Ida Rex, **Dylan G. Fischer** [1] and **Ryan Bartlett**, Evergreen Ecosystem Ecology Laboratory, Lab II 3265, The Evergreen State College, 2700 Evergreen Parkway NW, Olympia, WA 98505

A Decade of Understory Community Dynamics and Stability in a Mature Second-growth Forest in Western Washington

Running Footer: Forest Understory Community Dynamics

Four tables, Six figures

[1] Author to whom correspondence should be addressed. Email: fischerd@evergreen.edu

Abstract

It is often assumed that dominant forest understory communities are predictably associated with overstory tree species, yet several long-term studies suggest that understory communities are more independent of overstory change. We use a 10–year dataset to explore variation in understory communities in a mature second-growth temperate forest in Western Washington. We classify all recorded species into six growth-forms (graminoids, ferns, shrubs, subshrubs, saplings, herbaceous species), and introduced species, (collectively grouped) to analyze responses to overstory productivity, stand age, canopy heterogeneity, soil type, stand type, and proximity to a canopy-gap forming pathogen (*Phellinus weirii*), as well as overstory C changes though the decade. Plant diversity and cover declined marginally through time (Shannon's H' declined by 8%; and cover by 4.5%) as plots remained dominated by clonal species *Polystichum munitum* and *Gaultheria shallon.* Species richness decreased significantly by 23% between years (mean plot richness 10.02 in 2008 to 8.05 in 2018), and diversity, sub-shrubs, and shrubs generally declined with stand age. Shrubs were more abundant in conifer dominated plots. Ferns, and changes in ferns, were associated with presence of *P. weirii*, where cover increased in infected plots. Ordination results suggested community composition was correlated with changes in canopy cover (conifer forests) and stand age (deciduous forests). Changes in total plot C and canopy cover were also associated with diversity and total cover. Nevertheless, our results support incremental changes in understory communities on decadal time scales and limited predictability of the understory based on the overstory.

Keywords succession; understory; second-growth forests; carbon; *Pseudotsuga menziesii*

Introduction

Forest succession can result in complex stand structure dynamics with implications for understory species, especially in moist *Pseudotsuga menziesii* and *Tsuga heterophylla* forests of the Pacific Northwest (Franklin 2002, Reilly and Spies 2015). Nevertheless, variability in forest understory communities through time is not always well-understood (Halpern 1988, Halpern 1989, Van Pelt and Franklin 2000, Royo and Carson 2006, Sommerfeld et al. 2018, Chang et al. 2019). Understory plant communities have some predicable patterns at mid-succession (understory reinitiation; Franklin and Dyrness 1973, Franklin 2002), however several long-term studies suggest that understory communities are not always predictable based on overstory conditions (Halpern and Lutz 2013) and especially following disturbance (Fischer et al. 2016a, 2019). The succession of second-growth forests of the Pacific Northwest has been thoroughly studied with regard to tree species (Franklin and Dyrness 1973, Franklin 2002, Ishii et al. 2002, Reilly and Spies 2015), yet understory community change through time is not as well-understood (but see Thysell and Carey 2000, 2001).

Temperate forests in the Puget lowlands (Northwest Washington, USA) are renowned for their productivity and create potential for a mosaic of dynamic responses across variable microhabitat conditions as associated with stand age, canopy gaps, light attenuation and soil types (Franklin and Dyrness 1973, Ishii et al. 2002, Celis et al. 2019). Halpern and Lutz (2013) found that canopy closure following logging exerts a weak control on the understory communities, with 35% of their studied understory species displaying no coherent trend, and characteristics of the pre-closure vegetation were critical in determining the nature of change through succession. Similarly, Fischer et al. (2016a, 2019) found that within 20–30 years of a volcanic disturbance event, understory plant communities continued to change in both disturbed and undisturbed forest plots. Accordingly, changes in the understory plant communities may appear independent of changes in the overstory in a variety of forest ecosystems and different disturbances (e.g., McCune and Antos 1981, Rogers et al. 2008).

Research on change in understory plant communities of *P. menziesii* and *T. heterophylla* forests of the Pacific Northwest in response to factors such as overstory productivity, stand age and canopy composition (Halpern 1988, Ishii et al. 2002, Barbier et al. 2008, Halpern and Lutz 2013) has widespread applicability for a forest type spanning 1.2 million acres from Oregon to British Columbia (Barbier et al. 2008). While these forests are generally defined based on late-succession overstory conifers (Franklin and Dyrness 1973, Van Pelt and Franklin 2000), mid-age forests can be dominated by a mix of deciduous and conifer tree species (Kirsch et al. 2012), and small disturbances due to wind-throw and gap dynamics exert influence on understory communities and tree regeneration (Halpern 1989, Wright et al. 1998, Grandpré et al. 2011, Reilly and Spies 2015). Deciduous-dominated canopies may be associated with more diverse understories due to high light availability in the early spring before trees leaf-out (Barbier et al. 2008). Coniferous canopies may have more complex canopies, especially with age, resulting in greater abundance of microhabitats (Franklin and Dyrness 1973, Barbier et al. 2008). Further, modification of resource availability and heterogeneity by overstory species through changes in soil conditions, leaf litter, or water and light use can further impact understory diversity (Barbier et al. 2008, Bartels and Chen 2010). Interestingly, single type (conifer or deciduous) dominated canopies may have higher understory diversity than mixed overstories (Barbier et al. 2008) potentially due to greater light absorption (due to high LAI) by mixed species overstories. Understory communities may also be predicted by overstory biomass (carbon stocks) since more than half of variation in forest structural attributes can be accounted for by overstory biomass in regional-scale multivariate analyses (Reilly and Spies 2015).

In our study, we use a 10-year dataset from a mature, naturally regenerated, second-growth forest in the Lowland Puget Trough to examine detectable changes in understory plant diversity based on overstory conditions. We address four central questions regarding changes in cover, diversity, and community composition through time: First, how do species and growth forms (graminoids, ferns, shrubs, introduced and invasive species, tree saplings, subshrubs, and herbs) change over 10-years? Second, how do communities change in diversity and total cover over the same time period? Third, are the observed changes related to stand age, proximity to known pathogens, stand type (conifer, deciduous, or mixed), soil type or changes in overstory biomass carbon, canopy cover, or canopy heterogeneity? Fourth, how does community composition change over time and in relation to overstory variables?

Methods

Study Location

The study was conducted in the Puget lowlands of Western Washington, USA, situated within the Evergreen Ecological Observation Network (EEON), a long-term permanent plot network consisting of 44 plots throughout a 380–ha forest reserve managed by The Evergreen State College (Kirsch et al. 2012; Figure 1). The network was established in 2006 using a 250 m systematic sampling grid with a random start point, and fixed-area circular 10 m radius plots. The forest ecosystem is predominantly second-growth temperate rainforest. Based on the United States National Vegetation Classification (https://usnvc.org/ - last accessed 06/21/2022), the stands at this site best match associations intermediate between associations in the G237 group (*north Pacific red alder - bigleaf maple - Douglas-fir rainforest*), and G240 group (*north Pacific maritime Douglas-fir – western hemlock rainforest*) groups within the M024 macrogroup (Vancouverian coastal rainforest). More than half of the forest was clear-cut between 1937–1939, using early cable technologies (Kirsch et at. 2012), and accordingly the reserve represents a mosaic of stand ages (Figure 1; also see "Overstory Data" below). The area has an approximate average annual temperature of 10 °C, and an approximate annual rainfall of 127 cm, with high rainfall Oct. – June, and low rainfall in July – Sept. (Western Regional Data Center; https://wrcc.dri.edu/; last accessed 06/06/2021).

Soils are represented by similar post-glacial substrates throughout the sampling area. Twenty-nine plots were located on similar Alderwood gravelly sandy loam soil, with one plot each respectively located on Yelm fine sandy loam and Everett very gravely sandy loam. Further, seven plots were located on Giles silt loam soil; two plots are located on Skipopa silt loam; two plots on Kapowsin silt loam; and one plot on McKenna gravely silt loam. Two additional plots were located on Dystric xerochrepts soil, included within the sandy loam category. All plots are henceforth grouped into either a cohesive sandy loam (32 total plots) or silty loam (12 total plots) classification for statistical purposes (USDA web soil survey; https://websoilsurvey.sc.egov.usda.gov; last accessed 11/11/2021).

Understory Vegetation Survey

Understory vegetation was previously measured and described as primarily dominated by *Polystichum munitum*, an evergreen fern species, and *Gaultheria shallon*, a rhizomatous shrub in the family *Ericaceae* (Kirsch et al. 2012). In the current study, each of the 44 plots were surveyed for understory vegetation community composition, abundance, and richness in 2008 and 2018 during the spring–summer season using point-line-intercept transects. In each plot, a 10 m transect line was established in each cardinal direction, extending from the center of the plot to the plot boundaries. Intercept points were taken at intervals of 10 cm (100 points per transect). Every vascular plant species between 0–3 m in height intercepted at each point was recorded once, and then summed across each transect. Transects were averaged within each plot for estimates of percent cover. Each recorded species was classified into one of seven categories based on growth strategies or introduced status for analysis: graminoids (including sedges [*Carex* spp.]), ferns, shrubs, subshrubs, tree saplings, herbs/forbs and introduced species (including invasive species). Across all years, we used an abbreviated measure of species importance (I_a) calculated for each species as:

$$I_a = (\text{relative frequency} + \text{relative cover})/2.$$

Overstory Data

Across the study-area, forest overstory was dominated by a mixed canopy of *P. menziesii* with four codominant species: *Acer macrophyllum, Alnus rubra*, *Thuja plicata,* and *T. heterophylla* (described in Kirsch et al. 2012), and was classified as described above within the USGS National Vegetation Classification (Kittel et al. 2015). Methods for measurement of overstory tree size and growth are described in Kirsch et al. (2012), where all trees greater than 5 cm DBH (diameter at 1.4 m height) were measured within each plot using a nail installed at DBH on each tree. Plots were divided among three overstory stand classification types via biomass-based stand dominance (Table 1): conifer (single species dominance – *P. menziesii* or *T. plicata*), deciduous (including both single species dominance – *A. macrophyllum* or *A. rubra* – and *A. macrophyllum* and *A. rubra* co-dominance), and mixed conifer and deciduous overstory plots. Canopy cover was assessed in the field using a spherical convex densiometer (Forestry Suppliers, Inc., Rapid City, SD), at the center of each plot, during full leaf-out conditions in 2008, and again in 2022.

Canopy above-ground biomass carbon (C) and productivity (as represented by increases in biomass C) were assessed for each individual plot in both 2008 and 2018, using biomass formulas as calculated from the DBH of each tree within plot boundaries and the common assumption of 50% C for all biomass (Kirsch et al. 2012, Chojnacky et al. 2014). Briefly, we used taxa-specific equations based on tree DBH from Chojnacky et al. (2014) of the general form

$$\text{biomass} = e^{(b_0 + b_1 \, ln(\text{DBH}))}$$

where b_1 and b_0 are constants individually tailored to each taxa. Biomass was predicted separately for each tree per time step. Biomass was then summed across all trees in each plot and divided by plot area for estimates of overstory C (Mg ha^{-1}). Categorical classifications in changes in overstory C over the decade were determined by calculating percent change (d_{Carbon}), providing a means for classifying the nature of plot biomass change over 10 years where:

$$d_{\text{Carbon}} = (\text{Overstory C in 2018} - \text{Overstory C in 2008}) / \text{Overstory C 2008} * 100$$

Plots with ± 50% change were categorized as increased or decreased, while plots with less than 50% absolute change were marked as stable for graphical representation.

Overstory age was evaluated based on a combination of remote and ground-based methodologies. As land-ownership in 1968 (time of reserve establishment) was spread across more that 20 separate owners and parcels, the most reliable technique for assessing stand age was based on a combination of historic photographs and tree cores from the largest trees within aerially-delineated stands. First, aerial photos from 1939 (Kirsch et al. 2012) were used to map areas clear-cut in the late 1930s (Figure 1C). Next, remaining intact forest was compared with similar aerial photos from 1968 to determine stands that were cleared after 1939 and before the time of reserve establishment (1968). Second, the 1968 aerial photos were used to verify that stands not cut in the 1939 photo remained intact in the 1968 photo. Third, for uncut stands, we used an increment borer to core and age the largest trees within the remnant stands. Cores were taken as close to ground-level as possible (approx. 30 cm height), and trees were aged in the field adding five years to the oldest ring count to allow for seedling establishment and early growth. Maximum tree age from cores was then applied to stands as delimited from historic aerial photography matched with most recent (2017) photos. For plot locations within partially-cleared stands in 1939 photos, a similar approach was used, coring representative trees within stands delineated based on arial photos to determine stand age. Appropriate age estimates were then applied to each aerially-delineated stand (Figure 1C). Plots that were obviously cut in 1939, and not cut in 1968 (24 plots) were categorized as 80 years old for all analyses. Plots obviously cut in 1968 were categorized as 50 years old for all analyses (two plots). For plots that were not obviously cut in 1939 or 1968, tree cores indicated an oldest age of 129 years, and this age was thus assigned to all trees within similar stand types (12 plots). For the remaining plots where clearing status was not obvious in recent aerial photos due to partial clearing in 1939, increment borer-based data indicated ages spanning 50–104 years of age (six plots).

Variability in remotely-sensed canopy height was determined via publicly available LiDAR data from both 2008 and 2017 (https://lidarportal.dnr.wa.gov; last accessed 06/06/2021). We used a fixed area approach (Næsset 2002) where the standard deviation of canopy height within a 15 m buffer from the center of each plot as an index for roughness, with greater values in canopy height standard deviation representing greater canopy heterogeneity. This approach considers variability of the actual canopy regardless of tree identity rather than maximum height of each individual tree (Jeronimo et al. 2018). The fixed area index of roughness was computed for both years and a comparison of the indices between 2008 versus 2017 suggested nearly-identical ranking of plot canopy roughness regardless of year (slope for 2017–2008 plot canopy roughness regression = 0.97, ± 0.15 SE).

The presence of pathogens, specifically *Phellinus weirii*, commonly known as laminated root rot (due to its impact on wood properties in later stages of infection), was determined by field checking for indication of infection on nearby trees, recently fallen trees with exposed roots, and visible canopy gaps, both in the field and from 2017 LiDAR derived canopy height data. The primary form of *P. weirii* infecting *P. menziesii* and other conifers in the northwestern North America causes regular patchy mortality in *P. menziesii* but appears to be ineffective at damaging *T. plicata* canopies (Thies and Sturrock 1995). Deciduous species *A. macrophyllum, A. rubra*, are not susceptible to infections, and *T. heterophylla* is moderately tolerant, with increasing susceptibility based on proximity to surrounding infected *P. menziesii* stands (Childs 1970, Thies and Sturrock 1995). Laminated root rot is long-lived, spreading outwards from the infection center though root contact or infected woody debris, causing canopy gaps primarily due to windthrow – which are often recolonized by resistant or tolerant species, notably *A. macrophyllum* (Thies and Sturrock 1995), or non-shade-tolerant species (Childs 1970). As this pathogen is well-known in the forest types in the current study, examination of understories in affected and intact stands represented an obvious comparison.

Statistical Analysis

In all plots, we analyzed community diversity attributes using percent cover for all understory vegetation, number of species (richness) and diversity (Shannon’s H’). Shannon’s H’ diversity was measured as

$$H' = -\Sigma\, (p_i * ln(p_i))$$

Where p_i denotes the portion of the community percent cover represented by species *i*.

All recorded species' cover across all plots was compared between 2008 and 2018 using permutative ANOVA in the R package *lmPerm*, to account for non-normal distributions (Wheeler and Torchiano 2016). Next, each of the seven growth-form categories for both 2008 and 2018 were also compared across years using permutative ANOVA (*lmPerm*, as above). Total understory vegetative plot cover, species richness, and Shannon's H' were compared across years using ANOVA (after checking for normality). Single bi-variate analysis models where then constructed for each comparison to visualize variation between years, where slope of regression lines clarify trends through time (> or < 1:1).

To analyze the relative significance of overstory variables predicting understory vegetation within each year we used linear models (normal response variables) or permutative linear models (non-normal response variables; using the *lmPerm* package) including continuous and categorical predictor variables within each year of measurement. Each understory growth-form category was analyzed with respect to the influence of overstory biomass carbon (Mg C ha^{-1}), overstory stand age, overstory stand type, canopy roughness, soil type, and proximity to pathogens for each year. Species richness, diversity (as measured by Shannon's H') and total percent cover were also analyzed against all overstory variables within a linear model context.

We also compared decadal difference values between 2008 and 2018 measurements to determine if changes in species or growth form percent cover were related to the above predictor variables. All continuous response variables were compared against changes in all predictor variables, and also against categorical predictor variables. We first computed the change (hereafter denoted by $d_{subscript}$) in all variables between years, and independently for the ten most important species (based on I_a value). We then analyzed each dependent *d* value using linear models including all *d* values for continuous variables, percent change in carbon (d_{Carbon}), and categorical estimates of stand condition on all growth-forms. All analysis was conducted in the program R (version Rx64 4.1.0; R Core team 2021). In all instances, a *P*–value cut-off (α) of 0.05 was used to denote significance.

Community Analysis — We used community analysis techniques to model and analyze multivariate community change and differences based on predictor variables. Non–metric dimensional scaling (NMDS) ordination was used to visualize community profiles and decadal shifts in individual plot locations in multivariate space. Each ordination was constructed using relativized percent cover data, Bray-Curtis distance measures, and was based on a two-dimensional solution for the least stress configuration at convergence after a maximum of 999 randomizations. Relativization was performed using the *vegdist* function in the *vegan* package in R. We used 0.2 as a final solution stress cut-off along with a stress-plot to determine optimal dimensionality of ordinations (two dimensions in all cases). All NMDS ordination was conducted using the vegan package in the program R (version Rx64 4.1.0; R Core Team 2021; Oksanen et al. 2020), with Bray–Curtis distances generated using the *ecodist* package.

To determine statistical significance of community dissimilarity among years, between stand types (conifer, deciduous, or mixed), and between plots with and without the obvious presence of the pathogen *P. weirii*, we used permutational multivariate analysis of variance (PerMANOVA) using the *adonis* function in in the *vegan* package in R (Dixon 2003, Oksanen et al. 2020). Analyses included 1000 permutations and Bray-Curtis distance.

For continuous explanatory variables (e.g., diversity, percent cover, growth form abundance, stand age, canopy roughness, carbon) correlations were utilized to generate environmental vectors across ordination space using the *envfit* function in *vegan* (Dixon 2003, Oksanen et al. 2020).

Results

Growth Forms, Species, and Diversity Between Years

Overall patterns in understory community dominance remained relatively stable over the decade of study. Coverage of growth-forms remained relatively constant, possibly reflective of the consistent dominance of *P. munitum* and *G. shallon* (43% and 19% average cover respectively across all plots) (Figure 2; supplemental Figures S1, S2). Of the 80 recorded understory species (supplemental Table S1), 20% of plant species comprised 90% of overall cover, and this was similar in 2008 and 2018.

We observed limited change in individual species, with most species exhibiting non-significant fluctuations in abundance. The ten species with the highest I_a values displayed no significant change between years (supplemental Figure S2). Only seven out of the total 80 species recorded displayed significant differences: sapling *A. macrophyllum (P = 0.049),* recently naturalized annual herb *Geranium robertianum (P = 0.013),* perennial fern species *Polypodium glycyrrhiza (P = 0.044),* shrub *Frangula purshiana* (formerly *Rhamnus purshiana; P = 0.026*), perennial herb *Tiarella trifoliata* (*P = 0.028*), perennial shrub *Vaccinium parvifolium* (*P = 0.020*), and herb *Viola sempervirens* (P= 0.037). All above species decreased in cover, with the single exception of the introduced weedy species *G. robertianum,* which increased by 0.6 % (supplemental Figure S3). Further, 27 less-common native species (mean cover 1.3% ± 1.1% SE) sampled in 2008 were not recorded along transects in 2018. In 2018, 10 species were recorded which were not recorded along transects in 2008 (2.4% mean cover ± 2.5% SE; supplemental Table S1).

There were no significant differences between years in growth forms ($P > 0.05$). A direct comparison of 2008 and 2018 values in comparison to a 1:1 line shows how individual plots may have changed through time, with the expectation that values in 2008 should be predictive of values in 2018. Indeed, regression analysis of growth-forms (2018 percent cover by 2008 percent cover; Figure 2) yielded significant ($P < 0.05$) results for ferns, shrubs, saplings, subshrubs, and herbs. Graminoid and introduced species percent cover in 2008 was unrelated to percent cover a decade later ($P > 0.05$). Slopes were frequently < 1 for ferns, shrubs, subshrubs, and herbs. Individual growth-form abundance was generally not correlated with cover of other growth-forms ($r < 0.1$, $P > 0.05$). A single exception was for graminoids versus herbaceous species where decreasing graminoids cover was associated with increasing herbs (Pearson Coefficient $r = 0.31$, $P = 0.040$). Over-all, most growth form cover in 2018 was similar to 2008, but often slightly lower (below the 1:1 line).

Total percent cover of vegetation also displayed little variation between years, declining by 4.5% from 121.9% in 2008 to 117.4% in 2018, but not significantly ($P = 0.224$). Species diversity (H'), also did not change significantly during the 10–year study ($P = 0.252$). Average plot-level species richness decreased by 23% from 2008 to 2018 ($P = 0.003$) (Figure 2; Supplemental Figure S1). Significant relationships existed between years for richness, diversity (H'), and total percent cover, and with slopes of relationships frequently < 1, and most values under 1:1 lines (Figure 2).

Overstory Influence

Overstory Productivity— Standing overstory biomass C (Mg ha^{-1}), was not found to be a significant factor affecting percent cover for any growth-form in either 2008 or 2018 (Table 2). Overstory biomass C was also unrelated to stand type ($P = 0.143$ in 2008 and 0.146 in 2018). Further, understory community cover, richness, and diversity (H') in 2008 and 2018 were not affected by overstory C (Table 3). Overstory biomass C in 2008 was predictive of overstory biomass C in 2018 ($r^2 = 0.59$, $P < 0.001$), where biomass-dense plots increased in C more than biomass poor plots with a slope near 1 (slope = 1.06 ± 0.134 SE).

Stand Age—Subshrubs (2008, 2018) and Shrubs (2018) were negatively associated with stand age (Figure 3; Table 2). Species richness was not affected by stand age (Table 3), despite the decline in richness between 2008 and 2018. Understory species diversity (H'), however, declined with stand age in both years (Figure 4; Table 3). The youngest plots generally had deciduous canopies (mean age 79.5 years; Table 1; Figure 1C), conifer dominated plots were mid-aged (mean age 88.7), and the oldest plots had mixed deciduous and conifer cover (mean age 103.3).

Canopy and Stand Type —Stand type (as classified into three categories: conifer, deciduous, or mixed conifer and deciduous) had a significant association with shrubs in both 2008 and 2018, as well as subshrubs in 2018 (Table 2; Figure 3). The highest shrub cover for both years occurred on conifer-dominated plots ($P < 0.05$; Figure 3), while mixed overstory plots displayed the lowest percent cover. In contrast, 2018 subshrub cover was higher on deciduous dominated plots ($P < 0.05$). Other growth forms did not significantly differ by stand type in either year (Table 2). Understory species richness and diversity were also not significantly different among stand types in either year (Table 3). In 2008, total percent vegetation cover was the highest in conifer dominated plots and lowest in mixed-overstory plots (Table 3; Figure 4). Total cover among stand types was not significantly different in 2018 ($P > 0.05$). Conifer-dominated plots, tended to exhibit the highest canopy roughness compared to deciduous and mixed-canopy plots in 2008 ($P = 0.024$), yet not in 2018 ($P = 0.142$). Nevertheless, understory growth-forms (except graminoids), species richness, diversity, or cover were generally not significantly related to canopy roughness (Table 2; Table 3).

Soil type— Introduced species, as a group, were associated with soil type across both years where they had higher cover on silt loam soils (Figure 3). Herbaceous species also had higher cover on silt loam soils in 2008 (Figure 3) as did graminoids in 2018 (Table 2). In contrast, subshrubs had higher cover on sandy loam soils in 2018 (Table 2). Other growth forms, richness, diversity and percent cover remained unassociated with soil type in either year.

Presence of Pathogens— Fern coverage was lower in plots with presence of *P. weirii* (and hence proximity to large canopy gaps) in 2008 (Figure 3), yet not-significantly different in 2018 (Table 2) reflecting a positive change in ferns. In 2018 total percent vegetation cover was also higher in *P. weirii* infected plots (Figure 4; Table 3). All other growth-forms, as well as richness and diversity, were unaffected by the presence of *P. weirii* ($P > 0.05$; Table 3).

Measures of Change — In addition to analyzing relationships between response variables and overstory variables, we analyzed how decadal changes (d) in understory responded to overstory factors. Plots had higher d_{ferns} in presence of *P. weirii*, while d_{Grasses} increased with $d_{\mathrm{roughness}}$, and $d_{\mathrm{SubShrubs}}$ was significantly higher in deciduous forest types, and with increased $d_{\mathrm{canopy.cover}}$ (Table 4; Figure 5). Likewise, changes in sword fern (*P. munitum*; $P = 0.002$) and bracken fern (*Pteridium aquilinum*; $P = 0.013$) were positively associated with *P. weirii* infected plots, and *P. aquilinum* was also positively related to increased $d_{\mathrm{roughness}}$ ($P = 0.048$) (supplemental Figure S4). Changes in trailing blackberry, *Rubus ursinus*, was also positively related to $d_{\mathrm{canopy.cover}}$ ($P = 0.026$; supplemental Figure S4). All other d values for the top ten highest importance species in the data set (based on I_a value) where not significantly related to any tested factor ($P > 0.05$). Change in understory richness (d_{Richness}) was not significantly related to any measured variable including d_{Carbon}, stand age, forest type, $d_{\text{Total.cover}}$, $d_{\text{roughness}}$, soil type, or presence of *P. weirii* ($P > 0.05$). Nevertheless, $d_{\text{H'}}$ increased with d_{Carbon} (Table 4; Figure 5) and was unrelated to other factors. Interestingly, $d_{\text{Total.cover}}$ was positively (albeit weakly) related to $d_{\text{canopy.cover}}$, but was also unrelated to other factors (Table 4; Figure 5).

Community Ordination

Our NMDS ordination of all data from all years, and subsequent PerMANOVA, revealed multiple interesting patterns (Figure 6). A convergent two-dimensional ordination solution was found after 20 tries, and the final ordination stress was 0.096. Changes in individual plots between 2008 and 2018 are shown in Figure 6A where arrows connect measurements across years. Individual plots were variable in magnitude and direction of change through time, and year of measurement was not significantly associated with community composition in PerMANOVA analyses ($P > 0.05$; Figure 6A-C). Nevertheless, stand type ($P = 0.009$) and the presence of *P. weirii* ($P = 0.009$) were significantly associated with community differences. Stand type accounted for 22% of the variation in the PerMANOVA analysis (sums of squares), while presence of *P. weirii* accounted for 3.5% of variation (see supplemental Figure S5; $P = 0.013$). The continuous environmental variables stand roughness ($P = 0.0290$, $r^2 = 0.08$), age ($P = 0.0280$, $r^2 = 0.09$), and canopy cover ($P = 0.0270$, $r^2 = 0.09$) were also all significant vectors in ordination space, but overstory biomass C was not significant ($P = 0.09$) (Figure 6B). Roughness and canopy cover were best aligned with axis NMDS1, while age was best aligned with variation in axis NMDS2 (Figure 6B).

Shrub cover, total plot percent cover, grasses, introduced and herbaceous species, ferns, and bare ground were all significant vectors associated with different directional shifts in ordination space (Figure 6C). Vectors associated with individual species (Supplemental Figure S6) demonstrated that patterns in shrubs were largely driven by *G. shallon*, and patterns for ferns were largely aligned with the vector for *P. munitum*. The vector for *R. spectabilis* was inversely aligned with the vector for stand age, and was positively associated with vectors for introduced, graminoid, and herbaceous species. Interestingly, bare ground, canopy cover, and fern coverage had similar directional vectors, while stand age had an inverse correlation with grass, introduced species, and herbaceous cover (Figure 6B-C). Shrub cover and canopy roughness were also somewhat inversely aligned in 2D ordination space.

Finally, considering the 2018 data alone allows evaluation of patterns in the most recent measurement. The 2018 NMDS ordination analysis resulted in a convergent solution after 20 tries, and the final ordination stress was 0.087 (Figure 6D). Stand age, presence of *P. weirii*, stand type, and change in canopy cover ($d_{\text{canopy.cover}}$) were significant factors in our 2018 data PerMANOVA analysis (P = 0.0050, P = 0.0490, P = 0.0010, and 0.0210 respectively), while d_{Carbon}, and $d_{\text{roughness}}$ were not significant (P = 0.0819, and 0.1229 respectively). Plots with and without the canopy-gap forming pathogen *P. weirii* were equally distributed throughout the NMDS ordination space (supplemental Figure S5). Interestingly, the two significant vectors $d_{\text{canopy.cover}}$ ($P = 0.0030$, $r^2 = 0.22$) and stand age ($P = 0.0410$, $r^2 = 0.15$) were nearly orthogonal (Figure 6D), where $d_{\text{canopy.cover}}$ was aligned with variation along axis NMDS1, and especially variation in conifer stands. Meanwhile, age was best aligned with axis NMDS2, and variation within deciduous and mixed stands.

Discussion

Understory Through Time in Mid-Age Stands

In mid-succession, community change should become more apparent as understory communities expand in new canopy gaps (Thomas et al. 1999, Barbier et al. 2008, Sprugel et al. 2009, Bartles and Chen 2010, Grandpré et al. 2011, Kane et al. 2011). Nevertheless, since canopy closure provides a selection filter on potential species with respect to light tolerance, species may have been filtered out of the community by the time large tree gaps occur. In our study, we observed slight declines in canopy cover over ten years. Canopy cover in 2008 averaged 78.3% and declined slightly to 73.1% in 2018. We anticipated increases in species diversity through time (Franklin and Dyrness 1973, Franklin et al. 2002, Halpern and Lutz 2013, Reilly and Spies 2015). In contrast, we observed reductions in all diversity metrics (total cover by 4.5%, Shannon's diversity by 0.10 and species richness by 23%) even while canopy cover was stable or declining. Similarly, diversity and cover were inversely related to stand age. Nevertheless, the observed declines in diversity and density were consistent with Rogers et al. (2008), where increasing overstory dominance through succession selects for low cover and shade-tolerance (Urban et al. 1993) – but does not favor the establishment of new species. Over a quarter of the understory species recorded in 2008 declined or were absent in 2018. While the declines of diversity, richness and overall cover could be reflective of successional changes in the overstory (Sprugel et al. 2009, Bartels and Chen 2010, Su et al. 2019), they are also likely the result of small changes in microclimates and light conditions on the forest floor (Barbier et al. 2008, Halpern and Lutz 2013), and competition by more generalist species (Kennedy and Quinn 2001, Rogers et al. 2008). Further, less abundant species are also less likely to be accurately measured by point-line-intercept techniques which have inherent detection limits for rare species (in this case, species < 1% cover). Thus, despite statistically significant declines in some species, not all changes are necessarily ecologically significant. In the most striking examples of declining canopy cover in our study, where the pathogen *P. weirii* was present, we saw positive changes in ferns and more total cover by 2018, but such increases in high-biomass growth forms like ferns may come at the expense of a more diverse understory due to competition.

Observed changes in community metrics were likely emblematic of individual species and growth form responses – particularly declines in shrubs, annual herbaceous species, or increases of introduced and invasive species (Halpern 1989, Halpern and Spies 1995, Reinhart et al. 2006, Rogers et al. 2008, Halpern and Lutz 2013). It is probable that shrubs are more influenced by microhabitats compared to other growth-forms, as evidenced by declines in cover through time and sensitivity to overstory stand types (Halpern 1989; McKenzie and Halpern 1999, McKenzie et al. 2000, Dudney et al. 2021). Competition by dominant *P. munitum* and *G. shallon* can further reduce abundance of rare and disturbance-adapted species, as available forest floor is often over-shadowed by these large, shade-tolerant, clonal plants (Franklin and Dyrness 1973, Chang et al. 1996, Prescott 1994, Nelson et al. 2007) accounting for greater than 60% of the understory. Shrub density, particularly *G. Shallon,* may affect other species through nutrient, water or light competition, or inhibiting effects from leaf tannins (Chang et al.1996, Prescott 1994, Preston 1999). Previous studies at our field site have documented limited establishment on the forest floor dominated by *G. shallon* and *P. munitum* (Kennedy and Quinn 2001). Despite temporal and spatial overstory shifts, and minor decreases in relative abundance, these dominant species can keep a nearly uninterrupted ground cover and may control community composition and distribution (Franklin and Dyrness 1973, Prescott 1994, Wright et al. 1998, Mallik and Prescott 2001) which stabilizes though forest succession (Nelson et al. 2007).

Overstory stand carbon should correlate with light interception and LAI and could be a holistic metric predicting understory community diversity and composition. In fact, several plots in our study had dramatic (> 50%) declines in overstory carbon during the study period. Nevertheless, changes in stand C were rarely predictive of understory community response variables. Understory dynamics suggested a more complex model is needed to predict individual species responses or stability over decadal time scales – especially among the dominant shrub and fern growth forms. Models may need to better integrate clonal behavior in ferns and shrubs where clonal fragments may be as large as 12 m (Huffman et al. 1994), potentially importing resources from other microhabitats to bolster shrub persistence even when overstory biomass affects light conditions (McKenzie and Halpern 1999, McKenzie et al. 2000). Ordination of 2018 vegetation community composition in conifer forests was associated with canopy cover, and deciduous forest communities were more associated with stand age (Figure 6D). These relationships could suggest that increasing canopy cover in conifer forests play a similar role in influencing understory communities as increasing age in deciduous forests. Taken together, such results suggest that community convergence in stand types may occur with age and increases in canopy cover through time, despite declines in understory diversity and cover.

Understory Differences due to Stand Type

Measurable differences in structure and composition of coniferous or deciduous stands may also lead to variation in understory (Lezburg et al. 1999, Barbier et al. 2008, Halpern and Lutz 2013, Su et al. 2019). Stand type had measurable associations with the understory in our study (Tables 2-4; Figures 3-6) but likely not because of higher canopy heterogeneity (Messier 1992, Weber et al. 2014) – especially since the growth forms associated with stand type were not similarly responsive to canopy roughness. We did observed evidence of association between understory vegetation and soil type in our study in a limited number of cases – where introduced species and herbs were more abundant in silt-loam soils, and where sub-shrubs were more abundant in sandy-loam soils. Nevertheless, soil-type effects were mild, and may be confounded by effects of overstory on O-horizon conditions. Mixed conifer and deciduous overstories tended toward lower cover, diversity, and species richness in agreement with previous studies (Barbier et al. 2008, Rogers et al. 2008). Coniferous dominated stands within our study site displayed higher understory cover in 2008, and average shrub cover was approximately two times higher in conifer stands compared to both deciduous and mixed dominated stands (Figure 3). Nevertheless, change in shrub cover was minor in conifer stands, as was the change in cover of the dominant shrub species *G. shallon*. Meanwhile, deciduous-dominated plots had the highest average fern, graminoids, subshrub, herb, and sapling cover.

Seed production and dispersal within sites can be limiting factors during the understory reinitiation phase of succession (Lezburg et al. 1999), and mixed and deciduous-dominated stands in our study may create more microsites for new and introduced species. Nevertheless, understory dispersal strategies can be diverse (Halpern 1988, Halpern et al. 1999, Borcard et al. 1992), and our survey included a mixture of clonal (asexually reproducing) shrubs, ferns and herbaceous species combined with non-clonal species. Non-clonal species may have more dynamic regeneration pathways – via sexual reproduction, seed dispersal by natural forces (Halpern et al. 1999, Halpern and Lutz, 2013), or use of coarse woody debris (Kennedy and Quinn 2001), among others – and hence can be more impacted by the developments and shifts of microhabitats than dominant, colonizing species (Royo and Carson 2006, Compagnoni and Halpern 2009, Baker et al. 2015). Accordingly, we expected to see greater predictability of understory communities based on measures of canopy heterogeneity and changes in stand conditions. Nevertheless, species that need to establish via seed may require soil disturbance and microsites are not necessarily created or immediately associated with gaps without uprooting of trees. Only grasses showed a significant positive response to changes in canopy heterogeneity, and other significant changes were associated with either forest type (sub-shrubs) or presence of the gap-forming pathogen *P. weirii*.

Canopy gaps are often associated with distinct understory communities (Barbier et al. 2008, Halpern and Lutz 2013, Grandpré et al. 2011, Celis et al. 2019), particularly in relation to the creation of variable microhabitats (Zobel et al. 2021). Increasing species diversity can occur with the colonization of shade-intolerant species which would otherwise be shaded-out during succession (Thies and Sturrock 1995, Wright et al. 1998, Grandpré et al. 2011, Celis et al. 2019). In our study, presence of *P. weirii* was a significant factor in predicting response variables in some cases, but such effects were clearly not major predictors of the understory over-all (e.g., see *P weirii* ordination in supplemental Figure S5). The presence of *P. weirii* was associated with low fern cover in infected plots 2008 (Table 2), and greater increases in ferns over ten years. Total percent vegetation cover was also significantly higher in plots with *P. weirii* in 2018, possibly indicating the release from understory growth suppression with associated canopy gaps (Barbier et al. 2008, Kane et al. 2011). Importantly, canopy gap dynamics are possibly correlated with the dramatic increases in introduced species like *G. robertianum*, *I. aquifolium* and other non-native species adapted to canopy disturbance in mixed stands (Thies and Sturrock 1995, Reinhart et al. 2006, Barbier et al. 2008, Rogers et al. 2008, Jones et al. 2010, Dudney et al. 2021). Such findings may suggest there are shade-tolerant invasives that are persisting through canopy disturbances and increasing as stands slowly mature.

Within the context of our study, it is difficult to attribute community variance to a single physical factor. We had hypothesized that changes in overstory C could serve as a metric reflecting changes in stand structure with implications for the understory. Changes in overstory C were indeed significant for changes in community diversity, where diversity increased in locations that also saw increased C storage. However, such changes seem paradoxical when richness and diversity were declining over-all in these forest stands through time. Other idiosyncratic changes associated with canopy gaps (potentially increasing richness or diversity as a result of increased light), and increasing dominance of shade tolerant species (which may limit light for other species) may further complexify patterns. Even stand age, an important variable for several growth forms, community diversity and cover, was a significant predictor of less than half the tested response variables. The lack of greater significant relationships with stand age could be explained by larger relative influence of factors including stand type, as well as smaller unmeasured changes in microclimates (Chen et al. 1999, Gray et al. 2002, Su et al. 2019) and the stability of clonal species (discussed above). Our findings support complexity in individualistic understory associations with stand conditions, despite gradual declines in diversity through time in a maturing forest.

Conclusion

An examination of a decade of understory data across a naturally regenerated second-growth forest of mixed ages and stand type in Western Washington suggests some change in community composition associated with changes in overstory factors, and differences in nature of change based on overstory type (deciduous versus coniferous). In general, we found declines in diversity and shrub or sub-shrub cover with age, differences among stand types, and changes in community profile associated with stand age, type, and changes in canopy cover over a decade.

Surprisingly though, dramatic changes in overstory biomass (C) were not clearly associated with many understory changes. Overstory factors are not always the principal determinants of community change in these forests, or at least changes in understory and overstory may be occurring at different rates (Sensu McCune and Antos 1981). Despite over-all declines in diversity and changes in microhabitats, light gaps, overstory stand-type and roughness, changes in this highly productive understory community can be incremental on decadal time scales.

Acknowledgements

We thank members of the Evergreen Ecosystem Ecology Lab, the academic program Field Ecology 2006/8 and 2016. Alison Styring and Paul Przybylowicz were both instrumental in establishing the initial plot network study design. For field and lab support we specifically thank Justin Kirsch, Alexandra Kazakova, Jora Rehm–Lorber, Liam Mueller, Adam Martin, Rob Cole, Kyle Galloway, Pat Babbin, Josh Brann, Jordan Erickson, Katherine Halstead, Casey Broderick, Lindsey Wright, Emily Anderson. Hunter Stenovitch was instrumental in collecting canopy cover data in 2022. Rachel Brunner developed LiDAR methods for canopy heterogeneity in 2017. The Evergreen State College Computer Applications Lab provided significant logistical support in the early phases of this project. We are very grateful for reviews of this work by two anonymous reviewers and the section editor at Northwest Science. Joe Antos and Don Zobel also provided helpful feedback on this manuscript. Financial support has been provided by the Evergreen State College Foundation, Evergreen Faculty Sponsored Research Awards, The Evergreen Summer Undergraduate Research Fellowship, The Evergreen Fund for Innovation, and Microsoft Corporation.

Literature Cited

Baker, S. C., C. B. Halpern, T. J. Wardlaw, R. L. Crawford, R. E. Bigley, G. J. Edgar, S. A. Evans, J. F. Franklin, G. J. Jordan, Y. Karpievitch, T. A. Spies, and R. J. Thomson. 2015. Short and long-term benefits for forest biodiversity of retaining unlogged patches in harvested areas. Forest Ecology and Management 353:187-195.

Barbier, S., F. Gosselin, and P. Balandier. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved–A critical review for temperate and boreal forests. Forest Ecology and Management 254:1-15.

Bartels, S. F. and H. Y. Chen. 2010. Is understory plant species diversity driven by resource quantity or resource heterogeneity? Ecology 91:1931-1938.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73:1045-1055.

Celis, J., Halpern, C. B., and A. Muldoon. 2019. Consequences of reduced light for flower production in conifer-invaded meadows of the Pacific Northwest, U.S.A. Plant Ecology 220: 901-915.

Chang, C. C., C. B. Halpern, J. A. Antos, M. L. Avolio, A. Biswas, J. E. Cook, R. Del Moral, D. G. Fischer, A. Holz, R. J. Pabst, M. E. Swanson. and D. B. Zobel, D. B. 2019. Testing conceptual models of early plant succession across a disturbance gradient. Journal of Ecology 107:517-530.

Chang, S. X., G. F. Weetman, and C. M. Preston. 1996. Understory competition effect on tree growth and biomass allocation on a coastal old-growth forest cutover site in British Columbia. Forest Ecology and Management 83:1-11.

Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, B. L. Brookshire, and J.F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology variations in local climate can be used to monitor the effects of different management regimes. BioScience 49:288-297.

Childs, T. W. 1970. Laminated root rot of Douglas-fir in western Oregon and Washington. USDA Forest Service Research Paper PNW-102. Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Chojnacky, D. C., L. S. Heath, and J. C. Jenkins. 2014. Updated generalized biomass equations for North American tree species. Forestry 87:129-151.

Compagnoni, A., and C. B. Halpern. 2009. Properties of native plant communities do not determine exotic success during early forest succession. Ecography 32:449-458.

Dixon, P. 2003. VEGAN, a package of R functions for community ecology. Journal of Vegetation Science 14:927-930.

Dudney, J., R. A. York, C. L. Tubbesing, A. T. Roughton, D. Foster, S.L. Stephens, and J. J. Battles. 2021. Overstory removal and biological legacies influence long-term forest management outcomes on introduced species and native shrubs. Forest Ecology and Management 491:119-149.

Fischer, D., J. Antos, W. G. Grandy, and D. B. Zobel. 2016. A little disturbance goes a long way: 33–year understory successional responses to a thin tephra deposit. Forest Ecology and Management 382:236-243.

Fischer, D., J. Antos, D. Zobel, and A. Biswas. 2019. Understory succession after burial by tephra from Mount St. Helens. Journal of Ecology 355:1-42.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service Research Paper PNW–8. Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, and K. Bible. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest ecology and management, 155:399-423.

Grandpré, L., D. Boucher, Y. Bergeron, and D. Gagnon. 2011. Effects of small canopy gaps on boreal mixedwood understory vegetation dynamics. Community Ecology 12:67-77.

Gray, A. N., T. A. Spies, and M. J. Easter. 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. Canadian Journal of Forest Research, 32 :332-343.

Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69:1703-1715.

Halpern, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70:704-720.

Halpern, C. B., and J. A. Lutz. 2013. Canopy closure exerts weak controls on understory dynamics: a 30–year study of overstory-understory interactions. Ecological Monographs 83:221-237.

Halpern C. B., S. A. Evans, and S. Nielson. 1999. Soil seed banks in young, closed-canopy forests of the Olympic Peninsula, Washington: potential contributions to understory reinitiation. Canadian Journal of Botany 77:922-935.

Halpern, C. B., and T. A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5:913-934.

Huffman, D. W., J. C. Tappeiner II, and J. C. Zasada. 1994. Regeneration of salal (*Gaultheria shallon*) in the central Coast Range forests of Oregon. Canadian Journal of Botany. 72:39-51.

Ishii, H., and E. D. Ford. 2002. Persistence of *Pseudotsuga menziesii* (Douglas-fir) in temperate coniferous forests of the Pacific Northwest Coast, USA. Folia Geobotanica 37:63-69.

Jeronimo, S. M., V. R. Kane, D.J. Churchill, R. J. McGaughey, and J. F. Franklin. 2018. Applying LiDAR individual tree detection to management of structurally diverse forest landscapes. Journal of Forestry 116:336-346.

Jones, C. C., S. A. Acker, and C. B. Halpern. 2010. Combining local and large-scale models to predict the distributions of invasive plant species. Ecological Applications 20:311-326

Kane V. R., R. F Gersonde, J. A. Lutz, R. J McGaughey, J. D. Bakker and J. F. Franklin. 2011. Patch dynamics and the development of structural and spatial heterogeneity in Pacific Northwest forests. Canadian Journal of Forest Research 41:2276-2291.

Kennedy, P. G., and T. Quinn. 2001. Understory plant establishment on old-growth stumps and the forest floor in western Washington. Forest Ecology and Management 154:193-200.

Kittel, G., D. Meidinger and D. Faber-Langendoen. 2015. G240 *Pseudotsuga menziesii - Tsuga heterophylla / Gaultheria* shallon Rainforest Group. United States National Vegetation Classification. Fed. Geogr. Data Comm., Washington DC, US.. Available online at https://www1.usgs.gov/csas/nvcs/unitDetails/833261 (accessed 19 June 2022).

Kirsch, J. L., D. G. Fischer, A. N. Kazakova, A. Biswas, R. E. Kelm, D. W. Carlson, and C. J. LeRoy. 2012. Diversity-carbon flux relationships in a northwest forest. Diversity 4:33-58.

Lezburg, A. L., J. A. Antos, and C. B. Halpern. 1999. Belowground traits of herbaceous species in young coniferous forests of the Olympic Peninsula, Washington. Canadian Journal of Botany 77:936-943.

Mallik, A. U., and C. E. Prescott. 2001. Growth Inhibitory Effects of Salal on Western Hemlock and Western Red Cedar. Agronomy Journal 93:85-92

McCune, B., and J. A. Antos. 1981. Correlations Between Forest Layers in the Swan Valley, Montana. Ecology 62: 1196-1204

McKenzie, D., and C. B. Halpern. 1999. Modeling the distributions of shrub species in Pacific northwest forests. Forest Ecology and Management 114:293-307.

Mckenzie, D., C. B. Halpern, and C. R. Nelson. 2000. Overstory influences on herb and shrub communities in mature forests of western Washington, U.S.A.. Canadian Journal of Forest Research 30:1655-1666.

Messier, C. 1992. Effects of neutral shade and growing media on growth, biomass allocation, and competitive ability of Gaultheria shallon. Canadian Journal of Botany 70:2271-2276

Næsset, E., 2002. Predicting forest stand characteristics with airborne scanning laser using a practical two-stage procedure and field data. Remote Sensing of Environment. 80:88-99.

Nelson, C. R., C. B. Halpern, and J. A. Antos. 2007. Variation in responses of late-seral herbs to disturbance and environmental stress. Ecology 88:2880-2890.

Oksanen J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2020. vegan: Community Ecology Package. R package version 2.5-7. Available at https://CRAN.R-project.org/package=vegan (accessed 30 December 2021).Pabst, R. J., and T. A. Spies. 1997. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. Canadian Journal of Botany 76:298-315.

Prescott, C. E. 1994. Salal Cedar Hemlock Integrated Research Program: a synthesis. Faculty of Forestry, University of British Columbia, Vancouver.

Preston C. M. 1999. Condensed Tannins of Salal (*Gaultheria shallon* Pursh): A Contributing Factor to Seedling “Growth Check” on Northern Vancouver Island?. Plant Polyphenols 2. Springer, Boston, MA.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://www.R-project.org/ - (accessed on 12 December 2021).

Reilly, M. J., and T. A. Spies. 2015. Regional variation in stand structure and development in forests of Oregon, Washington, and inland Northern California. Ecosphere 6:1-27

Reinhart, K. O., J. Gurnee, R. Tirado, and R. M. Callaway. 2006. Invasion through quantitative effects: intense shade drives native decline and invasive success. Ecological Applications 16:1821-1831.http://dx.doi.org/10.1890/ES14-00469.1

Rogers, A. A., T. P. Rooney, D. Olsen, and D. M. Waller. 2008. Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 89:2482-2492.

Royo, A. A., and W. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Canadian Journal of Forest Research 36:345-1362.

Sommerfeld, A., C. Senf, B. Buma, A. W. D'Amato, T. Després, I. Díaz-Hormazábal, S. Fraver, L. E. Frelich, A. G. Gutiérrez, S. J. Hart, B. J. Harvey, H. S. He, T. Hlásny, A. Holz, T. Kitzberger, D. Kulakowski, D. Lindenmayer, A. S. Mori, J. Müller, J. Paritsis, G. L. W. Perry, S. L. Stephens, M. Svoboda, M. G. Turner, T. T. Veblen, and R. Seidl. 2018. Patterns and drivers of recent disturbances across the temperate forest biome. Nature Communications 9:1-9

Sprugel, D. G., K. G. Rascher, R. Gersonade, M. Dovciak, J. A. Lutz, and C. B. Halpern. 2009. Spatially explicit modeling of overstory manipulations in young forests: effects on stand structure and light. Ecological Modelling 220:3565-3575.

Su, X., M. Wang, Z. Huang, S. Fu, and H. Y. Chen. 2019. Forest understory vegetation: Colonization and the availability and heterogeneity of resources. Forests 10:1-17.

Thies, W. G., and R. N. Sturrock. 1995. Laminated root rot in western North America. USDA General Technical Report PNW–GTR–349. Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Thomas, S. C., C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. Ecological Applications 9:864-879.

Thysell, D. R., and A. B. Carey. 2000. Effects of forest management on understory and overstory vegetation: a retrospective study. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Portland OR.

Thysell, D. R., and A. B. Carey. 2001. Manipulation of density of *Pseudotsuga menziesii* canopies: preliminary effects on understory vegetation. Canadian Journal of Forest Research 31:1413-1525.

Urban, D. L., M. E. Harmon, and C. B. Halpern. 1993. Potential response of Pacific northwestern forests to climatic change, effects of stand age and initial composition. Climatic Change 23:247-266.

Van Pelt, R., and J. F. Franklin. 2000. Influence of canopy structure on the understory environment in tall, old-growth conifer forests. Canadian Journal of Forest Research 30:1231-1245.

Weber, A., J. P. Kimmins, B. Gilbert, Y. Lo, and J. A. Blanco. 2014. Multiple pathway succession in coastal Tsuga heterophylla, Thuja plicata and Abies amabilis forests on northeastern Vancouver Island, British Columbia. Canadian Journal of Forest Research 44:1145-1155.

Wheeler, B., and Torchiano, M. 2016. lmPerm: Permutation Tests for Linear Models. R Package version 2.1-0. Available at https://cran.r-project.org/web/packages/lmPerm/index.html https://cran.r-project.org/web/packages/BiodiversityR/index.html (accessed 19 June 2022).

Wright, E. F., K. D. Coates, and P. Bartemucci. 1998. Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position. Canadian Journal of Forest Research 28:1352-1364.

Zobel, D. B., J. A. Antos, and D. G. Fischer. 2021. Secondary disturbance following a deposit of volcanic tephra: a 30-year record from old-growth forest understory. Canadian Journal of Forest Research, 51:1541-1549.

Figure Captions

Figure 1. Map of plot locations with reference to dominant forest type (A), current forest coverage in recent Aerial imagery (B), historic forest treatment (C).

Figure 2. Linear regressions between 2008 versus 2018 cover for growth-form cover, species richness, species diversity (Shannon's H'), and total percent cover. Plot overstory carbon (C) change is represented in point color, with plots with increasing C indicated in dark gray, stable C in light gray, and decreasing C in black. Regression lines are indicated as solid lines on panels with significant relationships. Gray dashed lines represent 1:1 lines on regression panels.

Figure 3. Significant relationships between growth-forms in 2008 and 2018 against predictive overstory variables including presence of pathogen *P. weirii*, soil type, overstory age and stand type (conifer, deciduous, or mixed conifer and deciduous). Plot overstory carbon change from 2008 to 2018 is represented in point color, with plots with increasing C indicated in dark gray, stable C in light gray, and decreasing C in black. Significant linear regressions are represented by solid lines. Boxplots represent medians (black horizontal line) and quartiles along with outliers.

Figure 4. Significant results of community metrics versus overstory predictive factors overstory age and stand type (conifer, deciduous, or mixed conifer and deciduous) in 2008 and 2018. Plot overstory carbon change from 2008 to 2018 is represented by point color, with plots with increasing C indicated in dark gray, stable C in light gray, and decreasing C in black. Significant linear regressions are represented by solid lines. Boxplots represent medians (black horizontal line) and quartiles along with outliers.

Figure 5. Significant relations between changes in growth forms (*d*) against changes in overstory canopy from 2008 and 2018, as well as presence of pathogen *P. werii* and stand type

(forest type; conifer, deciduous, or mixed conifer and deciduous). Plot overstory carbon change from 2008 to 2018 is represented in point color, with plots with increasing C indicated in dark gray, stable C in light gray, and decreasing C in black.

Figure 6. Non-metric multidimensional scaling (NMS) ordination graphs displaying impact of overstory stand-type and year, in 2008 and 2018 (A-C), and in 2018 only (D). Each point is an individual plot in the respective years. In panels A-C, orbital lines represent 95% confidence orbitals around the centroid of each year (2008 – dashed line, vs 2018 – black line). In Panel D, convex hulls around distinct stand types are indicated by black (conifer), gray (deciduous), and dashed (mixed) lines. **A**: connecting arrows between individual plots in 2008 to 2018 show changes over the study period. **B**: significant vectors for stand structure metrics are fit to the ordination representing the directional correlation of roughness, age, and canopy cover. **C**: Similar to **B**, but vectors represent growth form categories. **D**: 2018 data demonstrated separation among stand types and significant vectors for changes in canopy cover through time (*d*.canopy.cover) and age.

TABLE 1. Stand* characteristics of EEON plots as classified by overstory canopy type in Olympia, WA, based on 2018 data. The metrics H’, Richness, and % Cover all pertain to 2018 understory measurements.

Overstory Stand Type	Dominant Species	n	Age (years)	Trees ha^{-1} (> 5 cm dbh)	Overstory C (Mg ha^{-1})	Soil Types	H'	Richness	% Cover
Conifer		20 [46%]	88.7 (±21.8)	379.0 (±168.8)	242.9 (±167.7)	17 Sand / 3 Silt	1.3 (±0.3)	8.3 (±2.5)	121.1 (±13.5)
	PSME	18	86.5 (±20.8)	372.6 (±178.3)	256.9 (±171.0)	15 Sand (Sand$_a$) / 3 Silt (2 Silt$_{g\,/}$ 1 Silt$_m$)	1.4 (±0.3)	8.2 (±2.6)	122.4 (±13.6)
	THPL	2	108.5 (±29.0)	414.0 (±44.6)	116.7 (±41.9)	2 Sand (Sand$_a$)	0.9 (±0.0)	9.0 (±1.4)	109.4 (±2.3)
Deciduous		12 [27%]	79.5 (±18.9)	394.9 (±146.5)	146.1 (±100.0)	7 Sand / 5 Silt	1.3 (±0.5)	8.5 (±4.1)	122.9 (±18.6)
	ACMA3	1	80.0	286.6	70.1	1 Silt (Silt$_g$)	1.0	6	114.3
	ALRU2	3	78.0 (±44.2)	509.6 (±178.3)	49.8 (±63.5)	3 Sand (Sand$_a$)	1.0 (±0.7)	5 (±3.0)	120.3 (±16.5)
	ACMA3 and ALRU2	8	80.0 (±0)	366.2 (±130.6)	191.6 (±86.0)	4 Sand (Sand$_a$) / 4 Silt (3 Silt$_{g\,/}$ 1 Silt$_y$)	1.5 (±0.5)	10.1 (±3.8)	125.0 (±21.1)
Mixed Conifer & Deciduous		12 [27%]	112.4 (±26.4)	312.1 (±203.8)	166.5 (±138.8)	8 Sand / 4 Silt	1.0 (±0.3)	7.2 (±2.4)	105.7 (±6.1)
	Mixed Canopy	12	112.4 (±26.4)	312.1 (±203.8)	166.5 (±138.8)	7 Sand (4 Sand$_a$ / 2 Sand$_d$ / 1 Sand$_e$) / 5 Silt (2 Silt$_{s\,/}$ 2 Silt$_k$ / 1 Silt$_g$)	1.0 (±0.3)	7.2 (±2.4)	105.7 (±6.1)

---

*Table values are weighted means of all data (± standard deviation), with the exception of ‘Number of Plots’, where values in brackets indicate total percentage of all plots, and ‘Soil Types’, where values in parentheses indicate number of plots located in each classification. ‘Sand’ represents plots located on Alderwood gravelly sandy loam soil (sand$_a$), Yelm fine sandy loam (sand$_y$), Everrett sandy loam (sand$_e$), or Dystric soils (sand$_d$); ‘Silt’ represents plots located on Giles silt loam soil (silt$_g$), Skipopa silt loam soil (silt$_s$), McKenna gravely silt loam (silt$_m$), or Kapowsin silt loam (silt$_k$). Standard deviation values are unapplicable for ACMA3 dominated stands – as represented only by one plot. Species abbreviations, utilizing USDA codes, are as follows Conifer: PSME: *P. menziesii;* THPL: *T. plicata.* Deciduous: ACMA3: *A. macrophyllum; ALRU2: A. rubra.*

TABLE 2. Summarized table of results* of linear models for growth form cover (graminoids, ferns, shrubs, introduced species, saplings, subshrubs and herbs) as predicted by overstory variables for 2008 and 2018.

		Overstory C (Mg ha^{-1})	**Stand Age**	**Stand-Type**	**Canopy Roughness**	**Soil-Type**	***P. weirii***	**d_{carbon}**
2008								
	Graminoids	1	0.7059	0.5464	**0.0347** (r^2 = 0.1)	1	1	N/A
	Ferns	0.8285	0.5458	0.4506	0.5252	0.0967	**0.0030** (r^2 = 0.20)	N/A
	Shrubs	0.7059	0.0762	**0.0024** (r^2 = 0.25)	0.9608	0.6604	0.4296	N/A
	Introduced	0.2213	0.9412	0.5570	0.34529	**0.0062** (r^2 = 0.15)	0.1808	N/A
	Saplings	0.7451	0.7059	0.4234	0.5158	0.9216	0.9608	N/A
	Subshrubs	0.8235	**0.0066** (r^2 = 0.17)	1	0.8627	0.5733	0.2776	N/A
	Herbs	0.78431	0.4444	0.39394	0.17735	**0.0374** (r^2 = 0.1)	0.31222	N/A
2018								
	Graminoids	0.0688	0.5916	0.5706	0.8628	**0.0201** (r^2 = 0.13)	0.3961	0.3269
	Ferns	0.7356	0.3960	0.5854	0.2151	0.2109	0.6386	0.0592
	Shrubs	0.6061	**0.0455** (r^2 = 0.06)	**0.0068** (r^2 = 0.23)	0.8235	0.9608	0.6154	0.3657
	Introduced	0.0552	0.8431	0.7541	0.7056	**0.0224** (r^2 = 0.12)	0.4082	0.2846
	Saplings	0.2662	1	0.5526	0.6545	0.7647	0.2492	0.9608
	Subshrubs	0.4655	**0.0393** (r^2 = 0.33)	**0.0358** (r^2 = 0.23)	0.7843	**0.0341** (r^2 = 0.31)	0.7451	0.2681
	Herbs	0.1125	0.9412	0.6196	0.6545	0.7255	0.2671	0.1718

*Significant results ($P < 0.05$) are in bold with r^2 values (calculated from sums of squares ratios) in parentheses

TABLE 3. Summarized table of results for linear models predicting community metrics (species richness, Shannon’s H’ diversity, and total percent cover) for 2008 and 2018 based on overstory variables. Significant results ($P < 0.05$) are in bold with r^2 values (calculated from sums of squares ratios) in parentheses.

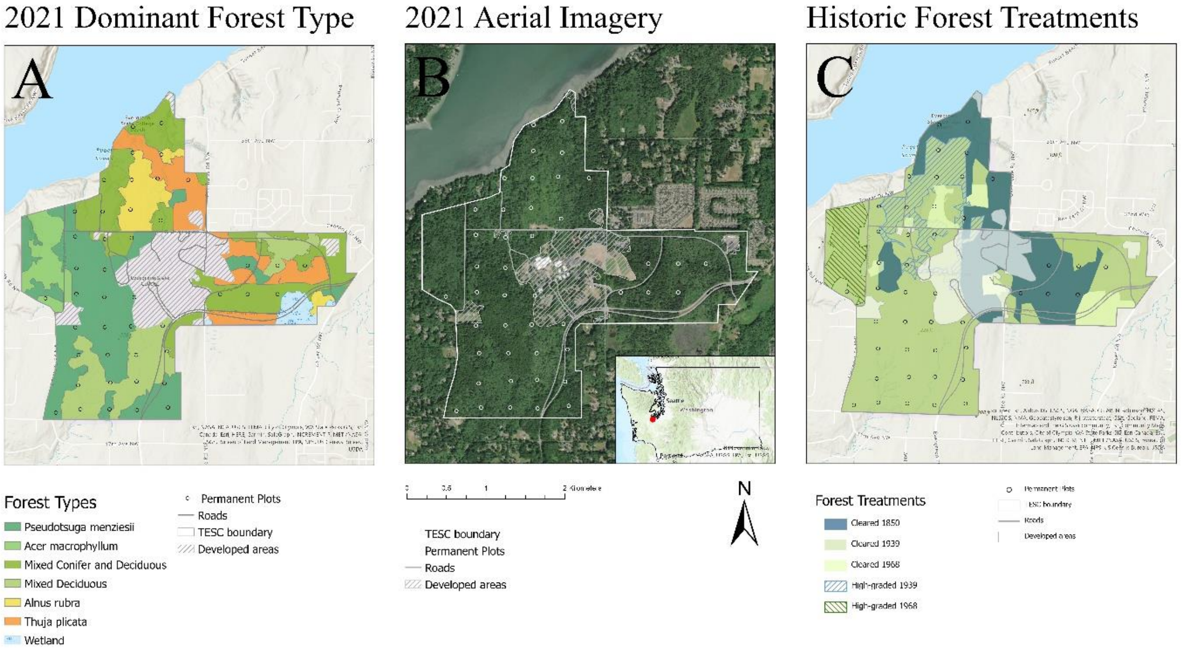
		Overstory C (Mg ha^{-1})	**Stand Age**	**Stand-Type**	**Canopy Roughness**	**Soil-Type**	***P. weirii***	$\boldsymbol{d_{\text{carbon}}}$
2008								
	Richness	0.6029	0.6429	0.3422	1	0.1414	0.2560	N/A
	H'	0.9559	**0.0114** ($r^2 = 0.15$)	0.5540	0.9363	0.3734	0.2044	N/A
	Total cover	0.8039	0.3678	**0.0404** ($r^2 = 0.16$)	0.5217	0.3804	0.7647	N/A
2018								
	Richness	0.8824	0.7843	0.8235	0.4545	0.6190	0.2101	0.3224
	H'	0.3473	**0.0024** ($r^2 = 0.21$)	0.6460	0.2508	0.8026	0.2893	0.8730
	Total cover	0.8039	0.0661	0.2142	0.2857	0.6333	**0.0449** ($r^2 = 0.08$)	0.8235

TABLE 4. Summarized table of results* for linear models predicting change (*d*) in growth forms and community metrics (species richness, Shannon's H' diversity, and total percent cover) from 2008 and 2018 versus changes (*d*) in overstory predictive factors.

	Stand Age	*P. weirii*	Stand–Type	Soil Type	d_{Carbon}	$d_{\mathrm{canopy.cover}}$	$d_{\mathrm{roughness}}$
Growth-Form							
$d_{Grasses}$	0.5436	0.0932	0.9980	0.0532	0.2198	0.8916	**0.0337** (r^2 = 0.1)
d_{Ferns}	0.7586	**<0.0001** (r^2 = 0.38)	0.9225	0.7104	0.9414	0.8111	0.2883
d_{Shrubs}	0.3572	0.4979	0.3334	0.4428	0.8317	0.1214	0.6953
$d._{Introduced}$	0.2670	0.0828	0.7990	0.9395	0.1868	0.3436	0.0789
$d_{Saplings}$	0.1683	0.1.883	0.2022	0.8376	0.1606	0.1287	0.3474
$d_{Subshrubs}$	0.59178	0.2018	**0.0436** (r^2 = 0.13)	0.4913	0.9558	**0.0213** (r^2 = 0.11)	0.2405
d_{Herbs}	0.3608	0.6075	0.6657	0.1108	0.8443	0.5749	0.4363
Community							
$d_{Richness}$	0.9987	0.6689	0.6757	0.1479	0.1189	0.8993	0.0713
$d_{H'}$	0.5377	0.6778	0.9402	0.301	**0.0002** (r^2 = 0.29)	0.0548	0.2196
$d_{Total\ cover}$	0.5719	0.4033	0.4216	0.5408	0.4204	**0.0080** (r^2 = 0.17)	0.4558

*Significant results ($P < 0.05$) are in bold with r^2 values (calculated based on sums of squares ratios) in parentheses.

Fig 1


2021 Dominant Forest Type

2021 Aerial Imagery

Historic Forest Treatments

Fig 2

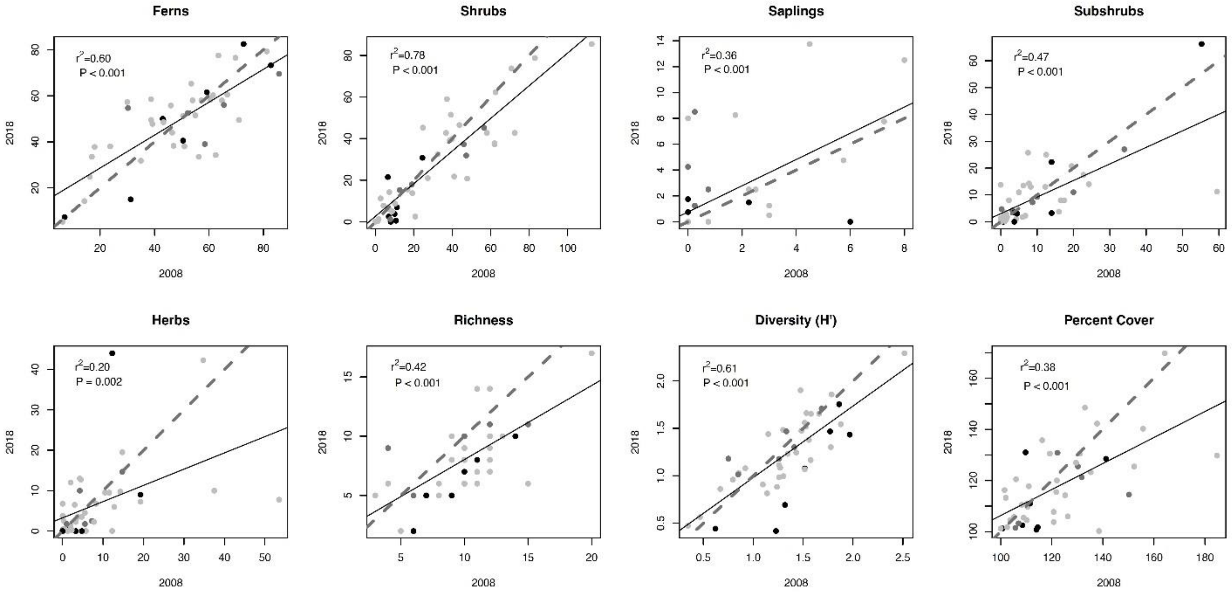
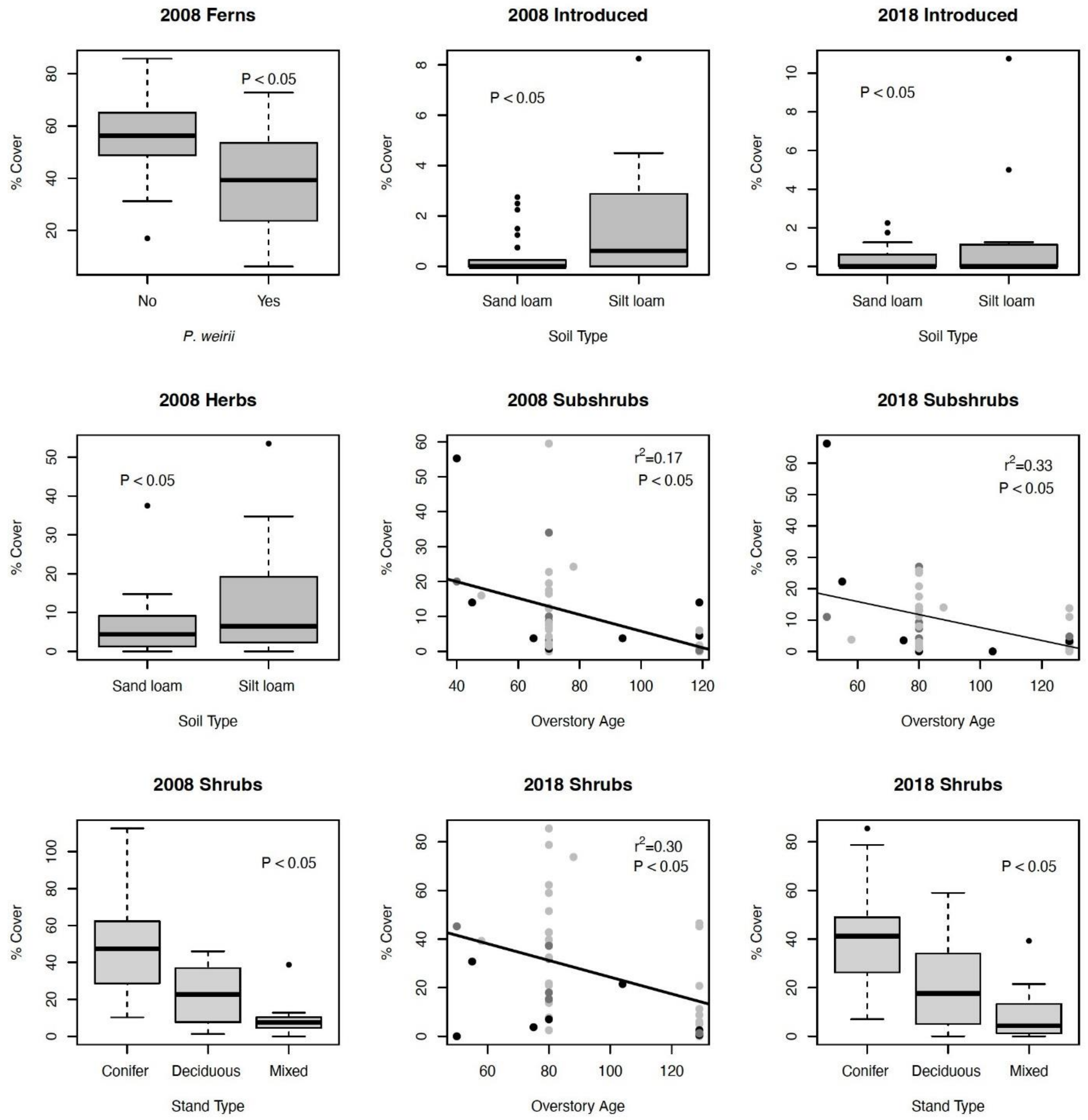

Ferns
r^2=0.60
P < 0.001
Shrubs
r^2=0.78
P < 0.001
Saplings
r^2=0.36
P < 0.001
Subshrubs
r^2=0.47
P < 0.001
Herbs
r^2=0.20
P = 0.002
Richness
r^2=0.42
P < 0.001
Diversity (H')
r^2=0.61
P < 0.001
Percent Cover
r^2=0.38
P < 0.001
2018
2008

Fig 3



2008 Ferns
% Cover
20
40
60
80
P < 0.05
No
Yes
P. weirii
2008 Introduced
% Cover
0
2
4
6
8
P < 0.05
Sand loam
Silt loam
Soil Type
2018 Introduced
% Cover
0
2
4
6
8
10
P < 0.05
Sand loam
Silt loam
Soil Type
2008 Herbs
% Cover
0
10
20
30
40
50
P < 0.05
Sand loam
Silt loam
Soil Type
2008 Subshrubs
% Cover
0
10
20
30
40
50
60
r^2=0.17
P < 0.05
40
60
80
100
120
Overstory Age
2018 Subshrubs
% Cover
0
10
20
30
40
50
60
r^2=0.33
P < 0.05
60
80
100
120
Overstory Age
2008 Shrubs
% Cover
0
20
40
60
80
100
P < 0.05
Conifer
Deciduous
Mixed
Stand Type
2018 Shrubs
% Cover
0
20
40
60
80
r^2=0.30
P < 0.05
60
80
100
120
Overstory Age
2018 Shrubs
% Cover
0
20
40
60
80
P < 0.05
Conifer
Deciduous
Mixed
Stand Type

Fig 4

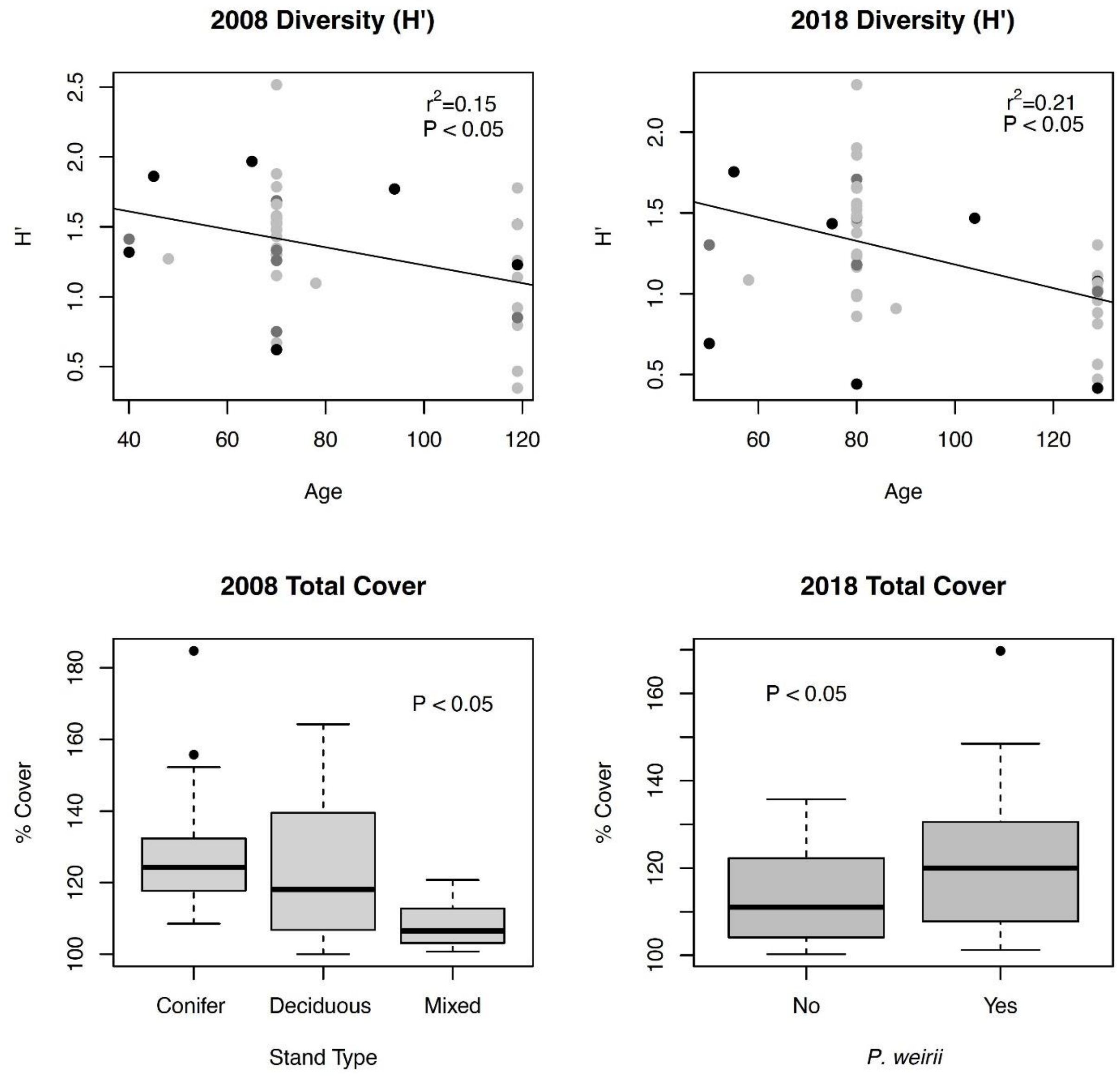

2008 Diversity (H')
H'
0.5
1.0
1.5
2.0
2.5
r^2=0.15
P < 0.05
40
60
80
100
120
Age
2018 Diversity (H')
H'
0.5
1.0
1.5
2.0
r^2=0.21
P < 0.05
60
80
100
120
Age
2008 Total Cover
% Cover
100
120
140
160
180
P < 0.05
Conifer
Deciduous
Mixed
Stand Type
2018 Total Cover
% Cover
100
120
140
160
P < 0.05
No
Yes
P. weirii

Fig 5

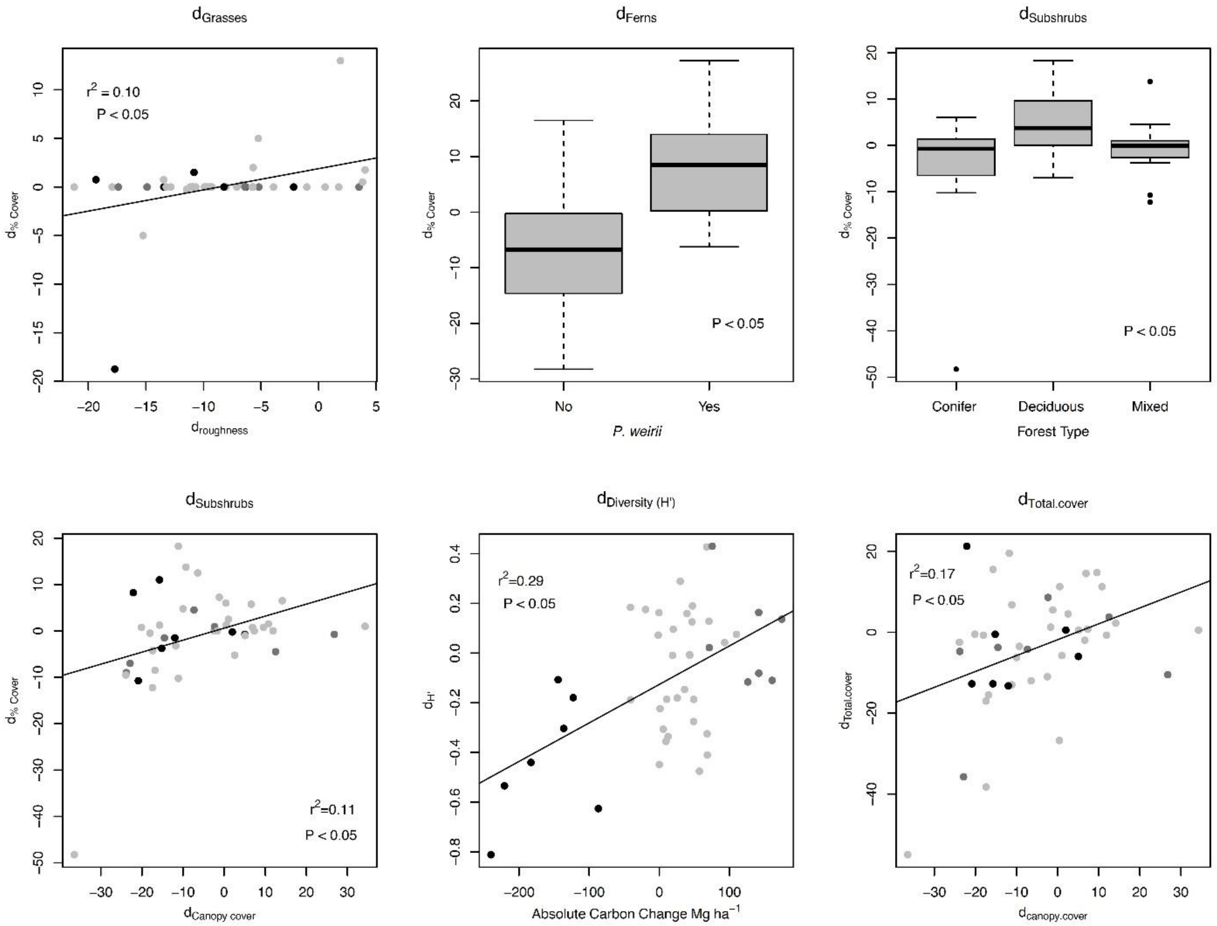
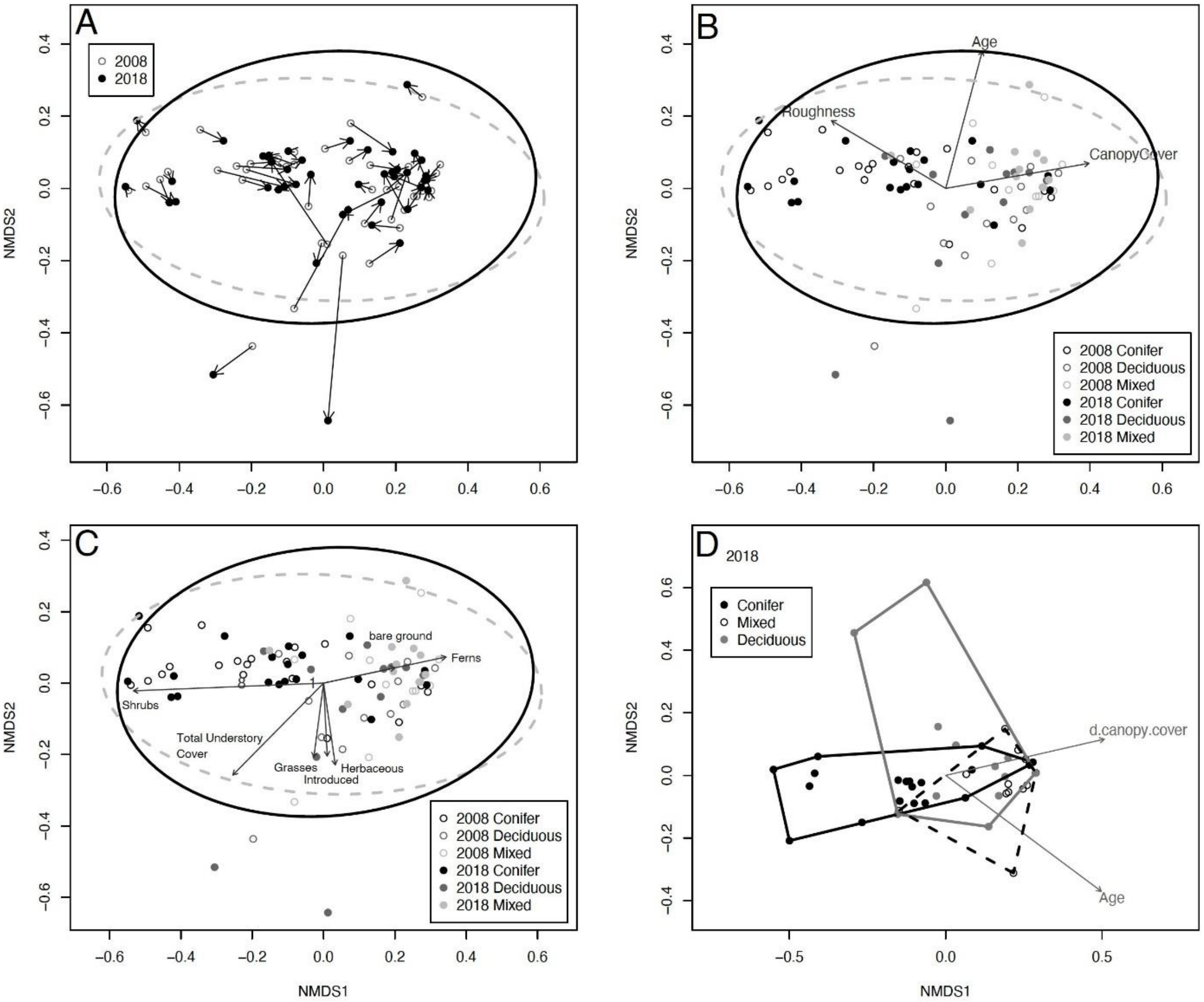

dGrasses
r2 = 0.10
P < 0.05
d% Cover
droughness
dFerns
P < 0.05
No
Yes
P. weirii
dSubshrubs
P < 0.05
Conifer
Deciduous
Mixed
Forest Type
dSubshrubs
r2=0.11
P < 0.05
dCanopy cover
dDiversity (H')
r2=0.29
P < 0.05
dH'
Absolute Carbon Change Mg ha−1
dTotal.cover
r2=0.17
P < 0.05
dcanopy.cover

Fig 6


A
2008
2018
B
Age
Roughness
CanopyCover
2008 Conifer
2008 Deciduous
2008 Mixed
2018 Conifer
2018 Deciduous
2018 Mixed
C
bare ground
Ferns
Shrubs
Total Understory
Cover
Grasses
Introduced
Herbaceous
2008 Conifer
2008 Deciduous
2008 Mixed
2018 Conifer
2018 Deciduous
2018 Mixed
D
2018
Conifer
Mixed
Deciduous
d.canopy.cover
Age
NMDS2
NMDS1
0.4
0.2
0.0
−0.2
−0.4
−0.6
0.6
−0.6
−0.4
−0.2
0.0
0.2
0.4
0.6
−0.5
0.0
0.5