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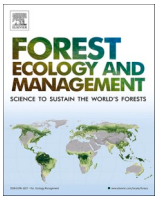

Effects of variable-density thinning on non-native understory plants in coniferous forests of the Pacific Northwest

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ABSTRACT

Old-growth forests serve as critical habitat for many sensitive species, but management practices have diminished their prevalence, and former regions of old-growth are now dominated by second-growth stands lacking the structural heterogeneity, diversity, and species richness that these older forests possess. In western Washington state in the Pacific Northwest of the United States, the Olympic Habitat Development Study was designed to address this issue and hasten the development of specific old-growth features in second-growth stands using variable-density thinning. One concern with such methods, however, is the potential to introduce non-native plants, which can have negative ecological and economic impacts. Here, we examine how variable-density thinning influences desirable forest characteristics, such as increased plant species diversity, versus the less desirable effects of non-native plant species introduction. We test two hypotheses regarding plant invasions. First, thinning would promote establishment of non-native, shade-intolerant species, but their abundance would gradually decline over time. Second, thinning disturbance and increased heterogeneity of canopy cover would initially promote understory richness of all species, although richness would decline over time with canopy closure and increased cover of shrubs and regenerating trees. We found that the number and cover of non-native species initially increased after thinning, peaking at 16 species present in variable-density thinned treatments in year three. By year 17, 11 species remained throughout the seven 6.5 ha treatment plots sampled, and cover was negligible. As predicted, species richness increased following thinning, however, native species richness remained elevated through year 17, contrary to our hypothesis. Furthermore, native species diversity also increased following thinning and remained higher in thinned treatments than controls through year 17. Our results show that variable-density thinning in temperate coniferous forests can enhance native, but not exotic, plant richness and diversity in the long term.

1. Introduction

In the Pacific Northwest of the United States, management practices have reduced old-growth cover by an estimated 72% since European contact (Strittholt et al. 2006), a trend similar to forest loss and modification observed globally as a result of logging, settlement, and agriculture (Nepstad et al. 1999, Wright and Muller-Landau 2006, Pichler et al. 2010, Brandt et al. 2017). By the early 1980s, it had become clear that the large-scale, even-aged management of Pacific Northwestern forests had caused a decline in populations of animal species that rely on old-growth ecosystems for habitat (Forsman et al. 1984; Lehmkuhl and Ruggiero 1991, Carey et al. 1992, Carey 1995). These management practices have resulted in a reduction of the structural complexity and spatial heterogeneity found in the old-growth forests relied upon by iconic species such as the Northern Spotted Owl, and hindered their development in regenerating stands (Spies and Franklin 1996). Thus, preserving and promoting development of old-growth habitats became a management priority in the Pacific Northwest (Curtis et al.1998), corresponding with increased consideration for sustainable forest management worldwide (McDonald and Lane 2004).

Certain management activities may enhance spatial heterogeneity (Stiers et al. 2018), one of many quantifiable characteristics of old-growth habitat (Franklin et al. 1986, Spies and Franklin 1991). The silvicultural method variable-density thinning (VDT) aims to accelerate

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the development of old-growth characteristics in second-growth stands (Carey 2003). In addition to spatial heterogeneity (achieved by removing trees in a non-uniform manner), these characteristics include faster tree growth and a deep, multilayered canopy promoted by thinning and the creation of gaps, as well as the retention of large snags and live trees.

One concern with VDT, however, is the potential for logging disturbance to introduce non-native plants or promote those already present, including those in the seed bank. Although not all non-native species are detrimental to the ecosystems they invade, some non-native species can have negative effects both ecologically (Wilcove et al. 1998, Pimental et al. 2000, Vitousek et al. 1996) and economically (Vitousek, et al. 1996, Pimental et al. 2000, Holmes et al. 2009), and their treatment can be difficult, time-consuming, and costly (Pimental et al. 2000, Vitousek, et al. 1996).

Both natural and anthropogenic disturbances can trigger non-native plant introductions (Hobbs and Huenneke 1992, Jauni et al. 2015) and the proliferation of non-native species is closely tied with anthropogenic disturbance (Decker et al., 2012; Forcella and Harvey, 1983) including logging (DeFerrari and Naiman 1994, Heckman 1999, Gray 2005, Sutherland and Nelson 2010). Following logging, successful establishment of non-native species may occur through the introduction of seeds by logging equipment or humans (Parendes and Jones 2000, Veldman and Putz 2010), via germination from the seed bank (Kellman 1974, Halpern et al. 1999, Sutherland and Nelson 2010), and by higher light levels favoring the growth of non-native species over shade-tolerant native forest plants (Heckman 1999).

While increases in resource availability following logging disturbance may allow non-native species to colonize, it can also benefit natives, resulting in increased richness of both species types (Belote et al. 2012). Understory native richness and diversity can have implications for ecosystem functioning (Hooper and Vitousek 1997, Loreau et al. 2001, Cardinale et al. 2004) and habitat (Carey 1996). Preserving species diversity has therefore become a concern in forest management (Lindenmayer and Franklin, 2002, Fedrowitz et al. 2014), as management activities in closed canopy forests have been shown to have lasting effects on plant species richness and diversity (Duffy and Meier 1992, Thomas et al. 1999, Wyatt and Silman 2010, Duguid and Ashton 2013, Dagley et al. 2018). These lasting effects may differ depending on the silvicultural methods used (Duguid and Ashton 2013, Fedrowitz et al. 2014, Chaudhary et al. 2016). Generally, less disruptive methods of timber harvest such as VDT and retention of uncut patches result in lower declines of understory richness, and may also enhance richness (Duguid and Ashton 2013, Fedrowitz et al. 2014, Chaudhary et al. 2016).

Although species richness is a valuable ecological metric, it has limitations, as it is a simple count that gives equal weight to all taxa (e.g. native or non-native) and can only be properly evaluated among identical sample sizes (Peet 1974). While also dependent on sample size, the measure of species diversity may provide a more complete picture of the functional characteristics of a plant community as it measures species evenness in addition to richness (Hill 1973). There are many hypotheses concerning the interactions between succession, disturbance, richness, and diversity (Roberts and Gilliam, 1995) which may explain the relation between silvicultural methods and understory species composition. The Intermediate Disturbance Hypothesis (Loucks 1970, Huston 1979) and the Environmental Heterogeneity Hypothesis (Ricklefs, 1977) are two such hypotheses, with the former relating diversity with disturbance frequency and the latter with heterogeneity of resource availability and environmental conditions such as microclimate. Per these two hypotheses, VDT may allow for greater species richness because it creates a mosaic of seral states, microclimates, and resource conditions that favor plant species which respond differently to disturbance frequency or severity and resource availability. In addition, because the thinning-induced spatial and resource heterogeneity is dispersed over the entire stand in VDT, richness and diversity will likely increase in parallel as this could also promote evenness throughout the stand.

In this study, several second-growth stands were treated with VDT, providing a unique opportunity to test the influence of disturbance associated with variable-density thinning on understory plant species richness, diversity, and invasion by non-native plant species in a forested setting over a timescale that is relevant to managers. We utilized up to 17 years of plant community data from this variable-density thinning experiment on the Olympic Peninsula in Washington, USA, to test two hypotheses regarding plant invasions and species richness and diversity. First, we hypothesized that thinning would promote the establishment of non-native, shade-intolerant species, but their abundance would gradually decline over time. Second, we hypothesized that thinning disturbance and increased heterogeneity of canopy cover would initially promote richness and diversity of all plant species, but that richness and diversity would decline over time with canopy closure and increased cover of shrubs and regenerating trees.

2. Methods

2.1. Study area description

The Olympic Habitat Development Study (OHDS) was initiated in 1994, initially funded by congressional direction to protect threatened and endangered species by maintaining and restoring forests with late-successional or old-growth characteristics (Thomas et al. 1990). Sites were selected within the Olympic National Forest (Olympic Peninsula, Washington) to be representative of coniferous forests likely to be managed in the future. Sites were of similar age (35–70 years) and structure, although they differed in elevation, slope, precipitation, and stand density (Fig. 1, Table 1). Dominant tree species in these sites were Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and Sitka spruce (*Picea sitchensis*); other common species were western redcedar (*Thuja plicata*), Pacific silver fir (*Abies amabalis*) and red alder (*Alnus rubra*). Three of the seven sites had been planted and four had regenerated naturally. Subsequently, two were commercially thinned (Fig. 1, Table 1). Thinning treatments for the current experiment were implemented over multiple years (1996 through 2003). Each of the 7 experimental sites contains two treatment stands (a minimum 6.5 ha each, Table 2).

2.2. Treatments

Treated plots consisted of three subtreatments: unthinned “reserve” areas (10% of the total stand area), logged “gap” areas (15% of the stand area), and a thinned matrix (75% of the stand; “thin”; Fig. 2). Pre-existing canopy gaps resulting from root rot or past harvesting were included in the total gap area. These gaps were generally 20 m by 20 m. Gap size was chosen to be less than the approximate mean height of overstory trees at each site to reduce the probability of future windthrow around gaps. Reserve areas were chosen based on presence of less common plant species, snag density, and concentrations of coarse woody debris. One uncut reserve was located in each quarter of the larger VDT plot and placed at least 20 m from gaps to minimize edge effects between subtreatment areas. In the thinned matrix, 25% of the original basal area was removed (mostly smaller trees of the dominant species). Trees were felled using chain saws and removed with both ground-based and skyline yarding (Table 1). Harvesting equipment was prohibited in the control treatment and reserve subtreatments to prevent damage to soil and vegetation.

2.3. Vegetation sampling

Prior to treatments, we conducted inventories of the total number of all plant species within each treatment stand at each site based on species occurrences in transects and Daubenmire plots located across a systematic grid. After treatments, a series of 5.64-m radius permanent

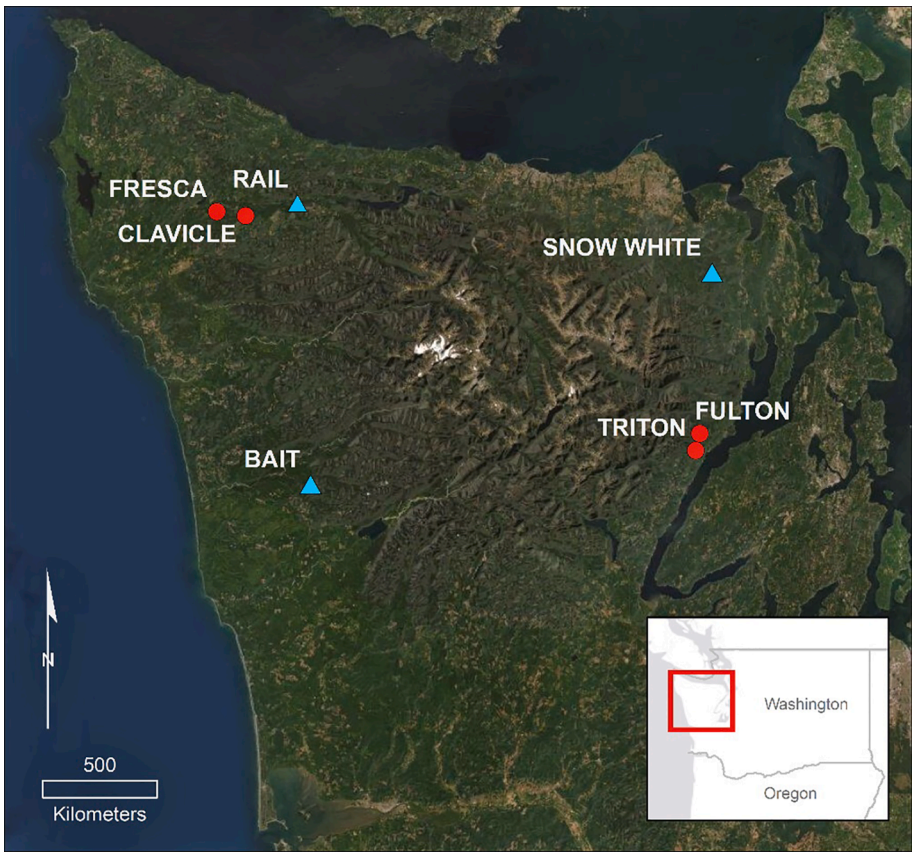

Fig. 1. Locations of study sites on the Olympic Peninsula. Plots thinned prior to treatment are indicated by blue triangles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

plots were established at grid points within each subtreatment in each VDT and control stand. In VDT treatments, these were distributed evenly among the three subtreatments using systematic stratified sampling, yielding approximately 6–8 plots per gap, reserve, and thinned subtreatment (Table 1). In the control treatments, 8–12 plots were established at grid points evenly spaced across each stand (Table 1). Plots were sampled every three to seven years across all sites, with some exceptions (Table 3). Post-treatment measurements involved visual estimates of cover of all plant species occurring within plots. Cover values between 10% and 95% were visually estimated in increments of 5%, anything less than 10% or over 95% was estimated to the nearest 1%, and anything less than 1% was estimated to the nearest 0.1%.

2.4. Statistical analyses

Plant species origins (native or non-native) follow designations in the USDA Plants Database (USDA NRCS, 2021). To examine how variable-density subtreatments (reserve, gap, and thinned) influenced the cover of introduced species over time, we compared the total percent cover of all non-native plant species in VDT subtreatments to that in control treatments across all survey dates.

To examine how VDT subtreatments influenced the cover of non-native plants over time after thinning (from three to seventeen years post-treatment), we used mixed-effects zero-inflated negative binomial models to accommodate the different numbers of plots sampled in subtreatments in different years, and the many plots lacking non-native plant species (overdispersion). We used the glmm ADMB package (Fournier et al., 2012) in the statistical program R (R Core Team, 2020). Because negative binomial models require integer values for the response variable, we rounded total non-native cover values over 1% to the nearest integer, and converted values smaller than 1% to 1%. Fixed predictors included subtreatment (as a categorical variable) and year since treatment (as a continuous variable), and their interactions. For comparisons between subtreatments and the control, the random effect of plot was nested within subtreatment, treatment stand, and site. We also performed the same analyses excluding the Bait site, which had very high non-native cover in some plots in year 7, to determine whether these values were influential in our models. We further examined how subtreatment influenced non-native species richness following thinning using linear-mixed effects models with the lme4 package in the statistical program R.

To test our second hypothesis that variable-density thinning would lead to an overall increase in plant species richness and diversity, we first compared total species richness between VDT and control treatments prior to treatment implementation, to ensure that there were not pre-existing differences in species richness between treatment stands across sites. We then separately compared species richness between VDT and control treatments over time after thinning. We calculated species richness as the sum of species present from surveys in each treatment stand at each sampling date to examine how treatments influenced total species richness over time. To examine how gap, reserve, and thinned subtreatments within VDT treatments influenced the equitability of species abundance (in addition to richness) we also computed species diversity—as the exponent of the Shannon index. This metric, which shares the same units as richness, reduces the importance of rarer taxa. It is often referred to as "effective diversity" or the "equivalent number of equally common species" (Hill 1973, Jost 2006; Eq. 1).

$$\exp\left(-\sum_{i=1}^{S} p_i log_b p_i\right) \quad (1)$$

Where p_i is the proportional cover of each of the i plant species per

Table 1
Summary of selected site characteristics at the seven sites of the Olympic Habitat Development Study (OHDS). Plant associations from Henderson et al. (1989). The abbreviation PCT in the Background column indicates pre-commercial thinning.

Site and Location	Elev. (m)	Precip. (mm/yr)	Plant Association	Background
Bait °N 47.5402, °W −124.0437	190–335	3175	CHF131 Western Hemlock/ Swordfern-Oxalis CHS136 Western Hemlock /Salal/Oxalis	Clearcut between 1951 and 1954, probably burned, replanted with DF. PCT in late 60s and early 70s. OHDS thinning used skyline yarding.
Clavicle °N 48.0451, °W −124.205	390–500	2360	CSF111 Sitka Spruce/ Swordfern - Oxalis	Clearcut in 1931. Burned and replanted the same year. OHDS thinning used ground-based yarding.
Fresca °N 48.0463, °W −124.2868	150	2650	CSF111 Sitka Spruce/ Swordfern - Oxalis	Clearcut about 1930, burned, natural regeneration, no treatment until study. OHDS thinning used ground-based yarding.
Fulton °N 47.6494, °W −123.0023	400–590	1450	CHS137 Western Hemlock/Salal/ Swordfern CHS139 Western Hemlock/ Oregon Grape/ Swordfern	Clearcut prior to 1929. Burned in 1929. Probably naturally regenerated. OHDS thinning used skyline yarding.
Rail °N 48.0622, °W −124.0701	275	2400	CHF131 Western Hemlock /Swordfern/ Oxalis	Clearcut about 1930, burned, natural regeneration, light thinning in 1986. OHDS thinning used ground-based yarding.
Snow White °N 47.9352, °W −122.9704	525–650	1850	CHS139 Western Hemlock /Oregon Grape/ Swordfern CHS137 Western Hemlock /Salal/ Swordfern CHS131 Western Hemlock/Salal	Clearcut around 1928, burned, planted with DF in early 1930s. Commercially thinned in 1970s. OHDS thinning used ground-based yarding.
Triton °N 47.6120, °W −123.0055	270–530	1450	CHS137 Western Hemlock /Salal/ Swordfern CHF132 Western Hemlock /Swordfern/ Foamflower	Clearcut prior to 1929. Burned in 1929. Probably naturally regenerated. OHDS thinning used skyline yarding.

treatment or plot, and S is the total number of plant species per treatment or plot.

We used linear-mixed effects models to compare species richness between treatments and native species richness and effective diversity among subtreatments within treatments following thinning with the lme4 package (Bates et al., 2015) in the statistical program R. Pre-treatment differences in native and nonnative species richness were compared with treatment designation as a fixed effect and site as a random effect. Post-treatment analyses included treatment-level species richness and year, and their interactions, as fixed effects and treatment stand nested within site as a random variable in the models. To examine plot-level native species richness and diversity over time, subtreatment and year, and their interactions, were considered fixed effects, and plot nested within subtreatment, treatment stand, and site were considered random variables in the model.

Table 2
Number of plots sampled per site and subtreatment by year.

		Number of plots			
Site	Subtreatment	Year 3	Year 7	Year 10	Years 15–17
Bait	Control	8	12	12	12
	Gap	6	8	8	8
	Reserve	6	8	8	8
	Thin	8	8	8	8
Clavicle	Control	0	12	12	10
	Gap	0	8	8	8
	Reserve	0	8	8	8
	Thin	0	8	8	8
Fresca	Control	6	8	8	8
	Gap	4	8	8	8
	Reserve	2	8	8	8
	Thin	4	8	8	8
Fulton	Control	8	0	0	8
	Gap	8	0	0	8
	Reserve	8	0	0	8
	Thin	8	0	0	8
Rail	Control	6	8	8	8
	Gap	4	8	8	8
	Reserve	2	8	8	8
	Thin	4	8	8	8
Snow	Control	8	12	12	12
	Gap	6	7	7	7
	Reserve	6	8	8	8
	Thin	7	9	9	9
Triton	Control	12	12	0	12
	Gap	8	8	0	8
	Reserve	8	8	0	8
	Thin	8	8	0	8

3. Results

Three years after treatments, there was significantly higher cover of non-natives in the gap and thinned subtreatments receiving variable-density thinning (VDT) compared to controls ($p < 0.00001$, Table 4, Fig. 3A). However, cover remained comparable between reserve areas within VDT treatments and control treatments throughout the study ($p = 0.30$, Fig. 3A). There were marked differences in non-native cover among subtreatments and some gaps did have large increases in non-native cover (maximum of 100% in year 7 at Bait). However, this was short-lived and cover declined to a mean of < 1% by the last survey year (Fig. 3A). Mean treatment-scale cover of non-natives was never higher than 4%, and it decreased significantly in thinned and gap subtreatments over time (Table 5, interactions between subtreatments and year: $p < 0.003$, Table 4, Fig. 3A). By the last sample (15–17 years), non-native cover did not significantly differ between control and gap and thinned subtreatments ($p > 0.17$, Fig. 3A). Analyses excluding the Bait site, which had very high (65–100%) cover of non-natives in five plots in year 7 (Fig. 3A) yielded similar results (Fig. S1, Table S1). Non-native species richness was also initially significantly higher in gap and thinned subtreatments compared to controls ($p < 0.0005$, Fig. 3B), but similarly, non-native richness declined over time (Fig. 3B, interactions

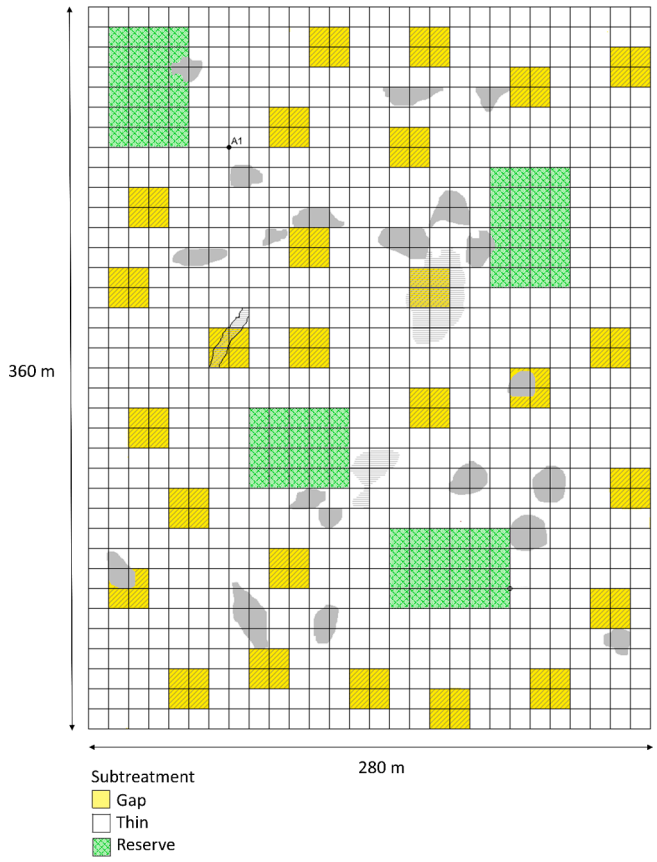

Fig. 2. This schematic shows an example of a variable-density thinning treatment at the 'Fresca' study site. Yellow regions denote 'gap' subtreatments, white regions are 'thinned' subtreatments, and green regions denote unthinned 'reserve' subtreatments. The gridpoint labeled 'A1' is an example plot location in the thinned subtreatment. Dark grey areas indicate natural openings and light gray stippling indicates windthrow areas with thin canopies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Dates of sampling by site. All sites were surveyed between June and August. 'Pre-trt' indicates the date that pre-treatment surveys were completed.

Site	Pre-trt	Year 3	Year 7	Year 10	Year 15	Year 16	Year 17
Fresca	1996	2000	2004	2007			2014
Rail	1996/1997	2000	2004	2007			2014
Snow White	1997	2002	2006	2009		2015	
Bait	1998	2002	2006	2009		2015	
Clavicle	1996/1998		2006	2009		2015	
Triton	1997	2006	2010			2019	
NF Fulton	1997	2007			2019		

between subtreatments and year: $p < 0.0009$). The control and VDT plots had three non-native species in common: cutleaf blackberry (*Rubus laciniatus*), wall lettuce (*Mycelis muralis*), and English holly (*Ilex aquifolium;* Table 4). Across all treatments, a total of 15 non-natives were present three years after treatment and, by the last sample (15–17 years), 11 species were found, all at very low abundances and frequencies (Table 5, Table 6). These tended to be widespread perennial ruderal species, with the exception of the biennials, foxglove (*Digitalis purpurea)* and bull thistle (*Cirsium vulgare)*. Relatively few

Table 4
Estimates of fixed effects of variable density thinning (VDT) subtreatments on non-native plant cover compared to controls, post-treatment year, and the interactions between VDT subtreatments and post-treatment year for zero-inflated negative binomial models. Bold values indicate significant differences at the $p < 0.05$ level. Degrees of freedom were approximated for nested mixed-effects models using the 'aov' function in the statistical program R, and are listed in the 'DF' column.

Level	Variable	Estimate	SE	z	p	DF
Subtreatment	Reserve	0.30	± 0.70	0.43	0.67	3, 18
Subtreatment	**Thin**	**2.37**	**± 0.63**	**3.78**	**0.000015**	**3, 18**
Subtreatment	**Gap**	**3.48**	**± 0.62**	**5.64**	**< 0.00001**	**3, 18**
Subtreatment	Post-treatment year	0.02	± 0.03	0.66	0.51	1, 40
Subtreatment	Reserve * post-treatment year	−0.03	± 0.05	−0.55	0.58	3, 40
Subtreatment	**Thin * post-treatment year**	**−0.14**	**± 0.04**	**−3.23**	**0.001**	**3, 40**
Subtreatment	**Gap * post-treatment year**	**−0.14**	**± 0.04**	**−3.13**	**0.002**	**3, 40**

species—English ivy (*Hedera helix)*, English holly (*Ilex aquifolium)*, and wall lettuce (*Mycelis muralis*)—are shade tolerant, suggesting that as the canopy closes further, cover will continue to trend downward.

Prior to treatment, richness of native and non-native species was similar between VDT and control treatments ($p = 0.67$ and $p = 0.68$, respectively, Fig. 4). Three to ten years after treatment, VDT treatments had higher species richness of both native ($p < 0.005$) and non-native plant species (all $p < 0.05$, Fig. 4) compared to control treatments during the same survey years. Species richness of native species remained significantly greater than the control treatment across all survey years (all $p < 0.004$, Fig. 4A), whereas non-native species richness declined over time in VDT treatments and did not significantly differ from controls by the last survey year ($p = 0.1$, Fig. 4).

Among subtreatments, native species richness and effective diversity were higher in gap and thinned subtreatments compared to controls, and these differences remained significant across all post-treatment sampling dates (all $p < 0.003$, Fig. 5, Table S). However, native species richness and diversity significantly declined in gap and thinned subtreatments over time (interaction between year and gap subtreatment; $p < 0.04$, Fig. 5). Species richness and diversity of native plants did not differ significantly between reserve and control plots in any survey year ($p > 0.3$, Fig. 5, Table S2). Frequencies of all native species, and native species classified by seral stages, are presented in the Supplement in Tables S3, S4, and S5.

4. Discussion

4.1. Non-native species cover and richness following variable-density thinning

Non-native species initially increased in cover after thinning and this corresponded with an increase in both native and non-native species richness. These patterns of increasing diversity following logging are in accordance with almost all other studies investigating the effects of disturbance in temperate forests of North America, as summarized by Sutherland and Nelson (2010). Results from other studies investigating the effects of logging on understory plant succession in Pacific Northwestern forests were similar to the results of this study, with non-native richness and cover peaking within the first decade following logging and

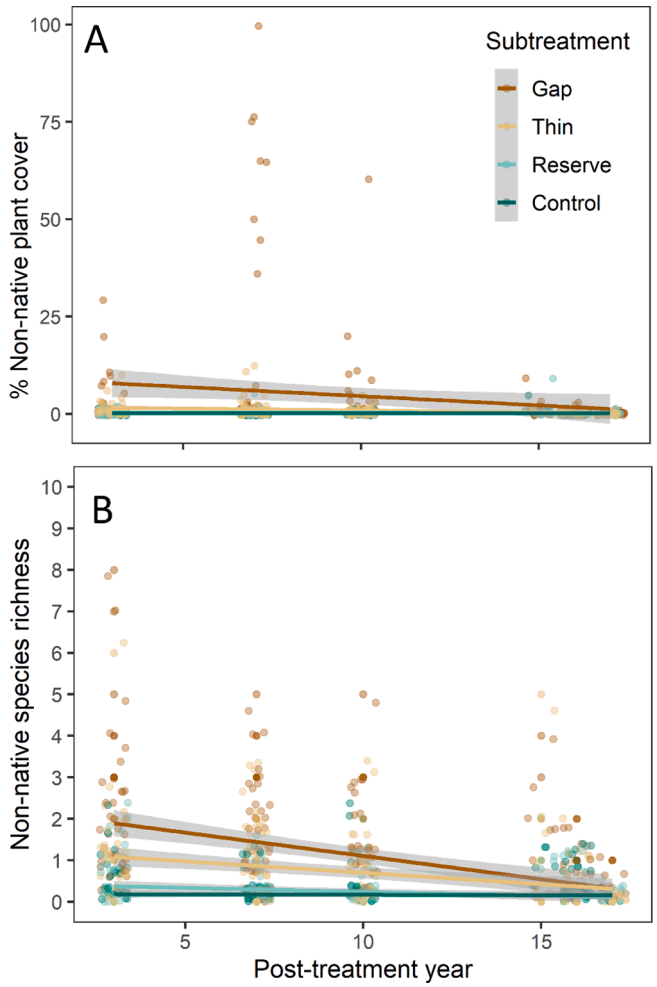

Fig. 3. Percent cover and species richness of non-native plants over time after variable-density thinning (VDT) subtreatments. (**A**) Percent cover of non-native plants per plot (points), and predicted mean percent cover of non-native plants over time per subtreatment and in control treatments (lines), ± 95% confidence intervals. (**B**) Species richness of non-native plants per plot (points) and predicted mean values per subtreatment over time (lines), ± 95% confidence intervals.

subsequent decreases in the second decade (DeFerrari and Naiman 1994, Gray 2005, Compagnoni and Halpern 2009). In general, higher rates of invasion and persistence correlate with more intensive tree removal (DeFerrari and Naiman 1994, Bailey et al. 1998, Gray 2005, Compagnoni and Halpern 2009), possibly due to an increase in available resources (Davis et al. 2000), and both native and non-native ruderal species may successfully colonize an area by opportunistically utilizing sunlight, water, and nutrients made newly available by logging. A possible advantage of VDT over clearcut harvesting is that its smaller gaps and lower light levels may limit non-native establishment and growth. In the case of clearcut harvesting, non-native cover can sometimes remain high. For example, in alder stands in the Hoh River watershed on the Olympic Peninsula, non-native cover exceeded 35% over 20 years after clearcut harvesting (DeFerrari and Naiman 1994). This contrasts sharply with our finding of an average of 1% non-native cover 15–17 years after VDT treatments. VDT, which results in less ground disturbance and light penetration to the understory, may limit the establishment or persistence of non-natives that benefit from large-scale disturbances. VDT may also prevent further spread of exotic species into undisturbed areas. In this study, gaps and thinned matrices were associated with higher non-native cover and richness than in reserve areas. Even in gaps, most individual plots retained very little (<1%) non-native cover at final sampling.

Table 5
Weighted mean cover of all non-native plant species present in control and variable-density thinning treatments across survey years. In variable-density treatments, mean species cover values per subtreatment were weighted based on the proportional area of sub-treatments (10% reserve, 15% gap, and 75% thinned).

Treatment	Species	Year 3	Year 7	Year 10	Years 15–17
Control	*Agrostis capillaris*	0	0	<0.1	0
	Cirsium arvense	<0.1	0	0	0
	Digitalis purpurea	0	0	<0.1	0
	Holcus lanatus	0	0	<0.1	0
	Ilex aquilafolium	0	0	<0.1	<0.1
	Mycelis muralis	<0.1	<0.1	<0.1	<0.1
	Rubus laciniatus	0	0	0	<0.1
	Veronica chamaedrys	<0.1	0	0	0
VDT	*Agrostis capillaris*	0	0	<0.1	0
	Cardamine spp.	0	0	0	<0.1
	Cirsium arvense	<0.1	<0.1	<0.1	0
	Cirsium vulgare	<0.1	<0.1	<0.1	<0.1
	Digitalis purpurea	<0.1	<0.1	<0.1	<0.1
	Hedera helix	0	0	0	<0.1
	Holcus lanatus	<0.1	0	<0.1	0
	Hypochaeris radicata	<0.1	<0.1	0	<0.1
	Ilex aquilafolium	0	<0.1	<0.1	<0.1
	Leucanthemum vulgare	<0.1	<0.1	<0.1	<0.1
	Lotus corniculatus	0	<0.1	0	0
	Mycelis muralis	0.65	0.14	<0.1	<0.1
	Rubus discolor	0	0	<0.1	0
	Rubus laciniatus	0.59	2.34	0.79	<0.1
	Rubus procerus	0	<0.1	0	0
	Rumex acetosella	<0.1	<0.1	<0.1	0
	Senecio jacobaea	0	<0.1	0	<0.1
	Senecio sylvaticus	<0.1	0	0	0
	Senecio vulgaris	<0.1	0	0	0
	Sonchus asper	<0.1	0	0	0
	Trifolium hybridum	<0.1	0	0	0
	Trifolium repens	<0.1	0	0	0
	Veronica chamaedrys	<0.1	<0.1	<0.1	0
	Veronica officinalis	<0.1	<0.1	0	<0.1

4.2. *Other factors influencing non-native cover and richness*

Factors other than disturbance from logging may influence the establishment of non-native species, including propagule pressure (Sutherland and Nelson 2010) and presence of a soil seed bank (Kellman 1974, Halpern et al. 1999). Prior to treatment, soil and litter seed banks were sampled at Bait, Fresca and Clavicle (Halpern et al. 1999). Seeds of cutleaf blackberry (*Rubus laciniatus*) were found in samples from Bait, the site where there was very high cover of this species shortly after thinning. The other non-native species found by Halpern et al. (1999) established after thinning, including wall lettuce (*Mycelis muralis*), bull thistle (*Cirsium vulgare*), oxeye daisy (*Leucanthemum vulgare*), foxglove (*Digitalis purpurea*), woodland ragwort (*Senecio sylvaticus*), and St. John's wort (*Hypericum perforatum*).

Once established, the traits of a non-native plant species may influence its persistence in its new environment. Ortega and Pearson (2005) theorized that non-native species may be classified as either "strong" or "weak" invaders. Weak invaders are more likely to persist at low levels for long periods while strong invaders have more negative impacts but are not very persistent. In Compagnoni and Halpern's (2009) study of invasibility of recently disturbed forests, the authors speculated that the non-native species occurring in low levels of abundance in the clearcuts and burned treatments of their study were weak invaders, referencing Ortega and Pearson (2005). In our study, cutleaf blackberry may be an example of a strong invader—found in several sites with very high cover in some plots in gaps at Bait, but vanishing by year 16. On the other hand, the relatively innocuous species, wall lettuce, persisted at many sites during the final year of sampling, though its cover steadily

Table 6
Frequency of non-native plant species in plots of the control treatment and in gap, reserve, and thinned subtreatments across survey years. Frequencies were calculated as the percentage of plots of each subtreatment type in which a species was present across all sites.

Subtreatment	Species	Year 3	Year 7	Year 10	Years 15–17
Control	*Agrostis capillaris*	0	0	2	0
	Cirsium arvense	2	0	0	0
	Digitalis purpurea	0	0	2	0
	Holcus lanatus	0	0	2	0
	Ilex aquilafolium	0	0	2	1
	Mycelis muralis	25	8	4	19
	Rubus laciniatus	0	0	0	1
	Veronica chamaedrys	2	0	0	0
Gap	*Agrostis capillaris*	0	0	13	0
	Cirsium arvense	17	6	3	0
	Cirsium vulgare	25	9	0	5
	Digitalis purpurea	31	30	10	7
	Hedera helix	0	0	0	2
	Holcus lanatus	3	0	5	0
	Hypochaeris radicata	8	5	0	0
	Ilex aquilafolium	0	0	0	2
	Leucanthemum vulgare	6	4	5	0
	Lotus corniculatus	0	2	0	0
	Mycelis muralis	72	45	28	25
	Rubus discolor	0	0	3	0
	Rubus laciniatus	17	17	28	5
	Rumex acetosella	11	4	3	0
	Senecio jacobaea	0	2	0	2
	Senecio sylvaticus	6	0	0	0
	Senecio vulgaris	3	0	0	0
	Trifolium hybridum	3	0	0	0
	Trifolium repens	3	0	0	0
	Veronica chamaedrys	3	11	3	0
	Veronica officinalis	0	0	0	5
Reserve	*Cirsium vulgare*	0	0	0	2
	Hypochaeris radicata	3	0	0	0
	Mycelis muralis	38	17	13	18
	Rubus laciniatus	13	2	3	0
Thin	*Cirsium arvense*	5	0	0	0
	Cirsium vulgare	3	0	0	0
	Digitalis purpurea	8	6	2	0
	Holcus lanatus	0	0	5	0
	Hypochaeris radicata	5	4	0	2
	Ilex aquilafolium	0	2	2	2
	Leucanthemum vulgare	0	0	0	2
	Mycelis muralis	67	49	27	20
	Rubus laciniatus	21	16	20	9
	Rubus procerus	0	4	0	0
	Rumex acetosella	3	0	0	0
	Senecio jacobaea	0	0	0	2
	Sonchus asper	3	0	0	0
	Veronica officinalis	0	0	0	5

decreased from year 3.

4.3. Understory species richness and diversity

The interactions between disturbance and diversity have been thoroughly studied, and many hypotheses have been brought forth to explain them, such as the Intermediate Disturbance Hypothesis. This hypothesis posits that the highest levels of diversity and richness are found in neither high or low disturbance environments, but rather ecosystems with moderate levels of disturbance (Loucks 1970). There are species which are more competitive and abundant in environments with fewer disturbances (Huston 1979), whereas other species are only found in environments with a higher frequency of disturbance. Similarly, the Environmental Heterogeneity Hypothesis, asserts that diversity in resource availability and variation in microclimate and substrate conditions that promote or inhibit germination or growth may correlate with higher plant species richness (Ricklefs, 1977). These

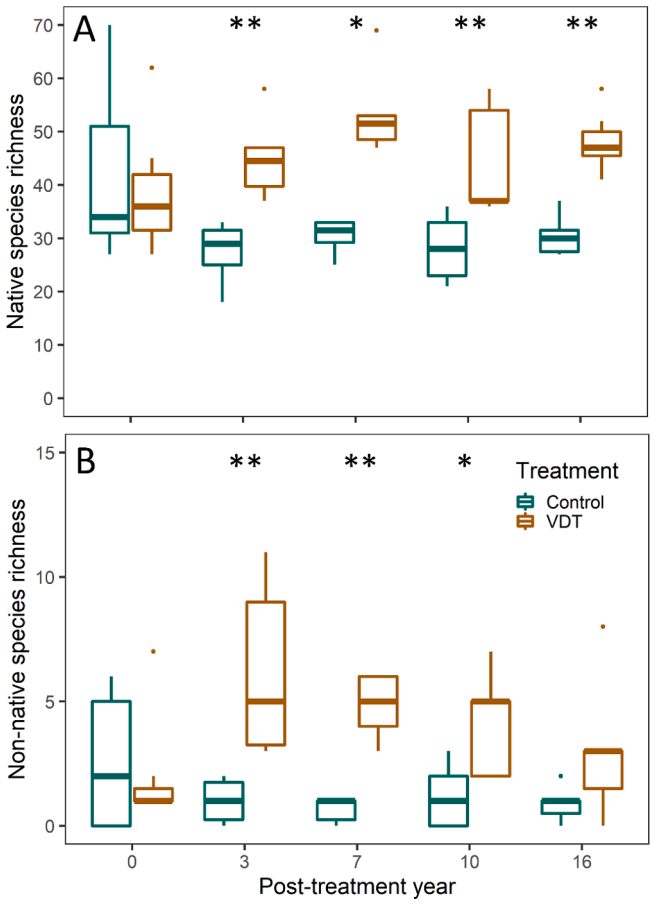

Fig. 4. Treatment-level richness before and after treatments for (**A**) native vascular plant species and (**B**) non-native vascular plant species. Boxes show the upper and lower quantiles, with medians indicated by the horizontal lines within, whiskers extend to 1.5 times the interquartile range except when limited by the data, and points indicate outliers. Asterisks indicate significant differences between variable density thinning (VDT) and control treatments in each survey year: * ($p < 0.05$), ** ($p < 0.005$). No statistical comparisons were made between pre-treatment richness and post-treatment richness as the metrics were collected using different methods.

hypotheses may help explain how variable-density logging disturbance increases plant species richness and diversity.

Some studies have found that large-scale logging may reduce plant species richness (Duffy and Meier 1992, Stapanian et al. 1997, Moola and Vasseur, 2004), while other studies have found higher levels of plant richness in managed forests (Heinrichs and Schmidt 2009, Belote et al. 2012, Boch et al. 2013). Other research has found the effects of logging on understory composition to be ephemeral (Albert and Barnes 1987, Ruben et al. 1999, Scheller and Mladenoff 2002, Duguid and Ashton 2013). Studies of variable-density thinning agree with our findings of increased diversity and richness following VDT (Ares et al., 2010; Davis and Puettmann, 2009; Puettmann et al., 2016; Thysell and Carey, 2001; Aukema, 2008), although these studies are of shorter duration than our study. Trends in diversity and species richness here are parallel, indicating that in our system, much of the contribution to diversity comes from the additional species present. However, our data collection and analyses focused on plot-level measurements, and because richness and diversity are both scale dependent (Hill 1973, Peet 1974), it will be beneficial for future research on landscape-level impacts of logging to consider richness and diversity at multiple spatial scales.

Duguid and Ashton's 2013 meta-analysis of logging effects on understory plant richness and diversity across North American temperate forest biomes suggests that successional stage at time of treatment and

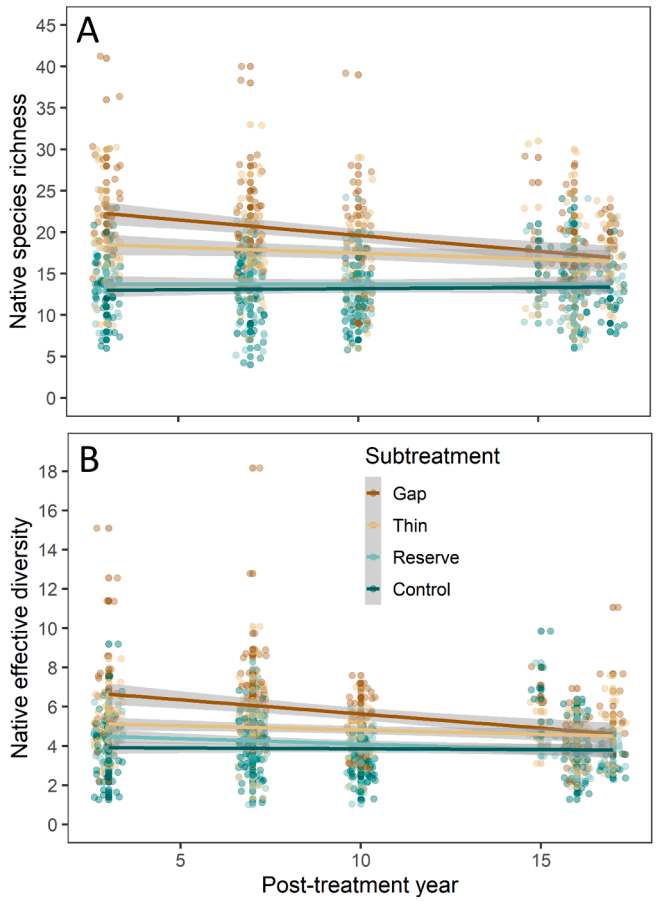

Fig. 5. (**A**) Native plant species richness per plot (points) and predicted mean values per subtreatment over time (lines), ± 95% confidence intervals. (**B**) Effective diversity of vascular native plant species per plot (points) and predicted mean values per subtreatment over time (lines), ± 95% confidence intervals.

method of harvesting is relevant in how the understory responds to tree removal. They found that studies examining even-aged management in stands greater than 50 years old had declines of understory plant diversity of approximately 28% in comparison to unharvested controls. In our study, we observed the largest increases in species richness and diversity and non-native cover in the thinned matrices and gaps when compared with the reserve subtreatment and the control.

Edge effects (e.g., changes in microclimate) associated with gap creation may enhance richness and diversity in adjacent areas, although it could be possible that the effect may differ with gap size, tree height, stand age, and other factors (Wilson and Puettmann, 2007). Research on the understory response to small canopy gaps has found that they do not significantly increase richness and diversity beyond the physical extent of the opening (Fahey and Puettmann, 2008). There is substantial evidence that gap creation modifies resource availability and microclimates in a localized manner (Canham et al. 1990, De Freitas and Enright 1995, Gray et al. 2002, Abd Latif and Blackburn 2010), with possible implications for the understory within the gap boundaries. Accordingly, we observed an increase in richness and diversity in the gaps similar to other studies examining the understory response to artificial openings in the canopy (Ares et al., 2009; Kermavnar et al., 2019).

Resource availability may influence species richness, and this is supported by the analysis of studies examining plant richness, diversity, and resource availability by Bartels and Chen (2010), who found that resource quantity (abundance of soil nutrients and light) interacted with stand development and succession to affect species richness. Spatial heterogeneity in the canopy resulting in increased yet varying light levels reaching the forest floor may also be a driver of increased understory richness following VDT. In a study of pre-commercial thinning in Douglas-fir forests, Thomas et al. (1999) found a weak but statistically significant relationship between understory vascular plant cover and light, and the effects of increased light reaching the understory persisted long after the canopy returned to a similar state as prior to thinning. Alaback and Herman (1988) observed similar results in western hemlock and spruce forests in Oregon, and the effects remained 17 years following thinning.

It should be noted that some chronosequence studies suggest that the effects of logging may persist for much longer than two decades (Duffy and Meier 1992, Wyatt and Silman 2010, Schmiedinger et al. 2012). Due to the temporal lag of impacts on vegetation following logging, longer-term studies examining the effects of differing management practices may be appropriate. Long-term, plot-level successional studies in the Pacific Northwest investigating the understory response to logging are sparse (but see Halpern and Spies 1995, Aukema, 2008, Compagnoni and Halpern 2009, Ares et al. 2010, Halpern and Lutz 2013) and the implicit assumptions made in chronosequences, such as comparability of environmental and stand conditions, can be problematic (Johnson and Miyanishi 2008). Furthermore, Tilman (1989) reported that only 2% of ecological studies collect data for longer than five field seasons, and a more recent meta-analysis by Estes et al. (2018) had similar findings for studies published between 2004 and 2014. Though we have up to 17 years of understory vegetation data here, and Halpern and Lutz (2013) have 45 years following clearcut harvesting and slash burning, additional studies on longer timescales would be valuable in gaining a better understanding of how forest management practices affect understory richness and diversity over time, as the full impacts may take longer to develop than the duration of our study.

5. Conclusion

To our knowledge, comparing the effects of variable-density thinning on non-native species introduction and native species richness and diversity has not previously been done at this spatial and temporal scale. However, analysis of tradeoffs over time between these metrics may be important to consider when deciding on land management options in forest ecosystems. Land managers are often concerned with the risk of persistent invasions of non-native plants due to their potential negative effects on native plants and animals. Our results show that this method of variable-density thinning in temperate coniferous forests can benefit native plant diversity, without lasting impacts due to increasing cover or richness of introduced species. Active management of stands through variable-density thinning is a promising option for the conservation and promotion of diversity (Carey 1998). It can accelerate the development of old-growth stand characteristics such as large diameter trees and multilayered canopies (Roberts and Harrington 2008, Comfort et al. 2010, Willis et al. 2018) and this study illustrates that it is also unlikely to result in decreases in diversity or large increases in long-term cover of non-native species.

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CRediT authorship contribution statement

Yianna Bekris: Writing – original draft, Writing – review & editing, Data curation, Investigation. **Janet S. Prevéy:** Writing – review & editing, Data curation, Visualization, Investigation, Formal analysis. **Leslie C. Brodie:** Supervision, Resources, Data curation, Investigation, Writing – review & editing, Validation, Methodology. **Constance A. Harrington:** Supervision, Project administration, Conceptualization, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119699.

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