Variation In Old-Growth Coast Redwood (Sequoia sempervirens) Reference Sites In Mendocino County, California

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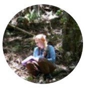

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VARIATION IN OLD-GROWTH COAST REDWOOD (*SEQUOIA SEMPERVIRENS*) REFERENCE SITES IN MENDOCINO COUNTY, CALIFORNIA

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ABSTRACT

Restoration and management of old-growth conditions in coast redwood (*Sequoia sempervirens* [D. Don] Endl.) forests are traditionally based on an idealized set of characteristics that occur in productive stands. We compared three old-growth sites to quantify variability among remaining reference stands of the central coast redwood range in Mendocino County, California. Two of the sites are protected from coastal influence, have rich alluvial soils, and relatively high visitor usage. The third site is in close proximity to the coast with variable soil conditions and little visitor access. We randomly sampled twenty, 20-meter circular diameter plots in each site to evaluate basal area, tree density, species richness, canopy cover, shrub cover, and herbaceous species cover. We conducted multivariate analyses including nonmetric multidimensional scaling (NMDS), perMANOVA, and indicator species analysis (ISA) to examine the structural clustering and compositional metrics among the sites. Results indicated a strong separation among old-growth reference sites in the NMDS ordination and significant differences in sites using perMANOVA. The inland sites had high tree density, basal area, herbaceous understory cover, and cover of *Oxalis oregana* Nutt., *Adenocaulon bicolor* Hook., and *Viola glabella* Nutt. The coastal site had a high abundance of *Trillium ovatum* Pursh (an old-growth associated species), high shrub cover in canopy gaps, diverse species assemblages, and relatively high abundance of woodland-adapted perennial species. ISA provided a distinct suite of understory species for each site. The unique characteristics and high variability among these sites may offer a new, and potentially more accurate, standard for restoration and management.

Key Words: Coast redwood, indicator species, old-growth, understory diversity.

Coast redwood (*Sequoia sempervirens* [D. Don] Endl.) forests have been altered by human practices to the extent that less than 5% of the primeval forest remains (Noss 1999). Much of what remains, including some of the most dramatic stands, are preserved in parks and reserves. These iconic stands have traditionally been considered ideal reference sites for restoration and management (O'Dell 1996, Giusti 2007), while the variation inherent in less productive stands is less often considered. Though coast redwood reach their greatest growth potential on stable alluvial flats (Stone and Vasey 1968), the range of *Sequoia sempervirens* is characterized by topographic variability and can include areas of unstable and unproductive soil conditions (Madej 2011). Often coast redwood forests do not develop the extraordinarily large tree diameters and high species dominance found in the most archetypal stands, regardless of the specific site conditions (Russell and Woolhouse 2012). Yet old-growth remnants are increasingly rare, particularly in the central range, and thus local old-growth stands are underutilized when considering reference sites and developing restoration targets (Russell and Michels 2010; Russell et al. 2014). Due to the unique structural and physiological characteristics of *S. sempervirens* (Sawyer et al. 2000; Busing and Fujimori 2005; Sillett and Van Pelt 2007; Lorimer et al. 2009; Madej 2010), reference sites from other forest types (e.g., Douglas-fir, mixed conifer-hardwood stands) yield few insights and may confound restoration objectives.

The dominance of herbaceous understory species in second-growth and old-growth stands varies (Table 1) by forest type and region (Duffy and Meier 1992; Jules and Rathcke 1999; Scheller and Mladenoff 2002). Pacific trillium (*Trillium ovatum* Pursh), for example, grows preferentially in old-growth Douglas-fir forests (Jules and Rathcke 1999) but at a lesser extent near timber harvest edges in coast redwood forests (Russell et al. 2000). In addition, shade adapted understory species such as calypso orchid (*Calypso bulbosa* [L.] Oakes), redwood violet (*Viola sempervirens* Greene), Douglas iris (*Iris douglasiana* Herb.), sugar scoop (*Tiarella trifoliata* L.), and vanilla leaf (*Achlys triphylla* [Sm.] DC.) grow favorably in old-growth stands and increase in abundance with time since harvest in second-growth stands (Russell et al. 2014). The fidelity of these species to old-growth conditions supports the assertion that understory herbaceous species may be indicative of disturbance intensity in previously harvested stands (Russell and Michels 2010). Yet, the distribution and dominance of herbaceous understory species is not uniform within old-growth sites; thus, understanding the variation in remaining

TABLE 1. Summary of cited studies that examine variability in second-growth herbaceous understory.

Citation	Region	Plot scale	Study finding
Duffy and Meier 1992	Appalachian Mtns	1m × 1m quadrat	No difference in herbaceous cover noted between old-growth and second-growth stands.
Jules and Rathcke 1999	Siskiyou Mtns	Various (avg: 150m^2)	*Trillium ovatum* recruitment decreased at old-growth forest edges.
Russell and Jones 2001	Coast redwood region	20m diameter	Understory cover higher in old-growth stands.
Scheller and Mladenoff 2002	Great Lakes region	2m × 2m quadrat	Statistically higher cover of shrubs in old-growth stands; all other taxonomic groups lower cover in old-growth. Differences in specific plants species not significant between groups.
Loya and Jules 2007	Coast redwood region	22.6m diameter	Understory species lowest in old-growth stands; three understory indicator species found in the old-growth stage.
Russell 2009	Coast redwood region	10m × 10 m quadrat	*Oxalis oregana, Athyrium filix-femina*, and *Vaccinium parviflorum* higher in older forest.
Russell and Michels 2010	Coast redwood region	20m diameter	Three coast redwood associated understory species favored on the older second-growth stands.
Russell et al. 2014	Coast redwood region	20m diameter	Two understory species (*Trillium ovatum* and *Viola sempervirens*) statistically higher in old-growth.

old-growth stands is essential for selecting prototypical reference sites.

The restoration paradigm in second-growth redwood stands currently promotes active management techniques (e.g., variable density thinning) to increase tree diameter, tree spacing, and the dominance of *Sequoia sempervirens* (O'Hara et al. 2010; Berrill et al. 2013). Although recovering second-growth stands do trend over time toward larger tree sizes, lower tree densities, and greater *S. sempervirens* species dominance (Russell and Michels 2010; Russell et al. 2014), defining restoration targets on short-term time scales (Foster et al. 1996) using iconic reference sites can lead to unrealistic expectations (Hilderbrand et al. 2005). Previous work in this part of the coast redwood range also noted high variation among sites (Michels and Russell 2010; Lambert 2012; Russell and Woolhouse 2012), yet the degree of this variation in remaining remnant old-growth stands in Mendocino County, California has yet to be quantified.

As such, we compared three remaining *S. sempervirens* old-growth reference sites in the central coast redwood range to examine variation in stand structure and species composition. We predicted that sites would exhibit significant differences in regard to stand density, basal area, and the cover of overstory (i.e., canopy), midstory (i.e., shrub), and understory (i.e., herbaceous) layers. We also predicted that significant variation among sites would manifest in understory indicators and in the abundance of individual understory species. Quantifying variation among the remaining old-growth reference stands in this region may reveal nuanced structural features or subtle stand characteristics for direct implementation or consideration in ongoing restoration efforts.

MATERIALS AND METHODS

Study Areas

Study sites are located in Mendocino County in Northern California in the central part of the range of *S. sempervirens,* which extends in a narrow coastal band from Curry County, Oregon to Monterey County, California (Little 1971). The region's climate is characterized by warm, mild summers and cool, wet winters (Sawyer et al. 2000) with frequent moisture inputs from coastal summer fog (Burgess and Dawson 2004). Topography within study sites is complex and highly variable, with slopes exceeding 30° in some areas and elevation ranging from 55 meters (m) to 361 m. Vegetation is representative of the central redwood range with canopy species including coast redwood (*S. sempervirens*), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco var. *menziesii*), and tanoak (*Notholithocarpus densiflorus* [Hook. & Arn.] Manos et al.) (Giusti 2007; Russell and Michels 2010). Common understory species characteristic of this region include sword fern (*Polystichum munitum* [Kaulf.] C. Presl), huckleberry (*Vaccinium ovatum* Pursh), California rhododendron (*Rhododendron macrophyllum* D. Don), redwood

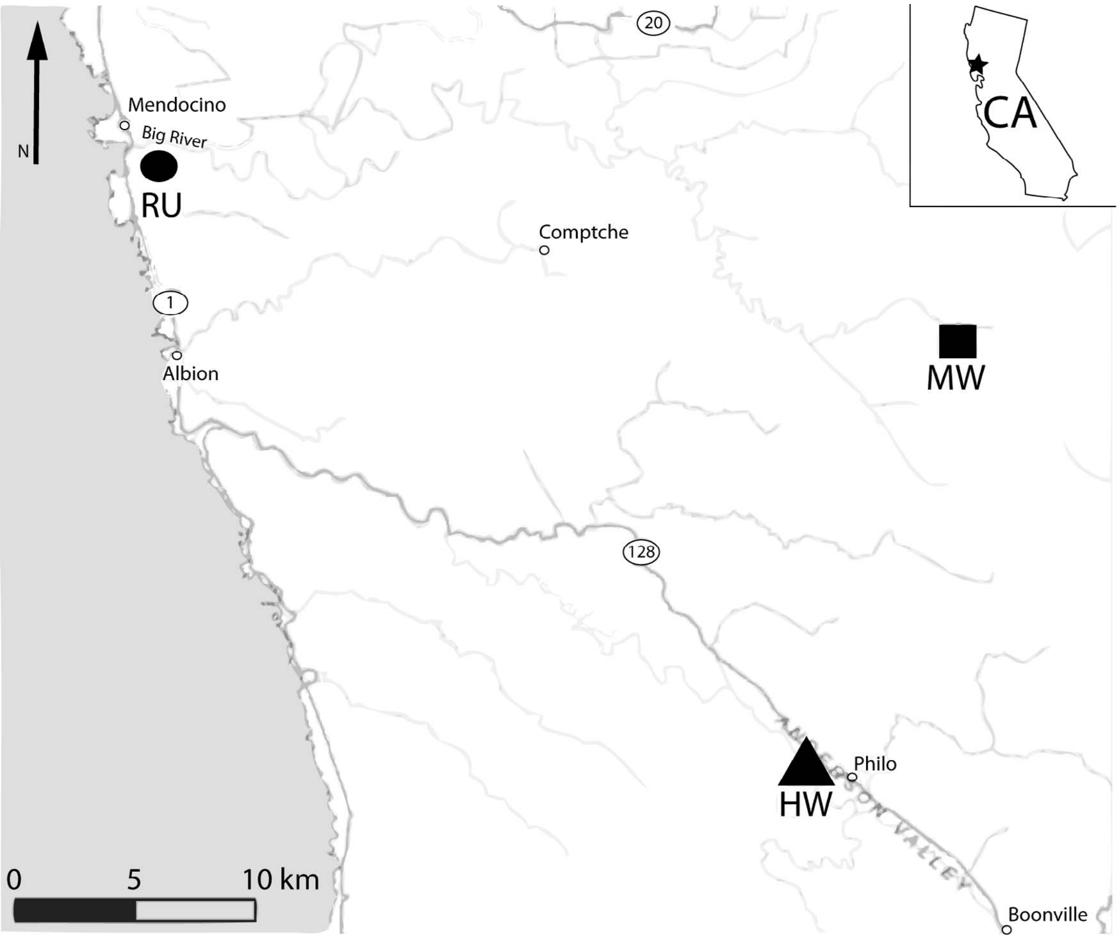

FIG. 1. Russell Unit (RU), Hendy Woods (HW), and Montgomery Woods (MW) old-growth coast redwood reference sites within Mendocino County, California.

sorrel (*Oxalis oregana* Nutt.), and western trillium (*Trillium ovatum*) (Russell and Michels 2010).

We selected old-growth reference sites using geographic information systems, land management history data (Rutland 2002), and regional knowledge of remaining old-growth stands in Mendocino County. Site selection criteria included old-growth stands (see Spies and Franklin 1996 for old-growth definition) dominated by *S. sempervirens*. We therefore selected the following three sites: 1) the 49-hectare (ha) Russell Unit, the smallest and most coastal of the three sites studied with nearly 24 ha of old-growth and residual old-growth forest located in the Brewery Creek watershed; 2) Montgomery Woods State Natural Reserve, a 462-ha alluvial redwood preserve located inland from the Russell Unit on Montgomery Creek; and 3) Hendy Woods State Park, a 342-ha preserve of old-growth coast redwood located in the Navarro River watershed (Fig. 1). All three sites are managed by California State Parks, and represent the largest remaining unharvested redwood stands in Mendocino County, with the Russell Unit being one of the few sizable old-growth stands remaining on the Mendocino coast (R. Pasquinelli, California State Parks, personal communication).

Comparison of physiographic variables among sites indicated similar conditions with regard to precipitation and air temperature (Rittman and Thorson 2006), but some variation in distance to the coast, slope incline, and soil complex (Table 2). Edaphically, Hendy Woods and Montgomery Woods are on well-drained, sandy to loamy alluvial soils in the Gschwend-Frenchman soil complex (USDA, NRCS 2012), while the Russell Unit site consists primarily of poorly-drained marine terraces of the Ferncreek sandy loam complex (Rittiman and Thorson 2006; USDA, NRCS 2012). Human use and access also varies among the sites with well-developed facilities and trail systems in place in Hendy Woods and Montgomery Woods, but no such facilities in the Russell Unit.

TABLE 2. Characteristics of three old-growth reference sites in Mendocino County, California. Seasonal ranges of precipitation, temperature, and soil data from Rittiman and Thorson (2006).

	Russell Unit	Hendy Woods	Montgomery Woods
Distance to coast	~1 km	~20 km	~34 km
Mean annual precipitation	100 cm–165 cm	100 cm–205 cm	100 cm–205 cm
Mean annual air temperature	11°C–12°C	6°C–17°C	6°C–17°C
Soil complex	Poor to moderately-well drained, loam-sandy, loam-clay	Well drained, loam-sandy loam	Well drained, loam-sandy loam
Elevation range	99 m–127 m	55 m–62 m	253 m–361 m
Slope range	2°–34°	0°–10°	0°–4°
Facilities	No facilities, trails, parking	Campsites, day use, visitor center, trails	Trails
Management	Little to none	Facilities, trail use, aesthetic	Trail use, aesthetic
Dominant canopy species	*Sequoia sempervirens*, *Tsuga heterophylla*, or *Pseudotsuga menziesii* var. *menziesii*	*Sequoia sempervirens*	*Sequoia sempervirens*

Field Methods

We conducted a pilot study using the relevé method (Cain 1938) to determine plot size and sampling intensity. We randomly located twenty, 20-m diameter (0.031 ha), circular sample plots within each of the three study sites using ArcMap (ESRI 2011) for a total of 60 plots sampled. We located sample plots a minimum distance of 20 m from adjacent plots, 10 m from special habitats such as riparian areas and rock outcroppings, and 200 m from main access roads to reduce edge effects (Russell and Jones 2001).

At the center of each 20-m diameter plot, we recorded physiographic characteristics including location, slope, and aspect using a handheld global positioning device and a 360° azimuth pocket compass. At plot center we also estimated canopy cover with a convex spherical crown densiometer using cover estimates taken in each cardinal direction (Michels and Russell 2010). Within each 20-m plot, we collected overstory, midstory, and understory species-level data (Table 3) following nomenclature from the Jepson Manual (Baldwin et al. 2012; Jepson Flora Project 2015). We identified and measured tree species using circumference tape to calculate the diameter at breast height (1.37 m) of each individual. We identified and recorded seedlings as the number of tree species less than 1.37 m tall. We estimated cover of midstory and understory layers using percent cover classes (Gauch 1982) consistent with previous research conducted in this forest type (Russell and Michels 2010). We estimated species cover in 1% increments up to 5%, 5% increments up to 25%, and 10% increments up to 100%. We also included a sub 1% cover class of 0.5%.

Statistical Methods

We used a multivariate approach to compare site-level characteristics among the three old-growth sites including nonmetric multidimensional scaling (NMDS) (Kruskal 1964; Mather 1976), perMANOVA (Anderson 2001), and Indicator Species Analysis (ISA) (McCune and Mefford 2011). The set of input variables we analyzed for NMDS and perMANOVA included total tree density, total basal area, percent canopy cover, percent shrub cover, percent herbaceous cover, total species richness, and percent cover of common old-growth associate species *Trillium ovatum* (Loya and Jules 2007) and *Oxalis oregana* (Russell 2009, Michels and Russell 2012). We also calculated descriptive statistics on these data to compare with multivariate results. We further evaluated a suite of understory species using percent cover for the ISA.

NMDS provides a characterization analysis to visually illustrate clustering in large, multivariate datasets but does not provide a significance metric. In order to augment our preliminary interpretations of NMDS results, we used perMANOVA to isolate differences among sites. We used a Bray-Curtis distance measure for both the NMDS and perMANOVA analyses due to its robustness for community data (McCune and Grace 2002) and a Monte Carlo randomization test to confirm the strength of the NMDS output. Following initial NMDS analyses, we used the recommended two-dimensions from the analysis output with a stability criterion of 0.00001. Subsequently, we calculated Pearson and Kendall Correlation values among the original data and the NMDS output data to determine which of the variables, if any, were associated with differences among plots and probabilities of co-occurrences.

We used ISA to determine if the presence of rare flowering herbaceous species functioned as site indicators. ISA intuitively compares the relative abundance and relative constancy of species within groups using a Monte Carlo randomization to test significance (Dufrêne and Legendre 1997). This method allowed us to determine if any species drove species assemblages unique to a particular old-growth site. Since ISA evaluates rare indicators of a habitat type, common species found on all sites are

TABLE 3. Canopy, woody sub-canopy, and herbaceous species encountered in the Russell Unit (RU), Hendy Woods (HW), and Montgomery Woods (MW). "X" denotes presence at each site.

	RU presence	HW presence	MW presence
Canopy Species Observed			
Abies grandis (D. Don) Lindl.	X	—	—
Notholithocarpus densiflorus (Hook. & Arn.) Manos et al.	X	X	X
Pseudotsuga menziesii (Mirbel) Franco var. menziesii	X	—	X
Sequoia sempervirens (D. Don) Endl.	X	X	X
Tsuga heterophylla (Raf.) Sarg.	X	—	—
Umbellularia californica (Hook. & Arn.) Nutt.	—	X	—
Canopy Species Encountered	5	3	3
Woody Sub-Canopy Species Observed			
Gaultheria shallon Pursh	X	—	—
Lonicera hispidula (Lindl.) Torr. & A. Gray	X	—	X
Rhododendron macrophyllum D. Don	X	—	—
Rosa gymnocarpa Nutt.	—	X	X
Rubus leucodermis Torr. & A. Gray	—	X	X
Toxicodendron diversilobum (Torr. & A. Gray)	—	X	X
Vaccinium ovatum Pursh	X	—	X
Vaccinium parvifolium Sm.	X	—	—
Woody Sub-Canopy Species Encountered	5	3	5
Non-Flowering Herbaceous Species Observed			
Athyrium filix-femina (L.) Roth var. cyclosorum Rupr.	X	X	X
Blechnum spicant (L.) Roth	X	—	—
Polystichum munitum (Kaulf.) C. Presl	X	X	X
Pteridium aquilinum (L.) Kuhn var. pubescens Underw.	X	X	X
Woodwardia fimbriata Sm.	—	—	X
Non-Flowering Herbaceous Species Encountered	4	3	4
Flowering Herbaceous Species Observed			
Achlys triphylla (Sm.) DC.	—	X	X
Adenocaulon bicolor Hook.	—	X	X
Aquilegia formosa Fisch. ex DC.	—	X	X
Asarum caudatum Lindl.	X	X	X
Calypso bulbosa (L.) Oakes	X	—	X
Cardamine californica (Nutt.) Greene	X	—	—
Clintonia andrewsiana Torr.	X	—	—
Galium triflorum Michx.	X	X	X
Lysimachia latifolia (Hook.)	X	X	X
Maianthemum racemosum (L.) Link	X	—	X
Maianthemum stellatum (L.) Link	X	X	X
Oxalis oregana Nutt.	X	X	X
Poaceae spp.	X	X	X
Prosartes hookeri Torr.	X	X	X
Stachys mexicana Benth	X	X	—
Tiarella trifoliata L.	X	X	X
Trillium chloropetalum (Torr.) Howell	X	X	X
Trillium ovatum Pursh	X	X	X
Viola glabella Nutt.	—	X	—
Viola sempervirens Greene	X	X	X
Whipplea modesta Torr.	X	—	X
Flowering Herbaceous Species Encountered	18	16	17
Total Species Encountered	32	25	29

excluded from the ISA. We found eleven understory flowering (i.e., non-Pteridophytes) herbaceous species common to all sites (Table 4), and as a result, did not include these species in the analysis.

RESULTS

The three old-growth coast redwood stands differed widely in structure and composition. Descriptive comparisons of input variables among sites suggested differences in structural characteristics and ground-layer metrics. Canopy cover, tree density, herb cover, and *O. oregana* cover were highest in Hendy Woods, while species richness, shrub cover, and *T. ovatum* cover had highest mean values in the Russell Unit, and total basal area peaked in Montgomery Woods (Table 5).

NMDS ordination illustrated a clear distinction among the old-growth sites. Monte Carlo randomization tests were significant for each axis ($P = 0.0196$) and minimal overlap existed among the Russell Unit when compared to Hendy Woods and

TABLE 4. Combined total percent cover of understory species observed in old-growth reference sites: Russell Unit (RU), Hendy Woods (HW), and Montgomery Woods (MW). Asterisk (*) denotes species used in indicator species analysis.

Flowering herbaceous understory species	RU percent total cover	HW percent total cover	MW percent total cover
*Achlys triphylla**	0	40	12
*Adenocaulon bicolor**	0	12.5	35.5
*Aquilegia formosa**	0	1	12
Asarum caudatum	4	17	0.5
*Calypso bulbosa**	4.9	0	0.5
*Cardamine californica**	16	0	0
*Clintonia andrewsiana**	43	0	0
Galium triflorum	8.2	7.5	27.5
Lysimachia latifolia	6.1	1.5	17.5
*Maianthemum racemosum**	8	0	2
Maianthemum stellatum	1.5	8	6
Oxalis oregana	135	780	481
Poaceae spp.	15	28.5	58.5
Prosartes hookeri	7.5	61.5	23
*Stachys mexicana**	1	34	0
Tiarella trifoliata	44.5	11.5	54.5
Trillium chloropetalum	6.5	5	18.5
Trillium ovatum	31.5	10.5	22
*Viola glabella**	0	29	27
Viola sempervirens	35.5	4.5	21.5
*Whipplea modesta**	6	0	5.5

Montgomery Woods (Fig. 2). As illustrated by the NMDS, most variation manifested among sites. Pearson Correlations (Table 6) ($r > |0.500|$) and the NMDS ordination characterized the Russell Unit as having high values of shrub cover, canopy cover, species richness and low values of *O. oregana* cover and total herb cover. Weaker correlations ($r > |0.300|$) indicated tree density and *T. ovatum* cover also reflected Russell Unit characteristics. Results of the perMANOVA ($F_{1,60} = 22.176$, $P = 0.002$) supported the NMDS analysis and Pearson Correlations findings. Pairwise comparisons among Montgomery Woods and Hendy Woods ($P = 0.0046$), Montgomery Woods and the Russell Unit ($P = 0.0002$), and the Russell Unit and Hendy Woods ($P = 0.0002$), indicated significant differences in variance among sites.

ISA for understory species demonstrated four indicator species for the Russell Unit, four indicator species for Hendy Woods, and six indicator species for Montgomery Woods (Table 7). Significant differences existed among groups of species that reached maximum indicator value within each site. Clintonia (*Clintonia andrewsiana* Torr.) had the highest ISA value for the Russell Unit, hedgenettle (*Stachys mexicana* Benth.) had the highest ISA value in Hendy Woods, and trail plant (*Adenocaulon bicolor* Hook.) had the highest ISA value for Montgomery Woods.

Qualitative observations (Table 2) support the findings that variation manifested between old-growth sites, especially when comparing the Russell Unit to Montgomery Woods and Hendy Woods. Yet, although the Russell Unit sample plots were generally more similar to one another than plots sampled in other sites, variation also existed in each site. Within the Russell Unit, the soil complex and dominant canopy species encountered was more variable. In this coastal site, soils varied from poorly drained to moderately-well drained and loam-sandy to loam-clay. In contrast, Montgomery Woods and Hendy Woods largely consisted of well-drained, loam to sandy loam soils. Further, qualitative observations of dominant canopy species varied within the Russell Unit, predominated by *Sequoia sempervirens*, *Tsuga heterophylla*, or *Pseudotsuga menziesii* var. *menziesii*. At Montgomery Woods and Hendy Woods, the dominant canopy species observed was *Sequoia sempervirens* throughout the sample plots. Topography within the Russell Unit was also more variable, ranging between 2° and 34° slopes, when compared to Hendy Woods (slopes did

TABLE 5. Descriptive characteristics (mean and standard error) of the three old-growth reference sites: Russell Unit (RU), Hendy Woods (HW), and Montgomery Woods (MW).

	RU mean (±SE)	HW mean (±SE)	MW mean (±SE)
Canopy Metrics			
Tree density (trees/plot)	13.8 (1.3)	36.0 (5.6)	18.8 (2.0)
Basal area (m2/ha)	5.1 (0.7)	12.9 (1.5)	15.7 (1.9)
Canopy cover (percent/plot)	84.6 (0.9)	88.3 (0.6)	84.1 (0.9)
Understory Metrics			
Shrub cover (percent/plot)	45.5 (5.0)	7.5 (0.9)	19.2 (4.0)
Herb cover (percent/plot)	15.6 (2.2)	46.8 (4.0)	40.3 (4.3)
Trillium ovatum cover (percent/plot)	1.6 (0.2)	0.5 (0.1)	1.1 (0.2)
Oxalis oregana cover (percent/plot)	6.8 (1.4)	39.0 (4.6)	24.1 (3.9)
Seedling density (seedlings/plot)	6.9 (1.2)	12.8 (2.2)	64.9 (12.9)
Sequoia sempervirens seedling density (seedlings/plot)	0.3 (0.2)	4.8 (1.8)	54.7 (12.0)
Diversity Metrics			
Total richness (species/plot)	17.8 (0.8)	12.9 (0.7)	15.6 (0.8)
Shrub richness (shrub species/plot)	6.0 (0.2)	3.0 (0.3)	4.6 (0.3)
Herbaceous richness (herb species/plot)	8.4 (0.8)	7.6 (0.5)	9.6 (0.7)

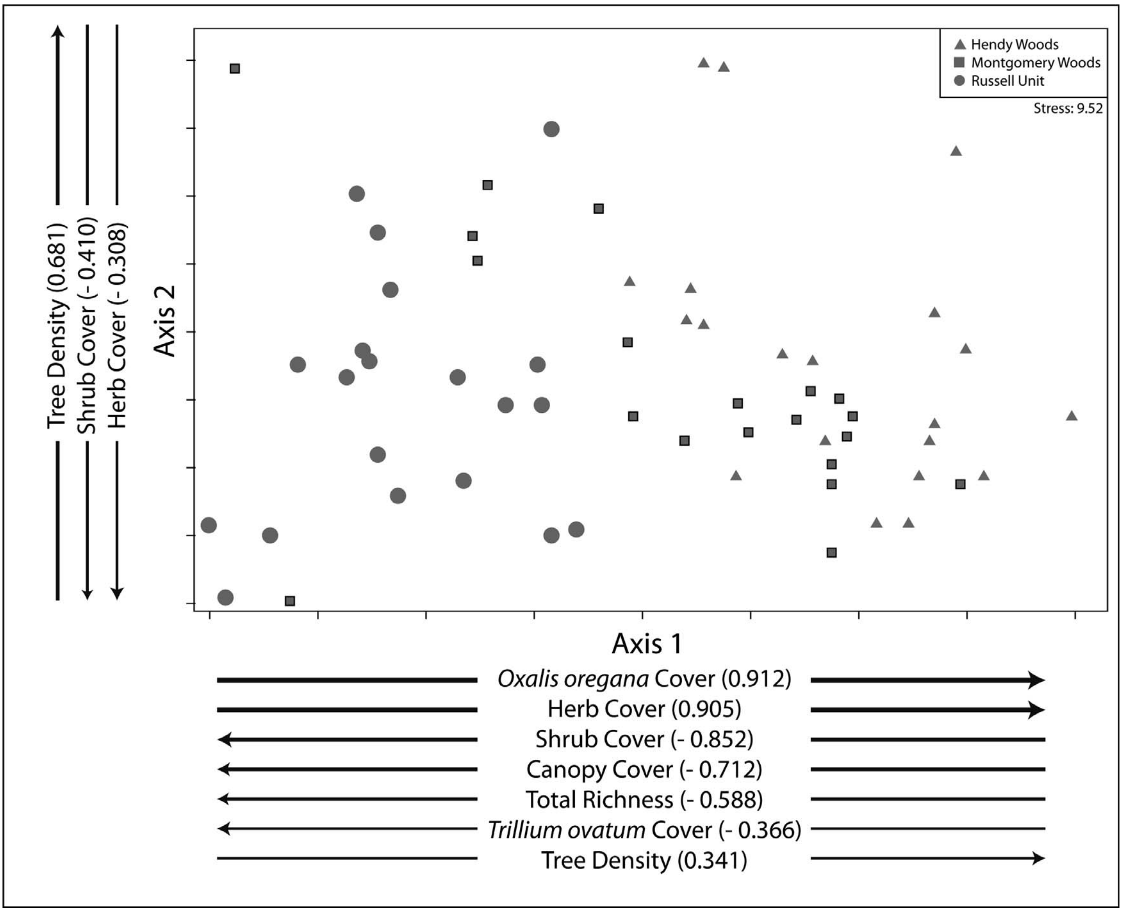

FIG. 2. Nonmetric multidimensional scaling main output for old-growth variables. Direction of influence (arrow direction) and strength (arrow weight) for variables with r > |0.300| indicated on each axis.

not exceed 10°) and Montgomery Woods (slopes did not exceed 4°).

DISCUSSION

The variation among these stands indicates greater landscape diversity and structural heterogeneity than is generally recognized in coast redwood old-growth forests. A variety of mechanisms may have led to the observed distinctions among these regional sites (i.e., microclimates, disturbance regimes, edaphic conditions, public access). Nonetheless, these findings still offer useful insights for current restoration paradigms.

Some of the variation found among these sites is likely explained by the Russell Unit's close proximity to the Pacific Ocean, which results in more frequent natural disturbances associated with coastal locations such as blowouts, salt spray, and strong winds (Wu and Guo 2006; Lorimer et al. 2009). These reoccurring, stochastic disturbances likely led to the openings of small canopy gaps and associated recruitment of otherwise suppressed species, as illustrated by the Russell Unit's high overall species richness yet low values in total understory cover, tree density, and basal area. Such gap disturbances increase niche partitioning and nutrient availability, allowing for a diverse assemblage of species to

TABLE 6. Pearson and Kendall correlations with ordination axes for stand structure and floristic data collected on the three coast redwood old-growth references sites in Mendocino County, California.

Variable	Axis 1 Pearson correlation (r)	Axis 2 Pearson correlation (r)
Percent *Oxalis oregana* cover	0.912	−0.289
Percent herb cover	0.905	−0.388
Percent shrub cover	−0.852	−0.41
Percent canopy cover	−0.712	0.443
Total species richness	−0.588	0.166
Total tree density	0.341	0.681
Basal area (m^2)	0.25	0.237
Percent *Trillium ovatum* cover	−0.366	−0.058

TABLE 7. Indicator species analysis comparisons on understory herbaceous species in the three old-growth reference sites in Mendocino County, California. Asterisk (*) denotes species with the highest indicator value in each stand.

	Indicator value	P-value
Russell Unit Indicator Species		
Calypso bulbosa	59	0.0002
Cardamine californica	55	0.0002
*Clintonia andrewsiana**	85	0.0002
Maianthemum racemosum	20	0.0534
Hendy Woods Indicator Species		
Achlys triphylla	42.3	0.0018
*Stachys mexicana**	68	0.0002
Viola glabella	41.4	0.0012
Montgomery Woods Indicator Species		
Galium triflorum	57.3	0.0002
*Adenocaulon bicolor**	59.2	0.0002
Aquilegia formosa	46.2	0.0002

TABLE 8. Potential qualitative characteristics of coastal old-growth sites and inland old-growth sites including representative photographs; symbols indicate high (+) or low (–) relative values. "0" indicates species not found in site(s).

Russell Unit	Site characteristic	Montgomery Woods and Hendy Woods
+	Species richness	–
+	Shrub cover	–
+	*Trillium ovatum* cover	–
+	*Clintonia andrewsiana* cover	0
–	Basal area	+
–	Tree density	+
–	Herbaceous cover	+
–	*Oxalis oregana* cover	+
–	*Stachys mexicana* cover	+
0	*Adenocaulon bicolor* cover	+
0	*Viola glabella* cover	+

flourish. These patterns of patch development are commonly observed in other old-growth stands in the Pacific Northwest (Wimberly 2002; van Mantgem and Stuart 2012).

While shade tolerant, old-growth associated species, such as *O. oregana* and *T. ovatum*, are present in the understory of each old-growth stand, *O. oregana* tended to dominate in Montgomery Woods and Hendy Woods (Sawyer et al. 2000; Loya and Jules 2007; Russell and Michels 2010). *Oxalis oregana*, a common species in coniferous forests (Russell and Michels 2010), is a strong competitor using vegetative spread via underground rhizomes as its main method of reproduction (Baldwin et al. 2012). In fact, most of the understory indicator species on each site (Table 7) are perennial, rhizomatous species found in moist, shady forests (Baldwin et al. 2012). The fertile alluvial soils of Hendy Woods and Montgomery Woods (Rittiman and Thorson 2006) in combination with low frequency of shrub canopy formation, is seemingly ideal for the proliferation of shade tolerant, moisture adapted species such as *O. oregana*.

While Montgomery Woods and Hendy Woods are both characterized by rich alluvial soils, nutrient-poor uplifted marine terraces also persist on the Russell Unit (Russell and Woolhouse 2012), which may account for some of the understory species variation among sites. Heavy shrub cover, common on marine terraces, reached maximum values in the Russell Unit. In addition, some species with significant ISA values observed in the Russell Unit, such as toothwort (*Cardamine californica* [Nutt.] Greene) and false Solomon's seal (*Maianthemum racemosum* [L.] Link) are most common in canopy gaps and open woodlands (Baldwin et al. 2012). The presence of species that prefer open woodlands may be related to edaphic conditions on the Russell Unit site.

Although the Russell Unit can be described as a site with a high degree of natural disturbance, the cover of *T. ovatum,* a species known to be sensitive to human disturbance (Loya and Jules 2007), was in higher abundance than on the other two sites. This finding suggests that natural and anthropogenic disturbances are not analogous. Both Hendy Woods and Montgomery Woods are managed for a high volume of visitor use, while the Russell Unit is not readily accessible to the public (i.e., no facilities, parking, or managed trails).

These findings support our hypothesis that significant variation exists among remaining old-growth reference sites in the central coast redwood region. Thus, we developed a qualitative matrix of potential indicators for potential application in restoration efforts (Table 8). Archetypal stands similar to Montgomery Woods and Hendy Woods may have relatively high tree density and basal area; herbaceous understory cover; cover of vegetatively spreading, shade tolerant understory species such as *Oxalis oregana*; and cover of perennial herbs including *Adenocaulon bicolor*, *Viola glabella*, and *Stachys mexicana*. In heterogeneous stands akin to the Russell Unit, dominant characteristics may include high cover values of sensitive understory species (*Trillium ovatum*), perennial *Clintonia andrewsiana* and other woodland-adapted perennial species, high shrub cover in canopy gaps, and diverse species assemblages. Potentially, incorporating these understory characteristics and other more subtle features of remaining old-growth stands will provide insight for restoration managers recognizing high variation in reference sites.

False assumptions of uniformity confound restoration targets. Thus, local site characteristics should be taken into consideration when designing active restoration projects. In developing future restoration efforts, biodiversity impacts to sensitive ground-layer species, overall species richness, and stand complexity should be carefully studied. Considering local stand variation could provide land use managers with additional references sites for comparison, more realistic restoration expectations, and a dynamic template for coast redwood restoration.

We recognize these findings represent a case-study scenario, and require augmentation for large-scale application. Although this study identifies differences in the few remaining old-growth coast redwood stands localized in Mendocino County, other stands may exist in this region or elsewhere that would further illustrate variation within this forest type. Additional research on other coast redwood old-growth stands would provide a stronger foundation to extrapolate these results. It is also important to note that causality among physical characteristics and biotic variables was beyond the scope of this study. Yet, the application of multivariate analyses, coupled with evidence from this case study in Mendocino County, reveals new insights for management of old-growth and recovering second-growth sites.

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