2-20-2014

Structure and Composition of Old-Growth and Unmanaged Second-Growth Riparian Forests at Redwood National Park, USA

Christopher R. Keyes
University of Montana - Missoula, christopher.keyes@umontana.edu

Emily K. Teraoka
Stillwater Sciences

Recommended Citation

Keyes, Christopher R. and Teraoka, Emily K., "Structure and Composition of Old-Growth and Unmanaged Second-Growth Riparian Forests at Redwood National Park, USA" (2014). *Forest Management Faculty Publications*. 48.
https://scholarworks.umt.edu/forest_pubs/48

Forests **2014**, *5*, 256-268; doi:10.3390/f5020256

OPEN ACCESS

forests

ISSN 1999-4907

www.mdpi.com/journal/forests

Article

Structure and Composition of Old-Growth and Unmanaged Second-Growth Riparian Forests at Redwood National Park, USA

Christopher R. Keyes [1],* and Emily K. Teraoka [2]

[1] Department of Forest Management, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA

[2] Stillwater Sciences, 850 G Street, Suite K, Arcata, CA 95521, USA; E-Mail: emily@stillwatersci.com

* Author to whom correspondence should be addressed; E-Mail: christopher.keyes@umontana.edu; Tel.: +1-406-243-5521; Fax: +1-406-243-4845.

Received: 12 December 2013; in revised form: 1 February 2014 / Accepted: 11 February 2014 / Published: 20 February 2014

Abstract: Restoration of second-growth riparian stands has become an important issue for managers of redwood (*Sequoia sempervirens* [D. Don] Endl.) forest reserves. Identifying differences between old-growth and second-growth forest vegetation is a necessary step in evaluating restoration needs and targets. The objective of this study was to characterize and contrast vegetation structure and composition in old-growth and unmanaged second-growth riparian forests in adjacent, geomorphologically similar watersheds at Redwood National Park. In the old-growth, redwood was the dominant overstory species in terms of stem density, basal area, and importance values. Second-growth was dominated by red alder (*Alnus rubra* Bong.), Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco), and redwood. Understory species were similar in both forests, with several key differences: *Oxalis oregana* Nutt. and *Trillium ovatum* Pursh had greater importance values in the old-growth, and *Vaccinium parvifolium* Sm., *Dryopteris* spp. and sedges *Carex* spp. had greater importance values in the second-growth. Notable differences in structure and composition suggest that restoration practices such as thinning could expedite the acquisition of old-growth characteristics in second-growth riparian forests.

Keywords: forest stand dynamics; *Sequoia sempervirens*; late successional forest; ecological restoration

---

1. Introduction

Forest restoration, or the silvicultural manipulation of second-growth stands to expedite the acquisition of old-growth forest characteristics, has emerged as a top priority for managers of forest reserves in northern coastal California [1–4]. Upland second-growth stands that emerged after the clearcutting of old-growth redwood forests are often characterized by conditions that foretell stagnation: very high tree densities, presence of non-native tree species, and suppressed stand growth and development [5–7]. Of equal importance are the region's riparian forests that connect upland forests with adjacent aquatic ecosystems. Riparian forest structure and composition have strong bearing on stream habitat quality [8–10], and they contain some of the most ecologically diverse and structurally complex vegetation of the Pacific Coast region [2,11–14], yet they have been substantially altered by past forest uses [10,15–17].

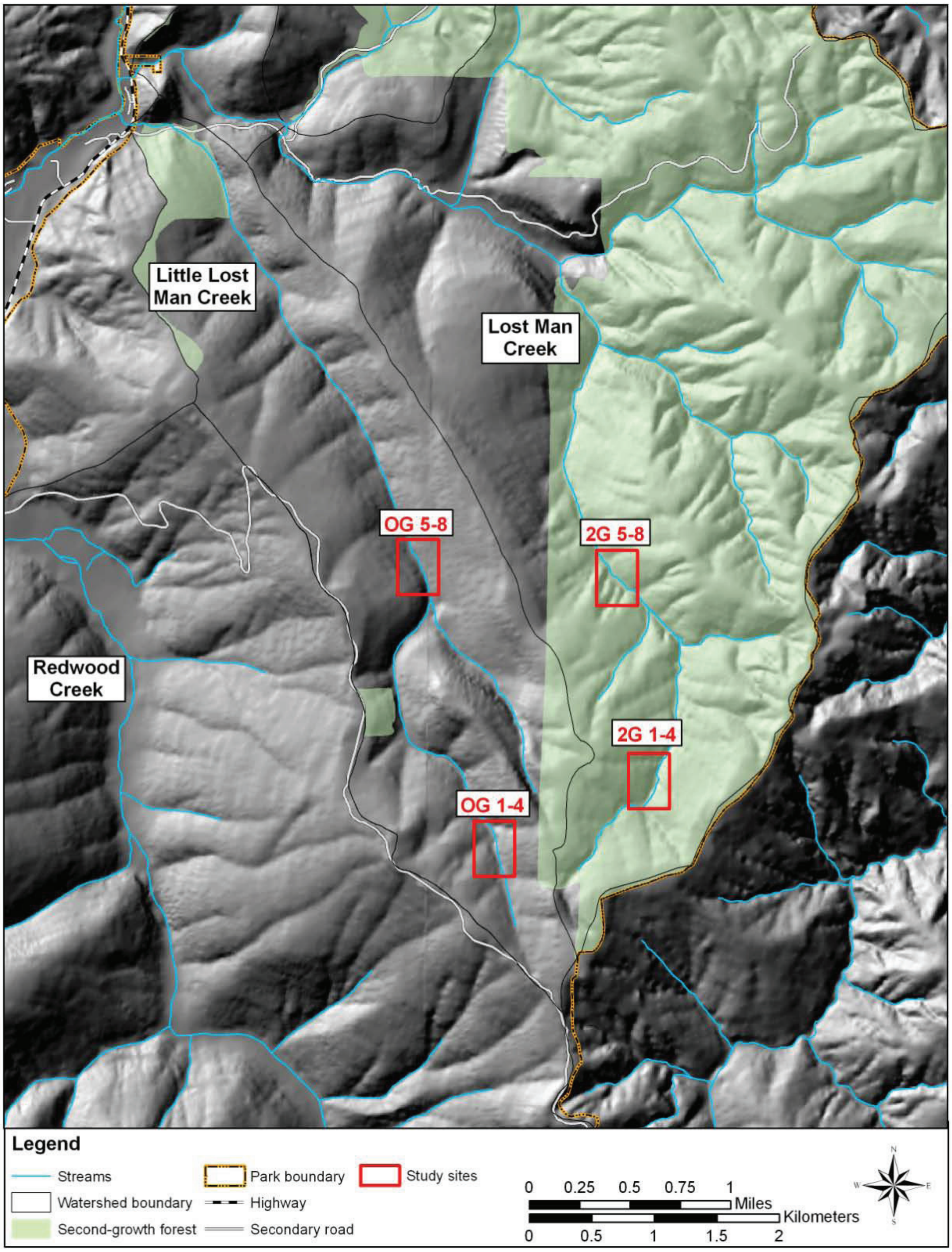
Historically, riparian forests in this region were the areas first targeted for logging because of the availability of large trees and the ease of transporting logs downstream [18]. One legacy of that history is altered riparian forest vegetation communities [10,15–17]. Second-growth riparian stands are believed to inadequately replace old-growth in their provision of important aquatic ecosystem services to streams and rivers, such as canopy shade, nutrients from arboreal detritus, structure and habitat from large woody debris, and stream bank stabilization [8,19–21]. Headwater streams are especially influenced by adjacent riparian vegetation in surrounding forests via shading and inputs of nutrients and organic matter [10,19,22]. Headwater streams comprise more than 80% of the cumulative channel length of northern California coastal watersheds, and 89% of streams within Redwood National Park [23].

Redwood National Park consists of a mix of old-growth and second-growth riparian forests. Past timber harvests heavily impacted more than one-third of the park's upland forests [24], and have influenced many kilometers of riparian forest. Yet, the structure and composition of second-growth riparian forests are poorly understood here and throughout the redwood region. No prior study has articulated the vegetative differences in stand attributes between old-growth and second-growth headwater riparian redwood forests. Such knowledge is vital to determining whether restoration efforts are necessary, and to establish reference conditions and objectives for riparian forest restoration practices. The purpose of this case study was to contrast forest conditions in two adjacent watersheds at Redwood National Park, and to provide insight for restoration planning.

2. Experimental Section

Study sites were located along first and second-order sections of Lost Man and Little Lost Man Creeks, two adjacent watersheds in Redwood National Park that are within 10 km of the Pacific coast of northern California (+41°17′15.72″, −124°4′5.19″; Figure 1). The two watersheds are geomorphologically similar, resulting in a watershed pairing that was designed to isolate harvesting history (logging) as the factor primarily responsible for any observed differences in riparian forest conditions. Few watersheds in the redwood region are pristine today, but the Little Lost Man Creek watershed is almost entirely (~89%) composed of undisturbed old-growth redwood forest of indeterminate age [23]. In contrast, 76% of the Lost Man Creek watershed was clearcut between 1954 and 1962 and left to regenerate naturally (it was outside the boundaries of Redwood National Park until park expansion in 1978), and thus consisted of 43–51 year-old even-aged stands at the time of the study.

Figure 1. Study location at Redwood National Park, USA (Little Lost Man and Lost Man Creeks). Plot numbers are indicated as OG (old-growth) 1–8 and 2G (second-growth) 1–8.



The climate of the area is coastal Mediterranean with average annual rainfall of 1706 mm, 90% of which occurs between October and April, and with temperatures generally ranging from 6 to 16 °C [25]. During the dry summer months, coastal fog extends inland up to 24 km from the coast. The region is characterized by steep, highly erodible landscapes of the Franciscan formation; they are often sheared and are susceptible to mass movement [26].

Sixteen 200 m^2 rectangular plots (20 m × 10 m) were installed; eight in the old-growth forest of Little Lost Man Creek and eight in the second-growth forest of Lost Man Creek (Figure 1). The stream channels at Lost Man and Little Lost Man Creeks are steep and sinuous, characteristics that physically defy sampling protocols. Thus, the plot shape and size reflected the greatest possible dimensions that feasibly sampled riparian forest conditions. The 10 m width reflects the widest possible plot that we could locate within the riparian forest strips occurring between the stream channel and the slope break above the incision. The 20 m length reflects the longest possible plot we could locate in the jagged stream courses. Plot selection criteria included the following attributes: inclusion of a flat valley floor or terrace immediately adjacent to the creek of at least 5 m wide, with an adjacent hillslope; a minimum of 50 m from the previous site; and absence of any major logging road (second-growth; skid roads and trails were acceptable). Plot location in the second-growth was determined first in order to avoid logging roads, and was achieved via the use of topographic maps and aerial photographs, and via field reconnaissance. Plots with matching stream order and elevation were then selected in the old-growth. To minimize variation in aspect and landform characteristics, all plots were located on the east side of creeks.

Sampling occurred from July to October 2005. Tree data were collected in the 200 m^2 rectangular plots immediately adjacent the stream's mean high water level. In each plot, species and diameter at 1.37 m (diameter at breast height; DBH) were recorded for all live trees greater than 10 cm DBH. Plant nomenclature followed that of the Jepson Manual [27]. Canopy cover was estimated three times in each plot using a concave spherical densitometer. In the second-growth, residual old-growth trees were noted as such. Basal area, stem density (trees ha^{-1}), and frequency were calculated for each species from plot data, and were relativized by dividing by the total value for the stand. Importance values (IV) [28] were calculated for each species by dividing the sum of basal area, stem density, and frequency values by 3 (or 2 when only 2 of the 3 measurements were available). IV is useful for highlighting differences between stands with similar species compositions, when those differences are not be apparent using a single measure [29–31]. Old-growth and second-growth metrics were compared using two-sample *t*-tests and Mann-Whitney U Tests (for non-parametric data) [32] and the medians of multiple groups of species were compared using Kruskal-Wallis Multiple Comparison *Z*-value tests [32] for those distributions failing normality tests. Statistical significance for all tests was determined at $\alpha = 0.05$.

Understory plant data were collected with a row of three 10 m^2 circular sub-plots spaced evenly within each rectangular plot. For each species of shrub and herb present, cover was visually estimated to the nearest percent. Each species was estimated independently; therefore, the total could exceed 100%. Relative frequency and cover were calculated, summed and divided by 2 to calculate an IV for each species. Shannon diversity (H') and evenness (J') based on H' were calculated for the understory in the old-growth and second-growth to compare species diversity and relative diversity [33]. The Jaccard Coefficient of Community was calculated for the understory in both forest types to compare the similarity of the two communities [28]. The Jaccard Coefficient of Community is an index of community similarity ranging from 0 (no species in common) to 100% (all species in common).

3. Results

3.1. Overstory Structure and Composition

Metrics of overstory stand structure differed significantly between the old-growth and the second-growth riparian forests. Stem density was significantly lower in old-growth (250 trees ha^{-1}) than second-growth (575 trees ha^{-1}) ($P < 0.04$; Table 1). However, the old-growth basal area was more than 6 times the second-growth, 396.1 m^2 ha^{-1} and 61.6 m^2 ha^{-1}, respectively ($P < 0.003$; Table 1). Mean canopy cover was significantly greater in second-growth than in old-growth ($P < 0.004$), but the magnitude of this difference was marginal: second-growth averaged 96% (SD 1.84) and the old-growth 92% (SD 3.02).

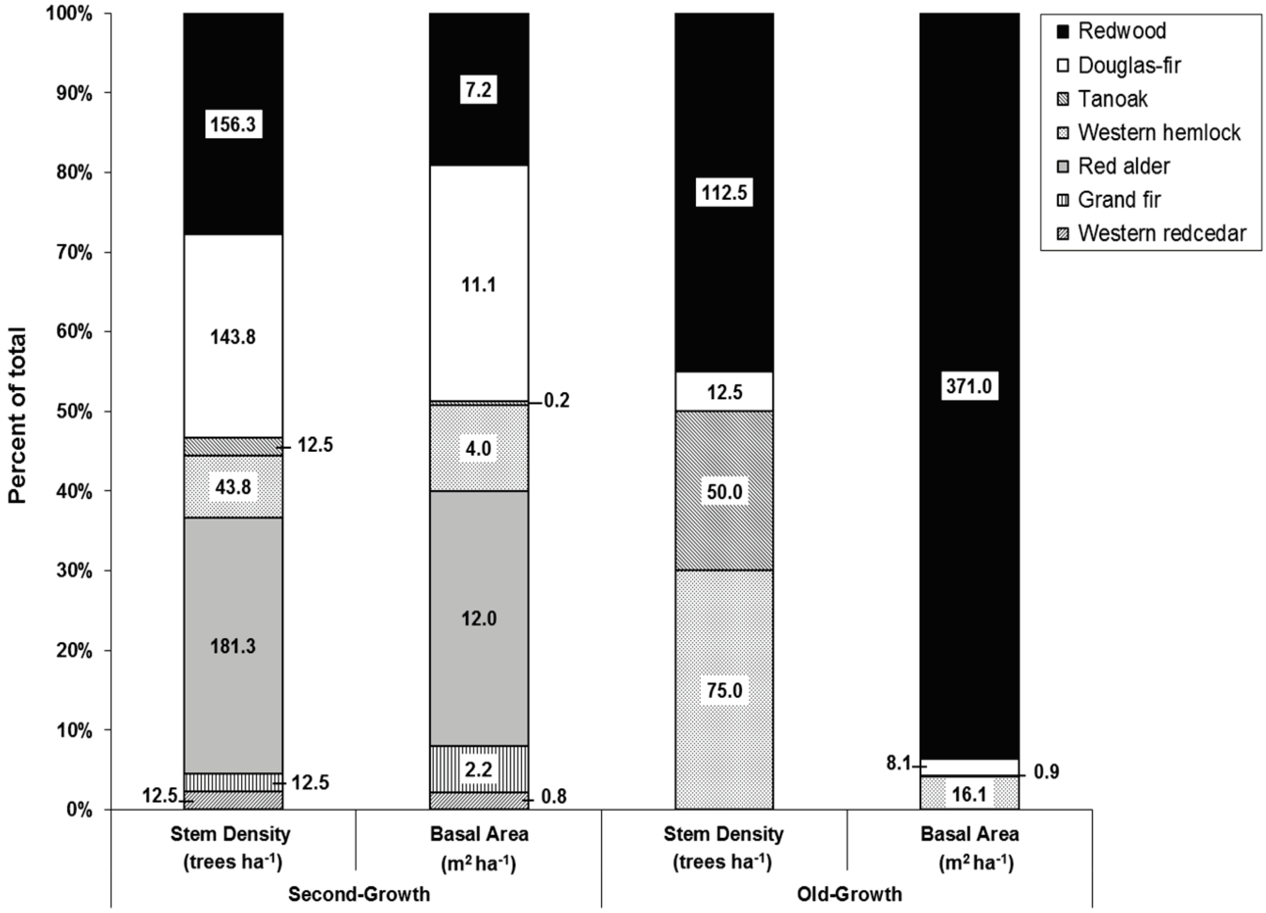
Table 1. Structural attributes of adjacent old-growth and second-growth riparian forests in Little Lost Man and Lost Man Creeks, Redwood National Park, USA.

Species	**Frequency (# plots)**		**Relative Frequency** [a] **(%)**		**Stem Density (trees ha^{-1})**		**Relative Density** [b] **(%)**		**Basal Area (m^2 ha^{-1})**		**Relative BA** [c] **(%)**		**Importance Value** [d] **(%)**	
	OG	2G	OG	2G	OG	2G	OG	2G	OG	2G	OG	2G	OG	2G
Douglas-fir	1	6	12.5	75.0	12.5	143.8	5.0	25.0	8.1	11.1	2.0	18.1	6.54	39.42
Grand fir	-	1	-	12.5	-	12.5	-	2.2	-	2.2	-	3.6	-	6.17
Red alder	-	7	-	87.5	-	181.3	-	31.5	-	12.0	-	19.5	-	46.21
Redwood	7	5	87.5	62.5	112.5	156.3	45.0	27.2	371.0	7.2	93.7	11.7	75.41	33.83
Tanoak	4	2	50.0	25.0	50	12.5	20.0	2.2	0.9	0.2	0.2	0.3	23.43	9.26
W. hemlock	7	2	87.5	25.0	75	43.8	30.0	7.6	16.1	4.0	4.1	6.5	40.52	13.05
W. redcedar	-	1	-	12.5	-	12.5	-	2.2	-	0.8	-	1.3	-	5.38
Rdwd rsdl[e]	N/A	2	N/A	25.0	N/A	12.5	N/A	2.2	N/A	24.0	N/A	39.0	N/A	22.14
Totals	N/A	N/A	N/A	N/A	250	575.0	100.0	100.0	396.1	61.6	100.0	100.0	-	-

[a] Relative frequency denotes number of plots that the species was found in divided by the total number of plots ($N = 8$); [b] Relative density denotes stem density of each species divided by the total stem density of all species; [c] Relative basal area denotes basal area of each species divided by the total basal area of all species; [d] Importance value (IV) denotes sum of relative frequency, relative density, and relative basal area divided by 3); [e] Rdwd rsdl denotes residual redwoods (in second-growth).

In the old-growth, redwood exhibited the largest quadratic mean diameter (204.9 cm; range 97.3–454.1 cm), was the tallest tree species by far, and made up the majority of the trees in the upper canopy (Figure 2). Relative to other species, redwood was the dominant tree in the old-growth on all levels, as it had the highest values of relative stem density (45%), relative basal area (94%), and IV (75.4%) (Table 1). The dominance of redwood in the old-growth, contrasts sharply with the second-growth where red alder and Douglas-fir were dominant (Figure 2). In the second-growth, red alder exhibited the highest IV (46.2%), followed by Douglas-fir (39.4%) and redwood (33%; Table 1).

Figure 2. Percent total basal area and stem density by species for adjacent old-growth and second-growth riparian stands (Redwood National Park, USA). Numbers indicate actual basal area or stem density; residual old-growth redwoods (second-growth) excluded.



3.2. Understory Vegetation

Understory plant species composition did not differ substantially between old-growth and second-growth riparian stands (Table 2). The Jaccard Coefficient of Community showed that old-growth and second-growth had 54% of species in common between the two communities, with 19 species observed in the old-growth stands (14 herbs and 5 shrubs) and 21 species in the second-growth stands (16 herbs and 5 shrubs) (Tables 2 and 3). Species unique to the old-growth were *Atriplex rosea* L., *Disporum hookeri* (Torr.) G. Nicholson, *Goodyera oblongifolia* Raf., *Rhododendron macrophyllum* D. Don ex G. Don, and *Rhododendron occidentale* (Torr. & Gray ex Torr.) A. Gray. Species unique to the second-growth were *Ranunculus uncinatus* D. Don, *Ribes* sp., *Rubus spectabilis* Pursh, *Rubus ursinus* Cham. & Schldl., *Dryopteris* sp., *Equisetum* sp., and *Asplenium* sp. Shannon diversity (H') and evenness based on H' (J') did not differ between old-growth and second-growth for all understory species combined ($P > 0.05$); however, H' and J' for shrubs were significantly greater in the old-growth ($P < 0.03$) whereas H' and J' for herbs was significantly greater in the second-growth ($P < 0.03$) (Table 3).

Table 2. Understory plant relative frequency, relative cover, and importance value (IV) in adjacent old-growth and second-growth riparian stands in Redwood National Park, USA. Species IV rankings are indicated.

Species	Relative Frequency [a]		Relative Cover [b]		Importance Value (IV) [c]	
	OG	2G	OG	2G	OG	2G
Adiantum sp.	4	4	0.1	0.4	2.2	2.3
Asplenium sp.	0	4	0.0	0.0	0.0	2.1
Athyrium filix-femina	17	21	0.4	1.8	8.67	11.37
Atriplex rosea	13	0	0.2	0.0	6.49	0.0
Blechnum spicant	67	67	15.4	10.6	41.03	38.72
Carex sp.	4	25	0.1	5.0	2.2	15.06
Disporum hookeri	8	0	0.2	0.0	4.3	0.0
Dryopteris sp.	0	29	0.0	1.1	0.0	15.15
Equisetum sp.	0	21	0.0	0.5	0.0	10.79
Galium sp.	17	21	0.3	0.5	8.58	10.710
Gaultheria shallon	58	50	11.4	8.6	34.94	29.33
Goodyera oblongifolia	8	0	0.1	0.0	4.2	0.0
Mahonia nervosa	8	8	0.6	0.4	4.5	4.4
Oxalis oregana	96	21	16.4	1.1	56.12	11.08
Polystichum munitum	92	96	50.7	52.6	71.21	74.21
Ranunculus uncinatus	0	8	0.0	0.6	0.0	4.4
Rhododendron macrophyllum	4	0	0.3	0.0	2.3	0.0
Rhododendron occidentale	8	0	1.4	0.0	4.810	0.0
Ribes sp.	0	4	0.0	0.1	0.0	2.1
Rubus spectabilis	0	8	0.0	3.6	0.0	6.0
Rubus ursinus	0	8	0.0	0.2	0.0	4.3
Trientalis borealis	4	4	0.0	0.1	2.1	2.1
Trillium ovatum	46	8	0.9	0.1	23.45	4.2
Vaccinium ovatum	4	4	0.2	0.2	2.2	2.2
Vaccinium parvifolium	21	38	1.1	12.0	11.06	24.74
Viola sempervirens	4	13	0.1	0.4	2.1	6.5

[a] Relative frequency denotes number of plots that the species was found in divided by the total number of plots ($N = 24$); [b] Relative density denotes percent cover of each species divided by the total percent cover of all species; [c] Importance value (IV) denotes sum of relative frequency and relative cover divided by 2; species IV rank noted (greatest (1) to least (10)).

No difference was detected between total understory cover in the old-growth and second-growth ($P = 0.48$). Shrub cover, however, was significantly greater in old-growth than second-growth ($P < 0.02$; Table 3). Herbaceous cover was significantly greater in second-growth ($P < 0.002$; Table 3). *Polystichum munitum* (Kaulf.) C. Presl had the highest relative cover of all plants found in the understory for both old-growth and second-growth, 52.3% and 71.2%, respectively. It also had the highest IV (Table 2). *Oxalis oregana* Nutt. cover was significantly higher in the old-growth than the second-growth (10.1% and 0.6%, respectively; $P < 0.001$) as well as the second highest IV in the old-growth (56%). It only had an IV of 11.0% in the second-growth (IV rank 8).

Table 3. Total number of understory species (s), average percent cover of individuals (N), Shannon diversity (H'), evenness using H' (J') average total percent cover for adjacent old-growth and second-growth riparian stands in Redwood National Park, USA (standard deviation in parentheses).

		s	N	H'	J'	Percent cover
Herbs	Old-growth	14	14.91 (9.62)	0.41 (0.14)	0.32 (0.11)	9.1 (7.7)
	Second-growth	16	16.38 (18.58)	0.29 (0.19)	0.23 (0.15)	52.3 (26.0)
Shrubs	Old-growth	5	7.29 (14.60)	0.11 (0.17)	0.14 (0.21)	39.0 (20.1)
	Second-growth	5	7.34 (8.96)	0.23 (0.13)	0.29 (0.16)	13.3 (13.5)
All	Old-growth	19	14.32 (9.60)	0.45 (0.17)	0.33 (0.13)	62.0 (22.7)
	Second-growth	21	11.34 (7.24)	0.45 (0.16)	0.32 (0.12)	52.9 (27.3)

4. Discussion

The overstory structure differences observed between old-growth and second-growth were consistent with other areas of the redwood region [5,7,34]. Lenihan [35] found an average canopy cover of 107.4% (SD 21.9) in old-growth forests in the upper portion of the Little Lost Man Creek watershed, which was similar to the canopy cover found in the old-growth riparian forest. Overall, the second-growth stem densities are relatively low compared to nearby upland second-growth forests at Redwood National Park [36,37]. This is not surprising, as riparian forests—especially on stream terraces—have generally exhibited lesser tree densities than adjacent upland sites in other areas of the Pacific Northwest [38–40]. The dominance of red alder in second-growth riparian forests is a common pattern in disturbed forests throughout the redwood region and Pacific Northwest [10,16,17,21,41]. Following the harvest of dense, conifer-dominated stands in Redwood National Park's Redwood Creek watershed, for example, Urner and Madej [15] noted the emergence of hardwood dominance (mostly red alder) for decades afterward.

The similar understory communities in old-growth and second-growth are not typical of other studies of upland forests in other areas of the redwood region or the Pacific Northwest. Typically, young forests have foliage concentrated high in the canopy with little to no understory, whereas old-growth forests have a diverse understory with a continuous distribution of foliage from the ground to the canopy [42]. An understory community with low species richness is a more typical characteristic of young stands in stem exclusion [43]. The similar total understory percent covers between old-growth and second-growth riparian forest was also atypical of upland forest studies in the area. In old-growth forests in the upper portion of the Little Lost Man Creek watershed, separate studies by Lenihan [35] and by Teraoka [36] observed average understory covers of 149% (range 77.5%–215%), and 73% to 164% (respectively). In upland second-growth stands of Lost Man Creek, Chittick [37] found understory cover ranging from 0 to 20% in the unthinned controls of the Holter Ridge Thinning Study. At a nearby ridge above Little Lost Man Creek, understory cover averaged 12% in the unthinned control of the Whiskey-40 Thinning Study. In both of those studies, thinning expedited stand development and boosted understory cover. At Holter Ridge, understory cover in thinned stands ranged 45% to 95%, and was negatively related to overstory tree density [37]. At the Whiskey-40, average understory cover in thinned stands ranged 24% to 93% [36].

Similarities in the old-growth and second-growth plant communities and understory plant covers could be attributed to several factors, including similar overstory canopy cover and site quality. Klinka *et al.* [44] showed that forest canopy cover and site quality had a strong influence on the percentage cover and species composition of understory communities. Differences from other (upland) areas in Redwood National Park could be attributed to wider tree spacing in riparian second-growth stands, or to increased soil moisture in riparian areas compared to more xeric upland sites. Riparian areas have generally been shown to have higher plant species diversity than upland areas throughout the Pacific Northwest [12,20], and within the redwood region soil moisture has shown to be a strong determinant of species composition [35,45,46]. The presence of red alder in the second-growth could also be affecting understory vegetation composition. In wet coastal forests of southeastern Alaska, Deal [47] found that most understory plant species had a higher percentage cover beneath canopies of red alder than those of conifers, and species-rich understories in low-density mixed alder-conifer riparian stands persisted for up to 45 years after logging.

Differences between old-growth and second-growth in shrub and herbaceous cover were consistent with other studies in the redwood region. Loya and Jules [48] found significantly higher shrub cover in old-growth redwood stands than in second-growth stands and higher herbaceous plant cover in young second-growth stands than old-growth stands. *Rhodendron occidentale*, *Trillium ovatum* Pursh, and *Oxalis oregana* had IV ranks in the top 10 in the old-growth, but low IV in the second-growth (Table 3). In contrast, *Carex* spp., *Dryopteris* sp., and *Equisetum* sp. all had IV ranks in the top 10 in the second-growth, but were absent or had low IV in the old-growth. *Trillium ovatum* and *Oxalis oregana* are common in old-growth redwood forests and have been described as old-growth stage indicator species [35,48,49].

Overall, because the differences in understory vegetation are modest, restoration efforts targeted at the understory composition (such as enrichment planting or natural recruitment) seem unnecessary. In the overstory stratum, however, striking differences in species dominance between old-growth and second-growth suggests the potential value of restoration practices (such as variable-density thinning [3,50]) that favor redwood. Because alder is a short-lived species (100 years) [51,52], this study's results do not indicate that thinning is essential to achieving redwood dominance over longer timeframes. However, restoration thinning could expedite the transformation of overstory dominance by targeting Douglas-fir and alder for reduction, thereby releasing overstory redwoods to achieve the proportionally greater dimensions and site occupancy that the species exhibits in old-growth.

Acknowledgments

This was a study of the Applied Forest Management Program at the University of Montana, a research and outreach unit of the Montana Forest & Conservation Experiment Station. Funding was provided by Save the Redwoods League. Staff at Redwood National Park assisted in data collection. We thank Morgan Varner (Mississippi State University), Sharon Kramer (H.T. Harvey & Associates), and Jason Teraoka (Redwood National Park).

Conflicts of Interest

The authors declare no conflict of interest.

References and Notes

1. Porter, D.; Gizinski, V.; Hartley, R.; Kramer, S.H. Restoring Complexity to Industrially Managed Timberlands: The Mill Creek Interim Management Recommendations and Early Restoration Thinning Treatments. In *Proceedings of the Redwood Science Symposium: What Does the Future Hold*; General Technical Report PSW-GTR-194; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 2007; pp. 283–294.
2. Lorimer, C.G.; Porter, D.J.; Madej, M.A.; Stuart, J.D.; Viers, S.D., Jr.; Norman, S.P.; O'Hara, K.L.; Libby, W.J. Presettlement and modern disturbance regimes in coast redwood forests: Implications for the conservation of old-growth stands. *For. Ecol. Manag.* **2009**, *258*, 1038–1054.
3. Keyes, C.R.; Perry, T.E.; Plummer, J.F. Variable-Density Thinning for Parks and Reserves: An Experimental Case Study at Humboldt Redwoods State Park, California. In *Proceedings of the 2009 National Silviculture Workshop*; Proceedings RMRS-P-61; USDA Forest Service Rocky Mountain Research Station: Fort Collins, CO, USA, 2010; pp. 227–237.
4. O'Hara, K.L.; Nesmith, J.C.B.; Leonard, L.; Porter, D.J. Restoration of old forest features in coast redwood forests using early-stage variable-density thinning. *Restor. Ecol.* **2010**, *18*, 125–135.
5. Chittick, A.J.; Keyes, C.R. Holter Ridge Thinning Study, Redwood National Park: Preliminary Results of a 25-Year Retrospective. In *Proceedings of the Redwood Science Symposium: What Does the Future Hold*; General Technical Report PSW-GTR-194; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 2007; pp. 271–280.
6. Teraoka, J.R.; Keyes, C.R. Low thinning as a forest restoration tool at Redwood National Park. *West. J. Appl. For.* **2011**, *26*, 91–93.
7. Plummer, J.F.; Keyes, C.R.; Varner, J.M. Early-Stage thinning for the restoration of young redwood—Douglas-fir forests in northern coastal California, USA. *ISRN Ecol.* **2012**, *2012*, doi:10.5402/2012/725827.
8. Keller, E.A.; MacDonald, A.; Tally, T.; Merritt, N.J. Effects of large organic debris on channel morphology and sediment storage in selected tributaries of Redwood Creek, northwestern California. In *Geomorphic Processes and Aquatic Habitat in the Redwood Creek Basin, Northwestern California*; Nolan, K.M., Kelsey, H.M., Marron, D.C., Eds.; United States Geological Survey: Denver, CO, USA, 1995; pp. P1–P29.
9. Lisle, T.E.; Napolitano, M.B. Effects of Recent Logging on the Main Channel of North Fork Caspar Creek. In *Proceedings of the Conference on Coastal Watersheds: The Caspar Creek Story*; General Technical Report PSW-GTR-168; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 1998; pp. 81–85.
10. Andrus, C.W. Woody Debris from the Streamside Forest and its Influence on Fish Habitat. In *Hydrological and Biological Responses to Forest Practices*; Stednick, J.D., Ed.; Springer Science and Business Media LLC: New York, NY, USA, 2008; pp. 211–235.

11. Spies, T.A.; Franklin, J.F. The Structure of Natural Young, Mature, and Old-Growth Douglas-fir Forests in Oregon and Washington. In *Wildlife and Vegetation of Unmanaged Douglas-Fir Forests*; General Technical Report PNW-GTR-285; Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H., Eds.; USDA Forest Service Pacific Northwest Research Station: Portland, OR, USA, 1991; pp. 91–109.
12. Naiman, R.J.; Fetherston, K.L.; McKay, S.J.; Chen, J. Riparian Forests. In *River Ecology and Management: Lessons from the Pacific Coastal Ecoregion*; Naiman, R.J., Bilby, R.E., Eds.; Springer-Verlag: New York, NY, USA, 1998; pp. 289–323.
13. Busing, R.T.; Fujimori, T. Dynamics of composition and structure in an old *Sequoia sempervirens* forest. *J. Veg. Sci.* **2002**, *13*, 785–792.
14. Zenner, E.K. Does old-growth condition imply high live-tree structural complexity? *For. Ecol. Manag.* **2004**, *195*, 243–258.
15. Urner, S.; Madej, M. Changes in Riparian Composition and Density Following Timber Harvest and Floods along Redwood Creek, California. In *Ecosystem Restoration: Turning the Tide*; Society for Ecological Restoration Northwest Chapter Annual Meeting, Society for Ecological Restoration Northwest Chapter: Tacoma, WA, USA, 1998.
16. Russell, W. The influence of timber harvest on the structure and composition of riparian forests in the Coastal Redwood region. *For. Ecol. Manag.* **2009**, *257*, 1427–1433.
17. Villarin, L.A.; Chapin, D.M.; Jones, J.E. Riparian forest structure and succession in second-growth stands of the central Cascade Mountains, Washington, USA. *For. Ecol. Manag.* **2009**, *257*, 1375–1385.
18. Magnuson, J.J.; Allendorf, F.W.; Beschta, R.L.; Bisson, P.A.; Carson, H.L.; Chapman, D.W.; Hanna, S.S.; Kapuscinski, A.R.; Lee, K.N.; Lettenmaier, D.P.; *et al. Upstream: Salmon and Society in the Pacific Northwest*; National Academy Press: Washington, DC, USA, 1996.
19. Vannote, R.L.; Minshall, G.W.; Cummins, K.W.; Sedell, J.R.; Cushing, C.E. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **1980**, *37*, 130–137.
20. Gregory, S.V.; Swanson, F.J.; McKee, W.A.; Cummins, K.W. An ecosystem perspective of riparian zones. *Bioscience* **1991**, *41*, 540–551.
21. Hibbs, D.E.; Bower, A.L. Riparian forests in the Oregon Coast Range. *For. Ecol. Manag.* **2001**, *154*, 201–213.
22. Bilby, R.E.; Bisson, P.A. Allochthonous *versus* autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. *Can. J. Fish. Aquat. Sci.* **1992**, *49*, 540–551.
23. Redwood National and State Parks. *Unpublished GIS Stream Layer for the Lost Man Creek and Little Lost Man Creek Watersheds*; Data stored at Redwood National and State Parks; South Operations Center: Orick, CA, USA, 2010.
24. Redwood National and State Parks. *Redwood National and State Parks' Strategic Plan: October 1, 2005–September 30, 2008*; USDI National Park Service, Redwood National Park: Crescent City, CA, USA, 2004.
25. Western Regional Climate Center. Data archives, Station 046498 in Orick, California; period of record: May 1937 to December 2009. Available online: http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca6498 (accessed on 5 May 2010).

26. United States Department of Agriculture. Soil Survey of Redwood National and State Parks, California, 2008. USDA Natural Resources Conservation Service. Available online: http://soils.usda.gov/survey/printed_surveys/ (accessed on 4 March 2010).
27. *The Jepson Manual: Higher Plants of California*; Hickman, J.C., Ed.; University of California Press: Berkeley, CA, USA, 1993.
28. Mueller-Duombois, D.; Ellenburg, H. *Aims and Methods of Vegetation Ecology*; John Wiley and Sons, Inc.: New York, NY, USA, 1974.
29. Curtis, J.T.; McIntosh, R.P. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecol.* **1951**, *32*, 476–496.
30. Goebel, P.C.; Hix, D.M. Development of mixed-oak forests in southeastern Ohio: A comparison of second-growth and old-growth forests. *For. Ecol. Manag.* **1996**, *84*, 1–21.
31. Barker, J.R.; Ringold, P.L.; Bollman, M. Patterns of tree dominance in coniferous riparian forests. *For. Ecol. Manag*. **2002**, *166*, 311–329.
32. Zar, J.H. *Biostatistical Analysis*, 4th ed.; Prentice Hall, Inc.: Upper Saddle River, NJ, USA, 1999.
33. Brower, J.E.; Zar, J.H.; von Ende, C.N. *Field and Laboratory Methods for General Ecology*, 3rd ed.; Wm. C. Brown Publishers: Dubuque, IA, USA, 1990.
34. Muldavin, E.H.; Lenihan, J.M.; Lennox, W.S.; Veirs, S.D., Jr. *Vegetation Succession in the First Ten Years Following Logging of Coast Redwood Forests*; Technical Report No. 6; USDI National Park Service, Redwood National Park: Arcata, CA, USA, 1981.
35. Lenihan, J.M. The Forest Associations of the Little Lost Man Creek Research Natural Area, Redwood National Park, CA. Master Thesis, Humboldt State University, Arcata, CA, USA, June 1986.
36. Teraoka, J.R. Stand Response to Restoration Silviculture in a Second-Growth Redwood Stand, Redwood National and State Parks. Master Thesis, Humboldt State University, Arcata, CA, USA, December 2004.
37. Chittick, A.J. Stand Structure and Development Following Thinning in a Second-Growth Forest, Redwood National Park. Master Thesis, Humboldt State University, Arcata, CA, USA, December 2005.
38. Means, J.E.; Harris, R.R.; Sabin, T.E.; McCain, C.N. Spatial variation in productivity of Douglas-fir stands on a valley floor in the western Cascades range, Oregon. *Northwest Sci.* **1996**, *70*, 201–212.
39. Pabst, R.J.; Spies, T.A. Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon, U.S.A. *Can. J. For. Res.* **1999**, *29*, 1557–1573.
40. Nierenberg, T.R.; Hibbs, D.E. A characterization of unmanaged riparian areas in the central Coast Range of western Oregon. *For. Ecol. Manag.* **2000**, *129*, 195–206.
41. Stubblefield, G.; Oliver, C.D. Silvicultural Implications of the Reconstruction of Mixed Alder/Conifer Stands. In *Utilization and Management of Alder: Proceedings of a Symposium*; Briggs, D.G., DeBell, D.S., Atkinson, W.A., Eds.; General Technical Report PNW-GTR-70; USDA Forest Service Pacific Northwest Research Station: Portland, OR, USA, 1978; pp. 307–320.

42. Franklin, J.F.; Spies, T.A.; Van Pelt, R.; Carey, A.B.; Thornburgh, D.A.; Berg, D.R.; Lindenmayer, D.B.; Harmon, M.E.; Keeton, W.S.; Shaw, D.C.; *et al*. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manag*. **2002**, *155*, 399–423.
43. Oliver, C.D. Forest development in North America following major disturbances. *For. Ecol. Manag*. **1981**, *3*, 153–168.
44. Klinka, K.; Chen, H.Y.H.; Wang, Q.; de Montigny, L. Forest canopies and their influence on understory vegetation in early-seral stands on West Vancouver Island. *Northwest Sci.* **1996**, *70*, 193–200.
45. Mahoney, T.M.; Stuart, J.D. Old-Growth forest associations of the northern range of coastal redwood. *Madroño* **2000**, *47*, 53–60.
46. Mahoney, T.M.; Stuart, J.D. *Status of Vegetation Classification in Redwood Ecosystems*; General Technical Report PSW-GTR-194; USDA Forest Service Pacific Southwest Research Station: Albany, CA, USA, 2007.
47. Deal, R.L. *Understory Plant Diversity in Riparian Alder-Conifer Stands after Logging in Southeast Alaska*; Research Note PNW-RN-523; USDA Forest Service Pacific Northwest Research Station: Portland, OR, USA, 1997.
48. Loya, D.T.; Jules, E.S. Use of species richness estimators improves evaluation of understory plant response to logging: A study of redwood forests. *Plant Ecol.* **2008**, *194*, 179–194.
49. Sawyer, J.O. Forests of northwestern California. In *Terrestrial Vegetation of California*, 3rd ed.; Barbour, M.G., Keeler-Wolf, T., Schoenherr, A.A., Eds.; University of California Press: Berkeley, CA, USA, 2007; pp. 253–295.
50. O'Hara, K.L.; Leonard, L.P.; Keyes, C.R. Variable-Density thinning and a marking paradox: Comparing prescription protocols to attain stand variability in coast redwood. *West. J. Appl. For.* **2012**, *27*, 143–149.
51. Newton, M.; Cole, E.C. Stand development and successional implications: Pure and mixed stands. In *The Biology and Management of Red Alder*; Hibbs, D.E., Bell, D.S., Tarrant, R.F., Eds.; Oregon State University Press: Corvallis, OR, USA, 1994; pp. 106–115.
52. Hibbs, D.E.; DeBell, D.S. Management of young red alder. In *The Biology and Management of Red Alder*; Hibbs, D.E., Bell, D.S., Tarrant, R.F., Eds.; Oregon State University Press: Corvallis, OR, USA, 1994; pp. 202–215.