Understory abundance, species diversity and functional attribute response to thinning in coniferous stands

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ABSTRACT

Alternative strategies for stand density management in even-aged coniferous forests may increase plant species and functional diversity. We examined the effects of fixed and variable density thinning on tree seedling regeneration as well as on abundance (indexed by cover) and richness of understory vascular plants 11 years after harvesting 45- to 66-year old forests dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) or western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) at three sites in western Oregon. Each site contained an unthinned control (CON), and thinning treatments selected to enhance overstory structural diversity and spatial variability within stands (HD, high density treatment at 300 trees ha^{-1}; MD, moderate density treatment at 200 trees ha^{-1}; VD300, VD200 and VD100, variable density treatments at 300, 200 and 100 trees ha^{-1}). Leave islands are included in HD and the other thinning treatments contain both leave islands and gap openings. Tree seedling regeneration was highly variable and generally increased with thinning. Cover of all understory species was greater in VD100 than in the control whereas richness was greater in HD and MD. Cover and richness of early seral species were greater in most thinning treatments than in the control. Understory plant communities were overwhelmingly dominated by native species. In general, vegetation dynamics was accelerated by thinning, especially in variable density treatments. Cover of N-fixing understory species was greater in VD200 than in the other treatments, and in MD and VD300 than in the control, whereas richness of understory N-fixing species increased in all thinning treatments. Cover of understory species with intermediate soil water requirements was greater in MD, VD200 and VD100 than in the control, whereas richness of these species increased in VD200 compared to the control, HD and VD300. Thinning promoted higher diversity of understory conditions without reducing density and species richness of crop tree regeneration, and seemed to increase functional effect and response diversity.

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1. Introduction

Preserving and enhancing biodiversity have become desirable forest management objectives in light of species loss and simplification of ecosystem structure and function worldwide (Roberts and Gilliam, 1995; Brunet et al., 2000; Odion and Sarr, 2007). Thinning has traditionally been aimed at increasing growth of residual crop trees and revenue. However, novel thinning strategies to increase overall biodiversity (Hartley, 2002), improve wildlife habitat (Hagar et al., 1996), accelerate the development of late seral forest characteristics (Lindh and Muir, 2004), and decrease fire hazard (Johnson et al., 2007) have gained interest, especially on public lands. Because of the interest to implement these new strategies, additional knowledge is needed concerning the effects of alternative thinning procedures for enhancing structural diversity and spatial variability on tree seedling regeneration and understory vegetation dynamics.

Thinning intensity as well as reproductive strategies, functional attributes, abundance of understory species, and inter- and intra-specific competition shape understory succession and vegetation community composition (Decocq et al., 2004; Roberts, 2004; Lindh, 2005; Smith et al., 2008). Understory abundance affects tree regeneration through competition for resources, changes in seedling environment, and modification of seedling–herbivore interactions (Gray and Spies, 1997; Kuehne and Puettmann, 2008). Rapid proliferation of native or non-native species (Nagai and Yoshida, 2006; Royo and Carson, 2006) following thinning, for instance, can negatively affect the establishment, growth, and survival of crop tree seedlings. Understory vegetation may either hide tree seedlings, thereby reducing herbivory, or create sheltered foraging areas for herbivores that selectively feed on tree seeds and seedlings (Saunders and Puettmann, 1999; Meiners, 2007; Royo and Carson, 2008). On the other hand, abundant regeneration, particularly of shade-tolerant tree species,

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Table 1
Environmental characteristics and pre-harvest features of the experimental sites in Oregon, USA. Ranges represent variation within sites.

	Keel Mountain	O.M. Hubbard	Bottomline
Ecoregion	Cascade Foothills	Coast Range	Coast Range, edge of Willamette Valley
Latitude, longitude	44°31′41″N, 122°37′55″W	43°17′30″N, 123°35′00″W	43°46′20″N, 123°14′11″W
Elevation (m)[a]	576–98	341–798	210–528
Mean annual precipitation (mm)[b]	1823	1351	1256
Slope (%)[a]	3–35	3–87	8–42
Soil type	Moderately to very deep, well drained Inceptisols (Dystrudepts)	Moderately to very deep, poorly to well drained Ultisols (Paleudults and Palehudults) and Inceptisols (Dystrudepts) from sedimentary and volcanic rocks	Deep to very deep, well drained Ultisols (Haplohumults and Palehumults) developed from sedimentary or volcanic rock
Size (ha)	90	89	100
Most abundant understory vascular plant species[c]	VAPA, POMU, OXOR, GATR, MANE, VIOLA	WHMO, HIAL, RUUR, TRBOL, POMU, FEOC	POMU, RUUR, GATR, PTAQ, VIOLA, COCOC
Harvest date	December 1997	September 1997	September 1997
Stand age at harvest (yr)	44	39	55
Harvesting method[d]	HD: cable MD: ground VD: ground	HD: cable, ground MD: cable, ground VD: cable, ground	HD: cable MD: cable VD: cable
Management history	Pre-commercial thin in 1964, and 1972	Pre-commercial thin in 1970, fertilized	None
Site index at year 50 (King, 1966)	39	36	42

[a] Elevation and slope were measured at the 0.1-ha overstory plot center.
[b] Precipitation was estimated from PRISM data for the period 1980–2005.
[c] POMU = *Polystichum munitum* Kaulf. C. Presl, VAPA = *Vaccinium parvifolium* Sm., RUUR = *Rubus ursinus* Cham. & Schlecht, OXOR = *Oxalis oregana* Nutt., GATR = *Galium triflorum* Michx., MANE = *Mahonia nervosa* (Pursh) Nutt., VIOLA = *Viola* sp., TRBOL = *Trientalis borealis* Raf. Spp. *latifolia* (Hook.) Hultén, PTAQ = *Pteridium aquilinum* (L.) (Kuhn), WHMO = *Whipplea modesta* Torr., HIAL = *Hieracium albiflorum* Hook., FEOC = *Festuca occidentalis* Hook., COCOC = *Corylus cornuta* Marsh. var. *californica* (A.DC.) Sharp.
[d] HD = high density thinning, MD = medium density thinning, VD = variable density thinning.

could produce secondary stem exclusion, markedly decreasing abundance of understory species (Alaback and Herman, 1988).

Thinning exerts varied effects on forest understories, which contain most of the plant diversity in temperate forest ecosystems. Changes following thinning are related to the intensity of disturbance to the overstory and understory vegetation and the forest floor. Understory response depends on associated environmental changes, pre-thinning understory composition, and reproductive and functional traits of resident and newly colonizing species (Bartemucci et al., 2006; Wilson et al., 2009). Stand density reduction can increase abundance of early seral species (i.e., species with maximum abundance in disturbed sites) (West and Osier, 1995; Wilson and Puettmann, 2007), trigger the proliferation of aggressive native and non-native taxa (Franklin et al., 2002; Gray, 2005), and negatively affect tall shrubs (Chan et al., 2006; Davis and Puettmann, 2009). Different responses to thinning, however, have been reported—e.g., low abundance and richness of early seral species 1–2 years after harvest (Halpern et al., 2005), no or very small increase in cover and richness of non-native species following harvest (Loya and Jules, 2008; Ares et al., 2009), and no effects on shrub cover when pre-harvest cover levels were low (Wilson et al., 2009).

Despite the widespread interest in preserving forest species for ecological, economic, and philosophical reasons, functional diversity—i.e., the value and range of functional traits of the organisms present in an ecosystem—may be more relevant than species richness for ecosystem functioning (Diaz and Cabido, 2001; Aubin et al., 2007; Voigt et al., 2007). This is because non-phylogenetically grouped species can have similar effects on dominant ecosystem processes or similar responses to environmental conditions (Lavorel et al., 1997). Stand density management can affect functional diversity by changing environmental conditions that affect biotic and abiotic components and lead to increase or decrease abundance and richness of functional effect types, func-

tional response types, or both (Bailey et al., 1998; Lookingbill et al., 2004). Functional response types are groups of species that respond similarly to a given disturbance (e.g., gap/forest interior species, drought-tolerant species), whereas functional effect types are groups of species that affect dominant ecosystem processes similarly (e.g., N-fixing species) (Lavorel et al., 1997). Increased functional diversity may enhance resilience, i.e., the capacity of an ecosystem to maintain desired ecosystem services in the face of fluctuating environmental conditions and human use (Folke et al., 2002), which would be an advantage to forest ecosystems increasingly stressed by global change.

Silvicultural strategies aimed at increasing heterogeneity in stand structure are of special interest for public lands in the Pacific Northwest region of the US. In this region, large areas have regenerated into coniferous stands that are simplified in terms of species diversity, structure, and function, compared to the old-growth forests that once occupied the sites. Thinning impacts on the understory have been evaluated by using post-harvest measurements over short periods (e.g., 1–8 years) (Chan et al., 2006; Nelson et al., 2007; Dodson et al., 2008; Lindh, 2008; Peterson and Anderson, 2009; Davis and Puettmann, 2009), chronosequence approaches (Puettmann and Berger, 2006), and retrospective studies on stands thinned more than 10 years ago (Bailey et al., 1998; Thysell and Carey, 2001; Lindh and Muir, 2004). Frequent measurements of the long-term effects of thinning following representative forest management practices at a large scale are necessary to fully understand the vegetation dynamics (Vallauri et al., 2002; Larsen and Nielsen, 2006). The Density Management Study (DMS) (Cissel et al., 2006; Peterson and Anderson, 2009), established in 1996 in western Oregon, follows a long-term approach to examine, among other objectives, the response of understory vascular plant vegetation to fixed and variable thinning intensities that create a broad range of residual stand structures and understory environments.

In this study, we examined forest understory response in abundance, species richness, and functional diversity to stand density

Table 2
Mean basal area (BA, m^2 ha^{-1}) and total height (HT, m) for upper, mid and lower canopy strata in coniferous stands in western Oregon 11 years after thinning.

Treatment	Upper canopy[a]		Mid canopy[b]		Lower canopy[c]	
	BA[d]	HT[e]	BA	HT	BA	HT
CON	53.8 ± 10.3	35.4 ± 1.0	1.3 ± 0.6	21.8 ± 3.6	0.2 ± 0.1	8.2 ± 4.3
HD	41.5 ± 6.6	34.8 ± 1.2	2.1 ± 1.2	25.2 ± 0.9	0.3 ± 0.2	10.2 ± 5.5
MD	33.0 ± 4.1	34.5 ± 2.4	6.2 ± 3.6	22.6 ± 0.9	0.2 ± 0.1	7.7 ± 3.9
VD300	35.3 ± 7.1	35.2 ± 0.6	3.9 ± 2.3	23.4 ± 4.2	0.0 ± 0.0	0.0 ± 0.0
VD200	29.4 ± 7.4	35.5 ± 1.1	1.7 ± 1.0	14.0 ± 7.2	0.1 ± 0.1	3.2 ± 3.2
VD100	29.2 ± 6.6	35.5 ± 1.4	3.1 ± 1.8	15.9 ± 8.0	0.3 ± 0.2	2.6 ± 2.6

CON = control; HD = high density, 300 trees ha^{-1}; MD = moderate density, 200 trees ha^{-1}; VD300 = variable density, 300 tree ha^{-1}; VD200 = variable density, 200 trees ha^{-1}; VD100 = variable density, 100 trees ha^{-1}.

[a] Grand fir, giant chinquapin, Douglas-fir, western hemlock.
[b] Big leaf maple, red alder, Pacific madrone, western red cedar.
[c] Pacific dogwood.
[d] We calculated stand basal area using bole diameter data taken at 1.35 m height for all trees ≥5 cm in diameter in each 0.1-ha plot.
[e] Height was measured in 10 coniferous trees and 6 hardwood trees in each 0.25-ha plot.

reductions 11 years after thinning. The primary objectives were to determine the effects of thinning operations producing a variety of spatial patterns and residual overstory densities on (1) survival of tree seedlings established after thinning; (2) total and individual plant species abundance (indexed by cover) and species richness in the understory; and (3) treatment-induced shifts in understory plants grouped by seral stage (early and late), origin (native and non-native), life form (tall shrub and clonal low shrubs), and functional effect and response type.

2. Methods

2.1. Study area and design

The three study sites (Keel Mountain, O.M. Hubbard and Bottomline) are in the western Oregon Cascades and Coast Range (Table 1). Pre-commercial thinning was applied to stands at Keel Mountain in 1964 and 1972 and at O.M. Hubbard in 1970. The O.M. Hubbard site was fertilized with 225 kg ha^{-1} of N applied from a helicopter in 1972. Mean annual precipitation estimated with the PRISM model (Daly et al., 1997) ranges from 1256 to 1823 mm with little precipitation from June to August. Sites are occupied by conifer stands (80 ha or greater) dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in age classes 40–60 years (Cissel et al., 2006). Hardwood trees were a minor component of all stands and were preferentially reserved during harvest. Common hardwoods were bigleaf maple (*Acer macrophyllum* Pursh), red alder (*Alnus rubra* Bong.), Pacific dogwood (*Cornus nutalli* Audubon), Pacific madrone (*Arbutus menziesii* Pursh,), and golden chinquapin (*Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmq.).

Overstory and understory pre-treatment data were not available; therefore, impacts of thinning treatments were assessed by comparison with unthinned control (CON) areas, which ranged in size from 16 to 24 ha. One set of five thinning regimes, each comprising 20–44 ha, was applied in 1997 at each site: (1) fixed high density treatment with 300 trees ha^{-1} (HD); (2) fixed moderate density treatment with 200 trees ha^{-1} (MD); (3) variable density treatment with 300 trees ha^{-1} (VD300); (4) variable density treatment with 200 trees ha^{-1} (VD200); and (5) variable density treatment with 100 trees ha^{-1} (VD100). In HD, 3–13% of the stand area was left unthinned in circular leave island reserves (i.e., patches of undisturbed forest trees) of 0.1, 0.2, and 0.4 ha. In MD, 4–18% of the stand area was cut in circular gap openings of 0.1, 0.2, and 0.4 ha, and 4–13% of the stand was left in circular leave island reserves of 0.1, 0.2, and 0.4 ha. In all three variable density treatments on each site, 4–18% of the area was left in circular gap openings and 4–18% was preserved in leave island reserves. Gap

openings and leave islands were of the same size as those in the fixed density treatments. Number of leave islands and gaps per ha by treatment ranged from 0.1 to 0.4, and from 0.3 to 0.4, respectively, reflecting differences in treatment area sites and operational constraints.

MD and VD200 had similar residual stand density and both included gaps and leave islands. Overstory and understory conditions in VD200, however, were more variable on smaller spatial scales and more likely to be influenced by neighboring treatment areas than did those in MD. In all treatments, distribution of residual trees was essentially even. Gaps and leave islands were spaced throughout the thinning treatments to accommodate harvesting operations without apparent bias caused by overstory and understory conditions. During thinnings, bole-only harvesting operations were used to minimize skidding damage to understory vegetation. Unmerchantable tree tops were left on site and logs were delimbed there as well. When bole delimbing was not completely accomplished on site, remaining limbs were removed at landings. Also, defective log portions were sometimes cut at landings. At Keel Mountain and O.M. Hubbard, slash left on landings was piled and some piles were burned. There was no slash treatment at Bottomline.

Overstory conditions 11 years after thinning are highlighted in Table 2. Basal area of the dominant overstory trees in CON and HD was greater than in all thinning treatments (Table 2). Basal area of trees in the mid and lower canopy layers, as well as average tree height for all layers, did not differ.

2.2. Vegetation plots

Seventy-seven permanent 0.1-ha circular overstory plots were installed in each site. The number of overstory plots in each treatment was 14 in CON, 21 in HD, 18–20 in MD, 6–8 in VD300, 7–8 in VD200 and 4–8 in VD100. Plots were located randomly within the treatment areas. If plot locations were less than 15 m from another plot or from treatment boundaries, however, a new location was randomly selected for that plot. Four 0.002-ha circular understory vegetation subplots were installed at 9 m in each cardinal direction from overstory plot centers. All measurements were taken 6 and 11 years after thinning, from June to September 2003 and 2008.

Tree regeneration was tallied by counting seedlings (0.15–1.37 m tall) by species in the vegetation subplots. Plant taxonomic nomenclature followed the USDA Plant Database (USDA-NRCS, 2005). In each understory vegetation subplot, we visually estimated total cover of bare soil, duff (decomposed organic material), ground-dwelling moss, litter (undecomposed or partially decomposed organic material), downed wood, and rocks. Total cover was also visually estimated for each understory plant

species in the understory vegetation subplots. Total cover was estimated as the percent of the vegetation subplot covered by the substrate types described above, using cover classes: 1%, 5%, and 10% and continuing in 10% increments to 100%. Overstory trees and shrubs >6 m tall were excluded from these measurements.

Species richness was calculated as the number of vascular plant species in the four subplots within each 0.1-ha plot (a total area of 80 m^2). Understory plant species were grouped as follows: (1) all plant species; (2) early seral species; (3) late seral species (generally shade-tolerant species that may eventually respond positively to canopy openings); (4) non-native species (species that are not native to western Oregon); (5) tall shrub species (>2 m in height); (6) low clonal shrub species ($\leq$2 m in height); (7) species that can potentially fix N; and (8) species grouped by soil water requirements into three classes: low, intermediate, and high. Species were assigned to groups based on published information (Halpern, 1989; Benson and Silvester, 1993; Thomas et al., 1999; Lindh and Muir, 2004; USDA-NRCS, 2005). The N-fixing status of all recorded understory species (excluding tree regenerating species) was known, whereas information on soil water requirements was only available for 37% of the species; only this subset was used in the corresponding analyses.

2.3. Quantitative and statistical analysis

We generated species–area curves using PC-ORD 4.0 (McCune and Mefford, 1999) to test whether the plant understory in each treatment had been adequately sampled. Both presence and cover data were used to calculate the distance between the centroid of the understory vegetation subsamples and the centroid of the whole sample, which represents a measure of dissimilarity among a set of items in a multidimensional space (i.e., the Sørensen distance, Sørensen, 1948). Species–area curves indicated that the number of understory vegetation subplots was sufficient to capture most understory species in all treatments. The number of 0.002-ha subplots (approximately 70 in CON, 100 in HD, 85 in MD, and from 40 to 50 in the variable density treatments) yielded a Sørensen distance <0, indicating that further increasing the number of subplots would provide very small increases in the number of species encountered.

Thinning effects on mean tree seedling density and richness, ground-substrate cover, and understory cover and species richness 11 years after thinning were analyzed using mixed model analysis of variance (ANOVA) with thinning treatment as a fixed effect and site as a random effect (Littell et al., 1996), and the MIXED procedure of SAS 9.1 (SAS Institute, 2004). The arcsine square root transformation was used to normalize the frequency distribution of proportional data (e.g., percent cover). Comparisons of treatment means used orthogonal contrasts with one degree of freedom.

Understory compositional change between years 6 and 11 after thinning were assessed by calculating the percent dissimilarity index (PD) (Faith et al., 1987) from data categorized by plant groups (i.e., early and late seral, non-native, tall and low shrubs) as follows:

$$PD = 100 \times \left\{ 1 - 2 \times \left[\frac{MIN(Xy_6, Xy_{11})}{Xy_6 + Xy_{11}} \right] \right\}$$

where MIN is the smallest of two values, X = cover or richness of understory species for a given plant group in year 6 (y_6) and year 11 (y_{11}) after thinning.

Percent dissimilarity for cover and richness (PD$_c$ and PD$_r$, respectively) ranges from 0 (no change in cover or richness from year 6 to 11) to 100 (complete change; e.g., no species in common in year 6 and 11). This index indicates extent of change but not the shift direction. Treatment effects on PD$_c$ and PD$_r$ were tested using a mixed model ANOVA and orthogonal contrasts with one degree of freedom.

Table 3
Tree seedling density (seedlings per ha) and richness (species per 80-m^2 area) 11 years after thinning in coniferous stands in western Oregon.

Treatment	Seedling density	Seedling richness
CON	750 ± 463 bc	0.7 ± 0.1 c
HD	2662 ± 699 bc	1.7 ± 0.2 b
MD	3487 ± 987 abc	1.6 ± 0.2 b
VD300	3150 ± 1327 abc	1.5 ± 0.3 b
VD200	5687 ± 1702 a	1.9 ± 0.3 ab
VD100	2937 ± 947 abc	2.2 ± 0.6 a

CON = control; HD = high density, 300 trees ha^{-1}; MD = moderate density, 200 trees ha^{-1}; VD300 = variable density, 300 tree ha^{-1}; VD200 = variable density, 200 trees ha^{-1}; VD100 = variable density, 100 trees ha^{-1}.
Values are means ± one standard error. Means followed by the same letter in a given column are not significantly different at $P \leq 0.05$.

We performed blocked multi-response permutation (MRBP) in PC-ORD 4.0 using cover data by species in subplots to test for differences in understory plant community composition among treatments. This procedure uses Euclidean distances and median alignment within blocks to control for site-to-site variation (McCune and Grace, 2002). The test statistic T indicates separation between groups and the statistic A represents within-group homogeneity compared to the random expectation. Indicator species analysis (ISA; Dufrêne and Legendre, 1997) was run in PC-ORD 4.0 with the same datasets as above to calculate the indicator value (IV) for understory plant species in the treatments. The IV measures the fidelity of species to treatments, using abundance and relative frequency of species within a given treatment (McCune and Grace, 2002). Statistical significance of IV was tested by using the Monte Carlo randomization test with 5000 iterations. Both MRBP analysis and ISA were run for all recorded understory species and after deleting rare species, which were species with less than two and three occurrences in the six treatments and three sites (excluding 56 and 88 species, respectively). Results were very similar with and without rare species in the dataset, indicating a weak effect of their presence on plant community ordinations. Therefore, results are presented for all species encountered.

3. Results

3.1. Tree regeneration

Tree seedling density displayed large variability among thinning treatments and study sites (Table 3). We found, however, a general trend indicating increased tree seedling density with lower residual overstory densities. Seedling density in VD200 was more than 7-fold greater than in CON (P = 0.001) (Table 3). Regeneration at Bottomline was scarce and dominated by Douglas-fir and bigleaf maple (approximately 50% abundance of each species). At Keel Mountain, western hemlock regenerated profusely, comprising 96% of seedlings. At O.M. Hubbard, the main regenerating species were grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) (64%), Douglas-fir (16%), madrone (9%), and bigleaf maple (6%). Seedling species richness was greater in all thinning treatments than in CON ($P \leq 0.02$), and in VD100 than in HD, MD and VD300 ($P \leq 0.02$).

3.2. Ground-substrate cover

There was little duff cover (<5%) in all treatments and less in the variable density treatments than in CON and HD ($P < 0.05$) (Table 4), whereas litter cover was lower in VD100 than in CON, MD and VD300, and it was lower in HD and VD200 than in CON ($P < 0.03$). Cover of ground-dwelling mosses was lower in VD100 than in CON and VD300 ($P < 0.03$). There were no significant differences in bare soil, downed wood, and rock cover (all < 1.5%) among treatments.

Table 4
Cover (%) of bare soil, duff, litter, downed wood, moss and rocks 11 years after thinning of coniferous stands in western Oregon.

Treatment	Bare soil	Duff	Litter	Downed wood	Moss	Rocks
CON	1.3 ± 0.5	3.6 ± 1.6 a	63.7 ± 10.0 a	1.3 ± 0.9	23.7 ± 6.2 a	0.7 ± 0.9
HD	0.9 ± 0.9	4.2 ± 1.1 a	37.0 ± 3.7 bc	0.9 ± 0.5	18.1 ± 3.6 ab	0.1 ± 0.1
MD	1.1 ± 0.2	2.9 ± 0.7 ab	45.8 ± 1.9 ab	1.1 ± 0.9	15.1 ± 1.6 ab	0.9 ± 1.4
VD300	0.6 ± 0.9	2.1 ± 0.9 b	45.8 ± 9.7 ab	0.6 ± 0.2	22.3 ± 8.2 a	0.2 ± 0.1
VD200	1.2 ± 0.9	2.5 ± 1.3 b	36.3 ± 6.2 bc	1.2 ± 0.9	15.2 ± 4.7 ab	0.0 ± 0.1
VD100	1.1 ± 0.9	2.2 ± 0.6 b	18.7 ± 8.1 c	1.1 ± 0.9	7.1 ± 3.3 b	0.3 ± 0.5

CON = control; HD = high density, 300 trees ha^{-1}; MD = moderate density, 200 trees ha^{-1}; VD300 = variable density, 300 tree ha^{-1}; VD200 = variable density, 200 trees ha^{-1}; VD100 = variable density, 100 trees ha^{-1}.
Values are means ± one standard error. Means followed by the same letter in a given column are not significantly different at $P \leq 0.05$. No significant differences were detected for treatment means not followed by letters.

Table 5
Cover (C, %) and richness (R, number of species per 80-m^2 area) of understory plant groups 11 years after thinning of coniferous stands in western Oregon.

Treatment	All species		Introduced species		Early seral species		Tall shrub species		Clonal low shrubs	
	C	R	C	R	C	R	C	R	C	R
CON	51.1 ± 19.2 b	48.0 ± 4.9 b	0.0 ± 0.1 b	0.0 ± 0.7 c	15.5 ± 4.2 b	3.9 ± 3.6 b	14.7 ± 6.4	3.0 ± 0.5 b	22.8 ± 16.6	2.7 ± 0.9 b
HD	63.3 ± 11.9 ab	76.3 ± 3.5 a	0.8 ± 0.3 ab	1.2 ± 9.6 ab	18.6 ± 4.6 ab	9.2 ± 0.9 a	16.9 ± 1.9	3.6 ± 0.7 ab	14.9 ± 6.6	3.0 ± 0.6 ab
MD	79.2 ± 15.8 ab	86.0 ± 13.6 a	0.6 ± 0.1 ab	1.1 ± 2.9 b	30.4 ± 7.8 a	8.4 ± 0.9 a	15.3 ± 3.6	3.6 ± 0.8 ab	21.6 ± 5.2	3.5 ± 1.2 ab
VD300	73.2 ± 17.3 ab	53.7 ± 5.4 b	0.6 ± 0.4 ab	0.9 ± 9.1 bc	25.5 ± 6.0 a	7.4 ± 4.2 ab	16.6 ± 3.6	3.6 ± 0.7 ab	26.3 ± 11.5	3.1 ± 0.9 ab
VD200	67.6 ± 16.8 ab	55.0 ± 3.5 b	1.3 ± 0.6 a	1.5 ± 7.9 ab	30.9 ± 7.7 a	10.3 ± 7.2 a	18.6 ± 1.1	4.4 ± 0.8 a	23.6 ± 12.1	3.3 ± 0.8 ab
VD100	83.8 ± 13.2 a	59.7 ± 7.3 ab	0.9 ± 0.1 ab	2.2 ± 9.9 a	32.6 ± 5.2 a	8.7 ± 8.0 a	18.2 ± 2.0	3.9 ± 0.4 ab	25.4 ± 10.3	3.9 ± 0.8 a

CON = control; HD = high density, 300 trees ha^{-1}; MD = moderate density, 200 trees ha^{-1}; VD300 = variable density, 300 tree ha^{-1}; VD200 = variable density, 200 trees ha^{-1}; VD100 = variable density, 100 trees ha^{-1}.
Values are means ± one standard error. Means followed by the same letter in a given column are not significantly different at $P \leq 0.05$. No significant differences were detected for treatment means not followed by letters.

3.3. Understory plant cover and richness

Thinning appeared to lead to increased cover and richness of understory species. Thus, cover of all recorded understory species was greater in VD100 than in CON ($P < 0.05$; Table 5). Richness of all understory species was greater in HD and MD than in CON, VD300 and VD200 ($P \leq 0.02$). Species richness was greater in HD and MD than in VD300 and VD200 ($P = 0.001–0.02$).

An example of the impact of increased species richness on understory vegetation patterns is shown in Fig. 1 for O.M. Hubbard.
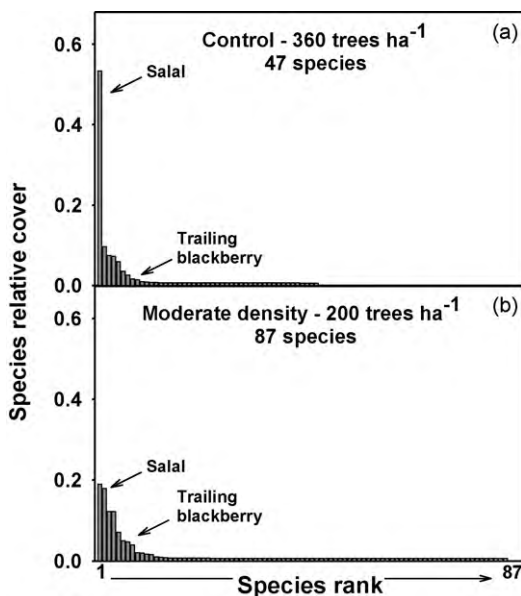

Fig. 1. Relative abundance of understory vascular plant species 11 years after thinning of coniferous stands at the O.M. Hubbard study site in western Oregon; (a) control treatment, and (b) moderate density treatment with a targeted density after thinning of 200 trees ha^{-1}.

In CON, we found a total of 47 understory species; salal (*Gualtheria shallon* Pursh) was the dominant species with a relative cover of 0.58 (Fig. 1a). In MD there were 87 understory species (Fig. 1b); relative abundance of salal was markedly lower than in CON, whereas abundance of other low clonal shrubs, such as the native trailing blackberry (*Rubus ursinus* Cham. & Schltdl), was greater in MD than in CON.

The understory plant communities were overwhelmingly dominated by native species in both cover and richness (Table 5). Mean total cover of non-native species varied from 0.1% in CON to 1.3% in VD200. Difference in cover of non-native species was only significant between these two treatments ($P = 0.02$). Mean total cover of native species ranged from 51% in CON to 81% in VD100 without significant differences among treatments. Richness of non-native species was greater in VD100 than in CON, MD and VD300 ($P \leq 0.05$), and in HD, MD and VD200 than in CON ($P \leq 0.04$).

As expected, cover of early seral species was greater in most thinning treatments than in CON ($P \leq 0.05$; Table 5) and represented 29–39% of the total understory plant cover. Thinning favored diversity of early seral species; i.e., species richness in all thinning treatments except VD300 was greater than in CON ($P \leq 0.02$). Cover (37–45%) and species richness (8.2–9.4 species per 80-m^2) of later seral species did not differ among treatments.

Cover of tall shrubs was similar in all treatments. Tall shrub richness, however, was greater in VD200 than in CON ($P = 0.02$; Table 5). Cover of low clonal shrubs varied from 14.9% in HD to 26.3% in VD300 without significant differences among treatments (Table 5). Richness of low clonal shrubs was greater in VD100 than in CON ($P = 0.02$).

Considering cover of all recorded species, there were differences in understory plant community composition between CON and both VD300 and VD100 (MRBP; $T = -1.6$, $P = 0.07$, A-stat = 0.04; $T = -1.4$, $P = 0.07$, A-stat = 0.05, respectively). Only two species and species grouped within the genus *Festuca* (fescues) had IVs with P close or equal to 0.05. Pacific bleeding heart (*Dicentra formosa* (Haw.) Walp.) (IV = 47.9; $P = 0.09$), a perennial, native herb indicative of closed canopy conditions was most associated with HD.
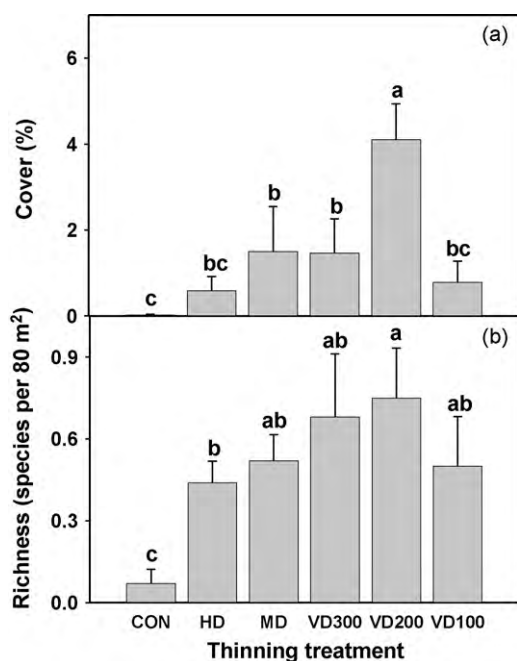
Fig. 2. Cover (a) and richness (b) of N-fixing species 11 years after thinning of coniferous stands in western Oregon. CON = control; HD = high density, 300 trees ha^{-1}; MD = moderate density, 200 trees ha^{-1}; VD300 = variable density, 300 tree ha^{-1}; VD200 = variable density, 200 trees ha^{-1}; VD100 = variable density, 100 trees ha^{-1}. Values are means ± one standard error. Mean values represented by bars under the same letter are not significantly different at $P \leq 0.05$.

Fescues (IV = 28.3, $P = 0.07$) and cutleaf blackberry (*Rubus lacinia-tus* Willd.), (IV = 43.6; $P = 0.05$) a deciduous, non-native low clonal shrub, thrive under open canopies, and had the greatest association with variable density thinning treatments.

3.4. Shifts in plant group composition from year 6 to year 11

Change in species composition from year 6 to year 11 expressed as percent dissimilarity in species richness and cover was generally greater in variable density treatments. For all species, PD$_r$ was greater in VD200 than in MD ($P = 0.03$; Table 6). PD$_c$ of non-native species was greater in VD200 than in CON ($P = 0.04$; Table 6). PD$_r$ for non-native species was greater in VD300 than in CON, HD, MD and VD200 ($P < 0.05$), and in MD, VD200 and VD100 than in CON ($P \leq 0.03$). PD$_c$ of early seral species was greater in VD300 than in VD200 ($P = 0.03$), whereas PD$_r$ was greater in VD300 than in CON ($P = 0.04$; Table 6). Early seral species tended to be slightly higher in cover and richness at Bottomline and O.M. Hubbard, and lower at Keel Mountain. Cover of late seral species did not change differently among thinning treatments from year 6 to year 11, but
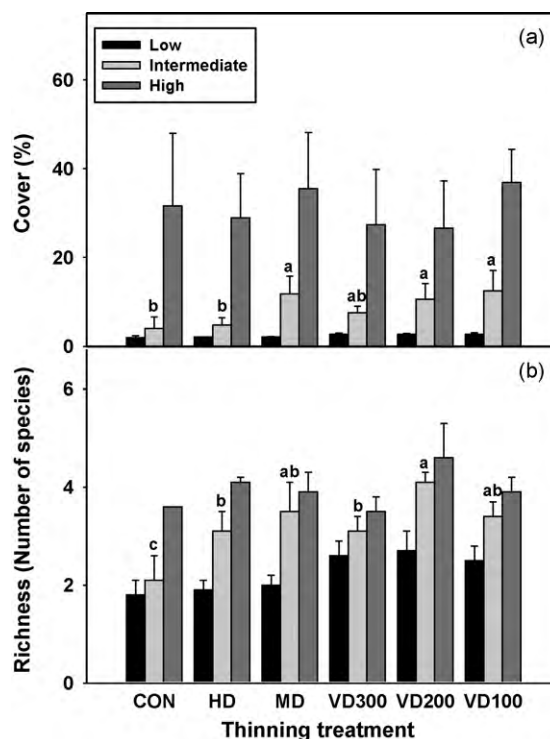

Fig. 3. Cover (a) and richness (b) of understory species sorted by soil water requirements 11 years after thinning of coniferous stands in western Oregon. CON = control; HD = high density, 300 trees ha^{-1}; MD = moderate density, 200 trees ha^{-1}; VD300 = variable density, 300 tree ha^{-1}; VD200 = variable density, 200 trees ha^{-1}; VD100 = variable density, 100 trees ha^{-1}. Values are means ± one standard error. Mean values represented by bars under the same letter are not significantly different at $P \leq 0.05$.

changes in richness were more intense in VD100 than in HD, MD and VD300 ($P \leq 0.03$). There were slight differences in change of cover and richness for tall shrubs from year 6 to year 11. PD$_c$ for tall shrubs was greater in VD200 than in VD100 ($P = 0.03$), and PD$_r$ was greater in CON than in VD100 (Table 6). PD$_c$ for low clonal shrubs was greater in VD100 than in CON, HD, VD300 and VD200 ($P \leq 0.04$; Table 6). These results indicate greater degree of compositional change through time in variable density treatments. PD$_r$ for low clonal shrubs was only greater in VD200 than in HD ($P = 0.04$).

3.5. Functional effect and response diversity

Cover of understory N-fixing species was greater in VD200 than in the other thinning treatments and CON ($P \leq 0.03$; Fig. 2a). It was also greater in MD and VD300 than in CON ($P = 0.01$ and 0.02, respectively). Richness of understory N-fixing species was

Table 6
Percent dissimilarity from year 6 to year 11 after thinning calculated for understory cover (*C*) and richness (*R*).

Treatment	All species		Introduced species		Early seral species		Tall shrub species		Clonal low shrubs	
	C	R	C	R	C	R	C	R	C	R
CON	14.9 ± 1.6	6.2 ± 0.5 ab	11.8 ± 10.8 b	0.0 ± 0.0 c	14.5 ± 1.4 ab	2.2 ± 0.7 b	19.1 ± 4.9 ab	12.7 ± 2.7 a	7.8 ± 4.6 b	5.4 ± 2.9 ab
HD	6.8 ± 1.0	1.9 ± 1.2 ab	16.0 ± 7.5 ab	17.1 ± 9.6 bc	11.4 ± 3.4 ab	3.6 ± 2.1 ab	13.3 ± 4.2 ab	5.5 ± 1.7 ab	8.4 ± 3.7 b	1.7 ± 1.2 b
MD	10.7 ± 7.4	0.6 ± 0.3 b	24.0 ± 13.2 ab	22.9 ± 2.9 b	13.8 ± 4.7 ab	5.2 ± 7.9 ab	11.2 ± 2.2 ab	5.8 ± 2.0 ab	15.4 ± 9.1 ab	7.0 ± 3.2 ab
VD300	11.6 ± 6.1	4.6 ± 1.4 ab	32.8 ± 10.8 ab	45.4 ± 9.1 a	21.9 ± 8.0 a	12.2 ± 6.0 a	22.2 ± 3.6 a	5.7 ± 2.9 ab	5.7 ± 1.4 b	2.5 ± 1.5 ab
VD200	13.3 ± 5.0	7.8 ± 3.0 a	45.2 ± 12.0 a	25.4 ± 7.6 b	6.2 ± 0.8 b	4.9 ± 7.7 ab	7.0 ± 4.7 b	7.5 ± 4.8 ab	5.5 ± 2.5 b	12.2 ± 4.3 a
VD100	8.1 ± 2.5	6.4 ± 4.0 ab	28.0 ± 1.5 ab	31.6 ± 9.9 ab	18.0 ± 4.7 ab	10.9 ± 5.2 ab	15.4 ± 6.1 ab	4.4 ± 1.5 b	27.3 ± 9.1 a	11.0 ± 4.9 ab

CON = control; HD = high density, 300 trees ha^{-1}; MD = moderate density, 200 trees ha^{-1}; VD300 = variable density, 300 tree ha^{-1}; VD200 = variable density, 200 trees ha^{-1}; VD100 = variable density, 100 trees ha^{-1}.
Values are means ± one standard error. Means followed by the same letter in a given column are not significantly different at $P \leq 0.05$. No significant differences were detected for treatment means not followed by letters.

greater in the thinning treatments than in CON ($P = 0.0001$–0.03; Fig. 2b). Among understory species that can potentially fix N, we found mostly herbs: American vetch (*Vicia americana* Muhl. ex Willd), desert deervetch (*Lotus micranthus* Benth.), garden vetch (*Vicia sativa* L.), and unidentified species within the genus *Lathyrus* (pea), *Lotus* (trefoil), and *Lupinus* (lupine). Scotch broom (*Cytisus scoparius* L. Link), a non-native and often invasive shrub, was also found in some plots. N-fixing species were more common at O.M. Hubbard and were almost absent at Keel Mountain. In the tree stratum, red alder (*Alnus rubra* Bong) was present in two of the three sites with very low average basal area (<0.1 m^2 ha^{-1}) but with a clumped distribution.

There were no differences in cover and richness of species with high and low soil water requirements among treatments (Fig. 3). Cover of understory species with intermediate soil water requirements was greater in MD, VD200 and VD100 than in CON ($P = 0.05$). In addition, richness of species with intermediate soil water requirements was greater in VD200 than in CON, HD and VD300 ($P \le 0.01$). The lowest richness for species in the intermediate class occurred in CON.

4. Discussion

4.1. Tree seedling density and ground substrata

Continuous tree seedling recruitment occurred in the three study sites after thinning. Most of the seedlings tallied 11 years after thinning likely originated after the sampling at age 6. This indicated that arrested succession caused by recalcitrant understory layers excluding tree regeneration did not occur. A similar trend was reported 5 years after thinning at the full suite of DMS thinning sites, although no statistical differences were found because of large variability in seedling density (Kuehne and Puettmann, 2008). Concordantly, there was large spatial variability in seedling density 11 years after thinning, although regeneration increased in all thinning treatments. Ample variability in forest regeneration often originates from microsite heterogeneity and seedling clustering (Fajardo et al., 2006; Mountford et al., 2006; Barbeito et al., 2009). The abundant regeneration we recorded in some areas may eventually decrease shrub and herb cover and diversity and require additional thinning of the regenerating trees. These interventions would also sustain growth of saplings, as shown after a second thinning at DMS sites (Shatford et al., 2009), although trade-offs between increased sapling growth and potential reductions in understory development should be considered when deciding target sapling densities. Overall, the tree regeneration trends at the DMS sites support the contention that slow seedling establishment periods may be common in coniferous forests of the U.S. Pacific Northwest after large disturbances (Poage et al., 2009; Shatford et al., 2009).

Decline in cover of ground-dwelling mosses after heavy thinning was consistent with previous research indicating that bryophyte richness and abundance decreased after reductions of canopy cover, possibly due to increased light and decreased substrate moisture (Beese and Bryant, 1999; Nelson and Halpern, 2005), and the accumulation of logging slash (Dovčiak et al., 2006). These effects, however, may depend upon the composition of the bryophyte community (Muir et al., 2006), the overstory species and the stand productivity [e.g., increased cover of ground mosses with thinning in stands dominated by *Picea sitchensis* (Bong.) Carr. (Alaback and Herman, 1988)]. Recovery of bryophyte abundance to that in the unthinned treatment, however, has been found as early as 10 years after thinning as noted in the Young Stand Thinning and Diversity Study in western Oregon (A. Ares, unpublished data).

4.2. Understory species cover and richness

The species-diverse understories at DMS sites were typical of mesic environments at low- to middle-elevations in the Pacific Northwest (Brockway, 1998). Increased understory plant cover and diversity after thinning at the DMS sites agreed with responses detected for temperate forests (McConnell and Smith, 1970; Thysell and Carey, 2001; Wienk et al., 2004; Metlen and Fiedler, 2006; Zenner et al., 2006; Dodson et al., 2008), although most of those studies were over shorter periods (1–4 years) than that in this study. These effects of thinning on forest understory have been attributed to reduce competition of overstory trees for light or below-ground resources (Harrington and Edwards, 1999; Thomas et al., 1999; Son et al., 2004). Thinning seems to have little or no effect on understory vegetation in forests growing at high latitudes or with understory plant communities having relatively low diversity (He and Barclay, 2000; Bauhus et al., 2001; Bergsted et al., 2008). Thinning can be considered an intermediate disturbance that is not as strong as severe disturbances (e.g., hurricanes, landslides) that may reduce diversity levels. In this study, ground substrata (i.e., bare soil, downed wood and rocks) appeared to have little effect on cover and richness of understory vegetation.

At the DMS sites, increased understory diversity after thinning was mostly caused by small increments in several rare species. Considered individually, these species would likely have little effect on ecosystem functioning, especially if they overlap with existing species having similar functional traits (Folke et al., 2004; Gleason et al., 2009). Only one native species (Pacific bleeding heart), one non-native species (cutleaf blackberry), and species within the genus *Festuca* exhibited high fidelity to thinning treatments at year 11 after thinning in the three DMS sites studied, compared to eight species (including cutleaf blackberry) in seven DMS sites at year 6 (Ares et al., 2009).

4.3. Understory compositional changes from year 6 to 11 after thinning

Judging by understory vegetation changes from year 6 to 11 after thinning, community change clearly accelerated in thinned compared to unthinned areas, particularly in the variable density treatments. Early seral species were generally an important component of the understory, and their cover remained stable with the exception of a slight decline at Keel Mountain. This is consistent with research in the Pacific Northwest forests indicating that early seral species persist for decades after clearcutting and reforestation (Puettmann and Berger, 2006). At the three DMS sites in this study, late seral species instead tended to decline from year 6 to year 11 after thinning, although their abundance was still greater than that of early seral species. The decrease in late seral species, however, may be a transient phenomenon. Twenty years after thinning young Douglas-fir stands, late seral herbs were more frequent in thinned stands than in unthinned stands (Lindh and Muir, 2004; but see Bailey et al., 1998).

The limited and declining abundance of non-native understory species after thinning at the DMS sites support the view that these species do not likely dominate vegetation communities at relatively high-elevation sites within forests that are not intensively managed and/or are not close to agricultural, urban or recreational areas (Halpern et al., 2005). This may be caused by seed dispersal limitation, microsite conditions preventing site colonization (Hellmann et al., 2008), and competition pressures by native vegetation. Non-native species sometimes increased significantly in richness after thinning, although their relative abundance remained low (Dodson et al., 2008; Nelson et al., 2008; Ares et al., 2009; Davis and Puettmann, 2009). This poses the risk of slow, incremental development of these species over time. Non-native species were not

common within DMS plots but are sometimes present along nearby forest roads and in landings (A. Ares, personal observation). Their decline during the last 5 years in this study supported the trend found in western Washington, where average cover of non-native species increased to 10.2% 1 year after variable density thinning of 55- to 65-year old stands of Douglas-fir, but then decreased to 7.1% at year 3 after harvest (Thysell and Carey, 2001).

Tall shrubs often sustain mechanical damage from harvest operations. Average height of salmonberry (*Rubus spectabilis* Pursh.), thimbleberry (*Rubus parviflorus* Nutt.), red huckleberry (*Vaccinum parviflorum* Sm.), and California huckleberry (*Vaccinum ovatum* Pursh.) decreased by about 40% immediately after harvest in thinned Douglas-fir stands in Oregon Coast Range, with full recovery noticed 8 years after harvest (Chan et al., 2006). At the three DMS sites, initial harvest damage on tall shrubs was probably limited in scale because of low-impact logging; most species within that group may have already recovered 6 years after thinning and did not experience major changes from then to year 11. Low clonal shrubs were initially released by thinning at DMS sites (Wilson and Puettmann, 2007). At year 11 after harvest, these shrubs may have ceased to expand, as they exhibited similar cover among treatments and only slightly higher species richness in the most intense thinning treatment compared to CON. Limited research data have suggested that response of clonal, late seral herbs to thinning is highly species specific (Nelson et al., 2007).

4.4. Functional response and effect groups

Greater cover and richness of N-fixing understory species after thinning at DMS sites suggest that the likelihood of maintaining the ecosystem function of N fixation is increased after partial harvest (sensu Norberg and Cumming, 2008), although actual N-fixation rates for these species are unknown. Results of this study agreed with findings in western Oregon indicating that understory N-fixing species were more abundant in young (50–100 years old) stands thinned 10–24 years earlier than in neighboring unthinned stands (Bailey et al., 1998). Some of these understory species have the potential to make substantial contributions to long-term soil N stores (e.g., 7–10 kg ha^{-1} yr^{-1} in McNabb et al., 1976), especially if further harvesting or disturbance reduce competition from overstory trees and understory species. Increased cover and richness of N-fixing species caused by stand density reduction and gap creation may further affect soil N cycling. For example, nitrogen mineralization rates often increase after thinning possibly because soil temperature (Thibodeau et al., 2000), soil water content (Chapin et al., 2002), litter quality (Thiel and Perakis, 2009), C limitation for microbes (Hope et al., 2003), and labile N from dead roots (Chen et al., 2002) all increase.

Increased cover and richness of understory species with intermediate soil water requirements after thinning at DMS sites suggest that these species benefited from augmented water availability after stand density reductions. This response was apparently not a short-term, episodic phenomenon because it was reflected in the understory vegetation cover and composition 11 years after thinning. Increased soil water content has been reported in gaps 2 years (Ritter et al., 2005), 6 years (Gray et al., 2002) and 9 years (Griffiths et al., 2010) after thinning, likely in response to reduce evapotranspiration and increased precipitation throughfall in openings. That effect was greater in gap centers and during the driest time of the year. Spatial differences in plant species composition, especially in larger gaps, supported these findings (Fahey and Puettmann, 2008). Differences in soil water content between gaps and the forest interior are likely to decrease with time because of root proliferation and vegetation encroachment in gaps, and lateral canopy development (Müller and Wagner, 2003; Muth and Bazzaz, 2002). No differences in soil water were often found in small gaps (<0.05 ha)

(Arunachalam and Arunachalam, 2000; Clinton, 2003; Albanesi et al., 2008). At the DMS study, a better understanding of canopy opening effects on understory vegetation would require measurement of key microclimatic factors across the different stand components; i.e., forest interior, leave islands and gaps.

Few studies have examined changes in vegetation composition in gaps in relation to microclimatic features. In a Hungarian beech forest, increased soil water in gaps had a strong effect on abundance of certain species (e.g., *Atropa belladonna* L, *Epilobium montanum* L., *Hypericum perforatum* L., *Stachys sylvatica* L., and *Urtica dioica* L.) (Gálhidy et al., 2006) supporting species-specific distribution patterns within gaps. On a broader scale, distribution of several understory species was found to be related to direct measures of soil water content in Oregon's western Cascades (Lookingbill et al., 2004) and British Columbia (Wang, 2000) suggesting that understory species are likely sensitive to soil water availability within predominantly mesic watersheds.

5. Conclusion

Thinning contributed to the development of a diverse plant understory in terms of overall diversity of species and plant groups differing in successional status, growth form, and structure, without decreasing tree regeneration or triggering plant invasions. This study provides evidence that thinning may impact ecosystem resilience, for example by enhancing functional effect and response diversity. Alternative silvicultural methods provide opportunities to manage for selected vegetation components, allowing both timber production and maintenance of ecological functions such as N fixation, wildlife habitat, and species diversity.

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