Comparison of Floristic Diversity between Young Conifer Plantations and Second-Growth Adjacent Forests in California's Northern Interior

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ABSTRACT

There is concern that intensive even-aged forest management in conifer plantations has resulted in the decline of plant species diversity and contributed to the rise of invasive species in western forests. This 3-year study assessed plant species richness, composition of vascular plant species, and presence of rare and nonnative plant species in 73 survey units (2,528 ac) on industrial forestland in northern California. Survey units were evenly divided between conifer plantations and adjacent managed uneven-aged forests in three regions of northern California: Sierra Nevada, Southern Cascades, and Klamath Mountains. We surveyed two forest types within these regions: mixed conifer and true fir. There was no significant difference in species richness between plantations and adjacent forests. Plantations tended to be richer in forbs and graminoids, whereas forests were richer in trees and shrubs. Herbicide applications in plantations significantly reduced shrub species richness, but the effect was short-lived. Rare plant species were equally distributed between plantations and adjacent forests, but plantations contained one additional nonnative plant species. Overall, our findings demonstrate that managed, even-aged conifer plantations maintain plant species richness at a level similar to adjacent managed, uneven-aged forests.

Keywords: species richness, clearcut, forest matrix, rare plant, nonnative plant

Concern over the loss of plant species diversity from intensively managed forests, particularly in areas where clearcut regeneration methods are used in plantation management, has increased in recent years. Critics argue that clearcutting alters the floristic composition of ecosystems, causing a net loss of species, a failure of plantations to return to preharvest levels of species richness, loss of rare species, and the spread of undesirable nonnative species across the forest landscape.

To evaluate the effect of management regimes on plant species diversity in conifer plantations (artificially regenerated, even-aged stands) and managed conifer forests (naturally regenerated, uneven-aged stands), managers need to understand how floristic composition varies between plantations and managed forests. Only then can they determine which regimes best balance timber production and biological diversity. Roberts and Gilliam (1995) reviewed plant diversity in forest landscapes and reported a wide range of findings based on different ecosystems, roles of disturbance, temporal and spatial scales, and models. It is not well understood whether the temporal pattern of species richness found in managed plantations is similar to that of uneven-aged, naturally regenerated forest matrixes (Halpern and Spies 1995), whether species richness levels in intensively managed plantations will return to preharvest levels (Gilliam 2002, McDonald and Fiddler 2006), whether rotation age is sufficiently long enough for understory plant species to recover to preharvest levels in managed plantations (DiTomaso et al. 1997, Battles et al. 2001, Roberts 2002), whether plantation management reduces rare species diversity, whether plantation management encourages the spread of undesirable nonnative species (US Forest Service 2004), or whether managed forests with multiple harvest entries can maintain species richness (Edwards et al. 2010).

This study addresses these issues by examining initial impacts of plantation management practices on plant species richness and by comparing species richness in plantations less than 12 years old to that in adjacent 60- to 90-year-old, uneven-aged, managed forest matrices. As recommended by several researchers (Halpern and Spies 1995, Roberts and Gilliam 1995, Thomas et al. 1999, Jules and Shahani 2003), we chose to focus on species richness for all vascular plants within four plant life form groups (forbs, graminoids, shrubs, and trees) at the plantation scale because plantations are the working basis for forestland management decisions. We sampled 73 survey units covering 2,528 ac across a diverse and broad forested area of northern California to provide both local and regional contexts for examining floristic differences. Our study had four objectives: (1) to quantify local species richness for plantations and surrounding uneven-aged managed forest matrices; (2) to compare and evaluate species richness among individual survey units across the study area; (3) to examine how uneven-aged forest matrix attributes and plantation treatment histories influence differences in survey unit species richness; and (4) to assess the incidence of rare plants and nonnative species in plantations and adjacent forest matrices.

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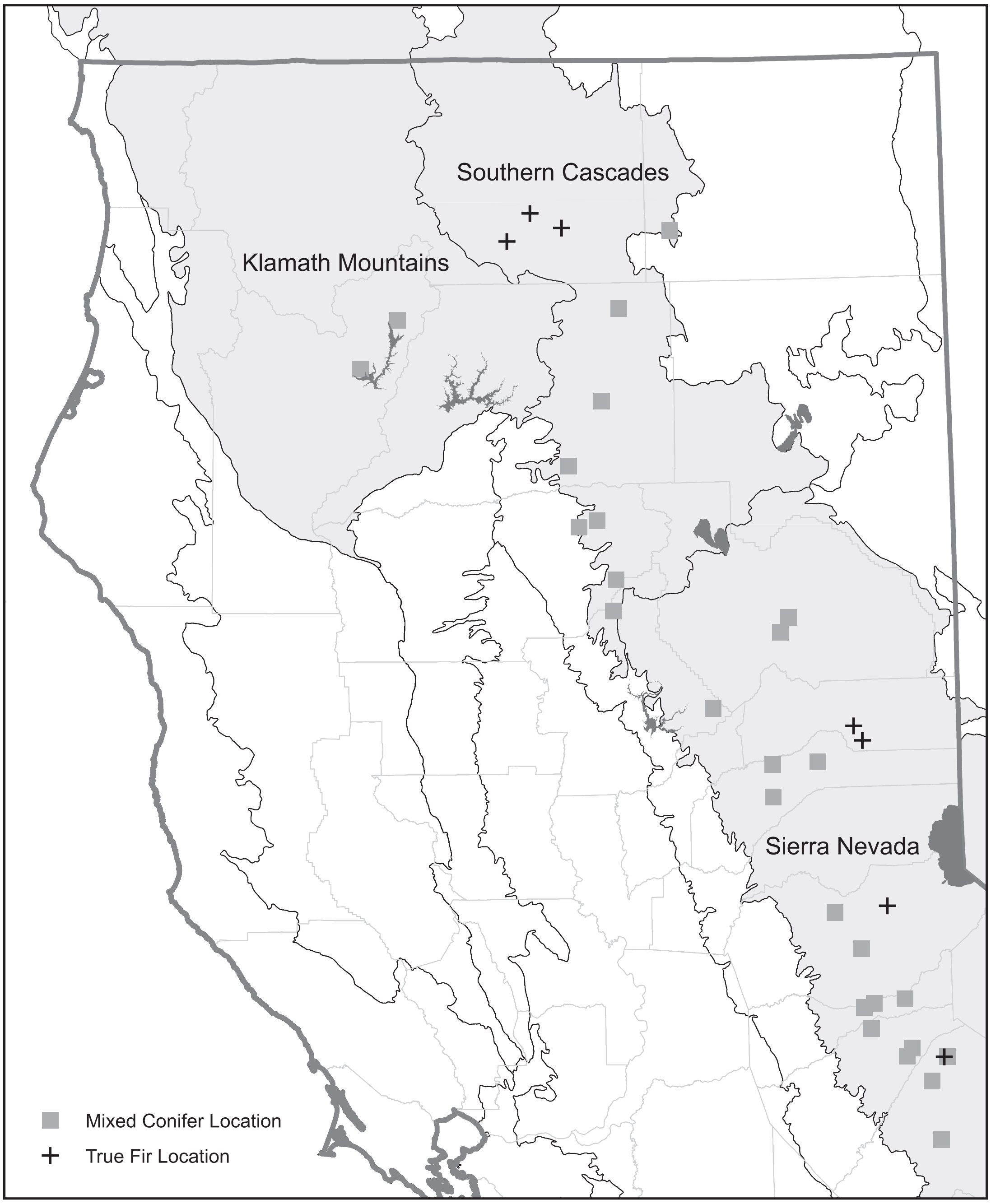

Figure 1. Ecological subregions and survey unit locations in northern California by forest type (Goudey and Smith 1994).

Data and Methods

Survey Units

We identified primary survey units across northern California consisting of recently established conifer plantations (hereafter called "plantations" or "plantation components") and adjacent surrounding second-growth conifer stands of comparable size and physical characteristics (hereafter called "forests" or "forest components"). Seventy-three survey units were chosen from 45 California state planning watersheds located in three ecological subregions (Goudey and Smith 1994). These regions include three floristic provinces (Sierra Nevada, Southern Cascades, and Klamath Mountains) (Hickman 1993) and two broad forest types (mixed conifer and true fir) (Figure 1). These forest types are commercially important timber-growing lands. Understory vascular plants account for the majority of species within these forests (Allen-Diaz 1988, Fites 1993, Christensen et al. 2008). The mixed-conifer type comprises five primary tree species of commercial importance: ponderosa pine (*Pinus ponderosa* var. *ponderosa*), Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), and incense cedar (*Calocedrus decurrens*). The true fir type has two primary tree species of commercial importance: red fir (*Abies magnifica*) and white fir (*Abies concolor*). Other conifers are common or occasional associates in varying mixtures within the true fir forest type. Management histories of second-growth mixed-conifer and true-fir stand types include multiple harvest entries over the past 100 years. Dominant overstory trees in both types range from 60 to 90 years of age. Mixed-conifer sites ranged in elevation from 3,100 to 6,500 ft, whereas true fir sites occupy elevations from 5,000 to 7,000

Table 1. Numbers of survey units and forest component characteristics by floristic province and forest type.

Floristic province	Forest type	No. of survey units	Canopy cover (%)	Canopy cover (SD)	Trees/ac	Trees/ac (SD)	Basal area (ft^2/ac)	Basal area (SD)
Southern Cascades	Mixed conifer	16	61	35	266	240	113	61
Southern Cascades	True fir	14	48	16	189	123	143	48
Klamath Mountains	Mixed conifer	4	92	45	278	187	91	30
Sierra Nevada	Mixed conifer	35	73	39	241	135	126	35
Sierra Nevada	True fir	4	51	9	255	82	113	35

ft. All sites are productive forestlands with an average site class of II (Dunning 1942), roughly equivalent to a site index of 80 to 100 ft at a 50-year breast-height age (Krumland and Eng 2005).

Plantation Characteristics

Plantations in this study were regenerated artificially following clearcutting of existing commercial tree species. One to two large California black oak (*Quercus kelloggii*) trees per acre were left for wildlife habitat on approximately 40% of the plantations. If necessary, brush was mechanically removed prior to planting. Plantations were planted with a variety of coniferous tree species, depending on site characteristics. Planting densities ranged from 350 to 450 trees per acre. Herbicides were applied to control brush and herbaceous species if a pest control adviser determined that competition would slow the growth of planted seedlings. In plantations where herbicides had been applied, surveys were not undertaken for at least 1 year after application. Twenty plantations had no herbicide applications. Average plantation size was 18.3 ac. All plantations had less than 30% canopy cover and were surveyed less than 12 years after establishment.

Forest Matrix Characteristics

Matrices delineating the forest component of survey units had varied management histories in both land tenure and methods of past harvest. Most commonly, timber stands regenerated naturally following a variety of harvests from 1870 to 1920. These harvests and periodic large wildfires removed most of the original old-growth timber. Remaining large-diameter trees were harvested frequently from 1920 to 1970, further reducing the frequency of large-diameter trees.

More recently, various forms of single-tree selection and thinning operations were applied at varying intensities to meet a range of management objectives. Stand-summary characteristics for forests were derived from tree inventory plots for each survey unit. Tree data were collected in a grid pattern at a frequency of one plot per 4 ac. The maximum time elapsed between tree data collection and floristic surveys was 6 years. If the forest component transect could not accommodate at least six plots, additional plots of similar composition outside the forest survey area were added as close to the area as possible. Plot summaries were reported for all trees ≥1 in. dbh. Forest component characteristics were calculated per acre for overstory canopy coverage, number of trees, and basal area (Table 1). Canopy coverage is expressed as the percentage of area occupied by the maximum vertical crown area projection of all inventoried trees. We did not deduct for overlapping crowns, so canopy coverage may be greater than 100% for dense stands. Each forest component was acceptably stocked with commercial tree species under the point count criteria of the California Forest Practice Rules (14 CCR 932.7) (California Department of Forestry and Fire Protection 2011). No logging, mechanical disturbance, or fire had occurred in forest components for 10 years prior to field surveys. Some forestlands were excluded from the study that otherwise fit the criteria for forest components, including land with substantial amounts of open ground, such as large landings, permanent roads, or brush fields.

Topography and land form of a plantation and its adjacent forest were similar. All survey units were part of timber harvest plans approved under the California Forest Practice Rules on industrially owned timberlands.

Field Sampling

Crews conducted fieldwork over three growing seasons (2004–2006). Field crews consisted of trained botanists, who performed botanical surveys, and research technicians, who established sample transects and collected nonbotanical information. During summer 2004, field-based pilot tests of various sampling methodologies were performed to identify the most efficient sampling scheme for determining species richness. Each sampling method included the time required to lay out units for surveying, conduct floristic surveys, and collect all other field data and involved both systematic and random plot placement, fixed-size plots of various dimensions, and systematic band transects across the entire survey unit. Systematic band transects 10 ft wide were determined to be the most efficient and could be methodically laid out by field crews in an objective and consistent manner. Transects laid out at 300-ft intervals (approximately 3% area coverage) included 80–90% of the plant species in test survey units. Transects spaced more closely improved results only marginally and were offset by losses in sampling efficiency.

Survey Methods

Transects were laid out in each survey unit to form a grid across each plantation and the forest components adjacent to either side (Figure 2). Transects were installed perpendicular to the baseline across the plantation (P) and extended into the surrounding forest components (F1 and F2) a distance equal to one-half the plantation transect length; nominally, $P = F1 + F2$.

Inventories were conducted along each transect in a 10-ft-wide band. Ground flags were placed every 100 ft along transects and at each segment transition edge between the plantation and forest components to clearly define sampling areas. The numbers of survey units and forest component characteristics by floristic province and forest type are given in Table 1. Total transect areas surveyed in all 73 survey units were 41.2 ac for plantation components and 38.5 ac for forest components. Detailed plantation area and transect sampling data are provided in Table 2.

The exterior edge of the plantation component of each survey unit is defined as a point along a transect halfway between the trees in the plantation and the drip line of the surrounding forest matrix. Transitions between forest and plantation components in terms of floristic composition and ground cover characteristics are usually

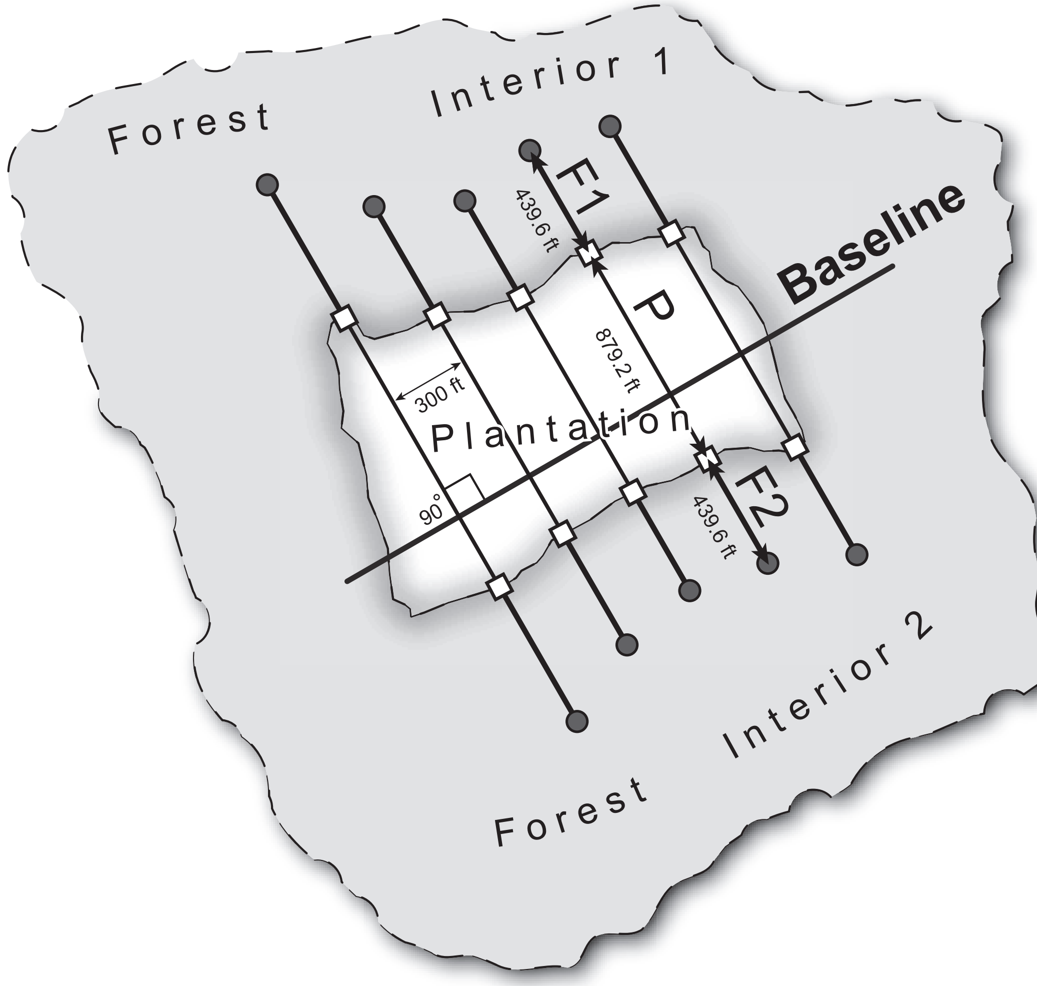

Figure 2. Nominal transect layout for a typical survey unit. P, plantation; F, forest.

Table 2. Plantation area and transect statistics for 73 survey units.

	Average	SD	Minimum	Maximum	Coefficient of variation (%)
Plantation area (ac)	18.3	8.6	1.9	46.2	
Number of transects per survey unit	3.3	1.1	2	8	
Single transect length (ft)	755	305	155	1720	22
Single transect area (ac)	0.17	0.06	0.04	0.40	22
Total transect length (ft) per survey unit	2471	1033	840	5111	
Total transect area (ac)	0.57	0.24	0.19	1.17	
Sample coverage (%)	3.4	1.3	1.7	11.6	

clearly defined and often abrupt. Transitional ecotones were not present, probably because of the short time frame between plantation establishment and when surveys were conducted. Because of variable topography and other unique field characteristics of each survey unit, the total length of transects for forest components for all survey units was 7% less than that for plantations. In approximately 60% of the plantation transects, we classified entry disturbances (e.g., temporary and access roads, skid roads from harvesting operations, tractor roads used in plantation establishment) proximal to or interpolated within the forest component with plantation components. Plantation transect lengths were subsequently extended to include those additional disturbances, with concomitant reductions in forest transect lengths. These disturbance adjustments accounted for approximately 1% of the entire transect length surveyed; an additional 6% were due to forest transect segments being terminated where forest type changed or property lines were encountered. For analytical purposes, surveys for forest transect segments (F1 and F2) adjoining a plantation were combined to create a single transect so that the number and transect-size distribution of forest and plantation components in each survey unit were as similar as possible.

Botanical Surveys

All plants within transect bands were identified to the lowest possible taxon following guidelines set forth by Hickman (1993). Each species was further classified into one of four plant life form groups: forbs (broadleaved herbaceous plants), graminoids (grasses, sedges, and rushes), shrubs, or trees. Ferns and associated fern allies were classified as forbs, as the modal incidence value was 0 (zero),

Table 3. Plantation unit richness accuracy assessment statistics. Bias means of >0 and ratio of means >1 indicate overestimates.

Plant group	Data means: Estimate ($E(SP_{UNIT})$)	Data means: Actual (SP_{UNIT})	Ratio of means ($E(SP_{UNIT})/SP_{UNIT}$)	Bias: Mean	Bias: *P* value	Bias: SD
ALL	79.2	77.7	1.02	1.55	0.22	10.8
Forbs	45.2	44.3	1.02	0.96	0.23	6.7
Graminoids	16.1	15.0	1.07	1.15	0.02	3.7
Shrubs	11.8	11.9	0.99	−0.05	0.85	2.1
Trees	6.7	6.6	1.02	0.16	0.12	0.9

$E(SP_{UNIT})$, estimated plantation unit richness; SP_{UNIT}, plantation unit richness; ALL, total number of species in all life-form groups.

and no more than three specimens were recorded in any survey unit. Botanical surveys were performed during the peak flowering period (late May to early September) for the majority of species in each of the three floristic provinces. We also documented and reported known locations of rare or endangered plants and nonnative plants recognized by the State of California and documented in the California Natural Diversity Database (California Exotic Pest Plant Council 1999, California Native Plant Society [CNPS] 2001).

Unknown Specimens

Plants that could not be positively identified were collected, and voucher specimens were deposited in the university and Jepson Herbaria at the University of California, Berkeley. Specimen records are available through the Consortium of California Herbaria (2010). Some unknown specimens, particularly small or young vegetative individuals, could not be identified more precisely than family or genus level.

Intuitive-Controlled Floristic Surveys

In addition to surveying individual transects in each survey unit, we conducted intuitive-controlled floristic surveys to determine more completely the number of vascular plant species present in plantations. Botanists systematically walked each plantation component and identified plants in all major habitats and topographic types, recording species not identified during plantation transect surveys. This method of surveying vascular plants was recommended by the USDI Bureau of Land Management (1999). For the purposes of this study, we consider intuitive-controlled floristic surveys to be a complete plant census. This method provides data for a check on sampling efficiency and we were able to use it to validate estimation methods based on transect data. We did not conduct complete surveys within forest components because of the excessive amount of additional fieldwork that would have been required to survey and establish forest boundaries.

Sample Size

As previously noted, the number of sample survey units at which we ultimately arrived (73 survey units; 2,528 ac) was based on a combination of site-specific criteria, the ability to perform botanical surveys during peak flowering periods, and funding. Although power analysis is another common method of determining sample size (Zar 1984, Aberson 2010), it is typically not performed with this type of species richness study. Therefore, we sampled as many survey units across each floristic province and forest type that were reasonably possible within the limits of this study.

Analytical Methods

Species Richness

We refer to the number of species in the plantation component of a survey unit as plantation unit richness (SP_{UNIT}) and to the forest component as forest unit richness (SF_{UNIT}). These terms apply to the number of species within each of the four plant life form groups, as well as the total number of species in all life-form groups (ALL species). We derived SP_{UNIT} from the intuitive-controlled floristic plantation component surveys. However, equivalent measures of SF_{UNIT} were not available. To derive SF_{UNIT} with a comparable basis for assessment, we used modeling approaches based on transect survey data (Gotelli and Colwell 2001). We denoted unit richness estimates for plantation and forest components as $E(SP_{UNIT})$ and $E(SF_{UNIT})$. We defined sample limit richness as the estimated richness of a survey unit component [$E(SP_{SLR})$ and $E(SF_{SLR})$] at a cumulative transect length equal to the total transect length of the plantation survey (PTTL). For plantation components, PTTL was coincident with observed sampling effort.

Rarefaction Modeling

We estimated unit and sample limit richness using parametric rarefaction models (Colwell and Coddington 1994) because they could be readily adapted to the continuous data collected in this study. Rarefaction models predict the number of species detected as a function of sampling effort and can be thought of as the smoothed, averaged, or expected value of all possible species accumulation curves that can be derived from a sample (Gotelli and Colwell 2001, Chao 2005). We used cumulative transect length as the measure of sampling effort.

Rarefaction Data.—Rarefaction data are derived from our botanical transects by tallying the number of species found against the cumulative transect length of any combination of transects sampled. This procedure produces a list of species richness data points from which subsequent modeling is based. We chose a method that uses all possible sample data in direct form with a maximum of eight transects in any survey unit. For each analysis, we generated every distinct data point at each species assemblage level j ($j = 1 \ldots T$). At most ($T = 8$), this produced 255 (2^{T-1}) data points. For a given assemblage level j, $C(T, j)$ data points were produced. However, permutations of all possible species accumulation curves indicated that there were equal numbers ($T!$) of possible data points at every assemblage level j and that they were all equally likely. We therefore assigned weights to each assemblage level in the form of $1/C(T, j)$ to ensure that each assemblage level contributed equally in subsequent parameter estimation.

Rarefaction Models.—Rarefaction models were developed to estimate species richness as a function of cumulative transect length sampled and are used to form comparable estimates of plantation and forest components. Rarefaction models used in this study have the implicit form $S(CL) = f(d_0, d_1, CL)$ where $S(CL)$ is the estimated number of species for a cumulative transect length of CL, and

Table 4. Summary of unit richness estimates and comparisons based on 73 survey units. Richness differences <0.0 and ratios <1.0 indicate that forest components were richer than plantation components. *P* values for RMA regressions are based on the hypothesis H_0:b_1 = 1.0.

	Mean unit richness		Richness difference			RMA regression				Ratio of means
Plant group	$\overline{(SP_{UNIT})}$	$\overline{E(SF_{UNIT})}$	$\overline{D_{UNIT}}$	*P* value	SD	b_0	b_1	*P* value	*r*	$(\overline{E(SP_{UNIT})}/\overline{E(SF_{UNIT})})$
ALL	79.24	77.85	1.39	0.50	17.70	3.83	0.93	0.55	0.82	1.02
Forbs	45.24	44.10	1.13	0.43	12.07	0.46	0.96	0.66	0.82	1.03
Graminoids	16.12	15.12	1.01	0.15	5.92	1.27	0.86	0.12	0.73	1.07
Shrubs	11.84	12.33	−0.49	0.23	3.43	−0.44	1.08	0.38	0.71	0.96
Trees	6.72	7.06	−0.34	0.09	1.70	−0.28	1.09	0.15	0.78	0.95

RMA, reduced major axis; $E(\overline{SP_{UNIT}})$, estimated plantation unit richness; $E(\overline{SF_{UNIT}})$, estimated forest unit richness; $\overline{D_{UNIT}}$, sample unit richness difference; ALL, total number of species in all life-form groups.

Table 5. Summary of sample limit richness estimates and comparisons based on 73 survey units. Richness differences <0.0 and ratios <1.0 indicate that forest components were richer than plantation components. *P* values for RMA regressions are based on the hypothesis H_0:b_1 = 1.0.

	Mean sample limit richness		Richness difference			RMA regression				Ratio of means
Plant group	$\overline{E(SP_{SLR})}$	$\overline{E(SF_{SLR})}$	$\overline{D_{SLR}}$	*P* value	SD	b_0	b_1	*P* value	*r*	$(\overline{E(SP_{SLR})}/\overline{E(SF_{SLR})})$
ALL	65.62	65.65	−0.03	0.98	13.81	0.25	1.00	0.99	0.83	1.00
Forbs	36.81	36.39	0.42	0.70	9.17	−1.01	1.02	0.91	0.84	1.01
Graminoids	12.52	12.11	0.40	0.40	4.12	0.42	0.93	0.56	0.75	1.03
Shrubs	9.99	10.51	−0.57	0.07	2.71	−0.41	1.10	0.13	0.74	0.95
Trees	6.29	6.58	−0.28	0.07	1.31	−0.76	1.17	0.02	0.86	0.96

RMA, reduced major axis; $E(\overline{SP_{SLR}})$, estimated plantation sample limit richness; $E(\overline{SF_{SLR}})$, estimated forest sample limit richness; $\overline{D_{SLR}}$, sample limit richness difference; ALL, total number of species in all life-form groups.

d_0, d_1 are general proxies for parameters to be estimated. We considered only two-parameter models to avoid possible overparameterizations. For each richness definition, we constructed 730 individual models (73 survey units × 2 components × 5 species groups). As suggested by Colwell and Coddington (1994), we tested several possible monotonically increasing functional forms for screening purposes to provide separate bases for sample limit and unit richness estimations.

Sample Limit Richness Model.—Sample limit richness models are used to provide comparable estimates of forest and plantation species richness based on observed levels of sampling effort. Sample limit richness estimates are close to empirical values observed in our botanical surveys. In this study, we compared candidate models for ALL species and for each individual plant life form group by examining regression total sums of squares and pooled mean square errors based on all survey units. The semi-log model (Gleason 1922) of the form $S(CL) = b_0 + b_1 \times \log(CL)$ was consistently 2–35% more efficient than other models and therefore was chosen as the functional form for subsequent estimations of sample limit richness.

Unit Richness Model.—Unit richness models are used to extrapolate sample data to provide an estimate of the total species richness in the forest or plantation component of a survey unit. We examined several bounded (asymptotic) model forms using only plantation component data. We evaluated model performance by comparing SP_{UNIT} to $E(SP_{UNIT})$ for ALL species, with secondary consideration given to the performance of individual plant life form groups. A cumulative band transect length equivalent to the area of the plantation was computed for each survey unit and used to predict $E(SP_{UNIT})$. On the basis of minimum forecasting bias and error variance, an exponential (SH) model of the form $S(CL) = A_{SH}[\exp(c/CL)]$ performed best overall. A_{SH} represents an asymptote, and c is a rate parameter. This model was first proposed by Schumacher (1939) for use in forest productivity studies. The SH model was also used to estimate forest unit richness.

Comparative Difference Measures

Four basic estimates for each plant life form group from each survey unit were available for subsequent analysis: $E(SP_{UNIT})$, $E(SF_{UNIT})$, $E(SP_{SLR})$, and $E(SF_{SLR})$. These estimates were based on the predictions of models discussed in the previous section.

We used two paired differences as dependent variables for assessment. For a plant life form group in any given survey unit, we defined sample limit richness difference as $D_{SLR} = E(SP_{SLR}) - E(SF_{SLR})$ and unit richness difference as $D_{UNIT} = E(SP_{UNIT}) - E(SF_{UNIT})$. We analyzed both difference measures by paired differences and analysis of variance (ANOVA)/covariance methods (Snedecor and Cochran 1967). Because difference measures are differences in estimates rather than measurements, they have variance components that are not included in analytical model formulations and therefore may underestimate overall model precision. We note, however, that under a null hypothesis [e.g., H_0: $E(D_{UNIT}) = 0$], acceptance is unaffected by negatively biased variance estimates.

We used *P* values as a means of assessing differences in species richness. In statistical significance testing, the *P* value is the probability of obtaining a test statistic at least as extreme as the one that was actually observed (D_{SLR} or D_{UNIT}), assuming that the null hypothesis is true (H_0: no difference between species richness within plantation and forest components). It is common to reject the null hypothesis when the *P* value is less than the significance level α, which is often 0.05 or 0.01. When the null hypothesis is rejected, the result is said to be statistically significant. Actually, *P* values are underestimated here, which makes the acceptance of no significant difference a conservative result.

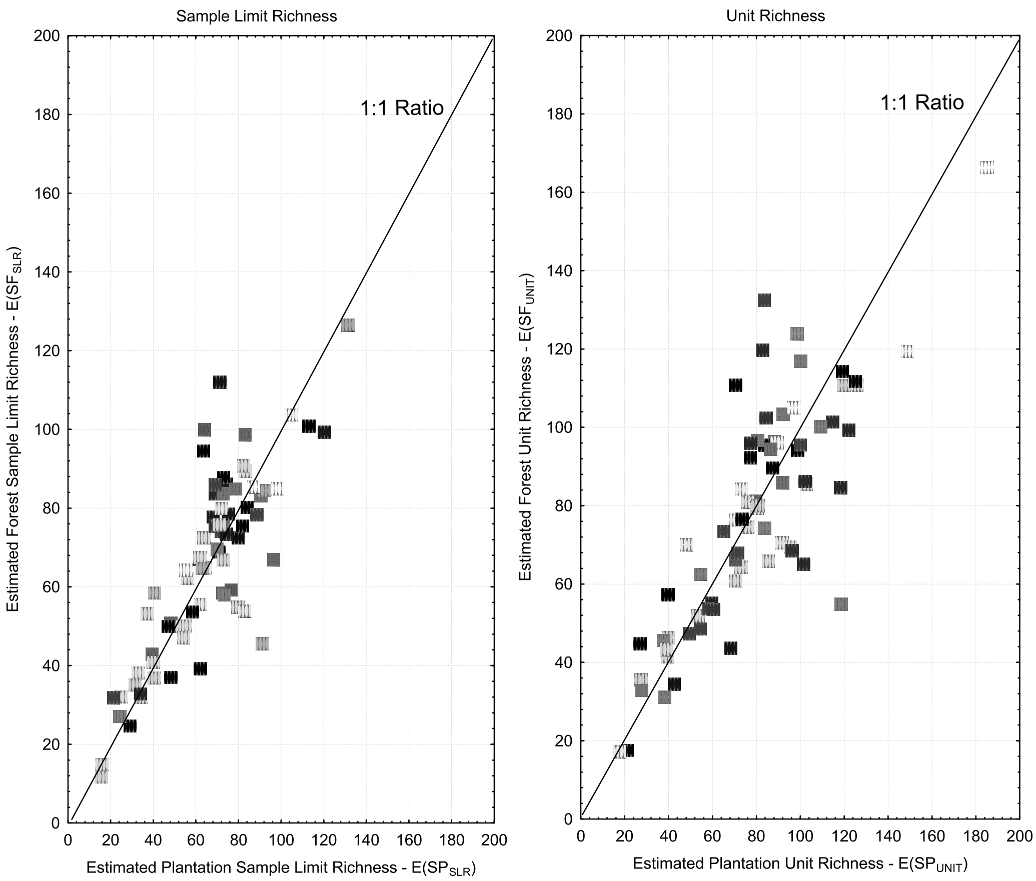

Figure 3. Estimated species richness for 73 paired plantation and forest components for the ALL species plant group (total number of species in all life-form groups). $E(SF_{SLR})$, estimated forest sample limit richness; $E(SF_{UNIT})$, estimated forest unit richness; $E(SP_{SLR})$, estimated plantation sample limit richness; $E(SP_{UNIT})$, estimated plantation unit richness.

We used additional diagnostics to aid in interpretation, including estimates of the following:

1. Ratios of means (e.g., $\overline{E(SP_{UNIT})}/\overline{E(SF_{UNIT})}$) provided proportionate views.
2. Reduced major axis (RMA) regressions (Sokal and Rohlf 1995) indicate the degree of linear association between respective component pair estimates. We used plantation components as independent variables [e.g., $E(SF_{SLR}) = b_0 + b_1 \times E(SP_{SLR})$]. Perfect linear (1:1) association between species richness in forest and plantation components would produce coefficient values of 0 and 1, respectively. Approximate likelihood ratio tests were used to test for 1:1 correspondence (e.g., H_0: $b_0 = 0$, $b_1 = 1$).
3. Pearson's product-moment correlation coefficients (r) for both richness definitions provided an index of variability between survey units. Values of $|r|$ in the range of 0.70+ indicate low levels of variability.

Seral Class and Species Composition

Seral Class.—Based on habitat descriptions in Hickman (1993), Fites (1993), *Flora of North America* (Flora of North America Editorial Committee 1993–2009), Barbour et al. (2007), and Sawyer et al. (2009), we classified species by habitat preference according to where they were most frequently found: in early seral or disturbed sites; in stands of intermediate age or open-canopy forests; or in late-seral, closed-canopy forests. We compared habitat preference between survey components by ANOVA.

Rare and Nonnative Plants.—The California Native Plant Society maintains a special status list of rare, threatened, and endangered plants in California (subsequently referred to as "rare plants"). Each rare plant is assigned a threat code as a means of classifying endangerment (CNPS 2001). Similarly, the California Invasive Plant Council maintains an inventory of nonnative and potentially invasive plant species that pose threats to native ecosystems. It categorizes nonnative plants by a criteria system that evaluates their degree of threat (limited, medium, or high) to native ecosystems (California Exotic Pest Plant Council 1999). We tabulated frequencies of occurrence of rare and nonnative plants by survey unit components as a means of summarization.

Results and Discussion

Species Richness

Field surveys identified a total of 738 unique species across the study area. We recorded a total of 694 species along band transects within the survey units (581 in forest components and 587 in plantation components). An additional 44 species were identified in the intuitive-controlled floristic surveys within plantation components. On average, 10% of the species encountered within a survey unit

Table 6. Univariate *P* values [H_0: estimated sample unit difference = 0] and proportion of variances (in parentheses) accounted for in unit richness differences by factor, life form group, and unit type. Bold entries have *P* values ≤ 0.05. Cells without entries have *P* values >0.10 and accounted for at most 1.0% of the variation.

Factor	Life form group				
	ALL	Forbs	Graminoids	Shrubs	Trees
Forest type					**0.03 (0.10)**
Province					
Herbicide application				**0.02 (0.12)**	
Elevation, ft.			**0.01 (0.08)**		
Plantation area, ac					
Total plantation transect length, ft					
Plantation age, years				0.08 (0.02)	
Canopy cover					
Basal area, ft^2/ac					

were classified as unknowns, and all unknowns were in the forb and graminoid life form groups. Overall, no significant differences in species richness were found between the forest and plantation components of survey units.

Unit richness model asymptotes (A_{SH}) estimated for both forest and plantation components were found to average 0.33 species higher than extrapolations. Table 3 summarizes data means, ratios of means ($\overline{E(SP_{UNIT})}/\overline{SP_{UNIT}}$), bias ($\overline{E(SP_{UNIT})} - \overline{SP_{UNIT}}$), and standard errors in forecasting for each plant life form group. Estimates were slightly high overall, but only the graminoids showed a significant bias ($P = 0.02$). Examination of the data indicates that two outliers were the apparent cause and occurred where sample data were not sufficient to clearly define asymptotic trends. We did not adjust for bias because there were no corresponding data for forest components, and subsequent comparisons with plantation components were based primarily on differences and proportions.

Average species unit richness estimates were 79 species for plantation components and 78 species for forest components (Table 4). Sample limit richness estimates ranged from 78 to 85% of unit richness estimates for each plant group and component except trees, where the value for both survey components was 93% (Tables 4 and 5). Neither richness difference measure was significant for any plant life form group at conventional confidence levels ($\alpha = 0.05$). As presented in Tables 4 and 5, species richness differences between survey units were close to 0, and ratio of means was close to 1. We did find, however, that plantation components were slightly richer in forbs and graminoids, and forest components were slightly richer in trees and shrubs.

The *P* values for RMA regressions indicate overall isometric relationships between forest and plantation richness for both difference measures and every plant group, with the exception of trees for sample limit richness. Correlation coefficients tend to range from 0.70 to 0.85, indicating significant and strong overall linear relationships between forest and plantation component richness (Tables 4 and 5). Individual survey units, however, could be quite variable, as can be seen in Figure 3 for ALL species. But overall, no significant differences in species richness were found between forest and plantation components of survey units. At the time of sampling, species richness in plantation components inventoried less than 12 years postharvest was similar to that of adjacent forest matrices, which represent preharvest species richness conditions for these forest landscapes with histories of multiple entries.

Effects of Unit Attributes and Herbicide Treatment on Species Richness

We analyzed the influence of specific factors on the richness differences of each plant life form group. Single-factor analyses of variance were used for categorical factors, and linear-regression slope tests were used for continuous factors. Sample limit and unit richness difference results were similar, so we reported only the latter. Categorical factors examined were floristic province, forest type, and herbicide class (none, herbicide application within 2 years of survey [HA ≤2YR], and last herbicide application 3 or more years before survey [HA ≥3YR]). Continuous factors examined were elevation, plantation age, plantation area, plantation total transect length, forest canopy cover, and forest basal area.

We found only a few factors to be significant ($P \leq 0.10$) in explaining differences in species richness for any of the life form groups examined, shown here in Table 6. Forest type was significant ($P = 0.03$) for the tree group. Examination of plantation records indicates that these differences are largely silvicultural and reflect different planting species mixes used in different forest types and locations.

Herbicide class ($P = 0.02$) was significant for the shrubs group within HA ≤2YR plantations. Contrasts indicate no difference between the "none" and HA ≥3YR classes. The HA ≤2YR class, however, averaged approximately three fewer species in plantation components, reflecting the response of targeted shrubs to the herbicide treatment or perhaps the time required for shrubs to establish following regeneration harvests. Although the impact on shrub richness was significant, it was short-lived; extirpation did not appear to have been an issue, and by the third year following application, the impact was no longer significant. Potential negative impacts of herbicide applications on the composition of understory vegetation are discussed by Halpern and Spies (1995).

We believe that a significant contributing factor explaining the lack of impact on species richness following herbicide applications in regenerating plantations in the HA ≥3YR class is that plant species likely sprouted or established from soil-stored or off-site seed after herbicide spraying. Results from this study support previous findings in western forests that herbicide treatments performed under current silvicultural methods do not reduce vascular plant diversity in plantations or that, if an impact is found, it lasts only about 2 years (DiTomaso et al. 1997, Battles et al. 2001, McDonald and Fiddler 2006). Forest managers should be aware that herbicide applications temporarily reduce shrub species richness. However, within 2 years of application, shrub species richness returns to pretreatment levels.

Plantation age ($P = 0.08$) for the shrub group also indicates that plantation components gained an average of 0.5 shrub species per year relative to forest components. Elevation is a highly significant factor ($P = 0.01$) for graminoid richness difference and indicates that forest components became one species richer per 500-ft gain in elevation in both forest types. Remaining factor/plant life form group associations had *P* values >0.10.

Seral Class

Overall, intermediate seral class species dominated both forest and plantation components in all survey units. The 738 species identified studywide were classified by seral class as 23% disturbance (170 species), 73.7% intermediate (544 species), and 3.3% late (24 species). The 694 species identified within the area transects broke down by seral class as 23.6% disturbance (164 species), 73.1%

Table 7. The average number of native and nonnative species per survey unit by life form group, seral class, and survey unit component. Numbers in parenthesis are sample standard deviations. Bold cells are significantly different (*P* values <0.05). *n* denotes the number of survey units where one or more life form group × seral class occurred in either the plantation or forest component. Cells with no entries had no observations. *r* is Pearson's correlation coefficient computed for the number of species found in the plantation and forest components of survey units.

		Native plants				Nonnative plants			
Life form group	Seral class	Plantation	Forest	*n*	*r*	Plantation	Forest	*n*	*r*
Forbs	Disturbance	**10.62** (5.56)	**6.95** (4.65)	73	0.75	2.10 (1.63)	1.40 (1.37)	63	0.71
	Intermediate	20.15 (9.36)	21.8 (10.15)	73	0.83	0.09 (0.33)	0.08 (0.34)	10	−0.16
	Late	0.94 (1.11)	2.78 (1.70)	66	0.54				
Graminoids	Disturbance	1.70 (1.30)	1.46 (1.09)	68	0.68	0.85 (1.02)	0.57 (0.88)	41	0.56
	Intermediate	7.53 (3.58)	7.44 (3.60)	73	0.72	0.34 (0.89)	0.34 (0.72)	22	0.57
	Late	0.02 (0.16)	0.03 (0.20)	5	−1.00				
Shrubs	Disturbance	2.60 (1.05)	2.32 (1.13)	72	0.54				
	Intermediate	7.03 (3.01)	7.60 (3.16)	73	0.77	0.06 (0.28)	0.04 (0.23)	8	−0.58
Trees	Intermediate	6.20 (2.17)	6.5 (2.60)	73	0.85				

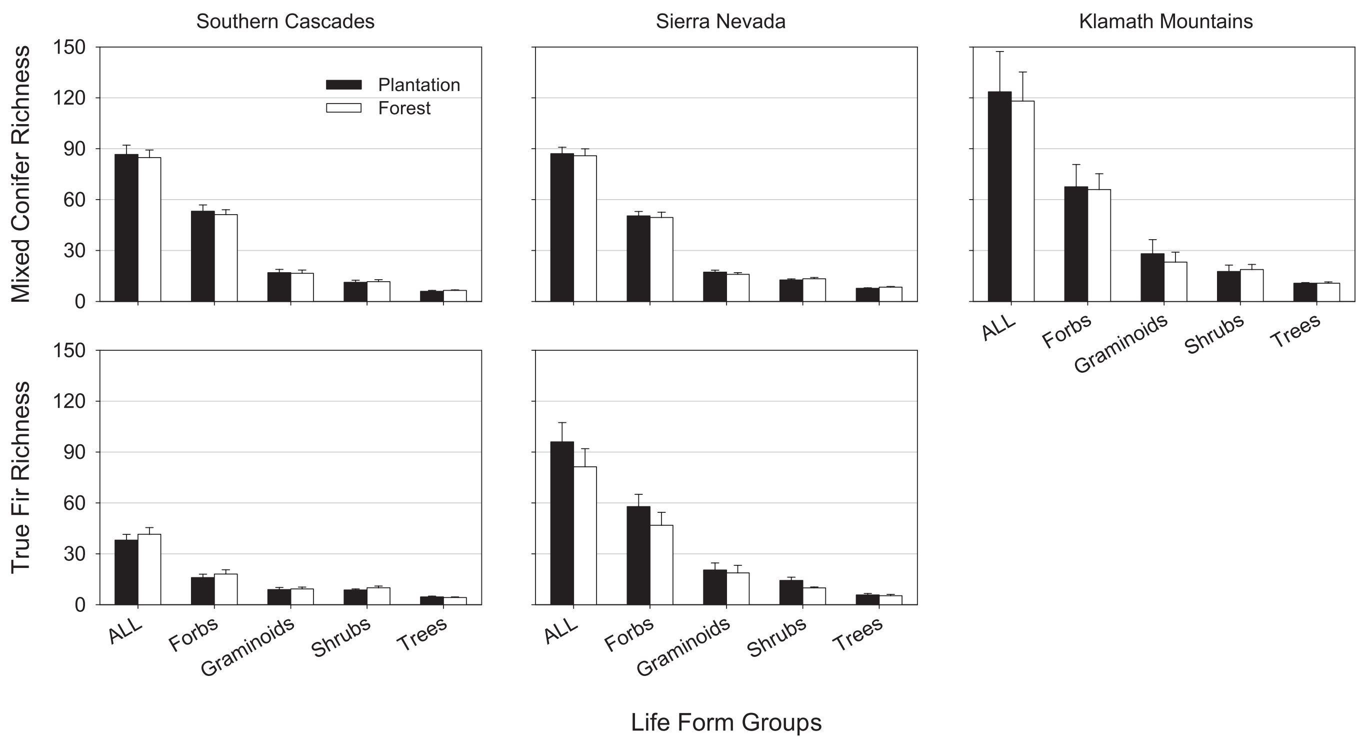

Figure 4. Comparison of forest type and floristic province by individual life form groups based on estimated forest and plantation unit richness. ALL, total number of species in all life-form groups.

intermediate (507 species), and 3.3% late (23 species). The additional 44 species found in the complete survey were classified as 13.6% disturbance (6 species), 84% intermediate (37 species), and 2.4% late (1 species). The average numbers of species delineated by life form group, seral class, survey unit component, native plants, and nonnative plants are presented in Table 7: significantly more forbs in the disturbance seral class were found in plantation components than in forest components, but these were the only life form group where significant differences were found between survey-unit components. The large number of intermediate seral species found within survey units reflects the heterogeneity of habitats within even-aged plantations and uneven-aged forest matrices and the ability of those species to respond favorably to disturbance over time. Results from this study support observations that following disturbance, individual species' postharvest responses and species richness are affected by the type of forest management used, an individual species' life cycle characteristics, and preharvest environmental and site characteristics (Roberts and Gilliam 1995).

Geographic Influence on Species Richness

We based our comparisons of forest type and floristic province on estimated forest and plantation unit richness. As Figure 4 shows, differences between forest and plantation unit richness for each life form group within a particular forest type and floristic province were not significant. We found little difference in unit richness between estimates for the mixed-conifer forest type in the Sierra Nevada (82 species) and Southern Cascades (86 species) floristic provinces, but the Klamath Mountains (113 species) floristic province had approximately 40% greater species richness. Species richness estimates within the true fir forest type were much higher in the Sierra Nevada (86 species) floristic province than in the Southern Cascades (42 species). There were no potential true fir forest type survey units that

Table 8. Number of survey units in which rare and other special status plants were present (73 total survey units).

Species	CRPR[a]	Number of survey units present		
		Plantation	Forest	Both
Arctostaphylos mewukka ssp. *truei*	4.2	1	1	1
Arnica venosa	4.2	1	0	0
Calystegia atriplicifolia ssp. *buttensis*	4.2	2	0	0
Ceanothus fresnensis	4.3	2	1	1
Clarkia virgata	4.3	1	0	0
Lomatium engelmannii	4	0	1	0
Penstemon cinicola	4	1	0	0
Rupertia hallii	1B.2	3	3	3
Smilax jamesii	1B.3	0	2	0
Thermopsis californica var. *argentata*	4.3	0	1	0
Thermopsis gracilis var. *gracilis*	4.3	0	1	0
Veratrum insolitum	4.3	1	1	1
Total		12	11	6

[a] The California Native Plant Society maintains a list called California Rare Plant Rank (CRPR), which categorizes the rarity of plants (California Native Plant Society 2001). It comprises four ranks, or categories: CRPR 1A, plants presumed extinct in California; CRPR 1B, plants that are rare, threatened, or endangered in California and elsewhere; CRPR 2, plants that are rare, threatened, or endangered in California but more common elsewhere; CRPR 3, plants about which more information is needed; and CRPR 4, plants of limited distribution—a watch list. More information can be found at the organization's Web site (California Native Plant Society 2001). In this table, we have added an extension to the CRPR denoting the level of endangerment for these species in forest and plantation survey units using a rank of 1 to 3, with 1 being the most endangered and 3 the least.

Table 9. Number of survey units in which nonnative plants were present (73 total survey units).

Species	Cal-IPC rating[a]	Number of survey units present		
		Plantation	Forest	Both
Agrostis stolonifera	Limited	2	0	0
Anthoxanthum odoratum	Moderate	0	2	0
Avena barbata	Moderate	1	0	0
Avena fatua	Moderate	1	1	0
Brassica nigra	Moderate	1	0	0
Bromus diandrus	Moderate	6	4	4
Bromus hordeaceus	Moderate	10	8	7
Bromus tectorum	High	36	18	18
Centaurea solstitialis	High	3	1	1
Chondrilla juncea	Moderate	1	1	1
Cirsium arvense	Moderate	14	14	11
Cirsium vulgare	Moderate	55	39	38
Cynosurus echinatus	Moderate	11	11	9
Dactylis glomerata	Limited	2	2	2
Erodium cicutarium	Limited	3	0	0
Geranium dissectum	Moderate	1	0	0
Holcus lanatus	Moderate	6	4	4
Hypericum perforatum	Moderate	7	5	3
Hypochaeris glabra	Limited	3	0	0
Hypochaeris radicata	Moderate	1	1	1
Isatis tinctoria	Moderate	2	0	0
Leucanthemum vulgare	Moderate	2	2	1
Lolium multiflorum	Moderate	1	1	0
Marrubium vulgare	Limited	2	0	0
Plantago lanceolata	Limited	1	3	0
Poa pratensis	Limited	1	1	0
Poa pratensis ssp. *pratensis*	Limited	1	6	1
Rubus discolor	High	6	4	2
Rumex acetosella	Moderate	20	17	14
Taeniatherum caput-medusae	High	3	1	1
Torilis arvensis	Moderate	10	10	9
Verbascum thapsus	Limited	33	14	13
Vulpia myuros var *myuros*	Moderate	9	8	5
Total		255	178	145

[a] The California Invasive Plant Council (Cal-IPC) publishes the Invasive Plant Inventory ratings (California Invasive Plant Council 2012). Each nonnative species is ranked high, moderate, or limited on the basis of the severity of its impact on California ecosystems.

met our sampling criteria located within the Klamath Mountains floristic province. Reasonably consistent proportions were observed within each plant group across all provinces for the mixed-conifer forest type, although the Klamath Mountains floristic province was consistently higher. Estimates for the true fir forest type in the Sierra Nevada floristic province were more than 100% greater than for the Southern Cascades for the ALL species group, with differences largely due to forbs. Although we did not find differences in species richness within individual survey units, we conclude that forest type and floristic province influenced overall level of species richness.

Presence of Rare and Other Special-Status Plants

When we analyzed transect survey data, we found 23 rare and other special-status plants within the survey units (Table 8). The complete surveys in plantations (described above, in the "Intuitive-Controlled Floristic Surveys" section), yielded six additional rare plant occurrences not found in plantation or forest transects but no new species. The California Native Plant Society lists two of the six species (*Rupertia hallii* and *Smilax jamesii*) as "rare, threatened, or endangered in California and elsewhere" (California Rare Plant Rank 1B), and state regulations require that specific plant protection measures be implemented when these plants are found where timber harvest operations are planned. The other 21 species found are classified California Rare Plant Rank 4: species having a limited distribution that have been placed on a watch list by CNPS. These special-status plants (also known as CNPS watch list species) currently require no extra protection during timber harvest operations (CNPS 2001). Based on individual table entries and the totals, forest and plantation components supported rare plants equally. Forest managers should be aware that rare and special species may be present in areas where forest management operations occur and should take measures to protect them.

Presence of Nonnative Plants

Based on transect data, we found 33 nonnative plant species in 65 of the 73 survey units (Table 9). Sixty-three plantation components and 58 forest components had one or more nonnative taxa. The complete plantation survey indicated 67 additional occurrences not found in plantation or forest transects and four new species: soft brome (*Bromus mollis*), common pokeweed (*Phytolacca americana*), common groundsel (*Senecio vulgaris*), and rat-tail fescue (*Vulpia myuros*). On the basis of the information in Tables 7 and 9, we found that plantation components averaged 1 species richer in nonnative species than forest components. On average, 3.48 nonnative species were present in plantation components and 2.44 nonnative species in forest components. Overall species richness within and between plantations and forests was not significantly affected by the presence of nonnative plants.

We found only 13 of 59 nonnative species listed as potential threats in the Sierra Nevada by D'Antonio et al. (2004) and conclude that managers need not assume that all documented nonnative plant species are highly invasive The entire upper quartile of nonnative plant occurrences in plantations comprise species found in a range of stable as well as ruderal plant communities and are not correlated per se with plantation management forestry operations (Bossard et al. 2000). Bull thistle (*Cirsium vulgare*) was the most common nonnative plant species in plantation and forest components. It is distributed throughout the world and occurs in both intact and destabilized plant communities (Bossard et al. 2000).

This species often dominates other herbs within plantations in the Sierra Nevada (McDonald and Tappeiner 1986), is known to reduce growth and yield of pine seedlings in plantations (Randall and Rejmanek 1993), and is therefore a frequent target of herbicide applications. Cheatgrass (*Bromus tectorum*) was also present in many survey units. This ubiquitous annual graminoid has virtually no effective control, and its range is still expanding (Novak and Mack 2001). Some species, such as Klamath weed (*Hypericum perforatum*), may not warrant extra prevention measures because of successful biocontrol efforts in the portion of its range where it has affected other economically important species. Other species, such as bull thistle, may warrant control if they reduce survival and growth of conifer seedlings in plantations (Randall and Rejmanek 1993).

Our results demonstrate the widespread nature of nonnative plants, and land managers may want to develop strategies to prevent further spread of specific species (US Forest Service 2001). Recently published research (US Forest Service 2008) can serve as a guide for landowners seeking to prevent and control nonnative plants as part of their forest management activities. These reports recommend that managers inventory nonnative plants, evaluate control methods at each site, and require off-road and earth-moving equipment and vehicles used for project implementation to be weed-free. They also recommend that mulches and seed sources be weed-free and that equipment, materials, and crews avoid areas infested with nonnative plants if there is a risk of spread to areas of low infestation.

Conclusions

Results from this study confirm that species richness varies by forest type and floristic province across the entire study area but indicate no difference in species richness between young plantations and managed forest matrices within the same forest types and floristic provinces.

At the individual survey unit scale (plantation and forest components), we found that forest type, floristic province, and elevation influenced overall species richness. In addition, we noted that there was a short-lived negative impact on shrub species richness in plantations where herbicides had been applied in the 2 years prior to the surveys but that shrub species richness quickly rebounded.

We found that plantation management does not significantly influence differences in species richness between plantations and surrounding managed forests because existing species tend to remain or repopulate both areas following harvest and subsequent regeneration. We suggest that future studies include simultaneous botanical surveys of plantations and adjacent forests, which would allow researchers to more accurately compare and evaluate species richness within the context of the local floristic province and silvicultural history.

We found that rare plants and special-status plants were equally distributed between plantations and surrounding managed forests but that plantations averaged one additional nonnative species. We encourage managers to be aware of rare and special-status plants that may be present in areas where forest operations occur and to implement effective protection measures to ensure their survival in future forest landscapes. We also found that nonnative plant species were widespread throughout the study area. Managers can follow suggestions outlined in the previous section to control their spread and take sensible precautions to protect existing native species from further impacts. Finally, we encourage additional, ongoing research on the effects of forest harvest operations on biological diversity at the management scale.

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