



# Peak plant diversity during early forest development in the western United States



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## ABSTRACT

Complex early-seral forests support biological legacies and unique understory vegetation (grasses, forbs, shrubs, juvenile trees) important to wildlife and ecosystem functioning. Intensive management in early-seral forest and other stages could reduce understory plant diversity and homogenize community compositions. Furthermore, the relative effects of management regime may vary at different stages of forest development. To what extent do taxonomic, functional and phylogenetic diversity vary by seral stage and/or ownership (a proxy for management regime) after accounting for climatic variation? For 2224 plant species sampled systematically at 16,330 sites in sixteen Plant Association Zones (PAZs) of Washington, Oregon and California, we estimated taxonomic, functional and phylogenetic diversity (both alpha = richness and beta = heterogeneity measures). Seral stage was inferred using forest structural metrics. Permutational multivariate analyses tested the relative effects of seral stage and ownership type. Across PAZs, a common motif emerged: low diversity in sparse, untreed stages indicated an accumulation period after stand-replacing disturbances, followed immediately by peak diversity in early sapling stages, after which gradually declining diversity coincided with the loss of shade-intolerant species during stand development and canopy closure. Departures from this motif tended to be in climatically less-permissive locations. More of the variation in diversity was explained by seral stage than ownership type (and their interactions were seldom significant). Discriminating the nuanced effects of different management regimes will require context-dependent proxies other than ownership. Identifying generalities in vegetation dynamics—and departures from those generalities—can help balance ecological and social objectives in rapidly changing forest landscapes.

## 1. Introduction

Awareness of the ecological importance of complex early-seral forests is now growing, even as their landscape proportion declines. Historically, forests naturally regenerating after canopy-removing disturbances comprised perhaps 5–20% of western US forestlands (Wimberly et al., 2000; Teensma et al., 1991; Agee, 2003) and 1–10% of eastern US forests (Lorimer and White, 2003). Yet recent changes in forestry practices and wildfire regimes of the western US have made early seral stages among the rarest in the region (Reilly and Spies, 2015). The landscape proportion of post-fire, early-seral forests declined from 5% in the 1940s to less than 2.5% in the late 20th century (Takaoka and Swanson, 2008). Changes in the distribution of seral stages across landscapes have unknown consequences for biological diversity. Declining proportions of early-seral conditions might reduce

plant biodiversity at landscape scales, which would have implications for organisms like birds, mammals and invertebrates that depend on plants for forage and habitat. We asked whether taxonomic, functional and phylogenetic diversity of plants varied predictably with seral stage and management regimes in temperate forests.

Structurally-complex early-seral forests host a diversity of plants and wildlife, including several early-seral obligates and opportunists (Swanson et al., 2014). Post-disturbance biological legacies and high fractions of hardwood shrubs provide irreplaceable habitat for a multitude of invertebrates, birds, reptiles and mammals (Hagar, 2007; Betts et al., 2010; Phalan et al., 2019). Likewise, post-disturbance canopy openings increase structural complexity and foster conditions required for certain plant species to establish (Halpern, 1989). During early forest development, the number and composition of plant species changes as a function of stem density and canopy closure (Lutz and

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Halpern, 2006). Understory plant species richness in early-seral forests can far exceed that of subsequent stages (Donato et al., 2009b), often peaking just 20 y after disturbances in high-productivity western US forests (Schoonmaker and McKee, 1988) and within a few decades in eastern deciduous hardwood forests (Gilliam et al., 2016). However, species richness is not only a function of time elapsed since disturbance, but also depends on the type and intensity of disturbances (Swanson et al., 2011). This suggests that understanding how diversity relates to forest development may also require knowledge of management regimes under different ownerships.

Linkages between ownership, forest management and plant diversity remain incompletely resolved. In western US forests, temporarily increased light availability can favor more understory plant species in plantation- and shelterwood-managed sites than in reserve-status stands (Battles et al., 2001). Yet, while logging may create a temporary high-light environment, subsequent intensive management may impede the development and persistence of full floristic diversity. Industrial management involving clearcutting and post-disturbance logging can also decrease plant diversity in forests of eastern and western North America (Roberts, 2002; Swanson et al., 2011). For example, in eastern Canadian mixed forests, logged/scarified stands saw an immediate decline in species richness attended by increased cover of graminoid functional groups and decrease of bryophytes on industrial privately-owned lands (Roberts and Zhu, 2002). Variation in forest structure is intimately linked to the management style and motivations of different landowners (Spies et al., 2002; Easterday et al., 2018). Multiple-use mandates on publicly-owned lands foster a mixture of management regimes, ranging from active silviculture to lightly-managed “reserved” status. By contrast, private industrial owners often seek to optimize timber production through vigorous silvicultural management. Categorizing forest lands by ownership provides a rough gauge of disturbance regimes (Kennedy et al., 2012; Easterday et al., 2018). Understanding disturbance regimes is important given that the agent, extent, duration and severity of disturbances exert strong control on successional trajectories and species diversity, in often nonlinear ways (Pickett and White, 1985; Walker and del Moral, 2003).

Quantifying diversity in forests can benefit from the complementary perspectives of taxonomic, functional and phylogenetic measures. Functional diversity observes that commonalities among species’ traits (or groups of traits) may be as ecologically relevant as taxonomic identities if traits impact individual fitness and vary predictably with environment (Shipley et al., 2016). Likewise, phylogenetic diversity presumes that taxonomic designations alone may conceal important information about evolutionary relatedness (Mazel et al., 2017). For example, a community possessing three closely-related pine species may be considered less “diverse” than another containing a pine, a sedge, and an aster. Thus, diversity may be simultaneously quantified by taxonomic units, their functions, and the degree to which they span the tree of life. Of interest is not only alpha-diversity (i.e., within-plot “richness”), but also beta-diversity (i.e., plot-to-plot “heterogeneity” of community compositions) (Anderson et al., 2011).

Recent attention to early-seral forest diversity has focused primarily on the US Pacific Northwest (e.g., Tepley et al., 2014; Hessburg et al., 2016; McCord et al., 2019; Downing et al., 2020) with some attention to California (DellaSala et al., 2014) or the eastern US (King and Schlossberg, 2014). To seek generality across climate and compositional gradients, we considered the US Pacific states of California, Oregon and Washington, which encompass some of the largest ranges of temperature and moisture in the continental US (Fig. 1). Specifically, we estimated richness (alpha) and heterogeneity (beta) components of taxonomic, functional and phylogenetic diversity for understory forest vegetation. Four hypotheses emerged. First, we expected plant diversity would be greatest in forest communities occupying earlier seral stages preceding canopy closure (H1). Second, we expected peak diversity in ownership types associated with intermediate management intensity (neither in industrial nor reserved status) (H2). Third, we tested an

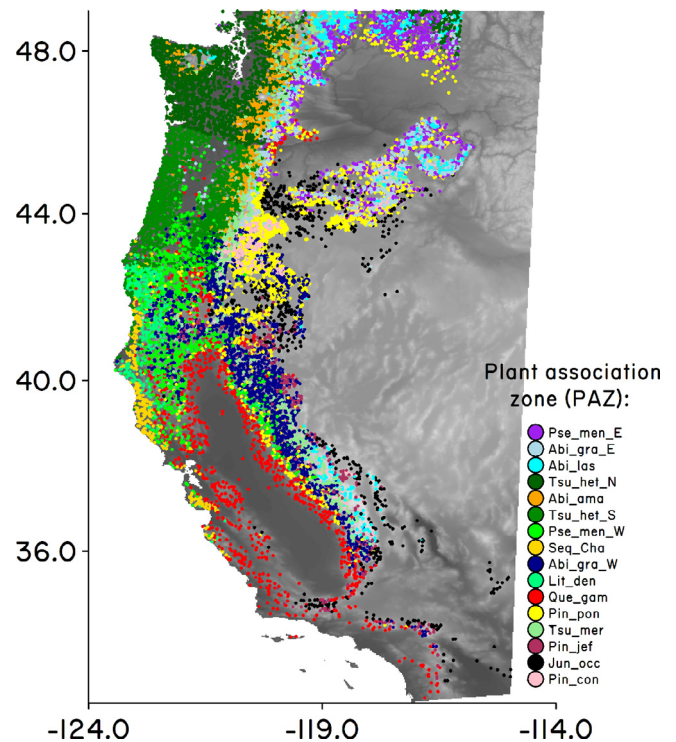


Fig. 1. Plant Association Zones (PAZs) at forest inventory plot locations in Washington, Oregon and California. Plots in each PAZ share similar climates, soils, terrains and potential natural vegetation across the 82.4-million ha study area. Analyses were conducted for each PAZ in parallel.

interactive effect such that the effects of seral stage would be modified by ownership (H3). Finally, we expected a significant ownership effect when focusing specifically on early-seral stages alone (H4). Identifying the conditions that constrain multiple dimensions of biological diversity can inform an ecological forestry approach to balance multiple objectives.

## 2. Methods

Computer code for analysis is available in Appendix S1 in Supporting Information. Statistical analyses were performed in R version 3.6.3 (R Development Core Team, 2020). Forest inventory data are publicly available at <https://www.fia.fs.fed.us/tools-data/>.

### 2.1. Sampling design and species abundances

We obtained abundances of understory vegetation sampled in the 10-y interval 2005–2014 at 16,330 sites in Washington, Oregon and California. Data originated from the US Forest Service’s Forest Inventory and Analysis (FIA) program (Woudenberg et al., 2010; Gray et al., 2012). FIA uses a nationally standardized sampling design that is systematically random and geographically representative: one site is randomly located in each cell of a hexagonal grid covering the US, and one plot (the sample unit) is then measured at each forested site (where “forested” is defined as  $\geq 10\%$  potential tree cover on undeveloped land  $\geq 0.41$  ha area and  $\geq 36.6$  m wide). Four 168-m<sup>2</sup> subplots comprise each 672-m<sup>2</sup> (0.0672-ha) plot.

In each sampled plot, trained crew members used FIA’s Phase 2 protocol to estimate vertically projected canopy-cover abundance for measured plant species. Measured species are the top four most abundant ones per growth form (i.e., graminoids, forbs, shrub/subshrub/woody vines, saplings, large trees) in each of the four subplots regardless of cover, or any species exceeding 3% cover. Our estimates are conservative in magnitude (because the protocol does not exhaustively

include all species) but include all taxa equally. When plots included multiple conditions (e.g., forested vs not) we used only information from conditions covering > 90% of the plot. Each species' abundance was the plot-level mean of its cover. Sub-specific taxa were lumped to species because subspecies concepts were not systematically applied in the field. Some individuals were only identified to genus (usually *Carex* or *Salix*) when field identification was prohibited. Nomenclature per USDA PLANTS (<https://plants.usda.gov>) was updated using concepts from Zanne et al. (2014) for constructing a phylogeny. The completely filtered and quality-checked dataset had a total of 16,330 plots containing 2224 understory plant species.

## 2.2. Environmental covariates

We determined ownership at each plot as a proxy for management intensity, comprising “reserved federal”, “available federal”, “private nonindustrial”, “nonfederal public”, and “private industrial” ownerships. At each plot location we queried climate data as 30-y annual normals spanning 1980–2010 from the ClimateNA database (Wang et al., 2016). To remedy collinearity among climate variables we used principal components analysis (PCA) based on the scaled and centered correlation matrix. We interpreted only the first two principal components (PCs) because they explained 78.3% of the variation in climate across the study area (43.4% and 34.9% respectively).

We also assigned each plot to a Plant Association Zone (PAZ hereafter) based on Henderson et al. (2011). PAZs were considered a blocking factor to account for variation from different climates, soils, terrains and potential natural vegetation across the large 82.4-million ha study area (Fig. 1). These are biologically meaningful groupings because plots in each PAZ share a common regional species pool, are spatially coherent, have similar potential productivity (as measured by mean annual increment), and share similar macroclimatic, edaphic and topographic features (Table 1).

Seral stage categories were based on stand structural development rather than measured age (Table 1). The FIA inventory measures on-site “stand age” from a plurality of trees in the predominant size-class; yet because this measurement describes the mean age of the cohort that most dominates the stand, it provides ambiguous information about actual time-since-disturbance (Stevens et al., 2016). Instead, we used a combination of tree canopy cover and quadratic mean diameter (QMD) to group plots into seral stages (Table 2), loosely based on Ohmann et al. (2007). To accommodate different rates and maxima of structural development among PAZs, we defined breakpoints for QMD not by absolute magnitude but rather by relative quantiles in each PAZ. Seral stage calculated this way loosely correlates with FIA's stand age

**Table 1**  
Summaries for Plant Association Zones (PAZ).

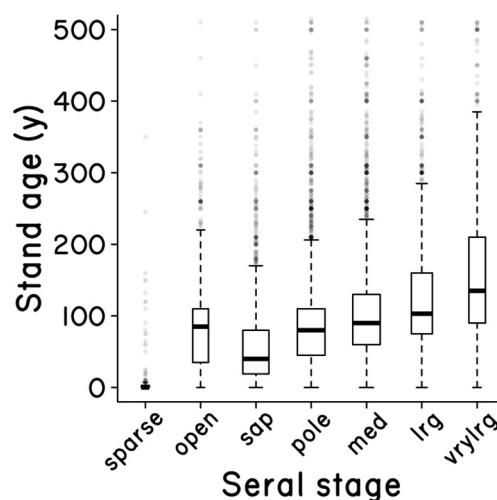
PAZ	PAZ species	MAT	MAP	CMD	MAI	QMDsoft	QMDhard	n
Pse_men_E	<i>Pseudotsuga menziesii</i>	6.6	618.2	457.2	4.2	26.7	2.3	1313
Abi_gra_E	<i>Abies grandis/concolor</i>	6.2	850.4	410.6	5.4	24.9	1.8	1237
Abi_las	<i>Abies lasiocarpa</i>	3.9	929.5	301.7	4.5	20.9	1.5	752
Tsu_het_N	<i>Tsuga heterophylla</i>	8.6	2034.3	221.5	10.0	27.2	11.7	1863
Abi_ama	<i>Abies amabilis</i>	6.5	2462.7	171.9	8.7	26.7	2.4	866
Tsu_het_S	<i>Tsuga heterophylla</i>	10.0	1954.5	307.9	10.0	34.4	13.0	1762
Pse_men_W	<i>Pseudotsuga menziesii</i>	11.5	1418.9	563.2	7.0	29.1	16.1	1115
Seq_Cha	<i>Sequoia sempervirens/Chamaecyparis nootkatensis</i>	13.1	1507.0	572.7	10.8	34.7	17.3	261
Abi_gra_W	<i>Abies grandis/concolor</i>	8.4	1188.8	515.2	6.9	30.0	5.7	1703
Lit_den	<i>Lithocarpus densiflorus</i>	12.1	2266.6	482.9	7.0	41.5	16.2	402
Que_gam	<i>Quercus</i> spp.	14.5	740.8	846.7	4.9	13.0	21.8	858
Pin_pon	<i>Pinus ponderosa</i>	7.6	599.9	590.7	4.1	26.9	3.2	1833
Tsu_mer	<i>Tsuga mertensiana</i>	4.9	1786.6	274.3	4.4	25.5	0.3	820
Pin_jef	<i>Pinus jeffreyi</i>	8.8	905.3	632.9	3.9	30.4	5.2	317
Jun_occ	<i>Juniperus occidentalis</i>	8.9	369.2	732.1	1.9	26.2	2.7	709
Pin_con	<i>Pinus contorta</i>	5.6	783.8	489.0	3.1	15.0	0.2	519

Abbreviations: MAT = mean annual temperature (°), MAP = mean annual precipitation (mm), CMD = climatic moisture deficit (mm), MAI = mean annual increment ( $\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$ ), QMDsoft and QMDhard = quadratic mean diameter of softwood, hardwood trees (cm).

**Table 2**

Definition of seral stages based on tree structural metrics. Quadratic mean diameter (QMD) breakpoints use quantiles per Plant Association Zone (PAZ).

Abbreviation	Seral stage	Canopy cover	QMD quantile
sparse	Sparse	< 10%	any
open	Open	10–30%	any
sap	Sapling	≥ 30%	0.15
pole	Pole	≥ 30%	0.25
med	Medium	≥ 30%	0.50
lrg	Large	≥ 30%	0.75
vrylrg	Very large	≥ 30%	0.90



**Fig. 2.** Covariation of seral stages with measured stand age, from forest inventory plots in Washington, Oregon and California. Seral stages were categorized based on field-measured tree canopy cover and quadratic mean diameter (Table 2). Box ends are the interquartile range (from 25th to 75th percentiles), midlines are medians, and points beyond whiskers are outliers > 1.5 times the interquartile range. Box widths are proportional to number of plots.

variable, but does not strictly depend on it (Fig. 2).

## 2.3. Plant phylogeny

For all 2224 understory plant species, we used the R package ‘V.PhyloMaker’ (Jin and Qian, 2019) to construct an ultrametric

**Table 3**

Test statistics for alpha-diversity in sixteen Plant Association Zones, from PERMANOVA. Bold face shows statistical significance at the 95% confidence level, indicating rejection of the null hypothesis of no difference in group centroids.

PAZ	Diversity	Seral			Owner			Seral × owner		
		F	R <sup>2</sup>	p	F	R <sup>2</sup>	p	F	R <sup>2</sup>	p
Pse_men_E	Taxonomic	15.9	0.07	<b>0.001</b>	1.2	0.00	0.282	1.1	0.02	0.372
Abi_gra_E		10.6	0.05	<b>0.001</b>	0.7	0.00	0.607	0.6	0.01	0.914
Abi_las		11.4	0.08	<b>0.001</b>	8.8	0.04	<b>0.001</b>	1.3	0.02	0.213
Tsu_het_N		15.0	0.05	<b>0.001</b>	7.5	0.02	<b>0.001</b>	0.9	0.01	0.526
Abi_ama		4.0	0.03	<b>0.001</b>	2.7	0.01	<b>0.033</b>	1.4	0.03	0.139
Tsu_het_S		14.9	0.05	<b>0.001</b>	4.6	0.01	<b>0.002</b>	1.9	0.02	<b>0.008</b>
Pse_men_W		5.6	0.03	<b>0.001</b>	4.2	0.01	<b>0.002</b>	1.3	0.02	0.225
Seq_Cha		3.1	0.06	<b>0.010</b>	1.5	0.02	0.202	0.9	0.06	0.528
Abi_gra_W		18.1	0.06	<b>0.001</b>	4.3	0.01	<b>0.003</b>	0.6	0.01	0.928
Lit_den		2.5	0.04	<b>0.017</b>	0.6	0.01	0.615	0.8	0.04	0.697
Que_gam		8.3	0.06	<b>0.001</b>	3.6	0.02	<b>0.008</b>	0.9	0.02	0.561
Pin_pon		33.1	0.10	<b>0.001</b>	5.4	0.01	<b>0.001</b>	1.3	0.01	0.128
Tsu_mer		10.8	0.07	<b>0.001</b>	4.1	0.02	<b>0.005</b>	0.6	0.01	0.888
Pin_jef		5.3	0.09	<b>0.001</b>	1.0	0.01	0.414	0.7	0.04	0.792
Jun_occ		35.3	0.23	<b>0.001</b>	2.9	0.01	<b>0.014</b>	1.2	0.03	0.197
Pin_con		4.9	0.05	<b>0.001</b>	2.0	0.01	0.101	1.2	0.04	0.265
Pse_men_E	Functional	16.1	0.07	<b>0.001</b>	3.8	0.01	<b>0.004</b>	2.2	0.04	<b>0.004</b>
Abi_gra_E		8.6	0.04	<b>0.001</b>	1.6	0.00	0.198	1.8	0.03	<b>0.022</b>
Abi_las		11.2	0.08	<b>0.001</b>	9.4	0.04	<b>0.001</b>	3.3	0.06	<b>0.001</b>
Tsu_het_N		6.4	0.02	<b>0.001</b>	4.3	0.01	<b>0.004</b>	1.6	0.02	<b>0.041</b>
Abi_ama		3.0	0.02	<b>0.004</b>	1.8	0.01	0.124	1.4	0.03	0.120
Tsu_het_S		18.4	0.06	<b>0.001</b>	3.8	0.01	<b>0.003</b>	1.4	0.02	0.120
Pse_men_W		3.3	0.02	<b>0.003</b>	5.7	0.02	<b>0.001</b>	0.8	0.01	0.747
Seq_Cha		1.9	0.04	0.094	2.8	0.04	<b>0.029</b>	0.9	0.05	0.590
Abi_gra_W		9.0	0.03	<b>0.001</b>	2.6	0.01	<b>0.038</b>	1.2	0.02	0.234
Lit_den		0.9	0.01	0.525	0.5	0.01	0.701	1.0	0.04	0.465
Que_gam		6.9	0.05	<b>0.001</b>	1.1	0.00	0.361	1.2	0.03	0.262
Pin_pon		16.0	0.05	<b>0.001</b>	5.3	0.01	<b>0.002</b>	1.0	0.01	0.512
Tsu_mer		6.7	0.05	<b>0.001</b>	1.9	0.01	0.100	1.2	0.03	0.234
Pin_jef		4.1	0.07	<b>0.002</b>	1.7	0.02	0.166	1.2	0.06	0.291
Jun_occ		5.5	0.04	<b>0.001</b>	2.4	0.01	0.050	0.9	0.03	0.620
Pin_con		2.9	0.03	<b>0.006</b>	0.9	0.01	0.440	0.7	0.03	0.811
Pse_men_E	Phylogenetic	15.6	0.07	<b>0.001</b>	2.5	0.01	<b>0.044</b>	1.4	0.02	0.105
Abi_gra_E		13.0	0.06	<b>0.001</b>	1.5	0.00	0.199	0.6	0.01	0.932
Abi_las		13.4	0.09	<b>0.001</b>	8.5	0.04	<b>0.001</b>	0.9	0.02	0.579
Tsu_het_N		12.0	0.04	<b>0.001</b>	3.1	0.01	<b>0.015</b>	0.7	0.01	0.840
Abi_ama		4.3	0.03	<b>0.001</b>	4.5	0.02	<b>0.001</b>	1.2	0.02	0.214
Tsu_het_S		13.0	0.04	<b>0.001</b>	3.6	0.01	<b>0.006</b>	1.5	0.02	0.066
Pse_men_W		5.9	0.03	<b>0.001</b>	5.7	0.02	<b>0.001</b>	0.9	0.02	0.640
Seq_Cha		3.1	0.06	<b>0.003</b>	1.6	0.02	0.181	0.9	0.05	0.540
Abi_gra_W		20.9	0.07	<b>0.001</b>	4.8	0.01	<b>0.002</b>	0.6	0.01	0.908
Lit_den		1.4	0.02	0.222	0.6	0.01	0.694	0.7	0.03	0.856
Que_gam		10.8	0.07	<b>0.001</b>	6.7	0.03	<b>0.001</b>	1.0	0.03	0.448
Pin_pon		33.1	0.10	<b>0.001</b>	2.0	0.00	0.086	1.3	0.01	0.155
Tsu_mer		12.0	0.08	<b>0.001</b>	5.0	0.02	<b>0.001</b>	0.6	0.01	0.889
Pin_jef		6.0	0.11	<b>0.001</b>	1.3	0.02	0.248	0.3	0.02	0.994
Jun_occ		29.7	0.20	<b>0.001</b>	0.4	0.00	0.766	1.8	0.04	<b>0.016</b>
Pin_con		5.6	0.06	<b>0.001</b>	1.0	0.01	0.426	1.4	0.05	0.120

phylogenetic tree based on the established super-tree of Zanne et al. (2014). Nodes in the phylogeny indicate divergence of taxa (speciation), and branch lengths indicate time since divergence. We calculated a phylogenetic variance-covariance matrix, assuming Brownian trait evolution, for estimation of phylogenetic diversity below. The complete phylogeny is in Appendix S2 in Supporting Information.

#### 2.4. Diversity measures

We calculated taxonomic, functional and phylogenetic diversities to provide complementary information. Measures of alpha-diversity considered “richness” components. Taxonomic species richness was simply the number of species recorded per 0.0672-ha plot. Functional richness was the number of unique growth forms (e.g., annual and perennial forbs, graminoids, shrubs and subshrubs, vines and trees). Phylogenetic species richness was the number of species per plot after discounting their evolutionary relatedness (Helmus et al., 2007). Intuitively,

phylogenetic diversity decreases towards zero as species become more closely related, and increases when species are more distantly related (i.e., covering a broader spectrum of the tree of life).

Measures of beta-diversity considered “heterogeneity” components. We defined beta-diversity as heterogeneity of multivariate dispersions, calculated as the distance to multivariate centroids in the space of a chosen dissimilarity measure (Anderson et al., 2006, 2011). This analysis used Bray-Curtis dissimilarities, corrected using shortest path step-across adjustment to account for any sites sharing no species in common (Oksanen et al., 2019). Prior to step-across adjustment, phylogenetic Bray-Curtis dissimilarities were weighted by branch length in the ultrametric tree, per Pavoine and Ricotta (2014).

#### 2.5. Statistical tests

We tested the effects of seral stage, management type, and their interaction on six diversity measures (three alpha, three beta). Before

analyses we assigned plots to PAZs as a blocking factor, with separate analyses for each PAZ. The alpha-diversity tests used permutational multivariate analysis-of-variance (PERMANOVA; Anderson (2001)), based on Euclidean distances, 999 permutations, and Type-I sequential sums-of-squares. Our implementation used the R function `vegan::adonis()` (Oksanen et al., 2019). With Euclidean distances, PERMANOVA becomes equivalent to conventional ANOVA, except model residuals are permuted to obtain *p*-values.

The beta-diversity tests used a permutational test for heterogeneity of multivariate dispersions (PERMDISP; Anderson et al. (2006)), based on Bray-Curtis dissimilarities, 999 permutations, bias correction, and spatial median as the multivariate centroid from which each group's dispersion was calculated. Our implementation used the R function `vegan::betadisper()` (Oksanen et al., 2019). Interactions in a 2-factor PERMDISP test, while technically possible, would yield ambiguous results (Anderson et al., 2006), therefore we tested effects individually and did not test an ownership-seral stage interaction for beta-diversity. Formally, PERMANOVA tests the null hypothesis that the within-group centroids (in terms of Euclidean distances) are equivalent among groups, while PERMDISP tests the null hypothesis that the average within-group dispersions (in terms of Bray-Curtis dissimilarities) are equivalent among groups (Anderson and Walsh, 2013).

For each diversity measure, we visualized diversity within each PAZ, ownership and seral stage as boxplots showing key quantiles (25th, 50th and 75th percentiles) of their empirical distribution. To identify any common motifs of diversity with respect to seral-stage, we also used R package 'crs' (Ma et al., 2015) to estimate cubic regression splines for each PAZ individually, as well as for all data aggregated across PAZs. These regression splines depict mean diversity as a nonlinear function of seral stage.

### 3. Results

Sampled forests of the western US harbored 2224 unique plant species (gamma-diversity). From 16,330 standardized plots, mean species richness was 12.1 (average alpha diversity), yielding an extremely high beta-diversity of 183.7 (Whittaker's beta-diversity = gamma/alpha - 1).

#### 3.1. H1: Diversity consistently greater in earlier seral stages

Seral stage was significantly associated with taxonomic diversity in all sixteen PAZs, and with functional and phylogenetic diversity in nearly all PAZs (Table 3). Across PAZs, alpha-diversity was consistently lowest in sparse and open stages, subsequently reached a peak in early-seral forests of sapling and pole-timber stages, then weakly declined during later forest development (Fig. 3A–C). Likewise, beta-diversity followed a similar motif whereby sparse and open stages were most homogeneous (Fig. 3D–F).

#### 3.2. H2: Diversity not consistently associated with ownership

After accounting for seral stage, ownership was significantly associated with diversity for only perhaps half of the PAZs (Table 3). Relative to seral stage, ownership always had very small effect-size (as measured by PERMANOVA pseudo-*F*) and poor explanatory value (*R*<sup>2</sup>). Ownership was significantly associated with diversity in some of the more productive, climatically moist PAZs (e.g., *Pseudotsuga menziesii*, *Abies grandis*, *Abies lasiocarpa*, *Tsuga heterophylla*). In the most arid, lowest-diversity PAZs (e.g., *Pinus jeffreyi*, *Juniperus occidentalis*, *Pinus contorta*), ownership was rarely significantly associated with diversity (Table 3).

#### 3.3. H3: No consistent seral stage–ownership interaction

After accounting for the individual effects of seral stage and

ownership, a significant interaction among these occurred in a slim minority of cases (Table 3). Primarily these significant interactions were in climatically moist, high-diversity PAZs (e.g., *Pseudotsuga menziesii*, *Abies grandis*, *Abies lasiocarpa*, *Tsuga heterophylla*) for functional diversity, but for few other kinds of diversity.

#### 3.4. H4: Early-seral ownership inconsistently related to heterogeneity

Considering only early-seral (sapling) stages, alpha-diversity was significantly related to ownership in only a minority of cases (Table 4). By contrast, early-seral beta-diversity had a significant relationship with ownership in nearly every PAZ (Table 5). Yet, the ranks of different ownership types were inconsistent when compared across PAZs (i.e., no single ownership type consistently had greater or lesser beta-diversity). For example, private industrial ownerships were top-ranked in *Sequoia sempervirens* and *Pseudotsuga menziesii* zones, but bottom-ranked in *Abies lasiocarpa*, *Tsuga mertensiana* and *Juniperus occidentalis* zones (Fig. 4). Available federal lands were often (but not universally) top-ranked.

#### 3.5. Diversity motif

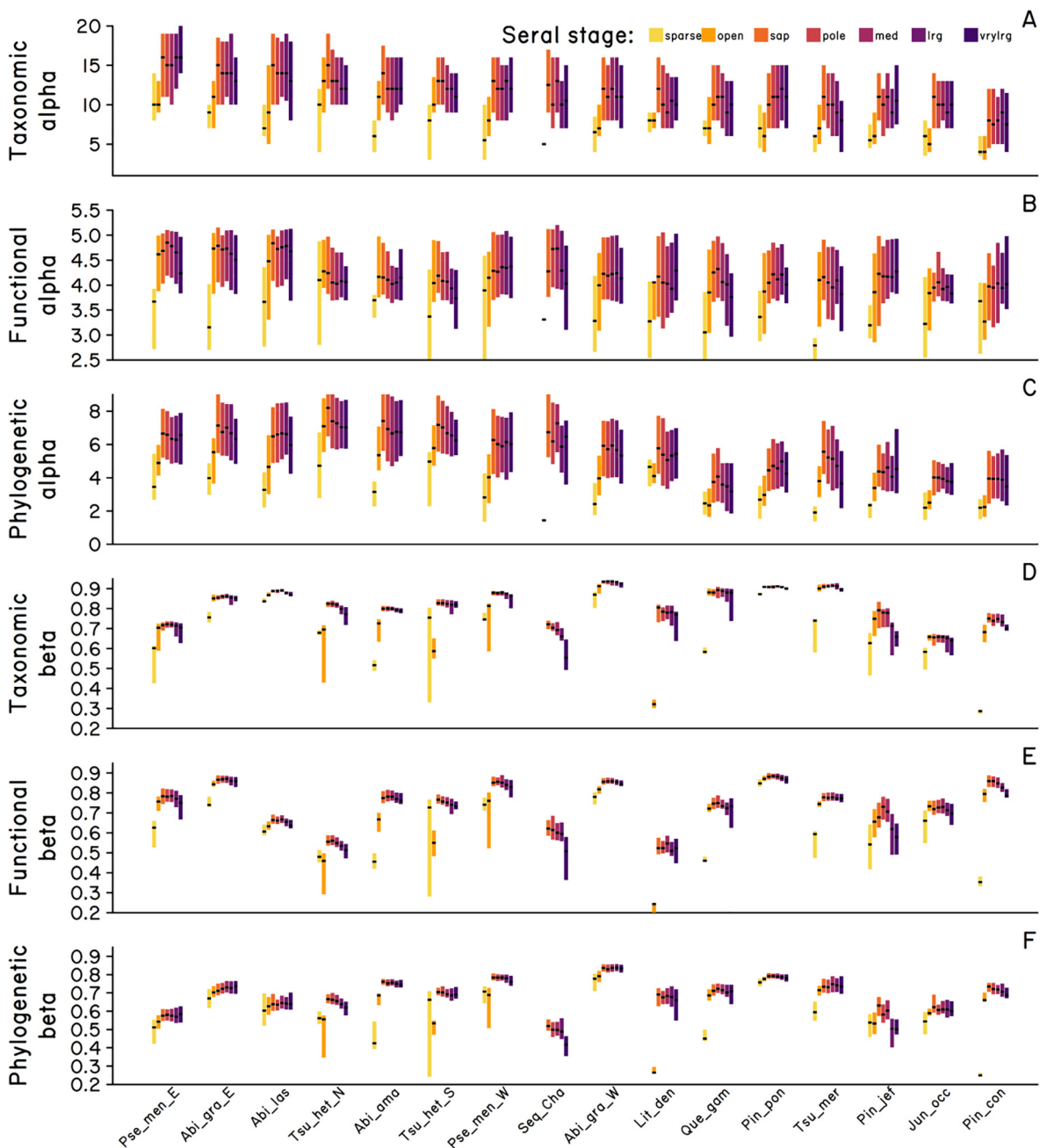
Diversity varied as a nonlinear function of seral stage, in a common motif across all six diversity measures and sixteen PAZs (Fig. 5). This motif exhibited lowest diversity in sparse and open seral stages, peaked in early sapling and pole-timber stages, and had a mild decline in subsequent mid- and late-seral stages.

## 4. Discussion

Among a wide range of habitats throughout the western US, we detected a recurrent “motif” of understory plant diversity through forest seral development. Specifically, the seral-stage motif consisted of minimal diversity in sparse and open stages, a strong peak in early sapling and pole-timber stages, and mildly declining diversity over subsequent mid- and late-seral stages as canopy cover and stand basal area increased. This held qualitatively true for taxonomic, functional and phylogenetic diversity measures. That the relationships between diversity and ownership were few, weak, and inconsistent suggests that ownership type is not a universal predictor of diversity in western US forests, but rather that effects may vary according to management practices in local contexts.

The diversity motif described above can be interpreted in terms of forest structural development. Low diversity in sparse, untreed pre-forest indicates that a period of species accumulation is required after stand-replacing disturbances, consistent with findings in watershed-scale studies (Lutz and Halpern, 2006). The immediate peak of species in sapling-stage early-seral forests indicates a mixture of species with overlapping tolerances based on life-history traits related to colonization, growth rates, and stress tolerance (Halpern, 1989). The gradual decline of diversity in mid- and late-seral stands thereafter is consistent with the elimination of shade-intolerant species during canopy closure (Larson et al., 2008). Despite its recurrence through the western US, predictions from this pattern may be complicated by the observation that structural development and community compositional change may occur at different rates (Larson et al., 2008). We also note that large-scale data, as presented here, may obscure specific compositional trajectories that depend on local site conditions.

Understory plant diversity following a disturbance is the result of biological processes (survival, vegetative or seed-bank regeneration, and immigration) as well as environmental modifications attributed to the disturbance itself: changes to microclimates, resource availability and structural heterogeneity (Roberts and Gilliam, 2014). The relative importance of these processes changes over the course of forest development. Peak levels of diversity in the sapling and pole stages can be attributed to persistence of early seral-affiliated plants (Hagar, 2007),



**Fig. 3.** Alpha- and beta-diversity, ordered by seral stage within each of sixteen Plant Association Zones. For each seral stage, the vertical bar is the interquartile range containing half of all values (from 25th through 75th percentiles), bisected by a black midline at the median (50th percentile). Seral stages are color-coded (early seral = warm colors, late seral = cool colors). Alpha-diversity for each plot is the count of species, functional groups, or phylogenetically-weighted species. Beta-diversity, as Bray-Curtis dissimilarity on a 0–1 scale, represents heterogeneity as the mean pairwise dissimilarity of each plot to all others with respect to abundance-weighted species, functional groups, or phylogenetically-weighted species.

concurrent with the advent of shade-tolerant understory plants. However, the persistence of a species (and its contribution to plot-level diversity) does not necessarily contribute to trophic functioning. For example, early-seral *Vaccinium* species often persist well into mid-seral stages, but as overstory cover increases their growth slows and they cease to flower and fruit (Anzinger, 2002). This means that a given species may contribute to taxonomic diversity without contributing much to ecosystem functions like berry or nectar provisioning. Further studies may elaborate on our generalized diversity patterns to explore turnover of specific ecological functions during early-seral stages.

Lower species richness in sparse or open pre-forest conditions, as defined here, does not necessarily indicate an absence of ecological values in early seral pre-forest. Early-seral specialist species often occur

in spite of temporarily reduced species richness in the initial stage immediately following disturbance. In the western US, these tend to be disturbance-adapted taxa such as *Ceanothus* spp., *Chamerion/Epilobium* spp., *Geranium bicknellii*, *Anaphalis margaritacea*, bryophytes such as *Ceratodon purpureus*, and many graminoids (Klinka et al., 1985, Franklin and Dyrness, 1988, Halpern, 1989). Some of these species provide important trophic or other functions such as nitrogen fixation, soil stabilization, and provision of fruits, seeds, nectar, or pollen. Given that the inventory sampling design relied on a 3% cover-abundance threshold and was not exhaustive, our alpha-diversity estimates may be revised upward if some taxa consistently occurred in only trace amounts after disturbances. This analysis may therefore be interpreted as giving abundance-weighted estimates, where taxa having at least 3%

**Table 4**

Test statistics for effect of ownership on *early-seral* alpha-diversity in sixteen Plant Association Zones, from PERMANOVA. Bold face shows statistical significance at the 95% confidence level, indicating rejection of the null hypothesis of no difference in group centroids.

	Taxonomic			Functional			Phylogenetic		
	F	R <sup>2</sup>	p	F	R <sup>2</sup>	p	F	R <sup>2</sup>	p
Pse_men_E	1.2	0.02	0.325	2.0	0.03	0.131	2.7	0.04	<b>0.028</b>
Abi_gra_E	0.8	0.01	0.533	0.8	0.01	0.524	0.6	0.01	0.655
Abi_las	2.5	0.06	0.074	1.1	0.02	0.359	2.2	0.05	0.104
Tsu_het_N	3.8	0.04	<b>0.004</b>	2.1	0.02	0.090	2.5	0.02	<b>0.039</b>
Abi_ama	1.8	0.03	0.126	0.7	0.01	0.624	1.6	0.03	0.175
Tsu_het_S	5.1	0.05	<b>0.002</b>	1.1	0.01	0.367	4.3	0.04	<b>0.002</b>
Pse_men_W	0.7	0.01	0.605	1.6	0.02	0.171	1.0	0.01	0.419
Seq_Cha	0.7	0.05	0.597	1.0	0.06	0.429	1.5	0.09	0.206
Abi_gra_W	1.0	0.01	0.417	1.3	0.01	0.276	1.4	0.02	0.236
Lit_den	0.7	0.03	0.596	0.8	0.04	0.500	0.7	0.03	0.559
Que_gam	1.8	0.05	0.140	0.1	0.00	0.992	1.9	0.05	0.116
Pin_pon	2.1	0.02	0.086	2.6	0.03	<b>0.043</b>	1.6	0.02	0.175
Tsu_mer	1.4	0.03	0.237	1.2	0.02	0.323	1.6	0.03	0.198
Pin_jef	1.6	0.10	0.194	4.0	0.22	<b>0.006</b>	0.9	0.06	0.530
Jun_occ	2.4	0.09	0.063	0.1	0.00	0.994	2.1	0.08	0.065
Pin_con	1.7	0.06	0.154	0.9	0.03	0.495	2.4	0.08	<b>0.046</b>

**Table 5**

Test statistics for effect of ownership on *early-seral* beta-diversity in sixteen Plant Association Zones, from PERMDISP. Bold face shows statistical significance at the 95% confidence level, indicating rejection of the null hypothesis of no difference in group dispersions.

	Taxonomic			Functional			Phylogenetic		
	F	R <sup>2</sup>	p	F	R <sup>2</sup>	p	F	R <sup>2</sup>	p
Pse_men_E	8.4	0.11	<b>0.001</b>	12.3	0.16	<b>0.001</b>	0.4	0.01	0.777
Abi_gra_E	26.6	0.29	<b>0.001</b>	16.0	0.20	<b>0.001</b>	0.7	0.01	0.616
Abi_las	276.8	0.87	<b>0.001</b>	77.6	0.65	<b>0.001</b>	31.7	0.43	<b>0.001</b>
Tsu_het_N	57.4	0.36	<b>0.001</b>	7.8	0.07	<b>0.001</b>	6.2	0.06	<b>0.002</b>
Abi_ama	102.5	0.67	<b>0.001</b>	10.9	0.18	<b>0.001</b>	36.9	0.42	<b>0.001</b>
Tsu_het_S	8.7	0.08	<b>0.001</b>	10.6	0.10	<b>0.001</b>	1.4	0.01	0.234
Pse_men_W	37.4	0.36	<b>0.001</b>	9.3	0.12	<b>0.001</b>	5.7	0.08	<b>0.001</b>
Seq_Cha	50.5	0.77	<b>0.001</b>	8.1	0.35	<b>0.001</b>	10.0	0.40	<b>0.001</b>
Abi_gra_W	1366.4	0.94	<b>0.001</b>	417.0	0.82	<b>0.001</b>	133.3	0.60	<b>0.001</b>
Lit_den	33.7	0.61	<b>0.001</b>	5.3	0.20	<b>0.002</b>	8.9	0.30	<b>0.001</b>
Que_gam	7.4	0.17	<b>0.001</b>	1.8	0.05	0.123	2.1	0.06	0.085
Pin_pon	90.9	0.50	<b>0.001</b>	43.0	0.32	<b>0.001</b>	12.7	0.12	<b>0.001</b>
Tsu_mer	413.4	0.89	<b>0.001</b>	202.2	0.79	<b>0.001</b>	45.2	0.46	<b>0.001</b>
Pin_jef	27.4	0.67	<b>0.001</b>	3.3	0.20	<b>0.025</b>	7.7	0.36	<b>0.001</b>
Jun_occ	12.8	0.36	<b>0.001</b>	7.1	0.23	<b>0.001</b>	7.7	0.25	<b>0.001</b>
Pin_con	294.1	0.91	<b>0.001</b>	208.4	0.88	<b>0.001</b>	91.4	0.76	<b>0.001</b>

cover contribute more than low-abundance taxa to overall patterns of diversity during early forest structural development. Although we assume this is sufficient to capture landscape-level diversity, a future calibration study using full species lists from USFS-FIA “Phase 3” plots could verify. Under this assumption, we recovered consistent and recurring diversity patterns across a wide array of climates, soils and terrain types harboring several thousand unique plant species.

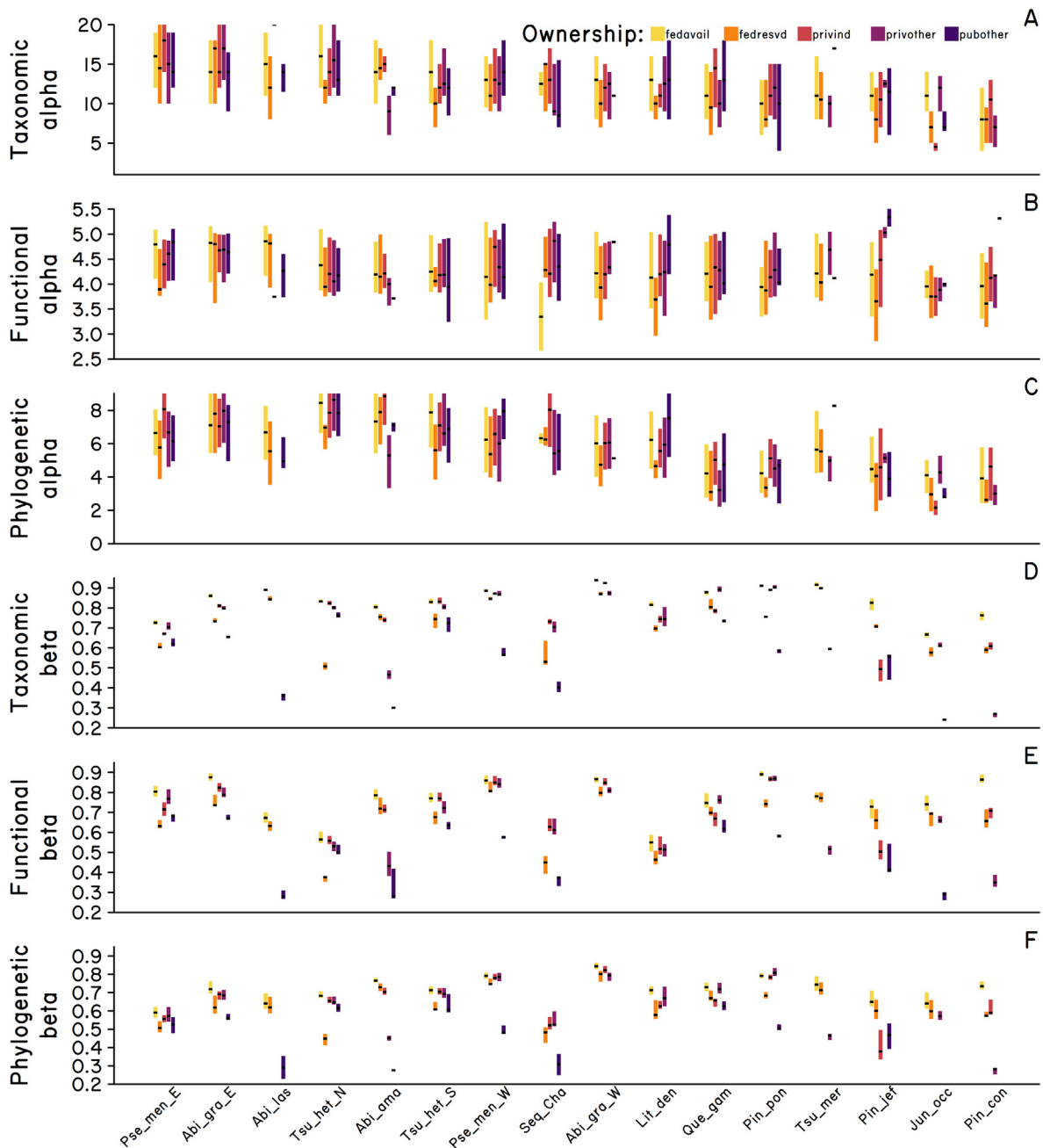
Our first hypothesis, of peak diversity in “early” seral stages, was supported with modification. While diversity did indeed peak in early-seral forest stages, it was drastically lower in sparse and open stages. This could be because open sites far from seed sources are dispersal-limited, or because exposed soil conditions limit establishment (Donato et al., 2009a). Alternatively, the expectation of high early-seral diversity is predicated on high structural and biophysical complexity typical of natural disturbances (Franklin et al., 2000, Swanson et al., 2011), which may or may not have been present. The low initial diversity we observed would be consistent with human-made disturbances (e.g., industrial logging) leading to simplified pre-forest stages. Since most industrial forest is managed to maximize occupancy

of mature trees through the use of herbicides and soil treatments, understorey vegetation may already have been reduced prior to logging.

The sapling stage is of paramount importance for plant community diversity. Forest management activities in the sapling stage may include herbicide application, hand slashing of competing vegetation, pre-commercial thinning to focus resources on commercial tree species, and supplementary planting (Smith et al., 1997, Tappeiner et al., 2015). These practices often reduce the number or abundance of plants, and may truncate the period during which open stand structure enables colonization by plants with a spectrum of shade tolerances (Sullivan and Sullivan, 2003). Few workers have examined greatly extended early developmental stages, but work following the 1980 volcanic eruption of Mt. St. Helens suggests that diversity may not peak for decades following a major disturbance when reforestation is not aggressive (Cook and Halpern, 2018, Chang et al., 2019). Indeed, large disturbances such as the Tillamook Burn, which are logistically impossible to reforest aggressively, exhibit a multitude of successional pathways (Bailey and Poulton, 1968). In our study, extended early-seral periods occurred in relatively few plots; therefore we likely underestimated peak values of alpha- or beta-diversity in plant communities during the early seral pre-forest period, especially as it may have manifested historically.

Ownership and management style are clearly linked to forest structure and availability of complex early-seral forests (Stanfield et al., 2002, Deal et al., 2015, Easterday et al., 2018). Therefore, it was surprising that our second hypothesis of diversity differences among ownerships was not more broadly supported. Also inconclusive were the third and fourth hypotheses that seral-stage effects would be modified by ownership. Curiously, early-seral alpha-diversity was not significantly associated with ownership, but early-seral beta-diversity was. This would be true if management of young forests altered the identity but not the number of species – as for example, when herbicides promote species turnover by selectively killing broadleaf forbs and trees but not conifer saplings (Miller and Miller, 2004; Iglay et al., 2010; Stokely et al., 2018). Likewise, Phalan et al. (2019) expected ownership to impact population trends of early-seral birds in the US Pacific Northwest, but found no appreciable difference between private industrial lands (where clearcutting prevailed) versus federal lands (where clearcutting ceased). Attitudes and behaviors are seldom unanimous within the same ownership type (Creighton et al., 2002), which implies that ownership categorization is too coarse to capture the nuanced management regimes of different landowners. Ownership would be a good proxy for management at large spatial scales only if it were very tightly coupled with realized disturbance type and intensity, which was likely not the case across our large and heterogeneous study area. Management and disturbance types affect organisms differentially: for plants, clearcutting may be functionally similar to other stand-replacing disturbances, but for wildlife the differences between clearcutting and natural disturbances are more profound (Imbeau et al., 1999, Zwolak, 2009). Better linking local-scale management histories to the national-scale forest inventory may be achieved through some combination of remote sensing, historical land-use archives, and systematic assessments like the National Woodland Owner Survey (Butler et al., 2016).

One principle for sustaining forests and their benefits is to balance ecological objectives with economic and cultural ones (Franklin et al., 2018). Estimating ecological diversity is fundamental to this. Forest workers now recognize that taxonomic measures alone cannot fully quantify how species function and how they are related. Measures of functional and phylogenetic diversity provide complementary information about “diversity” broadly defined (Srivastava et al., 2012, Tucker et al., 2018). In particular, phylogenetic diversity holds unique information about tree responses to climate change not otherwise revealed through taxonomic measures (Potter and Woodall, 2012). For western US plants in this study, variation in taxonomic diversity was fairly reflective of functional and phylogenetic diversity, perhaps in



**Fig. 4.** Alpha- and beta-diversity of early-seral stages, ordered by ownership type within each of sixteen Plant Association Zones. For each ownership type, the vertical bar is the interquartile range containing half of all values (from 25th through 75th percentiles), bisected by a black midline at the median (50th percentile). Ownership types are color coded (“available federal”, “reserved federal”, “private industrial”, “private nonindustrial”, and “nonfederal public”). Alpha-diversity for each plot is the count of species, functional groups, or phylogenetically-weighted species. Beta-diversity, as Bray-Curtis dissimilarity on a 0–1 scale, represents heterogeneity as the mean pairwise dissimilarity of each plot to all others with respect to abundance-weighted species, functional groups, or phylogenetically-weighted species.

part because members of at least one of the functional groups (graminoids) share both function and phylogeny. Nevertheless, taxonomic diversity as a unary metric cannot fully quantify the multidimensional effects of individual species on ecosystem functioning, especially for potentially disproportionate effects like nitrogen fixation or allelopathy. Further work should quantify how single species contribute uniquely to ecosystem functioning via “effect traits” like nutrient fixation, floral and fruit provisioning, herbivore forage, decomposition and carbon sequestration, as well as for human values such as bioindication and cultural values. Though many of these traits are indirectly represented by phylogenetic diversity, a deliberate mapping of phylogenetic diversity to ecosystem resource diversity (Thompson et al., 2015)

would be useful for conservation planning in a global change context. In changing climates, it may also be a challenge to balance the favorable microclimate effects of canopy retention at local scales (Zellweger et al., 2020) versus a broader, holistic strategy of maintaining a spectrum of forest structural stages across landscape scales. Further research could emphasize deliberately crafted silvicultural approaches to maximize the ecological value of intentionally created early-seral openings (e.g., Wheeler, 2012). It remains to be seen whether complex early-seral forests could represent potential hotspots of functional and phylogenetic diversity in the face of global changes.



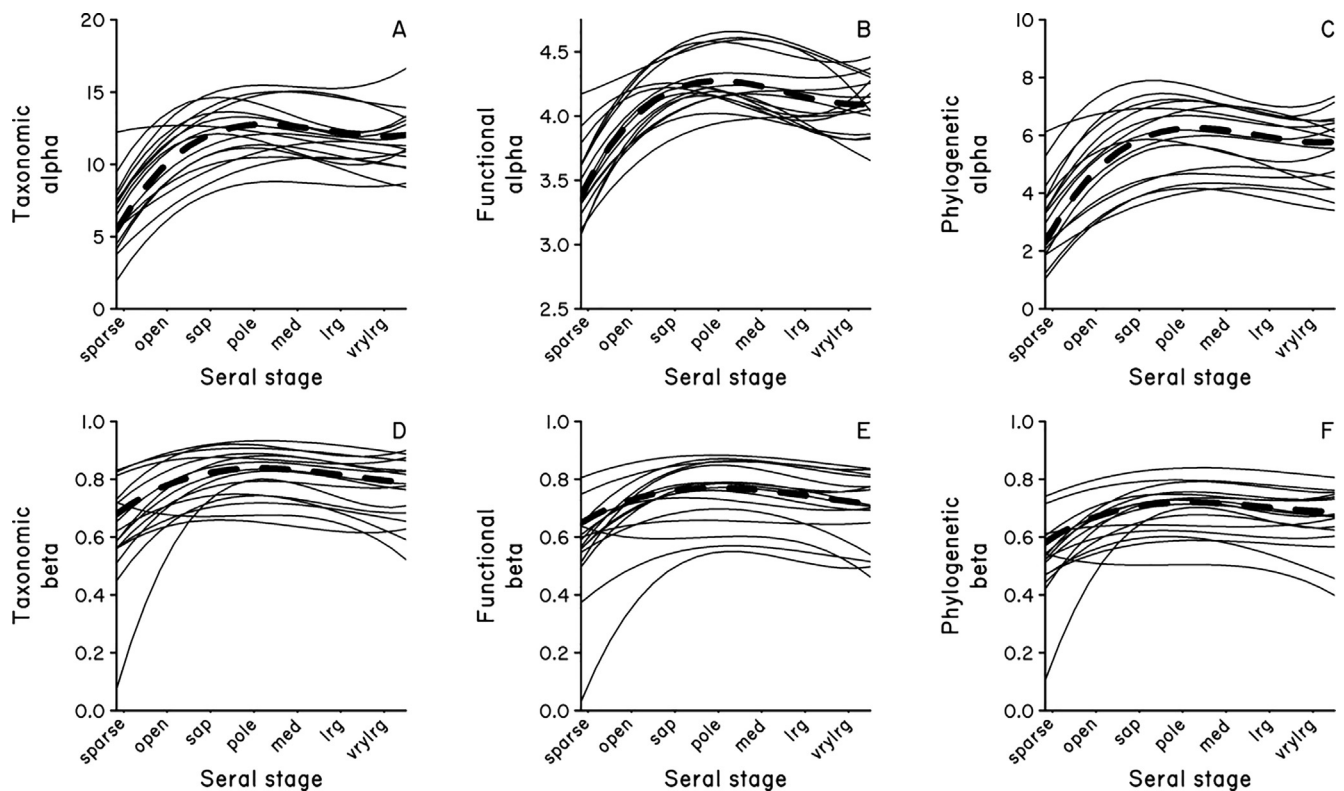


Fig. 5. Diversity motifs across forest seral stages. Each thin solid line is a smoothing spline function of diversity in response to seral stage, individually for each of sixteen Plant Association Zones. The thick dashed line is the canonical diversity motif across all ownerships and all PAZs in aggregate. The recurrent motif across all diversity measures exhibited lowest diversity in sparse and open stages, a peak in early sapling and pole-timber stages, and a mild decline in subsequent mid- and late-seral stages.

## 5. Conclusions

In conclusion, we detected a general motif of plant diversity development coincident with forest structural development across the western US. Such generality did not apply to diversity-ownership comparisons, suggesting that inferences about management effects may require context-dependent proxies other than ownership. Identifying generalities in vegetation dynamics—and departures from those generalities—can help balance ecological and social objectives in our rapidly changing forest landscapes.

## CRedit authorship contribution statement

**Robert J. Smith:** Conceptualization, Methodology, Formal analysis. : Writing - original draft, Writing - review & editing. **Andrew N. Gray:** Conceptualization, Methodology, Data curation, Supervision, Writing - review & editing. **Mark E. Swanson:** Conceptualization, Resources, Writing - review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Data accessibility

Forest inventory data are publicly available at <https://www.fia.fs.fed.us/tools-data/>. Computer code (R format) is provided in Supporting Information.

## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118410>.

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