

Use of species richness estimators improves evaluation of understory plant response to logging: a study of redwood forests

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Abstract The recovery of native understory plant communities after timber harvest has received a great amount of attention worldwide. However, most of these studies have ignored the potentially significant effects that differences in habitat across forest development may have on the species–area relationship, even though sampling efficacy among forest developmental stages may differ markedly as a result of equal sampling within stages. We examined vascular plant community structure in coastal redwood forests of northern California (USA) in forest patches in each of four forest stages that develop with forest age: Initiation, Closure, Mature, and Old-growth. We also used a set of traditional and novel approaches to assess sampling efficacy and guide our sampling design. We initially sampled 75 circular plots (0.04 ha) in stands within each forest stage across a 1,347 km² area. The species–area relationship suggested we had adequately sampled all stages after the first season of data collection, but non-parametric richness estimators (Incidence-based Coverage Estimator or ICE) and Michaelis–Menten means (MMMeans) rarefaction curves, indicated inadequate sampling of the older stages. Thus, we

added four more samples within the Old-growth forest stage, establishing a more equitable sample of all stages. Our full data set demonstrated significant differences between plant communities in previously harvested forests (‘managed’ = Initiation, Closure, and Mature) and ‘unmanaged’ forests (Old-growth). Though several understory species were present in all stages, a suite of Old-growth indicator and restricted species suggest that recovery of some species may take long periods in managed forests. Interestingly, a separate suite of common understory species were lacking in Old-growth, and species richness in this stage was lower than in the mature managed forests. We discuss how this departure from the prediction of peak richness in Old-growth may relate to fire suppression in Old-growth forests. Lastly, analysis of our initial, smaller sampling of plots suggested that Old-growth plots were the least species rich. However, additional sampling of the Old-growth stage demonstrated that Old-growth plots were as rich as Closure plots. This has important implications for all studies concerned with measuring recovery after forest disturbances; stage-dependent habitat-mediated differences that affect sampling efficacy may not be captured by traditional sampling methods.

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Introduction

In forests that are intensively managed for timber, community response to disturbance is of particular conservation interest because stand rotation logging imposes serial catastrophic disturbances to which forest species must respond (Jules 1998; Verheyen et al. 2003; Dignan and Bren 2003). This disturbance regime creates a patchwork of forest blocks, each at various stages of stand development and, therefore, a mosaic of habitats variously suitable for forest understory species. Because some species may recover slowly after disturbance (Moola and Vasseur 2004; Donohue et al. 2000), their persistence across the landscape will be dependent on several key factors, including rate of population increase, propagule abundance, dispersal mode, and the rate of harvest rotation. Site- and landscape-scale features of timber harvest disturbance may be particularly important for plants, which generally rely on seed dispersal to move from disturbed to suitable habitat. Thus, understory plant species must either persist through the disturbance or recolonize when, and if, the site becomes suitable again (Grime 1986).

The recovery of plant communities after timber harvest has been the subject of a large pool of literature (reviewed in Harris et al. 1982; Franklin 1982; Oliver and Larson 1996; and Franklin et al. 2002; for example). However, the results of these studies differ markedly (Dyrness 1973; Peet and Christensen 1988; Frost 1992; Sullivan et al. 2001; Battles et al. 2001; Costa and Magnusson 2002). For example, Greenberg et al. (1995) found an increase in species richness and diversity following post fire salvage logging in a fire-adapted sand pine scrub forest. In other cases, diversity initially decreased, especially among forest interior species (Meier et al. 1995; Roberts and Zhu 2002), then quickly recovered within a few decades (Peet and Christensen 1988; Hannerz and Hånell 1997; Gilliam 2002; Gilliam et al. 1995; Roberts 2002). This later pattern of community development was also documented in fixed plots measured prior to logging and 28 year later in a mixed Douglas-fir forest in the Pacific Northwest (Halpern and Spies 1995). In contrast, richness and herbaceous cover in eastern deciduous forests was lower in secondary forests recovering from timber harvest than in primary forests, even when the secondary forests were as old as 87 years (Duffy and Meier 1992). This

result is supported by studies in several other forest types (Peterken and Game 1984; Whitney and Foster 1988; Dzwonko and Loster 1989).

The diversity of these past findings may result in part because community recovery is systemspecific and influenced by numerous biotic and abiotic factors (Halpern 1989; Roberts and Gilliam 1995; Roberts 2004). Alternatively, while conflicting results may have system-specific, ecologically-based explanations, differences may also be attributable to habitat-specific effectiveness of sampling species richness. Though the species–area relationship is well documented, there is also a generally positive relationship between the number of individuals in a sample and richness (Colwell and Coddington 1994; Gotelli and Colwell 2001). So comparable samples will not necessarily be achieved using a sampling design with equal numbers of sampling units across different communities in which the number of individuals of a particular species varies significantly (Colwell and Coddington 1994). Thus, past studies that have used balanced sampling designs may have been inadequate for addressing the very questions they were intended to answer. Likewise, most studies that do not employ balanced designs have not addressed habitat-specific sampling efficacy (Peterken and Game 1984; Halpern and Spies 1995). A growing suite of analytical techniques has been developed recently to contend with estimating species richness where abundance varies (Gotelli and Colwell 2001; Longino et al. 2002), however none of these have been applied to studies which assess the recovery of forest diversity after logging.

In this study, we assessed the influence of clearcut logging on community structure and richness, and, more importantly, used a suite of newly developed analytical tools to provide a critique of traditional assessments of diversity recovery rates. In addition, ours is the first study to examine the effects of stand rotation logging on understory plant communities in redwood forests. The redwood forest system is ideal for asking how methods for assessing community metrics compare because it is a discrete system with a long history of intensive management similarly applied over the region, yet remnant unlogged stands exist in the matrix of managed forests. In this study, we explored the relationship between understory vascular plant diversity and forest development, time since disturbance, and environmental factors across

forest stages spanning new clearcuts to old-growth redwood forests.

Methods

Study area

We studied understory vascular plant community structure in redwood forests of central and southern Humboldt County, California, USA during the spring and summer of 2003 and 2004. The study included redwood forests of various ages across four ownerships: the Bureau of Land Management's Headwaters Forest, the City of Arcata's Jacoby Creek Forest, Humboldt Redwoods State Park (HRSP), and the Pacific Lumber Company (PL) holdings. The study area encompassed approximately 1,347 km². The majority of the study area has been clearcut at least once, and the timberland forests are a patchwork of cut blocks of various ages and developmental stages. Unlogged forest occurs in remnant patches across the landscape and was sampled from the Headwaters Forest, HRSP, and PL land.

Sampling design

A total of 79 plots were sampled during the flowering period of most forest species. Plot selection was restricted to redwood-dominated forests greater than 50 m from class-I and -II watercourses, at least 10 m from permanent, mapped roads, and at slopes between 20% and 60%. All aspects were sampled, but special habitats, such as riparian areas, forest wetlands, rock outcrops, and alluvial flats, were excluded. Each plot was located at least 250 m from other plots. Locations matching these criteria were generated in ArcView GIS 8.0 and located in the field using a Magellan® (San Dimas, CA) GPS receiver. At each location, temporary circular plots measuring 0.04 ha (11.3 m radius) were established for data collection.

To assess the relationship between understory plant community structure and stand development, we stratified samples in the field by assigning each plot to one of four forest developmental stages based on stand characteristics. The forest stage categories used were: Initiation—recently cleared (i.e., trees harvested), completely open-canopied plots; Closure—closed canopies, high stem density, small

diameter at breast height (dbh; mean = 40 cm), high small-stem mortality, and vertically undifferentiated canopies; Mature-closed to partially open canopies, lower stem density, larger dbh (mean = 60 cm), low small-stem mortality, and canopies with vertical structure due to dominant trees; and Old-growth—unlogged stands with very large trees (mean dbh = 133.4 cm).

To quantify understory vascular plant community structure, we recorded presence and cover of the entire vascular flora in the herbaceous layer in each plot. We defined the understory community physiognomically, arbitrarily separating the herbaceous layer from the shrub layer at 1-m. Each species was assigned one of the following cover classes: (1) <25%, (2) 26–75%, (3) >76. Nomenclature followed The Jepson Manual (Hickman 1993).

We recorded site characteristics at each plot to evaluate the relationship between community structure and environmental variables. We measured slope, aspect, and elevation, and visually estimated percent cover for canopy, shrub and herb layers as well as cover of bare mineral soil and woody debris. Each plot was assigned a woody debris decay class based on the average state of decay of all large pieces of woody debris. We also estimated the distance in meters from plot center to the interface between contiguous forest and forest opening, hereafter edge distance. In addition, the distance of each plot from the coast both linearly and by creek kilometers was determined from GIS data.

Since site quality affects rates of tree growth, stand descriptions related to tree size may lead to specious estimations of stand age (Watt et al. 2003; Andreasen and Tomter 2003), and, therefore, community compositional gradients associated with age of forest. To independently verify the chronological basis for our developmental stages, we estimated plot age for a random subset of the plots managed for timber using standard dendrochronology techniques. Forty-five plots were aged. One to seven trees from the dominant size-class cohort were selected from each aged plot. Cores that intersected the central pith were removed from each tree at breast height using tree ring increment borers. The cores were processed in the lab and the annual growth rings were counted under low magnification. The age of the oldest tree in the plot was used as plot age.

Analyses

Ordination

To assess the relationship between forest stage, site characteristics, and plant community composition, we used Nonmetric Multidimensional Scaling (NMS) with the Bray–Curtis distance measure conducted using the software PC-ORD (version 4.01; McCune and Mefford 1999). The joint plot feature with an r^2 -cutoff of 0.3 was used to explore correlations between site characteristics and community composition. Ordinations were performed on the full data set and on a subset of native plants only to tease apart the effect of early colonization of non-native species.

The data were prepared to improve multivariate fit and to facilitate interpretation of the results. Species that did not occur in more than 7.5% of the plots were excluded from analysis. One “Mature” plot was excluded due to insufficient site characteristic data; the final species matrix measured 78 plots \times 93 species. Edge distance was log transformed. The final matrix of site characteristics measured 78 plots \times 20 variables. Finally, we performed rigid visual rotations of the ordinations to maximize the percent variation explained along the two most dominant axes. Axes lacking interpretative value were not assessed.

Differences in community structure among forest stages were then assessed in PC-ORD using a Multiple Response Permutation Procedure (MRPP). All pair-wise comparisons of forest stages were made. We used a Bonferroni corrected critical value to maintain family-wide significance levels of $\alpha = 0.05$. The adjusted critical value was $\alpha/(\text{number of tests}) = (0.05/7 = 0.0357)$. For ease of interpretation, we present adjusted P -values instead of adjusted alpha.

Indicator species analysis

We assessed fidelity to each forest stage using an indicator species analysis (ISA) in PC-ORD (McCune and Mefford 1999). This analysis assigns a Dufrêne and Legendre (1997) indicator value, which describes the affinity of each species to each forest stage. For each species, indicator value differences among stages were tested using a Monte Carlo simulation of 1,000 runs with a critical value of $\alpha = 0.05$.

Richness estimators

Average richness

We used species richness to compare diversity among forest stages and to assess sampling efficacy within each stage. To determine whether there were differences in richness among forest stages, average sample richness was compared for the full data set and the non-native subset using Kruskal–Wallis One-way ANOVA in NCSS (Hintze 2001); these data did not satisfy parametric test assumptions. Native richness among forest stages was compared using ANOVA. All pair-wise comparisons were made using a Tukey–Kramer Multiple Comparisons test or, the nonparametric alternative, the Kruskal–Wallis Multiple-Comparison Z -value test. Bonferroni adjusted critical values were used for the Z -value multiple comparison tests.

Species accumulation and rarefaction curves

We also estimated total species richness with species accumulation and rarefaction curves. The accumulation and rarefaction curves can be used to compare richness across stages (Gotelli and Colwell 2001). In this study, however, the curves were used primarily to assess the validity of between-stage comparisons of richness. Valid comparisons can only be based on samples that adequately describe the richness of each habitat being compared. So, by assessing sampling efficacy of each stage, we determined which comparisons were likely based on adequate samples.

Sampling effectiveness can be inferred based on the behavior of the accumulation curve. Generally, sampling is considered adequate when the rarefaction or other richness estimator curve levels off asymptotically. A good estimator is one that becomes independent of sampling effort relatively early, remains stable, and is little affected by species patchiness or sample order (Gotelli and Colwell 2001). Richness estimates used to compare communities should be derived from effort-independent estimator curves.

Species–area curves were produced for each forest stage in PC-ORD (McCune and Mefford 1999). This software generates estimates of total species richness by iteratively subsampling randomly selected plots for each level of sampling effort (i.e., number of

plots) and calculating total richness for each run. The averaged estimates of total richness for each level of sampling were graphically portrayed as a plot of richness against number of plots.

Because richness estimates in sampled communities may differ due to differences in abundance of individuals, standard statistical techniques for comparing species richness may be misleading (Colwell and Coddington 1994; Chazdon et al. 1998). That is, one community may be more or less thoroughly sampled as compared to another using the same number of plots in each community if the number of individuals affects estimates of richness. Rarefaction techniques scale species richness estimates by individual abundance levels (Colwell and Coddington 1994; Colwell 2000; Gotelli and Colwell 2001).

For this reason, total species richness was also estimated using Michaelis–Menten rarefaction curves. We calculated Michaelis–Menten Means (MMMeans) curves using the computer program EstimateS (version 6; Colwell 2000). This is a sample-based rarefaction method that generates asymptotic estimates of total richness for each pooling level. Estimates are made once per pooling level by using the smoothed asymptotic estimator curve from a simulation of randomized plot order. This method suppresses the effect of outliers and produces a smoothed curve (Colwell 2000). We used the EstimateS default settings of sampling without replacement, parameter values fitted according to Raaijmakers' (1987) Eadie-Hofstee equation, and simulations consisted of 50 runs.

Non-parametric richness estimator

In addition to the species accumulation and rarefaction curves, we used EstimateS to generate non-parametric richness estimates. Some non-parametric estimators, such as the incidence-based coverage estimator (ICE), may provide reliable estimates of species richness at even low levels of sampling effort (Colwell and Coddington 1994; Chazdon et al. 1998; Walther and Martin 2001; Foggo et al. 2003; Brose et al. 2003). We converted the data to presence/absence and calculated the ICE (Lee and Chao 1994) using EstimateS. ICE uses the concept of statistical coverage to estimate true richness, including undiscovered species, based on the proportions of discovered rare species (Chazdon et al. 1998; Colwell

2000). The ICE estimates were generated for each forest stage using the EstimateS default definition of rare species as those that occur in 10 or fewer plots.

The species–area, MMMeans rarefaction, and non-parametric ICE curves were compared graphically to cross-verify the behavior of each estimator. Additional information regarding sampling efficiency was inferred from graphs of observed species richness, number of Uniques, and number of Duplicates. Uniques are the number of species that occur in only one sample, while Duplicates are those that occur in only two samples. These additional descriptors were calculated in EstimateS. Observed richness is the number of species in random simulated samples for increasing levels of sampling effort.

The EstimateS sample-based estimators can represent species density if plotted against the number of sample units or they can represent species richness if plotted against number of individuals (Colwell 2000; Gotelli and Colwell 2001). This report is concerned with species richness; however, the number of individuals was not tracked during data collection. Instead, we used the number of species occurrences within a forest stage as a reasonable proxy for abundance, and we plotted the number of occurrences along the abscissa (see Longino et al. 2002 for example).

Richness sampling curves that become effort-independent and stabilize suggest thorough sampling. Likewise, curves for Uniques and Duplicates should initially rise quickly with increasing numbers of individuals, then level off and decrease as sampling approaches true richness. This is because the probability of encountering a new species early in sampling is high, while only those species that are truly rare will remain infrequent as the community is more thoroughly sampled. However, estimators may behave differently for different data sets, and estimators that have been tested against benchmark datasets may not perform similarly for other datasets (Chazdon et al. 1998; Gotelli and Colwell 2001). For unstable curves, the ICE was considered a lower estimate of richness (Gotelli and Colwell 2001).

The rarefaction and richness estimators were used to guide further sampling. Preliminary results based on the first season of data collection suggested the need for additional sampling, especially of the Old-growth stage. Four additional plots were selected from the Headwaters Forest. This also served to include more coastal Old-growth forest sampling in the study.

Results

In the 79 plots sampled, we encountered 227 understory vascular plant species in 56 families. Seventy-three percent of these species, including the majority of herbaceous (69%) and all woody species, were native to California. We did not assess native status for species identified only to genus unless the genus is entirely composed of species native to California. Of the 79 plots, 19 were assigned to Initiation, 16 to Closure, 25 to Mature, and 19 to Old-growth. Most plot characteristics did not differ significantly among forest stages (Table 1). However, percent cover of the herb and canopy layers was predictably and significantly different among forest stages. Initiation plots had significantly less canopy cover and, with the exception of the Mature plots, more herbaceous cover than the other forest stages. Though canopy cover was greatest in the Mature stage, the three forested classes were statistically similar in canopy and herbaceous layer percent cover. Old-growth plots had significantly higher edged distance. Geographically, Closure plots were at higher latitudes than Mature and Old-growth plots.

And though there was some overlap in the ages of plots in each stage, the stages did represent distinct age categories.

Community analyses

Ordination

The NMS ordination of the full data set yielded a three-dimensional solution, which accounted for 80.2% of the variation in the data. Over the 400 iterations, the final stress in the solution was 17.76 and instability was 0.0025. Axes 1 and 2 alone explained 67.5% of the variation (Fig. 1). Though there was considerable overlap among Initiation and other managed plots and among forested managed plots and Old-growth plots, the Initiation and Old-growth plots formed distinct groups. The Initiation plot scores were negatively correlated along axis 1 and formed a cluster on the lower extreme of this axis, while the Old-growth scores were positively correlated along axis 1 and clustered opposite the Initiation plots. Together, the Closure and Mature plots formed a single but sparse cluster intermediate between these

Table 1 Summary of site characteristics by forest stage

	Initiation	Closure	Mature	Old-growth	P-value	Test	df
Number of plots	19	16	25	19			
Canopy cover	12.4 (14.8) ^a	69.4 (21.7) ^b	68.3 (15.2) ^b	62.4 (14.4) ^b	<0.0001***	ANOVA	77
Shrub cover	50.0 (21.3) ^{a,b}	38.4 (23.4) ^a	50.1 (28.0) ^{a,b}	63.2 (20.8) ^b	0.0304*	ANOVA	77
Herb cover	51.1 (28.7) ^{a,b}	22.6 (20.1) ^a	32.7 (20.0) ^{a,b}	22.0 (18.4) ^b	0.0014**	K-W	3
Soil cover	5.7 (8.0)	3.0 (7.7)	1.3 (2.6)	2.2 (4.1)	0.0808	K-W	3
Woody debris cover	34.2 (25.8)	38.4 (17.3)	32.9 (18.2)	28.2 (12.7)	0.5259	K-W	3
Slope (degrees)	24.9 (10.0)	28.3 (7.2)	27.4 (9.9)	31.9 (22.1)	0.4797	K-W	3
Elevation (m)	300.2 (148.5)	310.7 (95.3)	273.2 (117.5)	237.6 (113.9)	0.2907	ANOVA	73
Aspect (degrees)	198.7 (126.1)	210.1 (105.9)	195.5 (123.7)	137.7 (91.0)	0.1696	K-W	3
Edge distance (m)	3.7 (16.1) ^a	56.9 (83.1) ^b	63.4 (83.5) ^b	240 (296.7) ^c	<0.0001***	K-W	3
Woody debris decay	2.9 (1.6) ^a	4.3 (0.9) ^b	3.7 (1.4) ^{a,b}	4.6 (1.6) ^b	0.0086**	ANOVA	66
Linear distance from coast (km)	28.3 (7.4)	24.9 (5.7)	27.2 (6.7)	24.8 (6.5)	0.6527	K-W	3
Creek distance from coast (km)	43.9 (15.0) ^{a,b}	32.5 (11.5) ^a	41.1 (17.4) ^{a,b}	52.7 (20.5) ^b	0.0079**	K-W	3
Age	10.2 (7.8) ^a	37.3 (14.7) ^b	56.8 (15.5) ^c	–	<0.0001***	ANOVA	44
UTM east	41,6253.0 (6718)	414,310.5 (3817)	415,024.6 (6976)	416,783.3 (5395)	0.6468	K-W	3
UTM north	4,483,897.0 (13029) ^{a,b}	4,494,369.0 (8592) ^a	4,482,154.0 (15717) ^b	4,473,489.0 (15756) ^b	0.0004***	K-W	3

The mean values and standard deviations (in parentheses) for each of the measured site variables are presented by forest stage

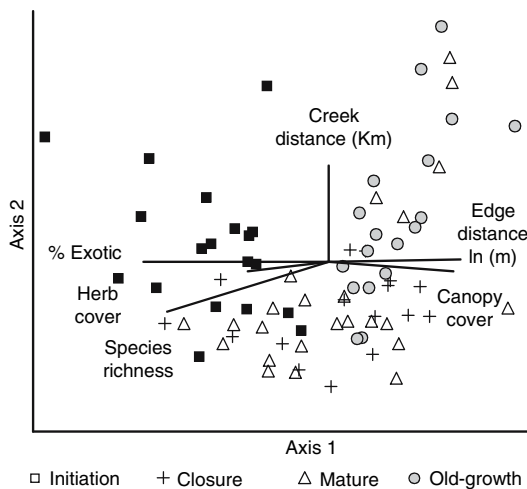


Fig. 1 Nonmetric Multidimensional Scaling ordination of the understory vascular plant community structure in 78 plots across four developmental stages of coast redwood forests. The symbols represent plots in each stage oriented relative to community structure similarity, while the vectors show the strength and direction of correlations among site characteristics and ordination scores where $r^2 > 0.3$

extremes. These three groups were also supported by the MRPP (Table 2). All pair-wise comparisons of stage, except Closure versus Mature, were significantly different. The Closure and Mature stages were indistinguishable ($P = 1.0$). Similar patterns emerged when assessing the native-only data (Table 2).

Few of the measured site characteristics correlated with the ordination scores. Notably however, edge distance (ln transformed) and percent canopy cover were positively correlated with ordination scores along axis 1 ($r = 0.63$ and $r = 0.70$, respectively) in the direction of the Old-growth plots, while species richness, percent non-native cover, and percent herbaceous cover were negatively correlated along this axis ($r = -0.81$, $r = -0.87$ and $r = 0.58$ respectively; Fig. 1).

Species richness

ANOVA suggests that average sample species richness was significantly different across forest stages (Kruskal–Wallis: $df = 3$, $H = 25.20$, $P < 0.0001$; Fig. 2). The Initiation plots were the most species rich, while Old-growth plots were the least rich. Richness of Closure plots was intermediate to Mature and Old-growth plots and was not significantly

different from either of these stages. The same pattern of species richness was found for the native-only data (ANOVA: $df = 78$, $F = 5.01$, $P = 0.0032$). Non-native species richness was also greatest in the Initiation plots and least in Old-growth plots, which had only one non-native species, English ivy (*Hedra helix* L.; Kruskal–Wallis: $df = 3$, $H = 41.3$, $P < 0.0001$).

Richness estimators

The herbaceous layer species richness data that were assessed with standard statistical techniques were also assessed using species–area curves (Fig. 3), MMMeans rarefaction curves, and ICE non-parametric richness estimators (Fig. 4). Species–area curves suggest that each stage was adequately sampled (Fig. 3). The species accumulation curves based on the area sampled stabilized at around 15 plots in each stage. The curves approach asymptotes in each stage, and the richness estimates agree with the ANOVA results.

The rarefaction and non-parametric estimators suggest that the Mature and Old-growth stages were not sampled thoroughly. The ICE estimates for both the Initiation and Closure stages stabilized at approximately 193 and 161, respectively, but they did not stabilize for the Mature and Old-growth stages. The MMMeans rarefaction curves did not stabilize, except in the Initiation stage, where the rarefaction and ICE curves converged at around 190 species. The estimator curves for the Closure stage also appeared to be nearing convergence as the maximum sampling effort was reached. The estimates did not converge on the observed species richness in any forest stage. The Uniques curves were broadly hump-shaped in the Initiation and Closure stages, whereas these curves for the Mature and Old-growth stages continued to rise as total sampling effort was reached. The Duplicates were still rising in the Closure stage but peaked and leveled off in the other forest stages.

Discussion

This study describes important differences between forest stages that can further our understanding about the role of disturbance in structuring communities. In particular, this study shows that understory vascular plant communities in redwood forests may recover

Table 2 Multiple response permutation procedure results for both full and native species only data showing all pair-wise comparisons for herbaceous layer communities in four coast redwood forest stages

	Forest stages	A	T	P-value
All herbs	All stages	0.045	−12.439	<0.0001*
	Initiation versus Closure	0.035	−8.064	<0.0001*
	Initiation versus Mature	0.032	−9.469	<0.0001*
	Initiation versus Old-growth	0.072	−15.371	<0.0001*
	Closure versus Mature	−0.001	0.149	1.0000
	Closure versus Old-growth	0.020	−4.191	0.0133*
	Mature versus Old-growth	0.021	−4.664	0.0145*
Native herbs	All stages	0.035	−9.457	<0.0001*
	Initiation versus Closure	0.026	−5.962	<0.0001*
	Initiation versus Mature	0.019	−5.194	0.0032*
	Initiation versus Old-growth	0.059	−12.216	<0.0001*
	Closure versus Mature	0.001	−0.289	1.0000
	Closure versus Old-growth	0.023	−4.529	0.0083*
	Mature versus Old-growth	0.021	−4.529	0.0176*

The agreement statistic (A) measures chance-corrected within-group similarity. The test statistic (T) describes separation between groups. Significance levels (P-value) were Bonferroni adjusted ($P \times (\text{number of tests})$) to maintain test-wide significance level of $\alpha < 0.05$. Significant differences are indicated with asterisks

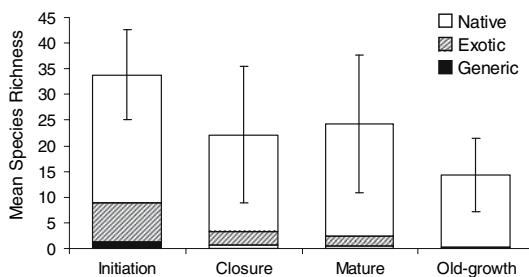


Fig. 2 Mean understory vascular plant species richness in each forest stage showing the proportion of native, non-native, and unassigned species. Species were not assigned native status if phenological conditions prevented identification beyond genus. Error bars show ± 1 SD of combined richness. The alphabetic coding shows the results of pair-wise comparisons among forest stages for each subset of the data. Results for the complete set are above the bars, the native results are shown in the native portion of the bar, and the non-native results are next to the non-native portion of the bar. Unassigned species were not compared separately. Within each data subset, corresponding letters indicate lack of statistical significance, while dissimilar letters show significant differences. There was one non-native species found in the Old-growth plots

relatively quickly after logging, yet a portion of the flora in Old-growth forest communities is lost after logging. This study also promulgates a method of assessing sampling efficacy that should be employed in other investigations where sampled communities

are compared for the purpose of understanding recovery of native systems in managed landscapes. This type of analysis may be most critical to field experiments for which sampling artifacts and the lack of experimental control are important concerns.

Community structure and disturbance

The results of this study run counter to a successional hypothesis predicting a spike in species richness immediately following logging due to non-native colonizers, followed by a trough in richness caused by canopy closure, and the eventual recovery of the pre-harvest community and peak of richness in the mature forest (Franklin et al. 2002). Community composition was markedly different between logged and unlogged forest types and between Initiation and older timberlands (Fig. 1, Table 2). But this difference was not attributable to early-colonizing non-native species, but rather an increase in native ruderals. Further, there was a suite of species restricted to and indicative of Old-growth (Table 3). While there was considerable overlap in the community composition among forest stages, the composition of even the oldest logged forests was different from unlogged forests. Thus, it may be that components of the understory plant communities of coast

Fig. 3 Species–area accumulation curves show the average number of unique species included in random subsamples for incremental increases in habitat coverage up to the total number of plots sampled. The curves for each forest stage rise quickly and level off near the asymptote

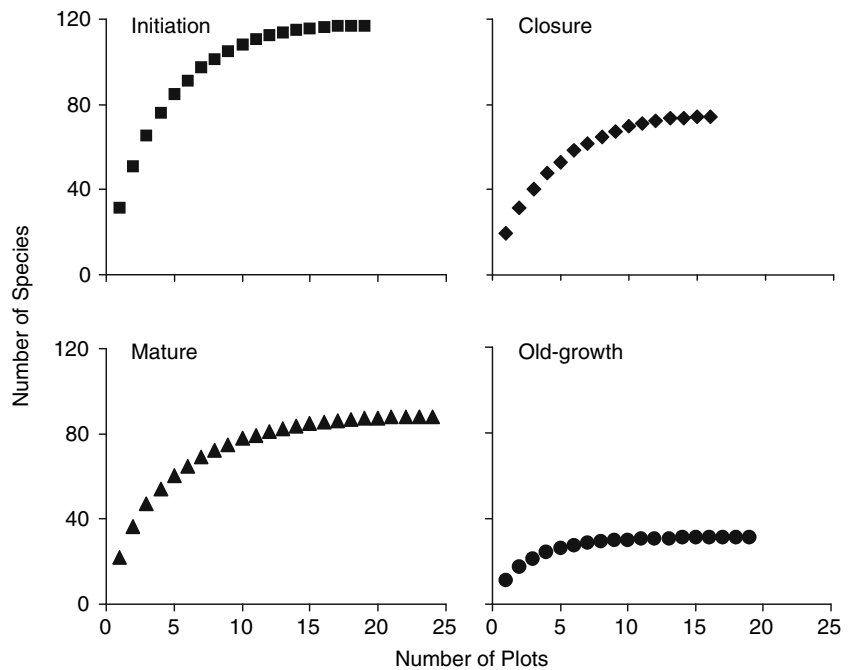
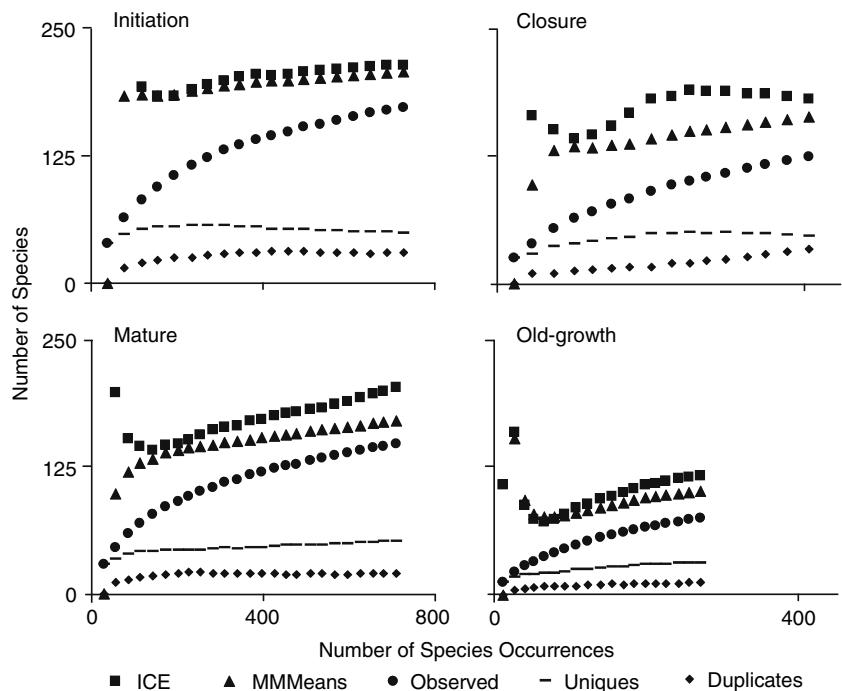


Fig. 4 Sample-based richness estimator (ICE) and rarefaction (MMMeans) curves show estimates of richness in each forest stage. ICE is the Incidence-based Coverage Estimator of total richness. MMMeans is the Michaelis–Menten Means rarefaction curve. Uniques and Duplicates are species that occur in only one and two simulated samples, respectively. Observed species richness is graphed for reference



redwood forests on timberlands do not recover during the period between logging. Short cycle stand rotation (i.e., 30–60 years) and permanent habitat features, such as logging roads, as well as high

impact soil disturbances associated with logging may distort community development dynamics in ways that prevent recovery of pre-logging forest conditions.

The ordination of the community data suggests a robust gradient associated with age and/or forest insularity. This age/insularity pattern is represented along axis 1, and the variables that correlate with the ordination scores along this axis follow a predictable pattern. Older plots have more canopy cover and are more insular, while younger forests are more species rich, support higher proportions of non-native species, and have more herb cover. And though canopy cover (Hannerz and Hånell 1997; Ross-Davis and Frego 2002) or the number of logging entries (Chen et al. 1992; Russell and Jones 2001; Godefroid and Koedam 2003; Kwit and Platt 2003; Foster et al. 1997) may explain global differences in community structure, fine-scale species- or guild-level differences illustrated by the ISA and the number and type of Old-growth restricted species suggests a subtle disjunction between logged and unlogged forests.

Assessing species-specific responses to logging is important because impacts to individual species may go unnoticed in community-level analyses. Yet, the subtleties evidenced by infrequent species may be as important as dominant species for community structure and recovery (Bruno 2002; Walker et al. 1999). Individual species assessments are especially pertinent when community analysis relies on species richness or other diversity metrics that do not differentiate between species. Species-specific differences in recovery are influenced by many factors, including habitat suitability (Gustafson and Gardner 1996; Vandermeer and Ricardo 2001; Bruno 2002), dispersal limitations (Matlack 1994; Clark et al. 1998; Sillett et al. 2000; Jacquemyn et al. 2001; Honnay et al. 2002), germination limitations (Primack and Maio 1992; Jules and Rathcke 1999; Dalling et al. 1998, 2002), and interactions among these factors (Verheyen and Hermy 2001). Interactions among these factors on timberlands are surely complex, and for some species there may be a lag between the initial disturbance and the population level effects (Tilman et al. 1994; Loehle and Li 1996).

We used ISA to describe species that may be at risk due to logging. While many native ruderal species appear to be positively affected by logging (Table 3), indicators of the Old-growth stage in this study were not generally striking. Western trillium (*Trillium ovatum* Pursh.) was an Old-growth indicator, reaching both peak frequency and abundance in

old forests, but it was not uncommon in other stages. Tan-oak (*Lithocarpus densiflorus* var. *densiflorus* (Hook. and Arn.) Rehder) was associated with Old-growth, most likely because it is generally actively removed from commercial timberlands to reduce competition with conifers. Heart-leaved twayblade (*Listera cordata* (L.) R. Br.) is the only Old-growth indicator species that appears obviously negatively impacted by logging. This ephemeral orchid likely requires dark moist forest conditions to persist, and plants do not likely survive conversion to open clearcut habitat (personal observation). And, though heart-leaved twayblade has light, potentially wind-dispersed seeds, most seeds probably fall relatively close to the parent plant (Machon et al. 2003). As such, dispersal into clearcuts or regenerating forests may be limiting in the recovery of this species. Finally, the indicator value for California milkwort (*Polygala californica* Nutt.) is likely a sampling artifact because the range of this species includes the southern Old-growth forest but does not extend into the coastal timberlands examined in this study (Hickman 1993; personal observation).

Eight infrequent species that occurred only in Old-growth plots (including heart-leaved twayblad) require specialized fungal associations for germination and/or growth (Rasmussen 1995). Six of these, *Cephalanthera austiniae* (A. Gray) A.A. Heller, *Corallorhiza maculata* Raf., *Goodyera oblongifolia* Raf., *Hemitomes congestum* A. Gray, and *Pyrola picta* Smith (also includes *P. picta* Smith f. *aphylla* (Smith) Camp), have distributions overlapping the entire study region. These species do occur on the managed lands included in the study (personal observation), but they did not occur in any logged plots. The total lack of these species from managed plots may be related to the impacts that logging has on fungi. There is some evidence that at least ectomycorrhizal fungal communities are able to recover rapidly after logging, though composition is altered (Jones et al. 2003). However, impacts to endomycorrhizal orchid fungi, monotropoid, and other specialized fungi may indirectly negatively impact vascular plant populations (Jules et al. 1999; Jules and Rathcke 1999). The conspicuous absence of these mycoparasites from all 60 managed plots, and the near absence of heart-leaved twayblade suggests that logging may negatively affect species by disrupting these mutualistic relationships.

Table 3 Indicator species for each forest stage

Stage	Species	I.V.	Mean	SD	P-value
Initiation	<i>Aira caryophyllea</i>	53.2	9.9	3.5	0.001
	<i>Anaphalis margaritacea</i> n	52.2	13.2	4.1	0.001
	<i>Cirsium vulgare</i>	39.4	11.7	4.1	0.001
	<i>Deschampsia elongata</i> n	66.7	10.9	4.1	0.001
	<i>Erechtites minima</i>	41.6	13.5	3.9	0.001
	<i>Hypochaeris radicata</i>	26.4	9.4	3.7	0.002
	<i>Leontodon taraxacoides</i>	27.3	7.7	3.7	0.002
	<i>Holcus lanatus</i>	27.2	10.7	3.8	0.003
	<i>Stachys ajugoides</i> n	29.6	10.5	4.0	0.005
	<i>Baccharis pilularis</i> n	24.6	9.5	3.9	0.006
	<i>Leucanthemum vulgare</i>	20.0	9.0	3.4	0.006
	<i>Sonchus asper</i>	22.7	7.7	3.7	0.006
	<i>Gnaphalium collinum</i>	26.1	12.2	3.8	0.007
	<i>Whipplea modesta</i> n	31.8	19.7	3.9	0.011
	<i>Cynosurus cristatus</i>	21.0	7.3	3.6	0.012
	<i>Iris douglasiana</i> n	25.7	14.1	3.9	0.017
	<i>Vicia tetrasperma</i>	18.9	8.2	4.0	0.022
	<i>Conyza canadensis</i> n	18.4	8.7	3.8	0.025
	<i>Galium aparine</i> n	21.1	10.9	4.1	0.025
	<i>Luzula comosa</i> n	15.7	7.1	3.3	0.031
	<i>Gnaphalium purpureum</i> n	16.2	8.0	3.7	0.034
	<i>Pteridium aquilinum</i> n	16.1	8.0	4.0	0.037
	<i>Torilis arvensis</i> n	16.1	8.2	3.6	0.041
	<i>Luzula parviflorus</i> n	16.2	8.4	3.7	0.042
	<i>Rubus parviflorus</i> n	20.5	12.5	4.1	0.047
Closure	<i>Abies grandis</i> n	21.8	12.9	3.9	0.036
	<i>Polystichum munitum</i> n	30.7	25.8	2.5	0.036
Mature	<i>Viola glabella</i> n	22.6	7.8	3.9	0.013
Old-growth	<i>Lithocarpus densiflorus</i> var. <i>densiflorus</i> n	39.3	18.5	4.1	0.001
	<i>Polygala californica</i> n	36.8	7.9	3.9	0.001
	<i>Trillium ovatum</i> n	32.0	21.7	3.7	0.016
	<i>Listera cordata</i> n	19.0	9.0	3.7	0.024

These species were significantly associated with their respective forest stages ($\alpha < 0.05$). Dufrêne–Legendre indicator values and the means and standard deviations as well as the *P*-values for the Monte Carlo simulations are given for each species. The superscript ‘n’ designates native species. All other species listed here are non-native

In addition to the intense nature of the initial disturbance, the frequency of logging disturbance may also affect the long-term population persistence of understory species and, thus, community resilience (Jules and Shahani 2003; Roberts 2002; Roberts and Zhu 2002). Though many forest understory species may either persist in or colonize young habitats, as we found for the majority of species, major changes in composition likely only occur over very long

periods (Dyrness 1973). Late colonizing species and the gradual expansion of remnant populations likely account for these changes (Halpern 1989). The differences in species composition between Closure and Mature stages in this study may suggest such slow changes. If these processes operate over the entire landscape, community structure and local extinction may be predicated, at least in part, by logging intervals.

Richness also differed among forest stages. Both native and non-native species richness was greatest in the Initiation stage. This was likely a result of the open canopy and disturbed soil conditions of this young stage (Dilustro et al. 2002). Often the early peak in richness is attributed to invading non-native species (e.g., Ross et al. 2002), but ruderal native species accounted for the majority of the additional species in the early successional habitats in this study. Old-growth forests were relatively species poor, and there were several common forest understory species conspicuously absent from the Old-growth plots. Studies in Douglas-fir, mixed conifer, and eastern hardwood forests, suggest that vascular diversity peaks in the oldest forests (e.g., Peterken and Game 1984), and there is a suite of Old-growth, or late successional, species that characterize this diversity (Jules et al. 1999). The results of the current work conflict with these studies.

The discrepancy between previous work and our study may result from several interacting factors. First, there may be unavoidable sampling artifacts due to the spatially clumped distribution of remnant Old-growth forest. In addition, the inland location of much of the Old-growth forest included in this study may have affected species richness. Creek distance (from the ocean) was correlated with the ordination solution (Fig. 1). Richness in forests may be positively correlated with precipitation and soil moisture (Bhattarai and Vetaas 2003; Härdtle et al. 2003). In redwood forests, fog, which decreases with increasing creek distance, is an important factor structuring understory communities (Harris 1987; Dawson 1998). It is likely that the coastal Old-growth forest in the study region supports a more diverse vascular plant community than that of the Old-growth forest we sampled. Finally, lack of disturbance may be another potentially important factor affecting community structure in the Old-growth plots in this study. The pre-settlement fire return interval in HRSP, from which most of the Old-growth plots were drawn, has been estimated to be 26 years (Stuart 1987), yet the shrub structure in these plots suggests that they have not burned recently, and there is no administrative record of fire in the portion of the park studied (Jay Harris, personal communication). Thus, the disturbance dynamics that structured observable Old-growth redwood plots in this study do not likely

represent “natural” conditions (Jacobs et al. 1985; Greenlee and Langenheim 1990). As such, the observed Old-growth forest may not represent a “control” or equilibrium understory community, and the value of comparisons between timberland and Old-growth reserve may be limited.

Richness estimators and accumulation curves

Though this study is the first to describe patterns of understory vascular plant diversity in redwood forests across a broad range of stand ages and developmental stages, it follows a long list of studies aimed at discovering the effects that logging has on the communities that exist between the timber. In some systems, vascular plant diversity may rebound quickly from logging (Gilliam 2002; Gilliam et al. 1995; Peet and Christensen 1988; Roberts 2002), while in others Old-growth communities may take long periods of time to recover (Peterken and Game 1984; Whitney and Foster 1988; Dzwonko and Loster 1989) or may not recover at all (Duffy and Meier 1992). Even though understanding community recovery is universally recognized as important to forest conservation, and though species richness is almost as universally used to investigate recovery rates, explicit evaluation of the effects of abundance and sampling efficacy on diversity metrics is not widely used in ecological studies. This study adds to the growing body of literature that examines the use of non-parametric richness estimators, species accumulation curves, and rarefaction curves to assess the validity of comparisons among communities.

Comparisons across forest stages amount to comparisons across habitats. Since each habitat may have idiosyncratic dynamics, within-stage sampling efficacy may differ across habitats. For instance, the “more individuals” hypothesis suggests that species richness is positively correlated with the number of individuals, which in turn varies with energy availability (Currie and Paquin 1987; Currie 1991; Gaston 2000). Availability of both energy and nutrient resources are drastically different across developmental stages in forests (Toky and Ramakrishnan 1983). For this reason, the number of individuals and species richness should be greater in recently disturbed forest habitat that has been released from canopy cover. Thus, for a fixed area in each habitat, a different proportion of the communities of those

habitats will be sampled if number of individuals (or biomass) correlates with richness.

Estimates of sampling efficacy suggested differences in sampling thoroughness across forest stages. Both species–area and richness estimator curves stabilized for the Initiation and Closure plots in this study. The ICE and MMMeans curves not only stabilized but also appeared to converge, suggesting agreement with the results of the species area curves for these habitats. Conversely, the Mature and Old-growth curves stabilized using the species–area approach, but they did not stabilize under rarefaction and non-parametric estimation. Furthermore, the curves for the older stages appear to be correlated with sampling effort. This suggests that the Mature and Old-growth habitats were not thoroughly sampled, which is contrary to the results of the species–area assessment.

There are several general implications of these assessments. First, within-habitat sampling efficiency may vary drastically among habitats. We sampled 25 Mature plots and only 19 and 16 Closure and Initiation plots, respectively. And though there are notable differences between the habitats of the Initiation and Closure stages, each was well sampled, whereas the Mature stage was likely undersampled even though more sampling effort occurred in this forest stage. Next, these results suggest that balanced sampling designs may be particularly poor at capturing the nuances of communities in forest habitats at different developmental stages. Finally, traditional tests may produce misleading results if the communities being compared are not thoroughly sampled.

Our results must be evaluated in light of the sampling efficacy assessment. The rarefaction and ICE results suggest that the community similarities among the Closure and Mature stages may be an artifact of under sampling the Mature stage. The ICE estimate for the Managed stage nearly converged on the estimate for the Initiation stage. Chazdon et al. (1998) and Longino et al. (2002) consider a rising ICE a good lower estimate of species richness, and the Mature stage estimator curve was still rising at maximal sampling effort. A more thorough sampling of the Mature stage may have resulted in an average richness similar to that of the Initiation stage and a community composition distinct from the Closure stage.

Assessment of the estimator curves for the Old-growth stage is less straightforward. The behavior of the curves for the Old-growth plots suggested insufficient sampling; all of the curves, except the Uniques curve, were rising moderately steeply as sampling approached completion. However, the Old-growth final richness estimate was still much lower than estimates for any other stage at almost any level of sampling effort. Understory habitat in the upland Old-growth forest may be completely occupied by woody shrubs (personal observation). In short, irrespective of sampling efficacy, vascular plant species richness in the Old-growth plots included in this study was truly lower than in all other forest stages.

While it is critical to understand community recovery in managed forest ecosystems, that understanding is contingent upon valid comparisons. To the extent that methodological shortcomings are masked by accepted protocols, our abilities to discover patterns in nature are diminished. Nonetheless, the methods used in this study to address sampling efficiency should by no means replace traditional tools. Nor should these be used uncritically. The behavior of the ICE was inconsistent in tests using tropical tree data for which total richness was known (Chazdon et al. 1998). However, these methods should be included in the ecological repertoire and used in conjunction with standard methods. This is especially relevant to studies that inform management of biodiversity, including the growing body of literature aimed at understanding the effects of logging on plant communities (e.g., Gilliam et al. 1995; Verheyen et al. 2003; Moola and Vasseur 2004). These studies have made numerous conclusions without assessing sampling efficacy.

Future comparisons between forest stages should be grounded in a thorough accounting of the species present in each community coupled with tests of within-stage sampling efficacy. This has long been recognized (e.g., Sanders 1968; Bunge and Fitzpatrick 1993), and methods for interpolating and extrapolating estimates that account for the relationship between number of individuals and species richness have been introduced in the ecological literature (Heck et al. 1975; Colwell and Coddington 1994; Gotelli and Colwell 2001). Yet these methods have not achieved widespread use (except see Goldberg and Estabrook 1998; Longino et al. 2002 for recent examples).

Conclusion

In light of the differences in sampling efficacy across forests stages, one might question the usefulness of biological conclusions drawn from this study. If diversity in the Mature and Old-growth stages was not fully captured, do the ordination, ISA, and other analyses instruct us? Indeed, a preliminary analysis, which included 15 Old-growth plots, suggested additional sampling in this stage. We collected more data, found more species, and reinforced the patterns found in the smaller data set. Unfortunately, the pattern suggesting further data collection was also reinforced. Importantly, the ordination and ISA results are unlikely to change regardless of the number of added plots. In these analyses, infrequent species, defined as those that occur in fewer than a percentage of plots, are removed to increase the signal to noise ratio. So the conclusions based on the common species are not likely to change. The ordinations do in fact tell us something about the relationships among forest stages even though the communities were not sampled thoroughly.

Analyses of species richness and diversity, both sensitive to differences in rare species, would change drastically if sampling efficacy, not number of plots, in each habitat was equal. This point is made quite clear by considering that equal area sampling between clearcut forest and Old-growth forest represents drastically different actual areas of sampling since there are large trees occupying habitat in one stage and none in the other. Therefore, the conclusions in this study based on species–area relationships were different than those based on non-parametric estimators and rarefaction curves, and the results that included the additional data were different from those including only the data specified by the species–area approach. Use of richness estimators can improve our evaluation of how logging impacts biological diversity and should be standard components of future studies.

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