

The effects of forest management on plant species diversity in a Sierran conifer forest

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Abstract

We used a large data set collected as part of a wildlife habitat study at the Blodgett Forest Research Station in the Sierra Nevada of California to assess the influence of management practices on vascular plant diversity in the mixed conifer forest. In addition to the existing data, we conducted botanical inventories in 32 plots (0.28 ha in size) from five different silvicultural regimes in 1997. Based on these inventories, understory species richness normalized to a total area sampled of 1.13 ha was significantly greater in plots under plantation (80 species) and shelterwood (77 species) management compared to plots in reserve sites (i.e., approximately 80 year with no active management, 48 species). This pattern in species richness was consistent in the larger data set. Based on 372 plots sampled between 1977 and 1996, plantations and shelterwoods routinely had the highest species richness and the reserve units routinely were the least rich. Stands under single-tree selection had species richness values closer to those of the reserve stands. The relative diversity observed in group selection plots varied from year to year. Based on the 1997 data, canopy closure and seedbed were significantly correlated to understory plant diversity. Plots that were more open and had more bare ground tended to have higher species richness. This result supports the suggestion that in addition to the total amount of biomass removed, post-harvest practices also affect plant diversity. There were considerable differences in the composition of the understory communities among silvicultural treatments. Plots under a group selection, single tree selection or reserve management regime had a greater proportion of late-seral vs. early-seral species and a lower proportion of introduced exotic species compared to plantations and shelterwoods. In this forest, more intensive management maximized species richness, but the lower intensity practices better conserved understory plants typical of late-seral stands. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Forest ecosystems provide habitat for a disproportionate share of the world's biological diversity. The recognition of the ecological and ethical importance of this biodiversity has motivated professional forestry to

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work toward maintaining this inherent diversity while also meeting the demand for wood products (Kapos and Iremonger, 1998; Perry, 1998; Seymour and Hunter, 1999). However, there is a critical lack of information about the potential effects of different types of management regimes on diversity patterns for many forest communities (Roberts and Gilliam, 1995b).

The mixed conifer forest of the Sierra Nevada, California is an example of a commercially important forest type where biodiversity will need to be maintained within the framework of active timber management. The mixed conifer forest extends throughout the Sierra Nevada, covering an area of 1.8 million hectares (Allen-Diaz, 1988). Only 8% of the mixed conifer forest is formally designated for conservation while 67% of this land is available for timber harvest (Davis and Stoms, 1996). It is a species-rich community. In particular, understory vegetation accounts for the vast majority of plant species in these forests (Fites, 1993; Shevock, 1996). Current harvesting options range from small clearcuts (most intensive) to single-tree selection (least intensive) followed by an array of post-harvest site preparation and tree planting strategies (Helms, 1994). The relative merits of these silvicultural techniques in regard to yield and tree regeneration have been well documented (reviewed in Helms and Tappeiner, 1996). Their impact on plant diversity is unknown.

We took advantage of existing data on vascular plant composition, collected to assess wildlife habitat in a Sierran mixed conifer forest, to examine the relationship between forest management and understory plant diversity. Between 1977 and 1997, there were 10 plant inventories in management units representative of the variety of silvicultural practices employed in the Sierra Nevada. This multi-year record of plant composition in stands with documented management histories greatly increases the temporal scope of inference. In 1997, we independently sampled understory vegetation in the different management units to meet several specific objectives: (1) to quantify current patterns in understory species diversity with taxonomic and statistical rigor, (2) to measure the correlation between plant species diversity, harvest intensity, and seedbed disturbance, (3) to evaluate the quality of the existing data in order to guide a retrospective analysis of the longer-term effects of forest management on plant diversity, and (4) to document any qualitative differences in the types of plants found in the various treatments.

2. Methods

2.1. Study site

The study was conducted at the Blodgett Forest Research Station in the northern Sierra Nevada, Georgetown, CA (38°52'N; 120°40'W). Olson and Helms (1996) provide a detailed description of Blodgett Forest, its management, and trends in forest growth and yield. Briefly, the central property of the research station consists of 1214 ha of mixed conifer forest divided in 109 management compartments (size range: 8–80 ha). The mixed conifer forest type is composed of variable proportions of five coniferous and one hardwood tree species (Tappeiner, 1980). Constituent canopy tree species include *Abies concolor* (white fir), *Pseudotsuga menziesii* var. *menziesii* (Douglas-fir), *Pinus lambertiana* (sugar pine), *Pinus ponderosa* (Pacific ponderosa pine), *Calocedrus decurrens* (incense cedar), and *Quercus kelloggii* (California black oak). All six tree species are common at the study site. The terrain in Blodgett Forest is flat or gently sloping and elevation varies from 1188 to 1463 m. The climate is characterized by cool, wet winters and warm, and dry summers. Mean annual precipitation is 158 cm; 78% falls between November and March. Typically, 35% of the precipitation falls as snow. Four major soil types are found on Blodgett. The soils derived from granodiorite parent materials include the Holland, Musick, and Bighill series. The fourth type, the Cohasset series, is developing in place on andesite parent material. These well-drained, loamy soils support a productive site in terms of wood volume growth (Olson and Helms, 1996; Natural Resource Conservation Service¹). Between 1900 and 1913, most of the forest was logged and then burned to reduce logging slash. The University of California, Berkeley has operated Blodgett Forest as a research and teaching facility since 1933.

The 109 compartments at Blodgett Forest are divided among even-aged management (40% by area), uneven-aged management (40%), and unmanipulated

¹ Natural Resource Conservation Service, National Soil Survey Center, United States Department of the Interior, <http://www.statlab.iastate.edu/soils/osd>.

reserves (20%). Even-aged treatments include plantations and shelterwoods. Plantations begin as small clearcuts (max. 8 ha), where all canopy trees are removed. After harvest the site is prepared and planted with a mix of the dominant canopy species. In shelterwood cuts, a residual stand of approximately 40 seed trees per hectare is left after the initial harvest. The seed trees are removed after natural tree regeneration is established (3–8 year after harvest). The two uneven-aged regimes include group and single-tree selection. Under group selection, approximately 11% of the compartment is harvested in small groups (max. 0.6 ha) every 10 years. Single-tree selection is also implemented on a 10-year cycle with trees removed in very small groups (<0.1 ha). Aside from fire suppression and prevention activities, no interventions have occurred in the reserve compartments since they were cut in the early 1900s. These five treatments represent a range of disturbance severity. In order of decreasing severity they are: plantation, shelterwood, group selection, single-tree selection, and reserve.

2.2. Field sampling

2.2.1. Plant inventory by the wildlife crew

Each compartment in the research station is divided into 121×121 m grids. The intersections of the grid lines mark the centers of permanent forest inventory plots. The plots are measured periodically to monitor forest composition and structure (max interval is 10 year). As part of a continuing effort to develop a comprehensive wildlife habitat classification system for Blodgett Forest, the species richness of the understory flora was assessed. The wildlife habitat plots are centered on the forest inventory plots and include all the area within a 30 m radius. Two wildlife technicians were trained to identify the common and conspicuous plants. This 2-person crew spent half an hour searching the plot and noting the presence of all the vascular plants they could find. Thus, a total of 1 person-hour was spent searching a 0.28 ha plot. Plant inventories associated with wildlife habitat assessments were conducted annually between 1977 and 1982, in 1984, and then annually again from 1993 to the present. Beginning in 1994, more thorough training in plant identification was provided to the wildlife crew.

2.2.2. Comprehensive plant inventory

In 1997, we inventoried 32 plots in 16 different compartments that included all five of the management regimes described above. The compartments were selected to represent both the differences in silvicultural treatments and environmental gradients in the research forest. Plots within compartments were chosen randomly. Ten of the 32 plots were also sampled by the wildlife crew who used their standard methods. For our inventories, we doubled the search time (2 person-hours per plot) and had a botanist familiar with the Sierra Nevada flora conduct the census. In addition, we surveyed a sequence of randomly selected plots under the same forest management to quantify the relationship between species richness and area sampled. Nomenclature follows Hickman (1993).

2.2.3. Sampling for plant abundance

We measured plant abundance in fourteen 10 m radius plots. These plots were nested inside a random subset of the larger plant inventory plots. The exception to the random assignment was that plots in group selection regimes were excluded from this more detailed assessment. A sufficient description of the vegetational and structural heterogeneity generated by this treatment requires a greater sampling effort that we could afford as part of this project. For each plot, we placed radial transects in the four cardinal directions. We used line-point sampling to quantify differences in seedbed type, herb-layer species abundance, and shrub-layer cover. Seedbed was divided into the following classes: bare mineral soil, leaf litter, woody litter, wood (e.g., intact logs), rock, and moss. The herb layer was defined as all vascular plants ≤ 1 m tall; shrubs were defined as vascular plants > 1 m and ≤ 2 m tall. Every 10 cm along the transects (400 points total), we noted the seedbed class and the species of the plants (if any) intersecting a vertically projected line. We recorded intersections separately for the herb, shrub, and tree layers. A list of all the plant species present inside the 10 m radius plot was kept.

2.3. Data analysis

In this study, the principal measure of species diversity is species richness, defined here as the number of species present in a particular management

regime. Species richness is a conceptually simple, operationally feasible, and widely reported measure of diversity (Magurran, 1988; Hellmann and Fowler, 1999). Furthermore, since richness is estimated from presence–absence lists and does not require information about abundance, it is the only diversity measure that can be calculated for the entire data set available at Blodgett Forest. The major drawback is the well known dependence of plant species richness on the size of the area sampled (Palmer, 1990), hence the need to document the site-specific relationship between local richness and sample area. We took an approach described by Colwell and Coddington (1994) to extrapolate the species accumulation curves from sequential plot sampling in four of the five management regimes. For each extrapolated curve, we calculated the average species richness as a function of the number of plots sampled. Because the order in which plots are added affects the shape of the curve, we calculated average richness for all possible permutations of the order-of-entry (e.g., 120 permutations when the number of plots sampled equals five). To estimate the asymptote (i.e., total species richness), the function was fit to a Michaelis–Menton saturating curve using a maximum likelihood procedure.

To evaluate the quality of the plant inventories conducted by the wildlife crew, species lists for the 10 plots that both crews sampled were compared. Capture rates were expressed as the ratio of the wildlife crew's richness estimate to our estimate. We also checked for under-counting (lumping) or over-counting (splitting) of species designations and for any consistent misidentification of particular taxa.

Based on the results of the species accumulation curves, we determined the minimum number of plots that provides a robust estimate of species richness for all silvicultural treatments (see Section 3). For treatments with more than the minimum number of plots, a mean richness value was calculated from 999 random simulations. From the simulations, a 95% confidence interval was also derived (Manly, 1997). By expressing richness relative to a standard sample area, estimated values can be directly compared.

For the plant abundance plots, two additional measures of diversity were calculated: the Shannon and Simpson indices (Magurran, 1988). These common diversity measures were included here to ease comparisons with other sites. We also used the result from

the plant abundance plots to document any correlation (Pearson product moment correlation coefficient) between species richness, canopy closure, and mineral soil seedbed.

To explore differences in the kinds of plant species found in each harvest treatment, plant species were divided into a priori categories according to successional status (late-seral vs. early-seral species) and place of origin (native vs. exotic). Assignments into successional class were based on an ecological guide to the mixed conifer plant association in the northern Sierra Nevada (Fites, 1993). Early-seral species were defined as plants not present in any of the late-seral stands sampled to develop the guide. Thus any generalists that occurred in both late- and early-seral stands were considered late-seral species in this analysis. Early-seral species were further classified as exotic or native in origin using the information in the Jepson Manual (Hickman, 1993).

3. Results

As expected, forest structure varied depending on the silvicultural treatment (Table 1). Trees in the reserve stands were massive, tall, and relatively numerous. Canopy cover was dense (87% closure) with little disturbance to forest floor (0.5% exposed mineral soil). At the other extreme, the trees were smaller and shorter in the plantations along with a more open canopy (73% closure) and more exposed mineral soil (13% exposed). Shrub and herb cover were greater in the even-aged treatments (Table 2). For the 14 intensively sampled plots, species diversity was greater in the even-aged plots by every measure. Plot-level species richness was negatively correlated to percent canopy closure, $r = -0.73$ ($p < 0.003$) and positively correlated to percent exposed mineral soil, $r = 0.52$ ($p = 0.05$). All of the abundant plants in the herb layer (Table 2) were widely distributed throughout the research station. For example, *Iris hartwegii* (Hartweg's iris) and *Trientalis latifolia* (starflower) were abundant in the plantations and the reserves, and *Ribes roezlii* (Sierra gooseberry) was common in three of the four regimes (Table 2).

The Michaelis–Menton function provided nearly perfect fits to the species accumulation curves ($r^2 > 0.99$, Fig. 1). The asymptotes of the curves, which

Table 1

Current forest structure in Sierran mixed conifer stands for four different management regimes at Blodgett Forest Research Station, Georgetown, CA^a

Treatment	Density (# ha ⁻¹)	Basal area (m ² ha ⁻¹)	Tree height (m)	Canopy closure (%)	Mineral seedbed (%)	Management history	Inventory dates
Plantation	506	19.4	10.2	73	13	Clearcut 1969, 1975	1995
Shelterwood	185	10.2	10.2	54	13	Initial harvest, 1979	1997
Single-tree	346	49.4	17.4	81	0.50	Last entered, 1993	1994
Reserve	531	79.9	21.9	87	0.50	No active management	1994, 1999

^a Only trees >11.4 cm in diameter at breast height (1.37 m) were included in the estimates of density, basal area, and mean tree height.

can be used as estimates of total species richness (Colwell and Coddington, 1994), were greater in the plantation and shelterwood than in the single-tree selection or the reserve unit (Fig. 1). Based on the shape of these curves, we chose four plots (1.13 ha) as a minimum sample area. This minimum reaches the saturating part of the curve in all cases (Fig. 1); additional plots make proportionally small additions to the estimate. Although the observed species richness based on a sample of four plots is still an underestimate of the total species richness (Hellmann and Fowler, 1999), the influence of the area sampled is greatly reduced, making possible precise and reliable comparisons among treatments.

In 1997, understory species richness at Blodgett Forest was significantly greater in the plantation and shelterwood regimes than in the reserves. In plantations, there were on average 80 species found in four plots compared to only 48 species in the reserve stands (Table 3). The 95% confidence intervals of these means did not overlap. Although single-tree selection units also had a much lower mean richness than the even-aged treatments, 58, the difference was not significant using the criterion of non-overlap of confidence intervals.

On average, the wildlife crew captured 68% of the species observed in our inventories. They did the best in the plantations finding 74% of the species present

Table 2

Vegetation cover, herb layer vascular plant abundance, and measures of species diversity in Sierran mixed conifer stands under different management regimes^a

Plantation (n=4)	Cover (%)	Shelterwood (n=2)	Cover (%)	Single-tree (n=2)	Cover (%)	Reserve (n=6)	Cover (%)
Tree layer	73	Tree layer	54	Tree layer	81	Tree layer	87
Shrub layer	47	Shrub layer	34	Shrub layer	13	Shrub layer	3
Herb layer	15	Herb layer	23	Herb layer	8	Herb layer	6
<i>Five most abundant species</i>							
<i>Ceanothus prostratus</i>	5.1	<i>Bromus carinatus</i>	5.2	<i>Quercus kelloggii</i>	2.4	<i>Trientalis latifolia</i>	1.5
<i>Ribes roezlii</i>	2.1	<i>Ceanothus integerrimus</i>	3.4	<i>Ribes roezlii</i>	2.2	<i>Chrysopsis chrysophylla</i>	1.4
<i>Rosa gymnocarpa</i>	1.9	<i>Rumex acetosella</i>	3.0	<i>Draperia systyla</i>	1.2	<i>Quercus kelloggii</i>	0.7
<i>Iris hartwegii</i>	1.0	<i>Calocedrus decurrens</i>	1.8	<i>Calocedrus decurrens</i>	0.7	<i>Chamaebatia foliolosa</i>	0.6
<i>Trientalis latifolia</i>	0.9	<i>Ribes roezlii</i>	1.7	<i>Symphoricarpos mollis</i>	0.6	<i>Iris hartwegii</i>	0.5
Richness	15.6 (1.8)	Richness	24	Richness	12	Richness	7.7 (2.4)
Shannon	2.12 (0.25)	Shannon	2.54	Shannon	1.90	Shannon	1.55 (0.34)
Simpson	6.43 (2.22)	Simpson	8.28	Simpson	5.12	Simpson	4.06 (1.53)

^a Results based on point intersect sampling (314 m² plot) in 1997 at Blodgett Forest Research Station, Georgetown, CA. Tree layer includes all vegetation >2 m in height; shrub layer includes vegetation ≤2 m and >1 m in height; herb layer includes vegetation ≤1 m in height. Measures of diversity reported as the mean of two plots followed by the standard deviation in parentheses for management regimes with more than two plots.

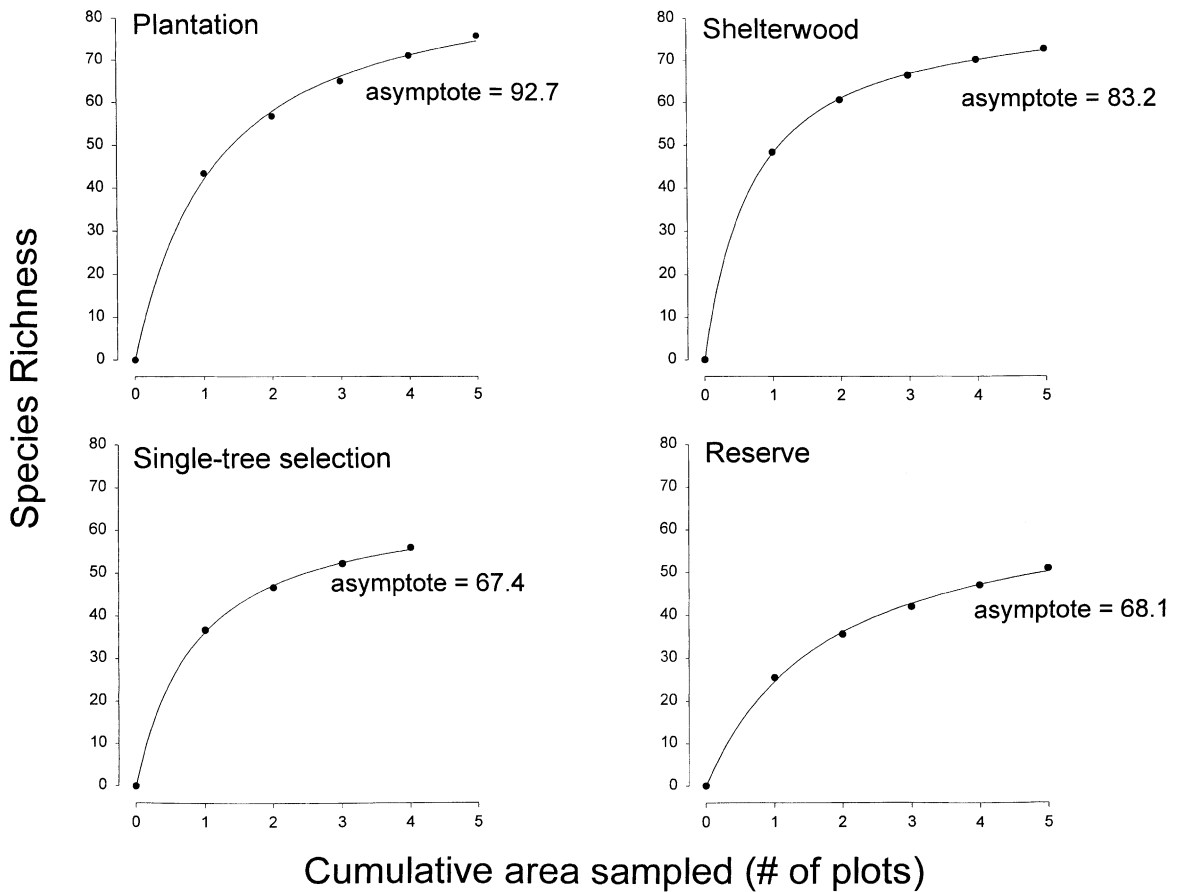


Fig. 1. Species–area relationships in mixed conifer stands under different management regimes at Blodgett Forest Research Station, Georgetown, CA. Results based on 1997 inventories of vascular flora in sequential plots 0.28 ha in area. The solid line shows the fitted Michaelis–Menton curve. The filled circles plot the cumulative mean richness for the number of plots sampled. Mean richness is calculated from all possible combinations of plot order-of-entry.

Table 3

Changes in species richness among Sierran mixed conifer stands under different management regimes^a

Year	Plantation	Shelterwood	Group selection	Single-tree	Reserve
1977	–	–	–	32 (26–39)	31
1978	34 (31–36) ⁹	–	–	23 (20–29)	23 (18–27)
1979	28 (21–31) ⁷	–	–	14 (10–19)	17 (14–20)
1980	–	–	–	32 (28–38)	28 (23–36)
1981	–	–	–	36 (29–39)	29 (26–32)
1984	31 (31–32) ⁷	–	–	–	23 (21–24)
1993	–	–	31 (28–37)	–	27 (21–35)
1994	65 (59–72) ¹³	–	66 (61–71)	–	42 (34–51)
1996	57 (51–67) ¹⁵	68 (62–71) ¹¹	63	–	46 (41–50)
1997	80 (74–87) ²⁴	77 (72–83) ¹²	52	58 (45–78)	48 (42–55)

^a Results based on yearly inventories conducted at Blodgett Forest Research Station, Georgetown, CA. Results are the mean richness values from 999 random combinations of four plots (total area sampled = 4 × 0.28 ha = 1.13 ha). Numbers in parentheses represent 95% confidence intervals of species richness. When only four plots were sampled, species richness is provided without confidence intervals. For plantation and shelterwood regimes, the superscript indicates the average age of the stands (years since harvest) included in the estimate.

and the worst in the shelterwood plots finding 61% of the total. In every plot, the wildlife crew noted fewer species. Misidentification of taxa was a minor problem — there were only a few repeated misidentifications. They simply did not find all the species present. In addition to the shorter search times, the wildlife crew was not trained to recognize the different species of grass (*Poaceae*). They also tended to lump species of asters (*Asteraceae*) and figworts (*Scrophulariaceae*). In spite of these absolute differences in species richness, the relative differences in species capture among management regimes were small. In other words, the wildlife crew's underestimates of plant species richness were consistent across treatments. For example, the pattern in species richness with management

regime was the same regardless of which 1997 data set (the complete inventories or the wildlife crew's inventories) was analyzed. This result suggests that the plant data collected for the wildlife habitat study could be used to examine relative differences in species richness among treatments with a reasonable degree of confidence. To further control the effect of variation in the crew's proficiency between sample years, we restricted our retrospective analysis to within-year comparisons.

The results from 1977 to 1996 supported the pattern observed in 1997. Species richness was greatest in plantations and least in reserves (Table 3). For the 10 years with at least four plots sampled in at least two different management regimes, reserve stands had the

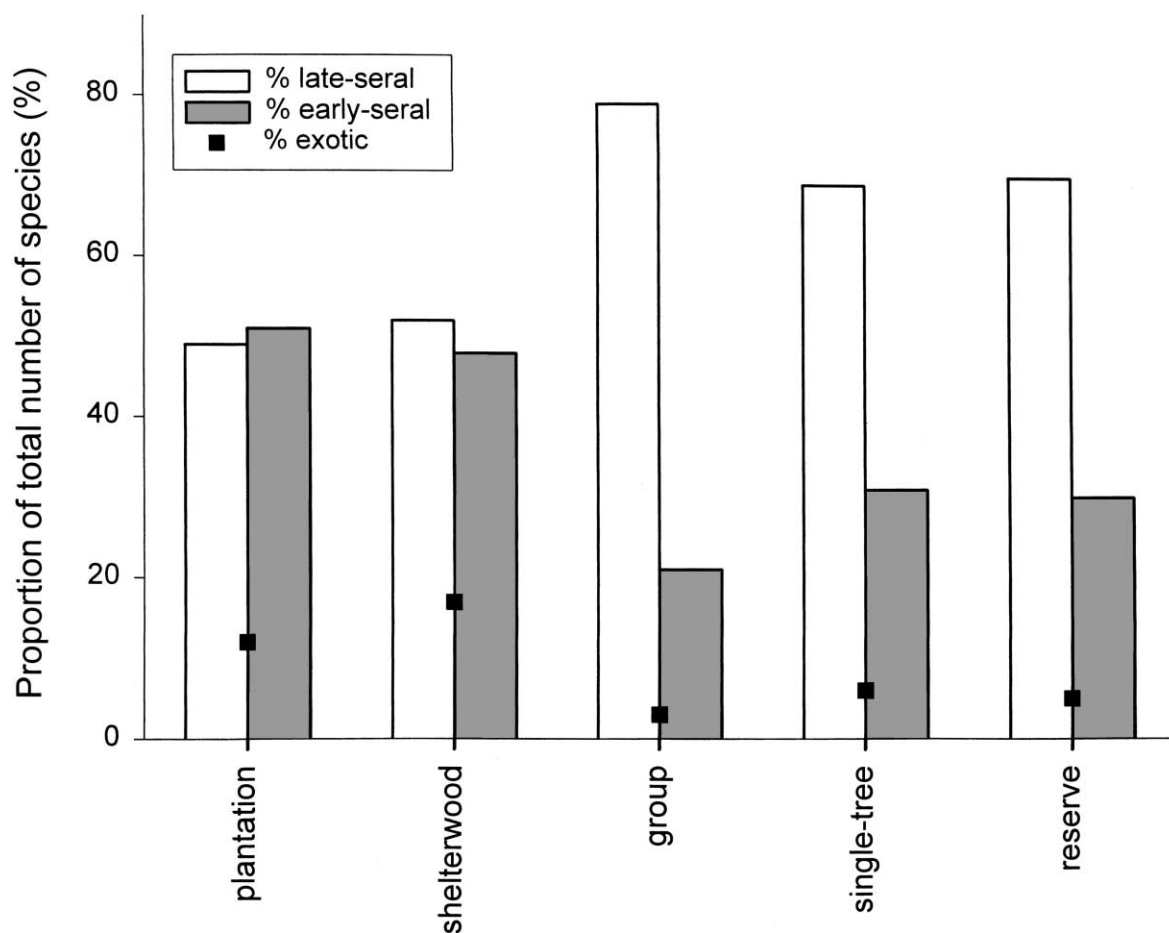


Fig. 2. Qualitative differences in understory vascular flora among the five management regimes at Blodgett Forest Research Station, Georgetown, CA. See text for definition of late-seral, early-seral species, and exotic species.

lowest mean richness nine times. For the six years that both plantations and reserve stands were sampled, plantations always had significantly higher species richness than reserves. Furthermore, plantations had the highest overall species richness four out of six years (Table 3).

Estimates of plant diversity under group selection management varied from year to year. In 1997 and 1993, species richness in group selection was indistinguishable from the reserve plots. In 1996 and 1994, richness in the group selection plots was greater than reserves and more similar to plots in even-aged management (Table 3).

There were major differences in the composition of the understory communities among silvicultural treatments (Fig. 2). Late-seral species were the majority ($\geq 69\%$) of plants in group selection, single-tree selection, and reserve stands. Of the early-seral species present in these stands, only one (group and reserve) or two (single-tree) were non-native species. In contrast, early-seral species accounted for half the species in the plantations and shelterwoods and several of them were introduced exotic species (six in plantations; seven in shelterwoods). Furthermore, the taxonomic distribution of plants varied among treatments. Species in the *Asteraceae* and *Poaceae* accounted for more than 25% of all species in the plantations and shelterwoods while contributing only 8% of the species in reserves.

4. Discussion

Despite concerns that forest management might decrease plant diversity (Gilliam and Roberts, 1995), most recent studies in temperate forests that measured management effects on understory species diversity report either no reductions, short-lived reductions, or increases in species richness following silvicultural intervention (Table 4). The results from the Sierran mixed conifer forest followed this trend: understory species richness was consistently greater in the managed stands (Table 3). However, there are at least three cases where plant species diversity was markedly reduced following clearcut harvests (Meier et al., 1995; Elliott et al., 1997; Qian et al., 1997).

Disturbance plays a leading role in many mechanistic models of species diversity. Among the alternatives, Roberts and Gilliam (1995b) argued that the

intermediate-disturbance hypothesis (sensu Connell, 1978) is most applicable to forest management. The intermediate-disturbance hypothesis predicts that species diversity should increase with increasing levels of disturbance up to a point, after which diversity declines. The underlying reasoning is that moderate disturbance prevents a few species from dominating resources but severe disturbance creates a stressful environment that few plants can tolerate.

For the range of treatments applied at Blodgett Forest, understory species diversity tracked the degree of disturbance. At the plot scale, percent canopy cover and available mineral soil seedbed were significantly correlated with species richness. These variables are related to two separate aspects of the silviculture. Canopy cover is a function of the timing and amount of wood volume harvested; whereas seedbed characteristics depend more on the post-harvest site preparation. The fact that both variables were related to species diversity supports previous results describing the importance of post-harvest practices in the ecology of managed forests (Roberts and Dong, 1993; Halpern and Spies, 1995; Gale et al., 1998). At the stand scale, the more intensive management regimes that removed more tree biomass and caused greater disruption to the forest floor (i.e., more disturbance) resulted in greater understory species richness (Table 3). The implication is that disturbances caused by silvicultural activities at Blodgett Forest fall within the “intermediate” range for this forest ecosystem. Presumably in the instances when management practices lead to decreased species richness, the interventions exceeded this intermediate level. Indeed, Qian et al. (1997) suggest that extensive clearcuts are atypical disturbances in coastal forests of British Columbia and assert that such harvests will always lower species diversity relative to old-growth stands. For the mixed forests in North Carolina, Elliott et al. (1997) mention the cumulative effects of clear-cutting in addition to other disturbances (e.g., air pollution, fire suppression, and grazing) as potential causes for the observed decreases in species richness. Meier et al. (1995) propose a mechanistically detailed hypothesis for the observed decreases in diversity in second-growth hardwood stands, but their fundamental argument is that clearcut logging is an extreme disturbance from which the herb community only very slowly, if ever, recovers.

Table 4

Effects of timber management on understory species diversity in temperate forests^a

Forest type and location	Harvest intensity	Effect on understory plant diversity
Mixed hardwoods, West Virginia, USA ^b	Even-aged, 20 year-old stands vs. > 70 year-old stands	No significant differences in species richness or Shannon index
Mixed deciduous and conifer forests, Maryland, USA ^c	2–90 years after clearcut harvest	No effect on species richness or Shannon index
Northern hardwood/oak-hickory forests, Pennsylvania, USA ^d	Various: range from clearcut to selection harvest	No significant effect on species richness
Central hardwoods, Indiana, USA ^e	Clearcut, group selection, single-tree, and mature reference stands	Species richness greater in clearcuts and groups; no differences in Shannon index
Beech forests, central Japan ^f	Shelterwoods vs. primary forest stands	No differences in species richness or Shannon index
Beech-dominated mixed deciduous forests, Denmark ^g	Various: range from clearcut to untouched	No difference in species richness or Shannon index between managed and untouched forest
Spruce-pine wetland forest Michigan, USA ^h	2–5 year-old stands following whole-tree harvest vs. adjacent uncut stands	Species richness significantly greater in harvested stands than uncut stands
Aspen-dominated northern hardwood forests, Michigan, USA ⁱ	≤15 year-old clearcut vs. 55–82 year-old second growth	Species richness and Shannon index greater in younger stands
21–27 year-old Douglas-fir plantations, Washington, USA ^j	Three intensities of precommercial thinning	Species richness increased with thinning intensity
Douglas-fir stands, Washington and Oregon, USA ^k	Clearcut, green tree retention harvest, and 65 year-old stands	Species richness significantly greater in green tree retention harvest than clearcut or 65 year-old stands
Young Douglas-fir stands, Oregon, USA ^l	0–28 year after clearcut harvest	Initial decline in species richness after harvest (2 year) followed by increasing richness with time
Mixed oak forests, Ohio, USA ^m	~70 year-old clearcut forest vs. >150 year-old primary forest stands	Species richness and Shannon index higher in primary stands but differences not significant
Cove hardwoods, southeastern USA ⁿ	10 pairs of matched secondary (logged) and primary forest stands	Species richness significantly greater in the primary stand for all 10 comparisons
Mixed hardwood and pine forests, North Carolina, USA ^o	0–16 year after clearcut harvest vs. mature forest before harvest	Sustained decreases in richness and Shannon index after harvest compared to pre-cut forest
Hemlock-fir forests, British Columbia, Canada ^p	40 year-old plantations vs. old-growth stands	Consistently lower species richness and Shannon index in plantations

^a Included in this summary are recently published results (1995 or later) with complete vascular flora inventories and comparable measures of diversity. Superscripts identify source.

^b Gilliam et al., 1995.

^c Yorks and Dabydeen, 1999.

^d Fredericksen et al., 1999.

^e Jenkins and Parker, 1999.

^f Nagaike et al., 1999.

^g Graae and Heskjaer, 1997.

^h Gale et al., 1998.

ⁱ Roberts and Gilliam, 1995a.

^j Thomas et al., 1999.

^k North et al., 1996.

^l Halpern and Spies, 1995.

^m Goebel et al., 1999.

ⁿ Meier et al., 1995.

^o Elliott et al., 1997.

^p Qian et al., 1997.

Halpern and Spies (1995) noted that in addition to the initial effects of logging and site preparation, other management activities (e.g., fertilization, herbicide application, grazing) can impact the composition of understory vegetation. Herbicides and grazing are among the tools used at Blodgett Forest to reduce the growth of aggressive shrubs and promote the growth of conifers (Helms and Tappeiner, 1996). In this study, the available data were not extensive enough to separate out the effects of initial vs. long-term management practices. However, the length of the record (10 surveys during a 20-year period) was long enough to incorporate both aspects of the silviculture systems and thereby provided an assessment of the totality of management influences on floral diversity.

Data quality is often an issue in retrospective studies. Our solution was to confront the limitations of the data and to extract only defensible insights. We used a simple measure of biodiversity — species richness — and estimated the quantity in such a way to control biases introduced by sampling intensity. This approach does not provide an estimate of total species richness but rather a reliable, relative index to compare treatments. Based on the 1997 quality assessment, the wildlife crew missed the infrequently occurring plant species and tended to lump together similar-looking species in difficult-to-identify families. However, the rank-order of species richness by management regime was insensitive to these omissions. While the proficiency of the contemporary wildlife crew was tested, there was no way to evaluate the species capture rates of past crews. There was a clear increase in species richness across all treatments after 1993 (Table 3), an increase that coincided with more time spent training the crew in plant identification. In spite of these weaknesses, the historical data record supported the 1997 results with remarkable consistency, lending strength to the conclusion that forest management as practiced at Blodgett Forest increases rather than decreases understory species richness.

Management practices at Blodgett Forest were associated with qualitative compositional differences in the understory plant community. Early-seral and non-native plants comprised a greater proportion of the species present in even-aged stands (Fig. 2). There were 22 species in the 1997 inventory occurring only

in plantations. Many of these species, e.g., *Agoseris retrorsa* (mountain dandelion) and *Calyptidium umbellatum* (pussypaws) are common in open disturbed sites. Reserves had 11 unique species, including two species of achlorophyllous orchids, *Cephalanthera austiniiae* (phantom orchid) and *Corallorhiza striata* (striped coralroot). Such differences in the understory plant community occur in other managed forests. For example, ruderal species were more frequent in logged northern hardwood forests (Fredericksen et al., 1999); the proportion of primary forest species was reduced in Japanese shelterwoods (Nagaike et al., 1999); species characteristic of open sites increased in importance in recently clearcut aspen stands (Roberts and Gilliam, 1995a); and invasive species accounted for 84% of the herb cover in clearcut sites in conifer forests of the Pacific Northwest, USA (North et al., 1996). Given that silvicultural interventions profoundly alter resource supply and microenvironments in forest stands, such shifts in the understory flora toward more “weedy” species are expected.

A challenge facing forestry is how to conserve regional biodiversity and to meet the demand for wood products. Any realistic strategy will have to include forests designated for preservation and for production (Hansen et al., 1991; Perry, 1998). The management plan of Blodgett Forest provides a specific example of this strategy and adds to the growing but still insufficient knowledge base describing effects of timber production on species diversity. At Blodgett Forest, more intensive silviculture practices were related to increases in understory species richness. However, less-intensive methods better conserved species typical of late-seral stands. Furthermore, ecological reserves were an essential part of the management mix. Perhaps as many as 11 late-seral species would be absent from Blodgett Forest if reserves were not included. As noted by Olson and Helms (1996), caution must be used when extrapolating the results from Blodgett Forest to other mixed conifer forests in the Sierra Nevada. The gentle terrain and high productivity of the site reduce the chances of serious soil degradation associated with timber removal. The compartments are small and interspersed, thereby minimizing the barriers to dispersal of forest herbs (sensu Meier et al., 1995). Also, the presiding management priority is sustainability. Thus, silvicultural activities

are implemented with technical competence and close supervision. A final warning is that we compared species diversity between managed stands and mature, second-growth reserves. Graae and Heskjaer (1997) observed that mature, second-growth stands often have lower plant diversity than old-growth stands because they have not yet reached the “degenerative” phase of development. The canopy openings and forest floor disturbance associated with tree-fall gaps in old-growth stands are considered crucial to biodiversity. Given these caveats, forest practices which take into consideration ecology as well as economics can effectively harvest timber and maintain plant species diversity in the Sierra Nevada.

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