



Understory floristic composition of planted western white pine stands in the northern Rocky Mountains

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ABSTRACT

Understory plants are an integral part of forests, serving a variety of functions that help maintain healthy ecosystems. The structure and composition of the understory are influenced by numerous biotic and abiotic factors, with light being critical. The introduction of the pathogen *Cronartium ribicola*, which causes white pine blister rust, into North America in the early 20th century led to the near total loss of western white pine (*Pinus monticola*) from moist forests of the Northern Rockies. Management is reintroducing blister rust-resistant western white pine across the landscape, but the effects on the understory are unknown. We examined the effects of stand structure and proportion of western white pine in the overstory on understory diversity of vascular plants in closed canopy stands dominated by blister rust-resistant western white pine across northern Idaho. Habitat series explained the greatest amount of variation (34%) in species presence-absence, while canopy cover accounted for 25%, basal area of all trees for 18%, and the proportion of western white pine composition by 14%. Our analysis revealed positive relationships between the proportion of western white pine in the overstory and both the presence of understory plants and the cover of several understory species. For both the presence and cover, separate sets of thirteen species were found to have a positive relationship with the proportion of western white pine in the overstory, with eight species in common. This research fills a knowledge gap by using data from a range of stands across northern Idaho with varying abundance of western white pine in the overstory to evaluate the relationship between the understory and overstory composition. As land managers plant more western white pine trees, we are likely to see the concomitant increase in understory plant diversity across the landscape, in addition to numerous other benefits, including disturbance resistance and resilience.

1. Introduction

Understory plants are an integral component of forest ecosystems. They provide a range of functions, including nutrient cycling, regeneration capacity, and microclimate modification for regenerating trees (Gilliam, 2007). This vegetation also provides important food, shelter, and habitat resources for wildlife ranging from arthropods to ungulates (Gill and Beardall, 2001; Proctor et al., 2012; Boch et al., 2013), and wildlife habitat use and behavior respond to changes to understory structure and composition (Dutra et al., 2011; Hanula et al., 2015). Site conditions can often be inferred from understory composition (Gilliam, 2007), where understory plants have formed the basis of habitat classification as indicator species (Daubenmire, 1968; Daubenmire and

Daubenmire, 1968; Cooper et al., 1991), making them useful as indicators of current and future ecological change (Dalle Fratte et al., 2019; Hedwall et al., 2019). The understory plant community is often shaped by forest overstory structure (Chávez and Macdonald, 2010), and understanding how the understory plant community responds to forest management has been a topic of growing interest in recent decades (Lencinas et al., 2011; Duguid and Ashton, 2013). In the moist mixed conifer temperate forests of the northern Rocky Mountains in the United States, there is limited to no information on how understory plant communities develop in managed stands. This information is needed to inform the consequences of land management focused on restoring species composition that contains western white pine (*Pinus monticola*) and create disturbance-resilient forests.

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Historically, western white pine dominated (>60%) this landscape (Neuenschwander et al., 1999). This began to change beginning in the early 20th century when white pine blister rust, caused by the pathogen *Cronartium ribicola*, was introduced into western Canada and the eastern United States in 1910 (Spaulding, 1911). By the 1960s, the continued widespread mortality of western white pine, failure to completely remove the alternate host gooseberry (*Ribes* spp.), lack of a successful antifungal to control the pathogen, and extensive salvage harvesting led to a shift in tree species composition across the landscape dominated by grand fir (*Abies grandis*) and western hemlock (*Tsuga heterophylla*).

Prior to the introduction of *Cronartium ribicola* and the subsequent salvage efforts, historical (i.e., pre-1910) western white pine stands were typically multi-aged with a diverse understory composed of trees, shrubs, and forbs (Larsen, 1923; Marshall, 1929). The physical structure of western white pine canopies allows a significant amount of sunlight to pass through and reach the understory (Wellner, 1948). Comparatively, other trees in the region, like grand fir, western hemlock, or western red cedar (*Thuja plicata*), have foliage that spreads out with deep crowns (Kershaw Jr and Maguire, 1996) and vertically layers creating multi-layered canopies that block substantial amounts of light to the understory (sensu Horn, 1971). For example, Canham et al. (1999) modeled light penetrating to the understory of mature interior hemlock-cedar forests of interior British Columbia and found that canopies of western hemlock and western redcedar had 12% and 11% of potential light in the understory compared to 30% light under lodgepole pine (*Pinus contorta*), which has a crown structure more like western white pine.

Tree species differences in light penetration through the canopy influence biodiversity and vigor of understory plant communities because sunlight controls levels of germination, photosynthesis, and microclimate (Young and Smith, 1980; Messier et al., 1998), among other processes. Bartels and Chen (2010) found that an increase in resource quantity may drive species diversity in understory communities, although resource-rich environments can promote dominance of species that establish earlier than others (Kardol et al., 2013). Given that the open canopy structure of western white pine is likely to result in an overall increase in the amount of light infiltration to the understory (Jain et al., 2004), we would expect to see greater species richness in such stands. Heterogeneous light environments, like those we hypothesize to exist in mixed stands with a large component of western white pine, have also been shown to structure diversity in the understory layer by partitioning resources across light and microclimate gradients (Halpern and Spies, 1995; Bartels and Chen, 2010).

While we cannot travel back in time (early 1900s) to fully understand the floristic nature of historical understories in western white pine-dominated stands, we do have photographs and descriptions from the past (Leiberg, 1899; Larsen, 1923; Marshall, 1929) which indicate that these forests contained a diverse abundance of understory vegetation. Since the planting of blister rust-resistant western white pine trees became widely practiced in the 1980s (Fins et al., 2002), plantations that contain this species are becoming a component of forests across the region. Currently, an integrated management approach that uses a combination of planted blister rust-resistant trees and natural regeneration of western white pine is being applied across the Northern Rockies (Forest Service, 2015). The increased abundance of western white pine and similar-aged mixed conifer plantations provides an opportunity to understand how the presence and abundance of western white pine influences understory plant community structure and assembly (Lindenmayer et al., 2000). This study tested the following hypotheses: (1) Understory species richness and total understory cover are positively correlated with the proportion of western white pine in the overstory but negatively correlated with stand density in closed-canopy stands, and (2) canopy cover is negatively correlated with the proportion of western white pine in the overstory and thus presence and cover of understory species that favor high light and partially shaded conditions is greater with more western white pine in the overstory.

2. Methods

2.1. Study area and plot design

Twenty-seven stands were selected within the historical range of western white pine-dominated forests of northern Idaho, USA (Haig et al., 1941). Six stands were near Priest Lake, Idaho (48°15'–48°27' N, 117°01'–116°44' W), four stands were in the Coeur d'Alene Mountains (47°48'–47°44' N, 116°08'–116°00' W), and seventeen stands were in the Clearwater Mountains (47°14'–46°43' N, 116°38'–116°02' W) (Fig. 1). All stands were even-aged and either planted with western white pine between 1960 and 2000, or of a similar age and dominated by either planted or naturally regenerated grand fir or western hemlock. Seventeen stands were on the Idaho Panhandle National Forests and Nez Perce-Clearwater National Forests, and ten stands were on private forest land. All stands sampled in 2018 (21 stands) met the following requirements: (1) average 12.7 cm diameter at breast height (1.37 m from the ground; diameter at breast height (DBH)) or larger, (2) greater than 50 percent western white pine by stems-ha⁻¹, and (3) accessible by road. In 2019, an additional six stands with western white pine composition between 25 and 50 percent by stem number were added. Stands were between 18 and 58 years old at the time of sampling.

Four 0.02-ha plots were established in each stand using the United States Department of Agriculture Forest Service Forest Inventory and Analysis (FIA) program plot design (Fig. 2) (Bechtold and Scott, 2005). A random point was chosen as the plot center on the first plot (i.e., the center plot). Subsequent plots were located 36.6 m, apart accounting for the slope at azimuths of 0°, 120°, and 240° from the plot center of plot one. All four plots were within the stand boundary and not in a drainage, old log landing, or skid trail. We established all four plots before starting measurements to ensure all plots fit within the stands. If all four plots did not fit within the stand using the FIA design, the distance between plots was shortened to 30.5 m, or the design was stretched to a linear design. If all plots did not fit using these options, the stand was not sampled.

2.2. Data collection

Data collected on the 0.02 ha (8 m radius) plots included the count and DBH of all living and standing dead trees by species. A random sample of two trees per species were selected for measurement of total height and crown length. Also, the habitat series for each plot was keyed out using the criteria specified in Cooper et al. (1991). Habitat series are defined by their “climax” tree species and can also include indicator understory species. Broadly defining habitat series by “climax” tree species, as was done in this study, provides an indication of the climate and soil moisture-holding capacity of the site. Eleven stands were classified in the western redcedar habitat series, eight stands in the western hemlock series, and eight stands in the grand fir series. The western hemlock series is the wettest series in the area, followed by western redcedar, and lastly grand fir within the mid-elevations of the stands in this study, where western white pine once dominated.

Canopy cover was estimated using a GRS Densitometer™ (Geographic Resource Solutions, Arcata, USA), which has been shown to produce similar canopy cover estimates to other indirect canopy cover tools in the Northern Rockies (Applegate, 2000). A cloth tape was laid across the 0.02-ha plot, oriented north to south, and another cloth tape oriented east to west, with the tapes crossing at the plot center. Canopy cover was measured at 30 points within each plot every 1.5 m along the cloth tapes at a height of 1.82 m. Additional densitometer measurements were collected along the east–west transect: Along the western transect, an additional measurement was taken 1.5 m due north of each measurement point, while along the eastern portion of the plot, an additional measurement was taken 1.5 m due south of each measurement point. At each of the 30 locations within the plot, the densitometer was used to determine if foliage or open sky was overhead. The number of points

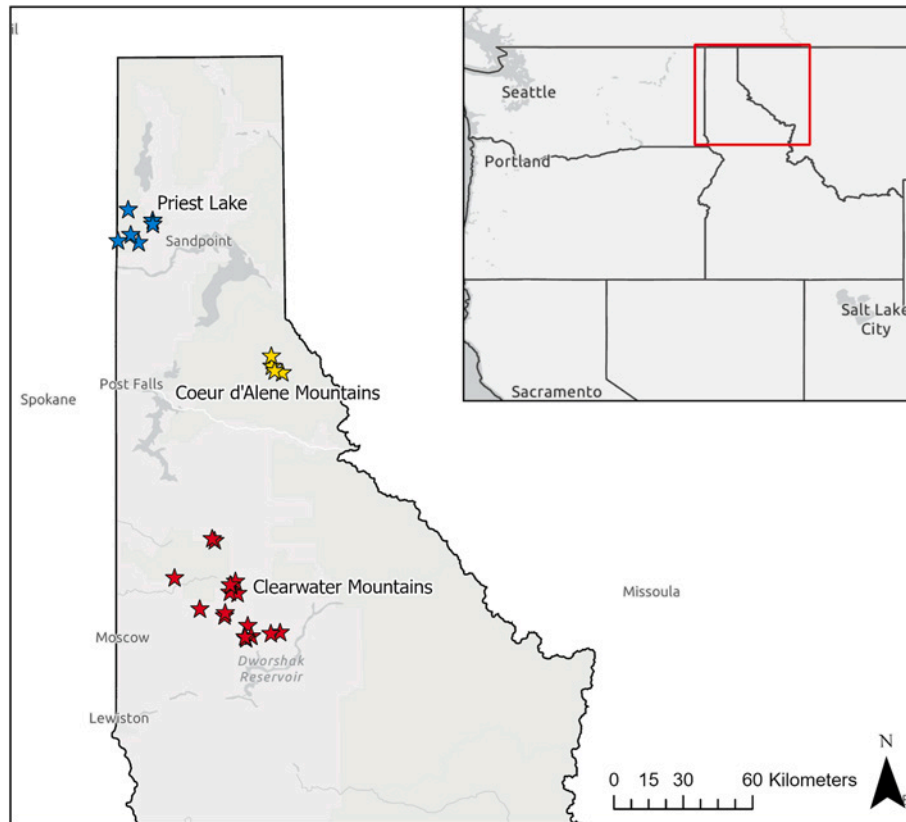


Fig. 1. The location of the 27 stands within the historical range of the western white pine forest type in northern Idaho, USA. Stands were located near Priest Lake (blue), in the Coeur d'Alene Mountains (yellow), and in the Clearwater Mountains (red).

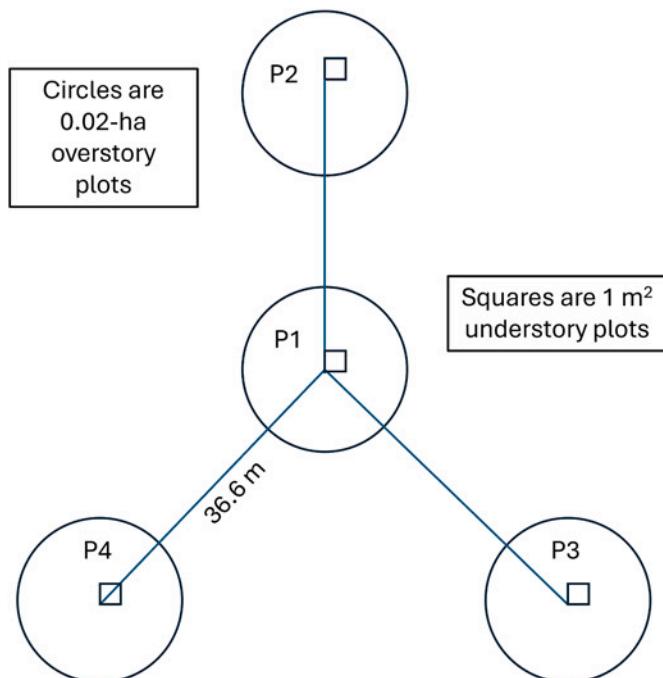


Fig. 2. Plot design used to sample the overstory and understory. The overstory was measured in each 0.02-ha round plot, while the understory was measured within the 1 m² square plots nested within the round overstory plots. Each overstory plot was located 36.6 m from the others. Plot 1 (P1) was established first, followed by plots 2–4 (P2–P4).

intercepting foliage was divided by 30 and multiplied by 100 to calculate canopy cover.

Understory vegetation was sampled within a 1 m² (1 m × 1 m) square plot oriented in the northeast quadrat of each overstory plot. The lower left corner of the 1 m² polyvinyl chloride (PVC) frame was placed at the center of the 0.02-ha plot. All vascular plant species less than 1.82 m tall within the 1 m² plot were identified to the species level except *Rosa* spp., *Viola* spp., *Mitella* spp., *Epilobium* spp., and grasses. Unknown species were collected in a plant press, given an identification number, and brought back to the lab for identification using field guides (Patterson et al., 1985; Parish et al., 1999). Ocular estimates of percent foliar cover of each individual species were recorded to the nearest five percent, with one percent indicating a trace amount of cover. The total cover for the vegetation plot could exceed 100 percent due to layering.

2.3. Statistical analysis

Data for the four individual plots were averaged to obtain values at the stand level ($N = 27$). Because our stands covered different land-ownership, if there was evidence of pruning of lower limbs and/or small stumps, the resulting binary variable for management history was either “managed” or “not managed”. Of the 27 stands, 10 had been managed and 17 had not been managed.

To examine the effects of stand and site characteristics on understory richness, generalized mixed effects models were fit using the glmmTMB package (Brooks et al., 2021). Mixed effects models were used to account for the hierarchical nature of stands within the region. Understory richness was fit with a Poisson distribution since the data were counts, while understory cover was fit with the beta distribution since the data were converted to a proportion prior to fitting. Full models tested various metrics of stand structure, species composition, and other covariates, including basal area of all trees, trees per hectare, canopy

cover, proportion of western white pine basal area, habitat series, and management history (managed or not managed). Variables that were not significant ($p > 0.05$) were sequentially removed from the model, starting with one non-significant variable at a time.

Analysis of species presence-absence and abundance as represented by cover was performed using the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen and Abrego, 2020). HMSC is a joint species distribution modeling approach (JSDM) (Ovaskainen et al., 2017), which accounts for the multivariate nature of communities and assumes species respond jointly to each other and the environment (Warton et al., 2015). The benefit of the HMSC method is that it allows us to ask questions such as whether the various understory plant species respond similarly or differently to stand structure, proportion of western white pine in the overstory, and habitat series. Species distribution modeling was performed using the HMSC package in R (Tikhonov et al., 2021).

For both presence-absence and cover, three models using the HMSC framework were fit to examine the amount of additional variation explained by including stand structure (i.e., basal area of all trees and canopy cover) and the proportion of western white pine basal area in the overstory from base models that only included habitat series. Habitat series was chosen since it is a proxy of various interacting environmental variables, including soils and climate (Cooper et al., 1991). The most complex models included habitat series, canopy cover, basal area of all trees, and western white pine proportion. Species presence-absence models were fitted using a probit distribution to account for the binary nature of the data, while the species cover models used a lognormal Poisson distribution. Model posterior distributions were sampled from four Markov Chain Monte Carlo (MCMC) chains, each run for 150,000 iterations, of which the first 50,000 were removed as burn-in and the remaining thinned by 100 for 1000 posterior samples per chain (Ovaskainen and Abrego, 2020).

All models included plant traits and phylogenetic relatedness of species as covariates to account for the variation in species niches by their traits and phylogeny. Two traits were included: (1) whether the species was native or exotic, and (2) the plant life form (tree, shrub, subshrub, or forb). Trait data were derived from the United States Department of Agriculture PLANTS Database (USDA NRCS, 2021). A phylogenetic tree was created using V.PhyloMaker (Jin and Qian, 2019) and included in the model to account for phylogenetic relatedness among the species in their response to the habitat series, stand structure, and overstory species composition. V.PhyloMaker uses a mega-tree (GBOTB.extended.tre) derived from published mega-trees (Zanne et al., 2014; Smith and Brown, 2018) and includes 74,533 species, making it the largest phylogeny of vascular plants at the time of publication. The specific tree created for this study used the scenario 3 method in the V. PhyloMaker package, where the new genus tip was bound to the half point of the family branch (Jin and Qian, 2019). Species traits accounted for a very small amount of variation in species responses to habitat series, stand structure, and proportion of western white pine in the overstory. In addition, a weak phylogenetic signal was detected. Although trait data and phylogenetic relatedness were included in the models, the

results focus on the environmental parameters (i.e., habitat series, stand structure, and proportion of western white pine in the overstory).

Model fit was evaluated both in terms of explanatory power (i.e., how well the model predicts the data used to fit the model) and predictive power (i.e., how well the model predicts data not used to fit the model). Predictive power of the models was calculated using k -fold cross-validation with five folds, where the data were fit into five folds, where one fold was used to fit the data, and the other four were used as training data (Ovaskainen and Abrego, 2020). Model accuracy for both explanatory power and predictive power was evaluated using root mean square error (RMSE) to calculate how close the best predictions were to the data. Model discrimination was expressed as area under the curve (AUC) (Pearce and Ferrier, 2000) and Tjur R^2 (Tjur, 2009) for the species presence-absence models and the pseudo- R^2 for the species cover models, which uses the Spearman rank correlation instead of the Pearson correlation for R^2 values (Ovaskainen and Abrego, 2020).

3. Results

3.1. Stand characteristics

Across the 27 stands sampled, stand ages ranged from 18 to 58 years old, with the oldest stands located on the grand fir and western redcedar habitat series (Table 1). Stands on the western hemlock habitat series had lower average trees per hectare and basal area per hectare of all trees, although the quadratic mean diameter was similar among the habitat series. Canopy cover ranged from 41% in a stand in the grand fir habitat series to 87% in a stand on the western hemlock habitat series. Overall, the proportion of total basal area in western white pine trees averaged 72%, 68%, and 56% for the grand fir, western redcedar, and western hemlock habitat series, respectively.

3.2. Species richness and total understory cover

Understory species richness across all stands averaged 10 species per stand and ranged from 3 to 15 species (Table 2). Understory coverage averaged 70% and ranged from 17% to 114%. Basal area of all trees was a common significant factor in both models and was negatively correlated with both understory richness and cover (Fig. 3 and Table 3). Canopy cover was negatively correlated with the proportion of western white pine in the overstory. For each 10% increase in western white pine, canopy cover declined by 1.5%.

3.3. Species responses to habitat series, stand structure, and western white pine composition

Explanatory power and predictive power of the HMSC models increased for both species presence-absence and species cover with the inclusion of stand structure represented by both canopy cover and basal area of all trees, and the composition of western white pine basal area proportion in the overstory (Table 4). Overall, the predictive power of the models was less than the explanatory power.

Table 1

Stand structure and western white pine composition expressed as a percent of basal area of all trees by habitat series. A total of 27 stands were sampled: 8 stands on the grand fir, 11 stands on the western redcedar, and 8 stands on the western hemlock habitat series. Values show the mean with ranges in parentheses.

Habitat series	Age	Trees per hectare	Basal area (m ² ·ha ⁻¹)	Quadratic mean diameter (cm)	Canopy cover (%)	Western white pine basal area (%)	Western white pine trees per hectare
Grand fir	31 (23–53)	666 (457–852)	30.1 (14.7–47.8)	24.2 (19.2–36.5)	63 (41–78)	72 (35–99)	469 (185–766)
Western redcedar	31 (19–58)	696 (358–1025)	29.6 (15.4–56.4)	23.7 (17.4–35.4)	68 (54–86)	68 (28–100)	446 (259–927)
Western hemlock	30 (25–37)	567 (383–840)	23.2 (13.7–28.7)	23.2 (18.3–28.1)	73 (64–87)	56 (8–99)	323 (74–754)
All stands	31 (19–58)	649 (358–1025)	27.9 (13.7–56.4)	23.7 (17.4–36.5)	68 (41–87)	66 (8–100)	416 (74–927)

Table 2

Number of understory species (richness) and mean sum of coverages (%) for understory species on square meter plots by habitat series. A total of 27 stands were sampled: 8 stands on the grand fir, 11 stands on western redcedar, and 8 stands on the western hemlock habitat series. Values show the mean with ranges in parentheses.

Habitat series	Richness	Sum of coverages (%)
Grand fir	10 (8–14)	76 (53–100)
Western redcedar	10 (5–15)	65 (17–114)
Western hemlock	10 (8–13)	72 (37–110)
All stands	10 (3–15)	70 (17–114)

Habitat series explained the greatest amount of variation (34%) in presence-absence when averaged across species, while canopy cover accounted for 25%, basal area of all trees for 18%, western white pine proportion for 14%, and the random effect of stand for 9%. Species cover variance was also most strongly explained by habitat series across all species, which accounted for 44% of the variation, followed by basal area of all trees (22%), percent canopy cover (15%), western white pine proportion (14%), and 5% from the stand-level random effect.

The directionality of the correlation between predictor variables and presence varied across species (Fig. 4), but some interesting trends were evident. The proportion of western white pine in the overstory had a positive correlation with understory species presence. The positive correlation occurred for 13 species, of which only three were tree species (*Tsuga heterophylla*, *Abies grandis*, and *Pinus monticola*). The other ten species positively associated with western white pine proportion are common understory species across northern Idaho, although none were positively correlated with the grand fir (ABGR) habitat series, a drier habitat series in the region. This suggests these species were less likely to occur on drier sites. Additionally, presence was predominantly

negatively correlated with basal area of all trees; the exception being *Tiarella trifoliata*.

Similar to the presence-absence model, results from the species cover model indicated only positive correlation between western white pine proportion and cover (Fig. 5). Excluding naturally regenerated tree seedlings, the cover of five species was positively correlated with western white pine proportion, including *Xerophyllum tenax*, *Tiarella trifoliata*, *Linnaea borealis*, *Aralia nudicaulis*, and *Solidago canadensis*. Besides *L. borealis*, these species had low percent cover within our plots, so there was not enough data to show a correlation with habitat series. Cover of four species was positively correlated with the basal area of all trees, *Prosartes hookeri*, *Galium triflorum*, *Osmorhiza berteroi*, and *Ade-nocaulon bicolor*, suggesting these species occurred in older stands with larger trees.

4. Discussion

Temperate conifer-dominated forests, such as the forests in the current study, commonly have lower understory floristic richness than broadleaved forests (Barbier et al., 2008). Therefore, it is not surprising that species richness averaged 10 understory vascular species (range 3–15) across all habitat series (Table 2), especially since Song (1997) found understory richness of 17 species of trees, shrubs, herbs, and grasses in old growth interior cedar-hemlock forests dominated by large lodgepole pine trees and numerous western hemlock and western redcedar trees ≤ 10 cm DBH in Interior British Columbia. Although the proportion of western white pine in the overstory was not correlated with understory richness and total cover, findings partially support our first hypothesis since understory species richness and total understory cover were negatively correlated with stand density (Fig. 3). Greater stand density often decreases light penetration to the understory and

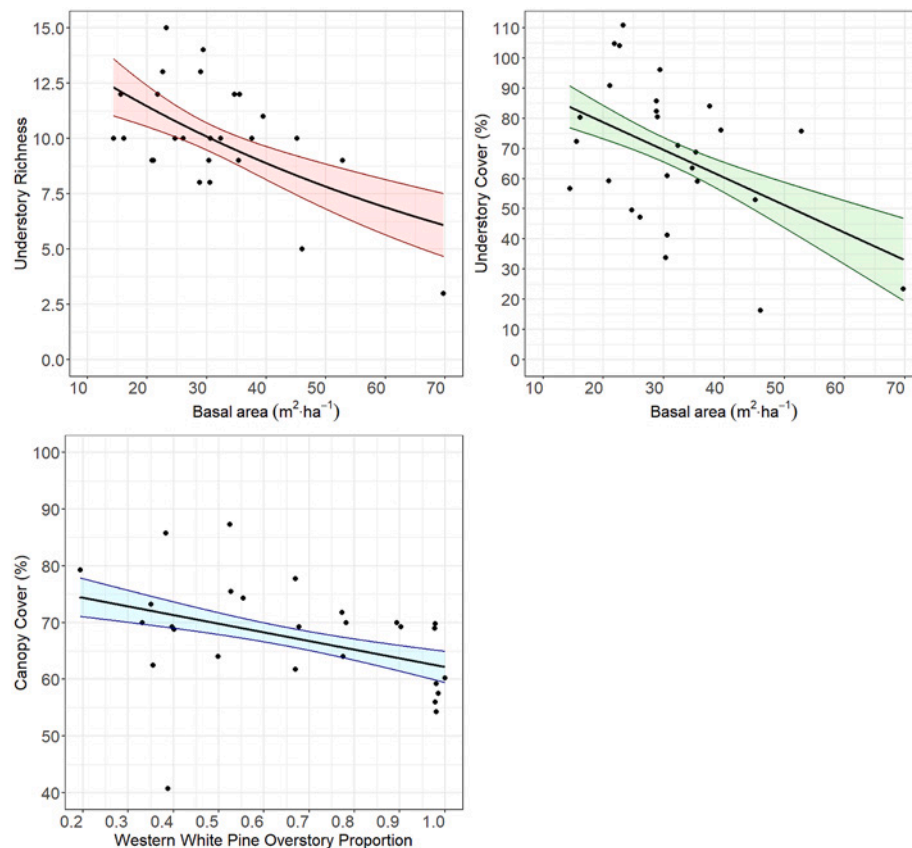


Fig. 3. Understory species richness in relation to basal area of all trees (top left), total understory cover in relation to basal area of all trees (top right), and canopy cover in relation to western white pine overstory proportion (lower left). $N = 27$ stands.

Table 3

Generalized mixed effects model parameters, standard errors, and *p*-values of parameters for the understory richness model fit with a Poisson distribution, the understory cover model fit with a beta distribution, and the canopy cover model fit with a Gaussian distribution. Region (Priest Lake, Coeur d'Alene Mountains, and Clearwater Mountains) was a random effect on the intercept in the models. Only parameters in the final models are shown. *N* = 27 stands.

Understory richness (Poisson distribution)			
	Estimate	Std. error	<i>p</i> -value
Intercept	2.693	0.177	<0.001
Basal area of all trees (m ² ·ha ⁻¹)	-0.013	0.006	0.023
Understory cover (Beta distribution)			
Intercept	0.819	0.113	<0.001
Basal area of all trees (m ² ·ha ⁻¹)	-0.009	0.003	0.007
Canopy cover (Beta distribution)			
Intercept	68.971	5.728	<0.001
Western white pine overstory proportion	-15.241	6.418	0.018
Basal area of all trees (m ² ·ha ⁻¹)	0.286	0.138	0.038

thus can influence the structure and composition of the understory (Wagner et al., 2011) and may be the cause of the negative correlation.

Our analysis found a positive association between the proportion of western white pine basal area and individual understory species presence and cover (Figs. 4 and 5), thus supporting our second hypothesis. Field observations confirm these statistical findings (Fig. 6). Thirteen understory plant species were found to have a positive association in terms of presence. Among these thirteen species were three trees, two shrubs, and eight forbs. Of the understory species, most typically grow in partial to full sunlight and diffuse light conditions (Crane, 1990; Snyder, 1991; Coladonato, 1993; Howard, 1993; Pavsek, 1993; Tilley, 2012; Wetherwax and Miller, 2012). The species favoring full sun conditions include *Thermopsis montana*, *Symphoricarpos mollis*, and *Solidago canadensis*, which commonly grow in woodland openings (Snyder, 1991; Coladonato, 1993; Pojar and MacKinnon, 2016). These three species only displayed positive correlation with western white pine, unlike more shade-tolerant species, *Xerophyllum tenax* and *Tiarella trifoliata*, which were also associated with the western hemlock series. Individual species cover, rather than presence, for five tree species and eight understory plant species was positively associated with the proportion of western white pine basal area. Although these plants are all native and common to northern Idaho forests, their light requirements range from full sun to moderate shade, with none associated with fully shaded conditions (Habeck, 1991; Snyder, 1991; Munger, 2006; Tilley, 2012; Wetherwax and Miller, 2012; FNA Editorial Committee, 2015; Hitchcock and Cronquist, 2018). Eight species (four of which were tree species) had a negative relationship between cover and basal area of all trees, but as the proportion of western white pine basal area increased within a stand, cover also increased, suggesting that the proportion of western white pine in the overstory may influence understory communities (Fig. 5).

Results show that as the proportion of western white pine in the overstory increased, canopy cover decreased (Fig. 3), which may help explain the positive correlations between western white pine in the overstory and the presence and cover of some individual species. Western white pine has unique characteristics that might explain this outcome. The crown and bole characteristics create an open canopy compared to grand fir, western hemlock, and western red cedar (Wellner, 1948). Its branches whorl around the bole in a very uniform manner, and its short, thin needles cluster at the end of upward ascending branches (Parish et al., 1999). It self-prunes as it grows, creating a high canopy with a clear bole that can become over 30 m high (Graham, 1990) (Fig. 7). This growth form allows sunlight to pass through the canopy, creating gaps and making direct sunlight available to understory species for a longer duration (Jain et al., 2004). Historical photographs of old-growth stands dominated by western white pine illustrate an understory rich in forb and shrub cover (Fig. 7b and c). With the widespread loss of western white pine in the northern Rocky Mountains, forests have become more dominated by grand fir and western hemlock, which have a different branching and needle structure (Kershaw Jr and Maguire, 1996). These species possess branches layered with flat needles oriented in sweeping sprays (Foiles et al., 1990; Packee, 1990) and thus minimize the amount of light reaching the forest floor (Canham et al., 1999) (Fig. 6a).

Changes in the light environment mediated by the relative abundance of western white pine appear to be a likely pathway by which the understory plant community is affected. There are, however, other factors that could also contribute to understory plant diversity, including variation in the soil nutrient profile and microbiome (Smith and Reynolds, 2015), wildlife use (Habeck and Schultz, 2015), site history, and site preparation method (Haeussler et al., 2004). Additional

Table 4

Explanatory and predictive power of the presence-absence models and the species cover models. The simplest models only included habitat series, then increased in complexity by adding stand structure (structure), which included both canopy cover and basal area of all trees, and finally, the inclusion of overstory composition (composition) represented as the proportion of the basal area occupied by western white pine trees. Shown are the means across all species, with the range of values across the individual species within parentheses.

Model	Species presence-absence					
	Explanatory power			Predictive power		
	AUC	RMSE	Tjur <i>R</i> ²	AUC	RMSE	Tjur <i>R</i> ²
Habitat series	0.87 (0.69–1.00)	0.39 (0.19–0.49)	0.104 (0.020–0.505)	0.45 (0.06–0.89)	0.43 (0.22–0.56)	<0.001 (–0.120–0.393)
Habitat series + structure	0.84 (0.65–1.00)	0.37 (0.14–0.48)	0.174 (0.030–0.515)	0.53 (0.17–0.95)	0.43 (0.21–0.58)	0.029 (–0.153–0.457)
Habitat series + structure + composition	0.87 (0.65–1.00)	0.34 (0.05–0.47)	0.262 (0.060–0.920)	0.56 (0.14–0.93)	0.43 (0.20–0.55)	0.031 (–0.157–0.431)
Model	Species cover (%)					
	Explanatory power			Predictive power		
	RMSE	Pseudo- <i>R</i> ²		RMSE	Pseudo- <i>R</i> ²	
Habitat series	3.16 (0.26–27.58)	0.228 (0.003–0.700)		3.92 (0.27–39.05)	–0.010 (–0.249–0.399)	
Habitat series + structure	3.51 (0.29–28.83)	0.241 (0.034–0.613)		5.73 (0.32–55.51)	0.032 (–0.151–0.343)	
Habitat series + structure + composition	3.79 (0.31–33.64)	0.264 (<0.001–0.795)		5.12 (0.35–34.52)	0.031 (–0.184–0.409)	

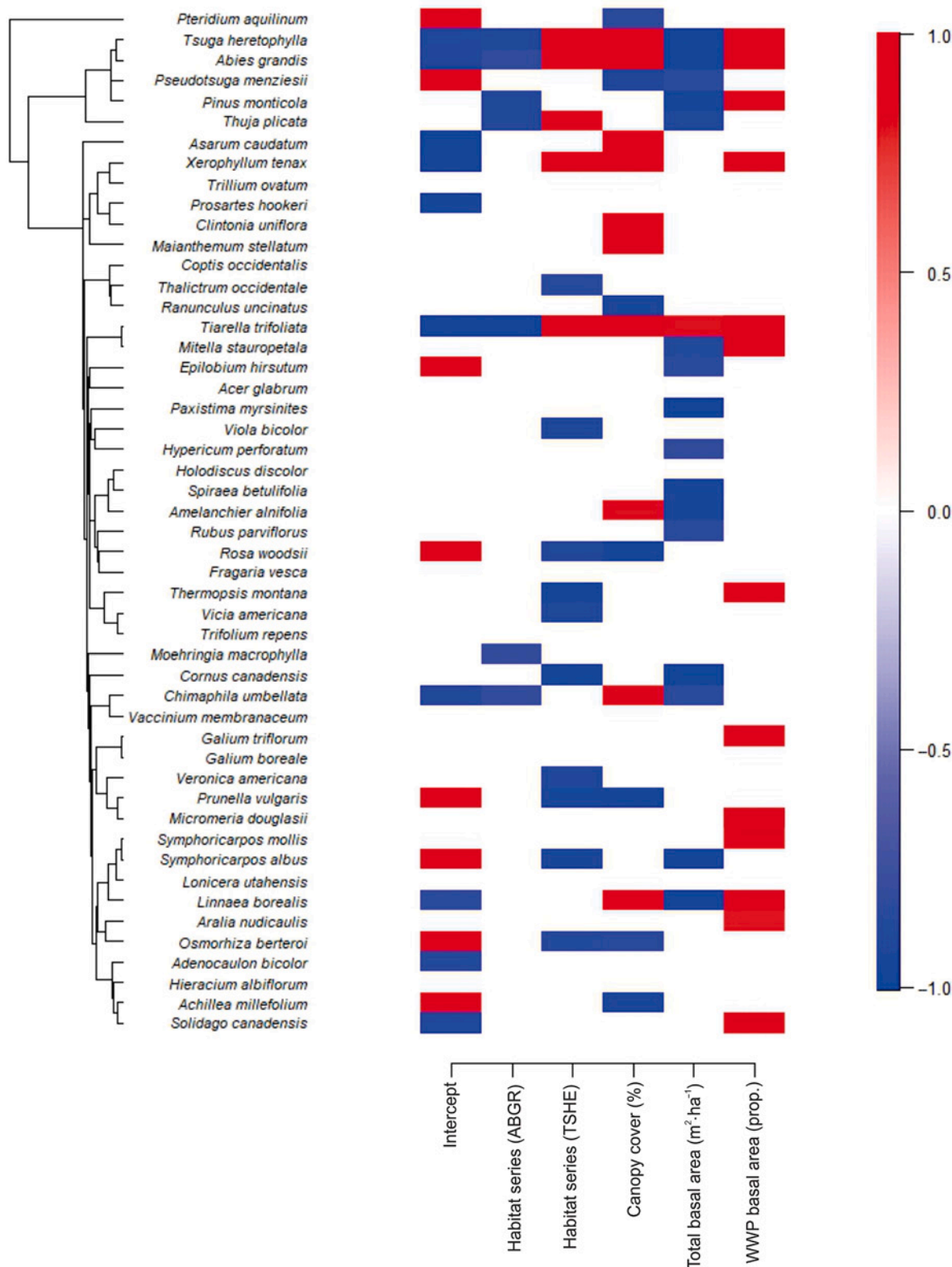


Fig. 4. Heat map showing the results of the HSMC analysis with all predictor variables included for presence. Darker red cells indicate greater positive correlation, while darker blue cells indicate more negative correlation. The figure shows grand fir habitat series (ABGR), western hemlock habitat series (TSHE), canopy cover (%), basal area of all trees ($\text{m}^2 \cdot \text{ha}^{-1}$), and the proportion of western white pine basal area (WWP basal area (prop.)). $N = 27$ stands.

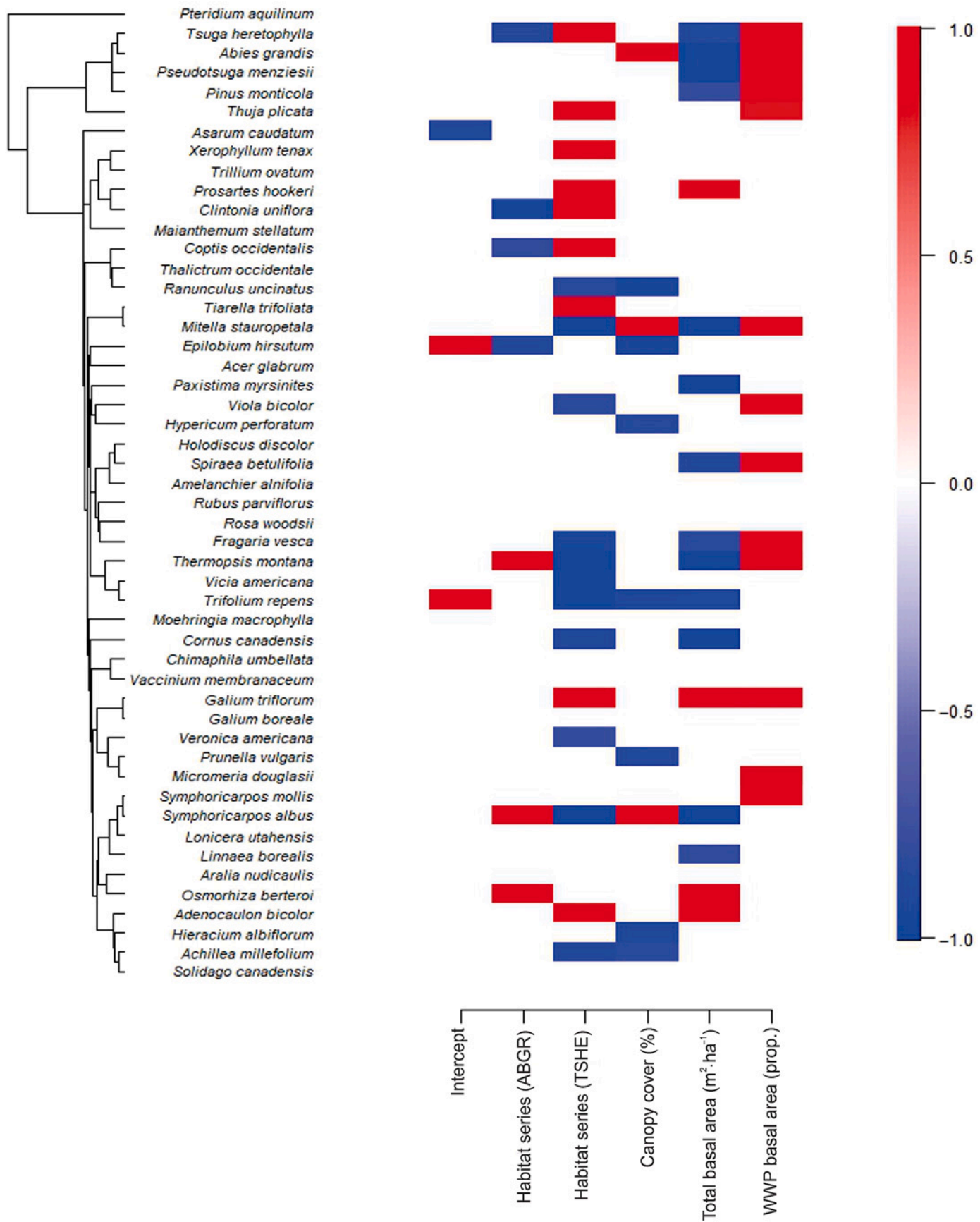


Fig. 5. Heat map showing the results of the HSMC analysis with all predictor variables included for species cover. Darker red cells indicate greater positive correlation, while darker blue cells indicate more negative correlation. The figure shows grand fir habitat series (ABGR), western hemlock habitat series (TSHE), canopy cover (%), basal area of all trees ($m^2 \cdot ha^{-1}$), and the proportion of western white pine basal area (WWP basal area (prop.)). $N = 27$ stands.



Fig. 6. Pictures of four of the twenty-seven stands sampled that represent the range of stand structure and species composition. **(a)** Quartz mountain: 19% western white pine, 25.1 cm DBH, and 30.3 $\text{m}^2\cdot\text{ha}^{-1}$ basal area of all trees, **(b)** Nat Brown: 68% western white pine, 20 cm DBH, and 29 $\text{m}^2\cdot\text{ha}^{-1}$ basal area of all trees, **(c)** Sleepy Wolf: 98% western white pine, 20.3 cm DBH, and 34.7 $\text{m}^2\cdot\text{ha}^{-1}$ basal area of all trees, and **(d)** vigor-quality: 100% western white pine, 33.8 cm DBH, and 39.5 $\text{m}^2\cdot\text{ha}^{-1}$ basal area of all trees.

factors can also influence the structure of the understory, including competition between the overstory and understory for water and nutrients, and mycorrhizal associations (Balandier et al., 2022). The stands selected for this study (Fig. 1) were chosen to represent a broad range of stand conditions across a wide geographical area on the windward side of the northern Rocky Mountains, and to mitigate potential local site-level impacts on the results. Nevertheless, these factors should be taken into consideration alongside light environment as potential contributors to understory plant community assembly in these forests.

The apparent relationship between western white pine in the overstory and the presence and cover of some understory species suggests that western white pine may play a role as a foundational species in forests (sensu Ellison et al., 2005). Due to the general lack of data and contemporary information regarding the plant communities found in historical western white pine forests, and the lack of existing stands with a major western white pine component, it has been difficult to assess the relationship between the species and the understory. This work fills a knowledge gap by considering data from a range of existing stands with varying amounts of western white pine in the overstory and evaluating the relationship between the understory community and western white pine in the overstory. The specific mechanisms and functional traits driving these changes in diversity remain understudied, but such information would offer an opportunity to better understand forest stand development and plant community assembly in these systems.

5. Conclusions

Western white pine has several attributes that make it an important species in the northern Rocky Mountains, and studies are indicating it may have been a foundational species that promoted disturbance resilience and overstory diversity (Marshall, 1929; Rehfeldt et al., 1984; Harvey et al., 2008). We found that the presence and cover of some understory species were positively correlated with western white pine, supporting this hypothesis. As more western white pine is reestablished across the landscape and becomes a larger component of stands in the future, this study indicates that we may see a concomitant increase in

understory plant diversity and abundance across the landscape. The understory species in this study are not threatened, but an increase in their abundance could have cascading effects on pollinators, wildlife, nutrient cycling, and other ecosystem services.

From a management perspective, reintroducing western white pine has a variety of benefits for landscape resiliency in addition to understory diversity. The species has numerous functional traits that allow it to prosper in the context of a variety of disturbances, including wind, ice, drought, disease, insects, and fire (Marshall, 1929; Rehfeldt et al., 1984; Harvey et al., 2008). These traits, which are primarily adaptations to the regional disturbance regimes, also have the capacity to modify the forest environment in a way that influences ecosystem dynamics and forest structure. This study provides the first examination of understory plant communities in young western white pine plantations, which is needed to further quantify the functional role and importance of western white pine and its contribution to floristic diversity.

CRediT authorship contribution statement

Andrew S. Nelson: Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Theresa B. Jain:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Jason Reinhardt:** Writing – review & editing, Writing – original draft, Data curation. **Eva K. Strand:** Writing – review & editing, Methodology. **Nicole Mutchler:** Writing – review & editing, Writing – original draft. **John Byrne:** Writing – review & editing, Supervision, Methodology, Data curation.

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Fig. 7. Examples of mature western white pine trees prior to the widespread loss of the species due to blister rust in northern Idaho. Photographs are from the Potlatch Lumber Company Photograph Collection at the University of Idaho. (a) White Pine King (1911), (b) Bovill Timber [05] (1913), and (c) Elk River Timber [03], (1913).

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 availability

Data are available upon reasonable request.

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