aspect. We found a non-linear relationship between stand age and richness, in which richness was highest in the youngest stands, reached a low in mid-aged stands (~55 years), then increased in the oldest stands. We also found that percent tree canopy cover was correlated with total understory cover, richness, diversity, and species composition. In general, young stands were characterized by high shrub and graminoid cover and old stands were characterized by an abundant herb layer. Our work suggests that a major component of our study landscape is currently entering the forest stage (canopy closure) characterized by low levels of vascular plant species richness and cover. We use our results to discuss the potential effects of future forest management on understory plants. © 2008 Elsevier B.V. All rights reserved.

**Keywords:** Canopy closure; Chronosequence; Old-growth forest; Species richness; Timber harvest; Understory herbs

## 1. Introduction

In forested regions worldwide, logging has converted vast areas of old, structurally diverse forests into young, even-aged plantations (Saunders et al., 1991; Groom and Schumaker, 1993; Spies et al., 1994; Gascon et al., 1999). Landscapes that were once dominated by older forest stands now consist of a greater proportion of young forest stands (Oliver and Larson, 1996). These young forests range from recently harvested sites where trees have not yet formed an interconnected canopy to forests entering stages of canopy closure and maturity. Because many landscapes now consist of a high proportion of young, structurally homogeneous forests, it has become increasingly important to understand the biological consequences of this large-scale habitat conversion (Gustafson and Gardner, 1996; Fahrig, 2001).

Studies which have assessed the effects of logging on forest biota have largely focused upon threats to rare or endangered taxa, with an emphasis on animal species (e.g., Forsman et al., 1984, reviewed in Andren, 1994). Meanwhile, the effects of large-scale logging upon common plant species of the forest understory have been less frequently studied (Duffy and Meier, 1992; Johnson et al., 1993; Roberts and Gilliam, 1995; Lindenmayer and Franklin, 2002). We conducted our study in Douglas-fir (*Pseudotsuga menziesii*) dominated stands in southwestern Oregon (Franklin and Dyrness, 1973), where almost no work has been conducted on understory plants in logged areas (see Kahmen and Jules, 2005). In these forests, maintaining a diverse understory layer is of conservation concern because understory species constitute the majority of vascular plant richness, providing habitat and resources for higher trophic-level species (Halpern and Spies, 1995).

A variety of approaches have been used to assess recovery of understory species following stand-replacing disturbance. For instance, permanent-plot studies have been used to directly address questions such as how understory plant species respond to clearcuts over time (e.g., Dyrness, 1973; Halpern, 1989;

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Roberts and Zhu, 2002). In coniferous forests of the Pacific Northwest, it appears that understory species richness and diversity tends to recover to pre-disturbance levels after just 20–30 years following clearcutting (Halpern and Spies, 1995). However, results from long-term permanent-plot studies are limited by duration (20–30 years) and, importantly, only provide insight into recovery processes prior to canopy closure.

Chronosequence studies provide an alternative approach to assessing plant species response to disturbance (Crocker and Major, 1955; Hibbs, 1983; Schoonmaker and McKee, 1988; Reiners, 1992; Foster and Tilman, 2000). Chronosequence studies utilize multiple sites that share similar biological and abiotic characteristics, yet vary in time since disturbance. Comparison of sites allows one to infer changes in composition for centuries following a disturbance event. One chronosequence study in coniferous forests of the Pacific Northwest (Spies, 1991) compared unmanaged young, mature and old-growth stands and found that few vascular plant species were restricted to old-growth forests. However, species composition varied between forest stages, with particular species displaying significantly greater frequency and cover in old-growth forests (Spies, 1991; Halpern and Spies, 1995).

We examined a chronosequence of 15 stands that ranged in age from 7 to 427 years to assess the relationship of understory composition with forest characteristics. The sites were restricted to the Siskiyou Mountains of southwestern Oregon, and were similar in underlying geology, elevation, slope, and aspect. In our study we described a suite of understory plant community measures (e.g., cover, diversity, and richness of vascular plant species in the understory) across the chronosequence. Understory vegetation trends were assessed both across the chronosequence and among classes of forest development. Specifically, we addressed the following questions: (1) What is the relationship of species richness and community composition with stand age? (2) Do species richness and community composition vary significantly among young, closed canopy and older stands? (3) Are any understory species either restricted to, or strongly associated with the three forest classes?

## 2. Methods

### 2.1. Study area

We conducted our study within Douglas-fir dominated forests in the Siskiyou Mountains of southwestern Oregon. The Siskiyou are a subset of the Klamath geologic province, a series of steep, deeply dissected mountains positioned between the Cascades to the east and the Coast Ranges of California and Oregon to the west (Coleman and Kruckeberg, 1999; Whittaker, 1960). We restricted our analysis primarily to the Sucker Creek watershed, a 250 km<sup>2</sup> drainage approximately 50 km inland from the Pacific Coast. Sucker Creek watershed is characterized by having a Mediterranean climate with cool wet winters and warm dry summers. While the region receives 110–175 cm average annual precipitation (USDA, 1995), only 9% of the precipitation occurs during the months of June through September (NCDC, 2000).

Our study was further restricted to mid- to high-elevations (1300–1500 m) on west to northwest facing slopes, a subset of the Sucker Creek watershed noted for its exceptionally high diversity in vascular plant species of the forest understory (Whittaker, 1960). The forest canopy is dominated by Douglas-fir and white fir (*Abies concolor*), while common species in the understory layer include shrubs such as wood rose (*Rosa gymnocarpa*), California blackberry (*Rubus ursinus*) and snowberry (*Symphoricarpos albus*), and herbaceous species such as trail plant (*Adenocaulon bicolor*), vanilla leaf (*Achlys triphylla*), anemone (*Anemone deltoidea*), Hooker's fairybells (*Disporum hookeri*) and western trillium (*Trillium ovatum*).

Past fire regimes for the Siskiyou Mountains were likely characterized by a complex fire history in which fire return intervals tended to be site specific and highly variable (Agee, 1991; Taylor and Skinner, 1998). Within mid- to high-elevations within the Sucker Creek watershed, the historic fire regime likely included frequently occurring fires of low- to moderate-severity and occasional stand-replacing fire events (Agee, 1991). The occurrence of frequent low-intensity fire was compatible with the development of old forests, which, prior to commercial logging, characterized 53% of Sucker Creek watershed (USDA, 1995). Thus, the watershed was comprised of large and well-connected blocks of structurally diverse older forests (USDA, 1995). The remainder of the watershed consisted of early-successional forest, riparian habitat, and open meadows.

Large-scale commercial clearcut harvest did not begin in Sucker Creek watershed until the early 1960s and lasted into the early 1990s (USDA, 1995). During this 30-year period, 34% of the late successional forests were harvested by clearcutting (USDA, 1995). Most clearcut sites were subsequently broadcast burned, and/or sprayed with herbicides, and replanted with Douglas-fir seedlings. This period of clearcut logging not only reduced the proportion of the watershed comprised of old forest habitat, but also altered the spatial distribution of old forests through forest fragmentation (USDA, 1995).

### 2.2. Study design

We selected 15 stands in which to sample vegetation. Considering that one of the primary objectives of this study was to assess the relationship between stand age and understory composition following stand-replacing disturbance, the ideal chronosequence would have been composed of young to old stands which all originated following a similar type of disturbance (see Foster and Tilman, 2000). Due to the absence of clearcuts greater than 45 years of age and the absence of recent stand-replacing fire events within the watershed, we constructed our chronosequence using six young stands (age 7–44) that regenerated following clearcutting and replanting with Douglas-fir, and nine older stands (age 90–427) which regenerated naturally following fire (Table 1). In the Siskiyou Mountains, the extremely patchy and site specific fire history resulted in expansive blocks of old forest habitat consisting of extremely small homogenous structural units, hereby referred to as stands (Bingham and Sawyer, 1991). Our study utilized

Table 1  
Stand attributes for 15 sites in the Sucker Creek watershed

Stand I.D.	Age 2003	Year cut	Broadcast burn	Stage class <sup>a</sup>	Mean DBH (cm)	S.D. DBH (cm)	% Open canopy	S.D. canopy	Slope (%)	Elevation (m)	Aspect (°)
1	7	1996	–	YY	–	0.0	96.9	3.3	21	1494	280
2	14	1988	1989	Y	10.4	0.8	75.9	13.9	21	1387	306
3	21	1981	1982	Y	18.6	2.0	19.4	20.8	25	1448	266
5	24	1978	1979	Y	21.7	4.5	28.0	29.7	31	1372	284
7	39	1964	1964	Y	37.8	2.3	16.3	14.7	24	1402	274
9	44	1959	1959	C	46.3	6.4	10.0	5.7	19	1295	284
10	90	–	–	C	80.4	4.2	9.6	1.6	31	1463	270
11	98	–	–	C	77.6	9.8	10.5	1.5	19	1451	282
14	119	–	–	C	84.8	13.4	13.4	1.9	27	1387	296
15	128	–	–	C	73.9	10.4	15.2	2.8	21	1433	290
16	179	–	–	O	85.6	12.0	18.1	4.9	10	1478	284
17	252	–	–	O	129.4	10.0	17.9	6.0	19	1494	294
18	273	–	–	O	110.2	4.9	16.9	3.9	17	1387	272
19	297	–	–	O	112.4	36.5	17.5	2.7	27	1417	270
20	427	–	–	O	142.0	65.8	23.3	8.2	23	1402	328

<sup>a</sup> Stage classes: Y = young; C = closed canopy; O = old. See Section 2 for description of stage classification.

one 50 m × 50 m permanent plot in each of the 15 stands. The plots are representative of each stand and were delineated in 2001 for a previous study focused upon the abundance of western trillium (see Kahmen and Jules, 2005 for details).

In order to limit environmental variation among plots, differences in underlying geology, elevation, slope, and aspect were kept to a minimum; plots were west to northwest facing (264–328°), between 1295 and 1495 m elevation, and had an average slope between 9 and 30% (Table 1). Although serpentinite and peridotite outcrops exist within the watershed, our study was restricted to soils with parent material of diorite or metasedimentary which bear similar plant communities throughout Sucker Creek watershed. To minimize edge effects (e.g., Chen et al., 1995) plots were at least 60 m away from the nearest road or clearcut edge.

Stand ages for unmanaged forests were estimated as the average age of the 10 largest trees using increment core samples taken within the 50 m × 50 m plot (Kahmen and Jules, 2005). Ages for managed stands were calculated based on time since broadcast burn, except for one case in which no broadcast burn occurred. For this stand, age was determined by the number of years following clearcut harvest (Table 1). That some stands in our study were initiated after broadcast burns and others after natural stand-replacing fires presents limitations to our study; these two types of fires may be quite different from one another (Walstad and Sandberg, 1990).

## 2.3. Data collection

### 2.3.1. Understory characteristics

To assess the composition of herbaceous and woody understory species, 20.2-m radius circular subplots were established in each 50 m × 50 m plot. Subplots were evenly spaced 10 m apart on a grid; subplots were at the intersections of five transects along topographic contours and four perpendicular transects. The vascular plants in the subplots were identified and their cover estimated. Nomenclature followed Hickman (1993). Percent cover was estimated for

all species ≤ 3 m in height, using the following increments: 0.5, 1 and 5–100% to the nearest 5%. This procedure allowed us to calculate a mean cover for each species, and a species richness and diversity (Shannon–Weiner  $H'$ ) value for each stand.

In an effort to obtain data on all species present throughout the growing season, we collected understory data in both early summer (9th June 2003–4th July 2003) and again in mid-summer (22nd July 2003–8th August 2003). In our analyses, we used the mid-summer data set except in the few cases where a species had senesced. In these cases, we used cover estimates from the early summer census.

### 2.3.2. Stand characteristics and classification

Tree canopy cover was estimated using a spherical densiometer. Densiometer readings, taken at breast height in each subplot, were used to estimate mean canopy openness (%) and variation in canopy cover for each plot. In addition, each stand was categorized *a priori* into one of three stage classes: young, closed canopy and old. Stand classification was modeled after stages described by Franklin et al. (2002), however our scheme used fewer categories due to the limited number of stands used in the chronosequence. Stands (and thus plots) categorized as young included recently clearcut sites with open canopies to sites in which the canopy was beginning to close but still had large light gaps. Closed-canopy stands included plots that had structurally homogenous canopies, to more open stands with the beginning of multi-tiered tree canopies. Stands of the older stage class were characterized by having large old trees, and fairly open tree canopies with a high degree of vertical diversification. Tree ages were not used to classify plots into stage classes.

## 2.4. Data analysis

Because we examined the potential influence of several stand attributes on understory vegetation, we first assessed the statistical independence of the attributes; Spearman rank correlations were used to test for significant correlations

between stand age, slope, elevation, aspect ( $^{\circ}$ ) and canopy cover. Next, Spearman rank statistics were used to examine correlations between stand attributes and species richness, diversity, total % graminoid, herb, shrub, and total % understory cover (excluding conifers). For these analyses, subshrubs (herbaceous plants with a slightly woody base) were included in the herb category. For all our multiple correlation tests, we present uncorrected  $p$ -values.

We used two-parted, piecewise regression (Toms and Lesperance, 2003) to describe the relationship between species richness and stand age. Piecewise regressions are useful in estimating ecological breakpoints such as the distance threshold for which an edge effect ceases to influence species composition. In this study, piecewise regression was used to estimate the breakpoint at which richness switched from having a negative to a positive relationship with stand age. The software NCSS 2001 was used to conduct the regression (Kaysville, UT, USA). Spearman rank tests were then used to describe correlations between stand age and richness for the two subsets of data divided by this breakpoint.

To assess whether species composition differs among young, closed canopy and old stands, we used nonmetric multidimensional scaling (NMS) with the Sorensen distance measure (PC-Ord version 4.01; McCune and Mefford, 1999). We used NMS because of its effectiveness in assessing non-normal data sets (McCune and Grace, 2002). Conifer data was excluded from the ordination that allowed for better detection of patterns in shrub and herbaceous composition. Additionally, only species which occurred in at least 4 of the 15 stands were used, leading to a data set of 74 species. In using the NMS ordination, the slow and thorough “autopilot function” was used to select the optimum dimensionality for the ordination. This selection process included 40 runs with original data and 50 Monte Carlo randomized runs (McCune and Grace, 2002). The coordinates for the final configuration were rotated by stand age, which improved interpretability, without changing the cumulative variance represented by the axes. We then assessed the relationships between stand attributes and species composition (i.e., axis scores) using Pearson correlation tests.

Differences in understory species composition between the three classes were tested using Multiple Response Permutation Procedure (MRPP) with the Sorensen distance measure (McCune and Mefford, 1999). MRPP is similar to a Multivariate Analysis of Variance (MANOVA), but is better suited to assess community data because distributional assumptions of normality and equal variance are not necessary. Finally, a Kruskal–Wallis one-way ANOVA and a multiple comparison Z-value test were used to test for differences in various stand attributes between classes.

Indicator species analysis (ISA; Dufrêne and Legendre, 1997; McCune and Mefford, 1999) was used to identify species with an affinity to one of the three classes: young, closed canopy and old. Indicator values (IVs) combine relative cover (proportion of total cover) with frequency of occurrence among stands to express the degree of affinity exhibited by individual species to any one of the specified classes. A Monte Carlo

simulation, using 1000 randomizations was used to test for significant differences in IVs among the three stage classes.

### 3. Results

In the 15 stands, we found 129 vascular plant species: 8 broadleaf trees, 5 conifers, 25 shrubs, 81 herbs, and 10 graminoids. Fifty-six percent of these species were found in only 1–5 stands, 19% in 6–10 stands and 23% occurred in 11–15 of the stands. The vast majority of species (~98%) were native; only three non-native species were found: *Cirsium vulgare*, *Hypericum perforatum* and *Tragopogon pratensis*. These three species were found only in managed stands, where they occurred at low cover. Douglas-fir and white fir were present in all stands, and the other conifer species occurred only in a few (1–3) of the stands. A complete list of all observed species is available from E.S.J.

No significant correlations were found between any of the stand attributes (stand age, slope, elevation, aspect and canopy openness). Although not significant, there was an interesting relationship between stand age and canopy openness; canopy openness was the highest in the youngest stands, declined in mid-aged stands and then increased in the oldest stands (Fig. 1). Tree canopy cover was significantly correlated with richness

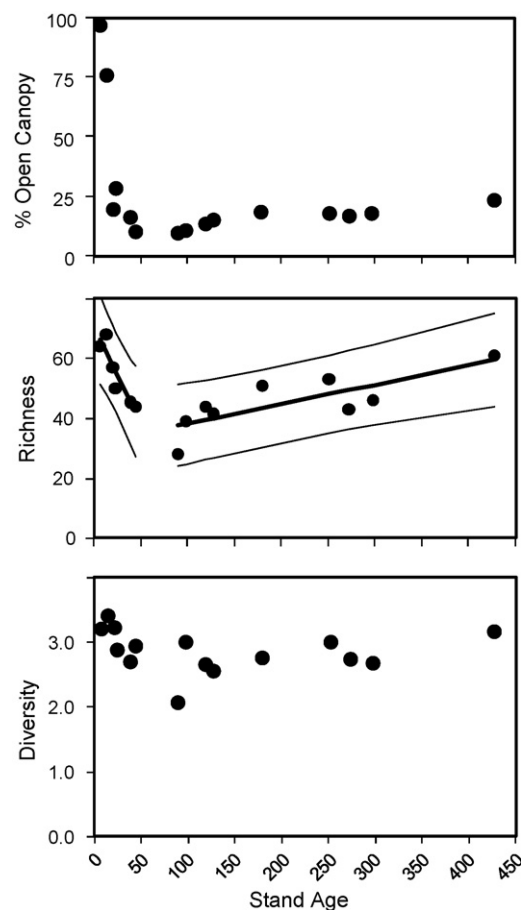


Fig. 1. Species diversity, richness, and % open canopy across stand ages. For richness, piecewise-polynomial regression was used to generate the two-parted mean response and 95% confidence intervals shown.



( $r_s = 0.904$ ,  $p < 0.0001$ ), diversity ( $r_s = 0.661$ ,  $p = 0.007$ ) and total percent understory cover ( $r_s = 0.811$ ,  $p = 0.0002$ ). These measures all peaked in the youngest, most open stands, then reached their lowest measures in stands with the greatest degree of canopy closure and finally rose in older forests (Figs. 1 and 2).

Shrub and graminoid cover were negatively correlated with stand age ( $r_s = -0.650$ ,  $p = 0.009$ ,  $r_s = -0.651$ ,  $p = 0.009$ ). Graminoids and shrubs exhibited their highest percent cover in the youngest stands and declined with age, reaching their lowest levels in mid-aged to old stands (Fig. 2). In contrast, understory herb cover was positively correlated with stand age ( $r_s = 0.600$ ,  $p = 0.018$ ), reaching its highest levels in the oldest stands (Fig. 2).

The piecewise-polynomial regression used to describe the relationship between stand age and richness generated two

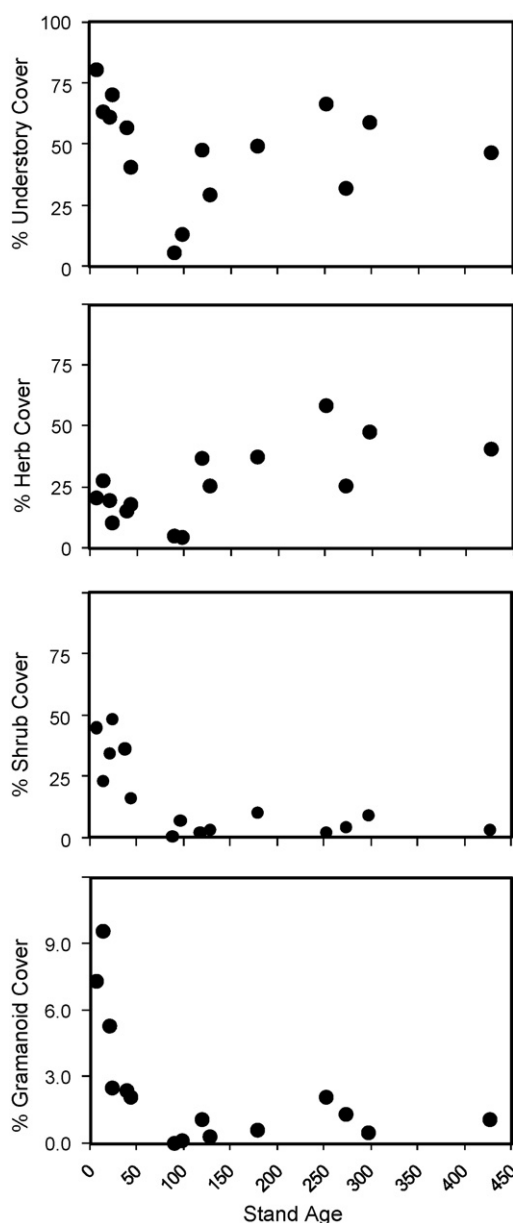


Fig. 2. Relationship between stand age and % graminoid, % shrub, % herb, and % total understory cover.

Table 2

Correlations between stand attributes and the NMS ordination axes (Spearman's  $r$ )

	Axis 1	Axis 2	Axis 3
Stand age	<b>0.763</b>	−0.002	−0.418
Canopy openness (%)	−0.221	<b>0.554</b>	0.291
Slope	−0.414	−0.179	−0.046
Elevation	0.250	−0.022	0.044
Aspect	0.333	0.341	−0.318
S.D. of canopy openness	<b>−0.644</b>	0.462	0.347

Bolded values indicate significant correlations ( $p \leq 0.05$ ).

separate linear equations: if stand age  $\leq 55$  years, then species richness =  $70.69 + -0.65 \times (\text{stand age})$ , and if stand age  $\geq 55$ , then species richness =  $31.65 + 0.065 \times (\text{stand age})$  (Fig. 1). In stands  $< 55$  years in age, species richness was negatively correlated with stand age ( $r_s = -0.942$ ,  $p = 0.005$ ), while in stands  $> 55$  years in age, species richness was positively correlated with stand age ( $r_s = 0.783$ ,  $p = 0.013$ ).

Understory community composition changed along the age canopy openness gradients. The best NMS solution was a 3-dimensional model that captured 91.7% of the variation in community structure with 77.7% being captured by the first two axes. It took 79 iterations to reach an NMS solution with a stress level of 5.7 ( $p = 0.0196$ ). Axis 1 was positively correlated with stand age ( $r = 0.763$ ), and negatively correlated with the standard deviation of canopy cover ( $r = -0.644$ ; Table 2). Axis 2 was positively correlated with % open canopy ( $r = 0.554$ ; Table 2). The ordination illustrated that stands from both the young and old stages formed distinct clusters (Fig. 3). Closed-canopy stands exhibited a wide degree of variation and overlapped with stands from the old stage (Fig. 3). MRPP confirmed that all three stages differed in species composition (Table 3).

The Kruskal–Wallis test revealed that canopy openness and species richness were significantly higher in both the young and old stage classes than in the closed-canopy class (Table 4). Shrub and graminoid cover were the highest in the young stage class, while herb cover peaked in the old stage class (Table 4).

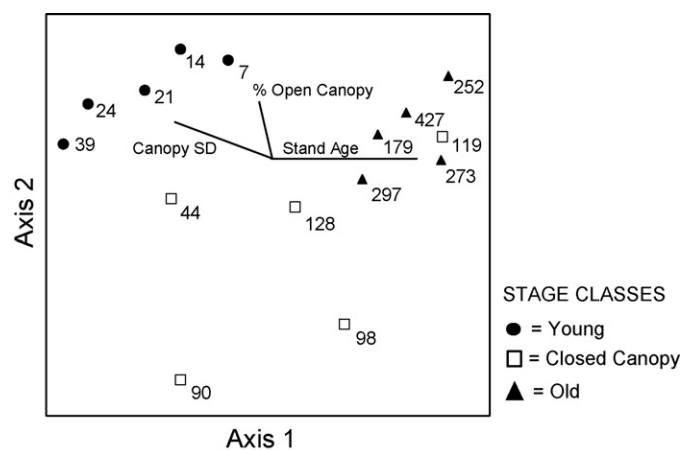


Fig. 3. Nonmetric Multidimensional Scaling ordination of understory species across a 420-year chronosequence. Vectors represent correlations with ordination scores where  $r^2$  value  $\geq 0.300$  (Table 2). Canopy S.D. represents the standard deviation around mean canopy cover per stand.

Table 3

Differences in species composition among three forest stage classes and pairwise comparisons between each stage class using MRPP

Stage classes	A	T	p
All stages	0.1712	−5.9027	0.0001
Young-closed canopy	0.1086	−4.3936	0.0026
Young-old	0.2378	−5.4122	0.0016
Closed-canopy-old	0.0752	−2.7280	0.0184

Note: The agreement statistic (A) measures chance corrected within-group agreement. If all stands within a stage class were identical, A = 1. If stand heterogeneity were equal to expectation by chance, A = 0; values <0.1 are common in community ecology (McCune and Grace, 2002). T represents the difference between stage classes; the more negative T, the greater the difference between classes.

Indicator species analysis revealed that 29 species exhibited a notable affinity to one of the classes: 16 species for the young stage, 1 for canopy closure, and 12 species for the old stage class (Table 5).

#### 4. Discussion

Theoretical models of stand dynamics (Harris et al., 1982; Franklin, 1982; Oliver and Larson, 1996; Franklin et al., 2002) predict that in temperate coniferous forests: (1) understory species richness will tend to peak in young, recently initiated stands with open canopies, (2) as stands become more closed, richness will decline to its lowest levels, and (3) as canopies re-open in older more structurally diverse stands, richness will again increase. Although understory plant communities represent an important component of biodiversity in Pacific Northwest forests, surprisingly few studies test these predictions through all stages of stand development (but see Halpern and Spies, 1995). Likewise, only a handful of studies specifically document reductions in understory richness during canopy closure (e.g., Schoonmaker and McKee, 1988; Lezberg, 1998; Moola and Vasseur, 2004; Tyler and Peterson, 2006).

In this study, we demonstrated that species richness was significantly associated with canopy openness and stand age across our chronosequence. Richness showed a steady decline as young stands entered canopy closure conditions, where richness reached its lowest level. Richness then increased in older stands as light increased. The piecewise-polynomial

Table 4

Summary of plot characteristics by forest stage class

	Young	Closed canopy	Old	p
Number of plots	5	5	5	
Canopy openness (%)	47.3 (36.7) <sup>a</sup>	11.7 (2.4)	18.7 (2.6) <sup>a</sup>	0.0060
Shrubs	37.2 (9.8)	5.7 (6.3) <sup>a</sup>	5.8 (3.5) <sup>a</sup>	0.0081
Herbs	18.7 (6.4) <sup>a</sup>	18.0 (13.2) <sup>a</sup>	42.0 (12.1)	0.0185
Graminoids	5.7 (2.8)	1.1 (1.7) <sup>a</sup>	1.1 (0.7) <sup>a</sup>	0.0113
Total understory	66.4 (9.4) <sup>a</sup>	26.8 (18.2) <sup>b</sup>	50.5 (13.2) <sup>a,b</sup>	0.0097
Richness	56.8 (9.5) <sup>a</sup>	39.2 (6.6)	50.8 (6.9) <sup>a</sup>	0.0140

Average values (±1 standard deviation) are shown. p-Values are for comparisons across the three stage classes (Kruskal–Wallis). Shared letters (a, b) indicate a lack of statistical differences between the two classes ( $p > 0.05$ ; Kruskal–Wallis multiple comparison Z-value test).

Table 5

Indicator values for species in three stage classes

Stage class	Species	Y <sup>a</sup>	C	O	p
Young	<i>Ceanothus velutinus</i>	100	0	0	0.001
	<i>Ribes sanguineum</i>	99	0	0	0.001
	<i>Elymus glaucus</i>	98	0	0	0.001
	<i>Sambucus mexicana</i>	95	0	1	0.001
	<i>Rubus parviflorus</i>	87	6	2	0.007
	<i>Symphoricarpos albus</i>	86	5	7	0.013
	<i>Arctostaphylos patula</i>	80	0	0	0.007
	<i>Epilobium angustifolium</i>	80	0	0	0.010
	<i>Rubus leucodermis</i>	80	0	0	0.007
	<i>Ribes lobbii</i>	79	0	1	0.009
	<i>Penstemon anguineus</i>	78	1	0	0.010
	<i>Iris chrysophylla</i>	76	0	1	0.031
	<i>Pteridium aquilinum</i>	73	2	16	0.015
	<i>Rubus ursinus</i>	66	25	9	0.056
	<i>Achillea millefolium</i>	65	3	1	0.027
	<i>Rosa gymnocarpa</i>	55	13	32	0.059
Closed canopy	<i>Chimaphila menziesii</i>	5	63	24	0.028
Old	<i>Trillium ovatum</i>	23	16	57	0.059
	<i>Osmorhiza chilensis</i>	21	16	59	0.003
	<i>Galium</i> sp.	20	25	50	0.065
	<i>Achlys triphylla</i>	9	17	75	0.002
	<i>Clintonia uniflora</i>	4	4	83	0.003
	<i>Ribes lacustre</i>	4	0	73	0.020
	<i>Adenocaulon bicolor</i>	2	15	79	0.015
	<i>Corallorhiza maculata</i>	2	16	65	0.030
	<i>Smilacina stellata</i>	2	10	85	0.025
	<i>Anemone oregana</i>	1	1	55	0.057
	<i>Goodyera oblongifolia</i>	0	27	67	0.025
	<i>Senecio bolanderii</i>	0	3	51	0.088

Y = young; C = closed canopy; O = old.

<sup>a</sup> Only species with ( $p < 0.10$ ) are reported.

model used to describe the non-linear relationship between richness and stand age estimated that stands ~55 years in age will be the most species poor. Additionally, when stands were categorized into stage classes, richness was found to be significantly lower in the closed-canopy stage class than in either the young or the old classes.

The three stage classes were significantly different in understory species composition. Young stands were composed of relatively high shrub, graminoid and herb cover. In contrast, cover of shrubs, graminoids and herbs was low in the closed-canopy stands. In the oldest stands shrub and graminoid cover remained low, yet herb cover was significantly higher than in the other two stage classes. In previous work, the presence of an abundant herbaceous layer was associated with a decrease in stand density, an increase in the distribution of large trees, and the passage of long periods of time (centuries), during which populations of dispersal-limited and slow recolonizing herbaceous species are thought to gradually expand (Halpern and Spies, 1995; McKenzie et al., 2000).

In combination, these results suggest that young stands entering canopy closure will lose richness over the coming decades, reaching a low point during the closed-canopy stage. Because 34% of late successional stands in our study area were logged in a 30-year period beginning the 1960s (USDA, 1995), we predict a significant decrease in understory diversity over

the next four decades. The proportion of closed canopy, species poor forests will exceed the proportion represented in Sucker Creek watershed prior to the onset of clearcut harvest.

#### 4.1. Young stands

Numerous studies that assess short-term understory response to clearcutting find that species richness tends to be as high as or higher than pre-disturbance levels within just a few years after canopy removal (Dyrness, 1973; Swindel and Grosenbaugh, 1988; Halpern, 1989; Reiners, 1992). Furthermore, in the well-studied H.J. Andrews Experimental Forest in the western Cascades of Oregon, not only was richness high soon after clearcutting, but ~75–90% of the original forest species were present soon after clearcutting, and diversity ( $1/D$ ) returned to pre-harvest levels after approximately 20–30 years (Halpern and Spies, 1995). The remarkable resilience in the understory layer of these Douglas-fir forests is attributed to the ability of many species to sprout from underground structures such as roots and rhizomes, and/or rapidly recolonize a site soon after disturbance (Halpern, 1988; Schoonmaker and McKee, 1988; Halpern and Spies, 1995; Lezberg et al., 1999).

Our results support conclusions of previous work, in that young stands age 7–39 had high richness and diversity. Species composition included sclerophyllous shade intolerant invaders such as *Ceanothus velutinus* and *Arctostaphylos patula*, and also included a large component of species common to the oldest stands such as *A. triphylla*, *Osmorhiza chilensis*, and *T. ovatum*. Additionally, that only one plant, *Goodyera oblongifolia*, occurred in the majority of the oldest stands, though was completely absent from the young stage class, provides further evidence that many herbs associated with the oldest stands likely survived clearcutting, or quickly recolonized clearcut sites.

#### 4.2. Closed-canopy stands

In our study, species richness was the lowest in the closed-canopy stage class. Given that this class included stands just entering canopy closure and stands exiting this stage, our results may actually underestimate projected reductions in richness for young managed stands. Similarly, it is also possible that the silvicultural practice of single species (i.e., Douglas-fir), even-aged management may lead to greater structural homogeneity and light limitation during canopy closure than found in natural stands (Hansen et al., 1991; Halpern and Spies, 1995). In either case, managed plantations may experience reductions in richness and understory cover that are as low or lower than those measured in the most species poor stands in our chronosequence (see unmanaged stands age 90 and 98).

The reduced richness and cover of understory species in closed-canopy stands is generally attributed to low light availability, which can severely limit the growth and survival of many species (Alaback, 1982; Klinka et al., 1996; Lezberg, 1998). Although species associated with older forests are typically shade tolerant and capable of maximizing brief and unpredictable exposure to direct light (Chazdon and Pearcy,

1991), some may not be able to endure long periods of extreme light limitation associated with closed-canopy stands (Alaback, 1982; Klinka et al., 1996; Lezberg et al., 1999). For forests of the Pacific Northwest, little data exist concerning which species can survive canopy closure versus species which must rely upon dispersal from another site once conditions become more favorable (but see Tappeiner and Alaback, 1989).

In a study from the western Olympic Peninsula, data suggest that many species common to older forests can survive in closed-canopy stands, yet are greatly reduced in cover (Lezberg et al., 1999). In a related study (Halpern et al., 1999), many of these same species common to older forests were scarcely represented in the seed bank of closed-canopy stands. Poor seed bank development suggests that population expansion of species in older forests may be heavily dependant upon either that species' ability to persist through canopy closure, or the species' ability to disperse into an area once light conditions improve. For most understory species throughout Pacific Northwest forests it is unknown which mechanism enables plant species to populate older forests as they exit the canopy closure phase.

#### 4.3. Old stands

Old stands in our study were characterized by having the greatest cover of understory herbaceous species. While shrub and graminoid species were not as abundant in old forests, a diverse understory of herbaceous plant species peaked in these older forests. Interestingly, we did not find that these herbaceous species were restricted to the oldest stands. This result compliments studies from the Cascades and Coast ranges of the Pacific Northwest that indicate there is a suite of species that reaches their greatest frequency and abundance in old stands, yet are also found in younger forests (Spies, 1991; Halpern and Spies, 1995).

#### 4.4. Potential long-term implications

In Sucker Creek watershed, and many other watersheds throughout the Pacific Northwest, it remains to be seen whether plantations will be subject to even age (rotational clearcut harvest) or uneven age (selective) management. Nonetheless, because some plantations within the study area are designated as “matrix” under the Northwest Forest Plan, it is possible they will be subject to rotational clearcut harvest (USDA, 1995). The potential impacts of repeated clearcut harvest upon understory communities are not well understood. For instance, it is unknown whether young regenerating stands subject to repeated clearcut harvest will produce significantly different floras than those harvested from original old forest stands. Previous work suggests that recovery and expansion of the herbaceous understory layer may be correlated with pre-disturbance herb abundance (Halpern and Franklin, 1990). Therefore, young forests resulting from harvesting relatively young (60–120 years) secondary stands prior to the development of an abundant herb layer might be significantly different in composition from those that have resulted from the harvest of

older, more structurally diverse stands. Given this scenario, species which reach peak cover in stands of the oldest stage class may be particularly susceptible to loss if stands are clearcut prior to the development of an abundant herbaceous understory layer.

Further, because many herbaceous species are highly limited in their ability to disperse across large distances (Brunet and Von Oheimb, 1998; Bossuyt et al., 1999; Verheyen and Herour, 2001), the spatial distribution of potential seed sources across the landscape may become an important factor governing species recovery. For example, studies that have assessed dispersal rates into stands of varying distances from old forest patches demonstrate that stands closer to potential propagule sources have greater richness in “old forest” species than more isolated stands (Matlack, 1994; Singleton et al., 2001). Therefore, the high degree of fragmentation in our study area might result in greater distances between young stands and old forest patches, which may slow the recovery of understory diversity (Jules, 1998; Vellend, 2003; Butaye et al., 2002; Tyler and Peterson, 2004).

Finally, our study emphasized the extent to which age, and the changes in canopy openness that accompany it, may be related to species composition. However, age is likely correlated with a multitude of factors not assessed in this study such as large diameter woody debris, litter and duff accumulation, snag density, microbiotic soil communities, and daily temperature fluctuation (Spies et al., 1988; Hansen et al., 1991; Roberts and Gilliam, 1995; Meier et al., 1995). Although there is a growing body of literature suggesting that selective harvest may successfully increase species richness (Bailey et al., 1998), influence canopy structure, and encourage the development of multi-layered stands (Bailey and Tappeiner, 1998; Busing and Garman, 2002), silvicultural prescriptions may not serve as an adequate surrogate for the passage of time, including its role in forest development and the structuring of understory communities (McKenzie et al., 2000).

#### 4.5. Conclusions

Due to the paucity of permanent-plot studies that directly assess long-term response of understory communities to stand-replacing disturbance, the spatial chronosequence approach can serve a valuable role. By assessing a 420-year chronosequence, we were able to demonstrate that a large proportion of the landscape (young tree plantations) was entering the most species poor stage in stand development (canopy closure stage). Although this stage may not threaten any species with extinction, even at the stand-level, the dominance of the landscape by closed-canopy conditions is likely to change the abundance of many common understory herbs in our study area. In addition, the potential for managed stands to become subject to repeated disturbance, either by repeated clearcutting or increased fire intensity associated with plantations (Weatherspoon and Skinner, 1995; Key, 2000; Odion et al., 2004), may result in the attrition of understory herb richness. Without intervention, many species may become increasingly restricted to the remnant older

stands in which they now reach peak abundance. Whether selective timber harvest alone may serve as an adequate surrogate for the passage of time in developing old forest attributes in plantations may eventually be answered by the continued surge in research on the effects of thinning (e.g., Thomas et al., 1999; He and Barclay, 2000; Thysell and Carey, 2001). Future studies in our study area should specifically address whether thinning can be compatible with the retention of biodiversity in the forest understory while at the same time meeting other management objectives.

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