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Short-term bryoid and vascular vegetation response to reforestation alternatives following wildfire in conifer plantations

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Keywords
Aspect; Bryophytes; Fire; Mixed-species plantings; Plantation management; Shrub removal; Site conditions; Vegetation dynamics; Vegetation removal

Abbreviations
ISA = indicator species analysis;
MRBP = blocked multi-response permutation procedure;
NMS = non-metric multidimensional scaling;
sph = stems per hectare

Nomenclature
USDA (2007)

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Abstract

Question: How are dynamics of early-seral post-fire vascular plant and bryoid (terrestrial mosses, lichens, and fungi) vegetation impacted by reforestation activities, particularly manual vegetation removal and planting density? Does the relationship between vegetation dynamics and vegetation removal differ between harsh (west-facing) and moderate (east-facing) aspects?

Location: Five high-severity burn plantation forests of *Pseudotsuga menziesii* in southwestern Oregon, USA.

Methods: Plantations severely burned in a recent wildfire were planted with conifer seedlings as a four-species mixture or a monoculture, at two different densities, with and without manual vegetation removal. A subset of plots was also planted on a contrasting aspect within each plantation. The contrasting aspects differed in potential solar insolation and were indicative of moderate (eastern exposure) and harsh (western exposure) site conditions. Covers of shrub, herbaceous and bryoid vegetation layers were measured during reforestation activities 2–4 yr after the fire. Dynamics of structural layer cover and community composition were compared among treatments with analysis of variance and multivariate analyses (non-metric multidimensional scaling and blocked multi-response permutation procedure).

Results: Structural layer cover and community composition differed between areas that received reforestation treatments and untreated areas. However, variability within treatments in a plantation was greater than variability within treatments across plantations. Effects of vegetation removal on composition and structure were more evident than effects of planting or altering planting density. Vegetation removal decreased cover of tall and low shrub and the bryoid layer, and increased herbaceous layer cover. Bryoid community and low shrub structural layer responses were more pronounced on moderate aspects than on harsh aspects. Vegetation removal shifted vascular plant community composition towards exotic and annual species.

Conclusions: These reforestation treatments may be implemented without substantially altering early-seral vegetation community composition dynamics, especially in areas with harsh site conditions. Site conditions, such as aspect, should be evaluated to determine need and potential effects of reforestation before implementation. Monitoring for exotic species establishment should follow reforestation activities.

Introduction

On much of the publicly owned forest in the USA, post-fire forest management goals have changed in recent years from a focus on rapid conifer regeneration to include multiple objectives. These objectives typically include the maintenance of species and structural diversity, or accelerated development of late-seral habitat characteristics (Curtis et al. 1998). Management alternatives designed to meet these diverse and continually

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evolving management objectives are needed (Puettmann et al. 2009). Reforestation activities provide opportunities to meet a variety of ecological and restoration objectives, in addition to more conventional timber production objectives (Puettmann et al. 2009; Paquette & Messier 2010). For example, reforestation in other ecosystems, such as degraded tropical forests, has been demonstrated to be an effective means of accelerating the development of diverse, natural forests (Lamb 1998).

Previous human activities and disturbance regimes have a significant impact on the outcomes of management practices and the response of forests to disturbances (Lamb 1998; Wilson et al. 2009). Naturally regenerated forests typically result in mixed species stands that exhibit high resilience to changing conditions following fire (Trabaud et al. 1985; Turner et al. 1997; Wang & Kemball 2005; Donato et al. 2009; Swanson et al. 2010). In contrast, fire within established monoculture plantations can result in distinct conditions, such as lack of biological and structural diversity, owing to homogeneous overstory and understory size, structure and species composition. Because of these factors, burned plantations may benefit from management activities designed to help meet specific restoration objectives (Lamb 1998; Maestre & Cortina 2004; Swanson et al. 2010). For example, lack of conifer establishment because of competition from other vegetation and limited seed sources (Hobbs et al. 1992; Maestre & Cortina 2004) may hinder recovery of burned plantations. In such cases, reforestation with a native conifer mixture and low-intensity vegetation control to ensure seedling survival (but not maximum growth) is a viable management option (Hobbs et al. 1992). This type of management can result in spatially and structurally heterogeneous forests that can more closely resemble naturally regenerated forests (Paquette & Messier 2010).

Reforestation activities generally occur shortly following disturbances, such as wildfires. This initial post-disturbance period is coincident with the development of early-seral plant communities (Cremer & Mount 1965; Trabaud et al. 1985; Turner et al. 1997; Wang & Kemball 2005; Kayes et al. 2010). Early-seral plant communities provide many important functions in post-fire forests, including prevention of erosion, replenishment of soil organic matter, nitrogen fixation in association with microorganisms, provision of wildlife habitat and facilitation of the establishment of late-seral species (Chapin et al. 1994; Swanson et al. 2010; Walker et al. 2010). Early-seral forests also support organisms and processes not present in closed canopy forests, allow nutrient renewal in ecosystems, and are 'hotspots' of biodiversity (Halpern 1988; Swanson et al. 2010). In addition, early-seral species can shape the future vegetation dynamics of ecosystems (Turner et al. 1997; Ghermandi et al. 2004; Walker et al. 2010; Young & Peffer 2010). Early-seral plant communities can promote understory diversity of later successional stages by retaining seed sources and herbaceous species with limited dispersal capabilities (Lamb 1998; Aubin et al. 2008).

Through direct and indirect effects, pre- and post-fire forest management activities have the potential to alter early-seral vegetation composition, structure and function by increasing soil disturbance, reducing duration of forest recovery, and homogenizing forest conditions and genotypes (Loumeto & Huttel 1997; Swanson et al. 2010). The effects of forest management practices on conifer growth and establishment are well documented in the drier portions of the Pacific Northwest (Pabst et al. 1990; Hobbs et al. 1992; Tesch et al. 1992). However, there is little documentation of the impact of reforestation practices on the dynamics of early-seral vegetation structure, composition, and function.

The primary objective of this study was to examine the dynamics of early-seral vegetation structural layers and plant communities within post-fire reforestation treatments designed to meet management objectives, such as natural recovery, enhancing tree diversity, and ensuring conifer establishment. A second objective was to compare early-seral vegetation structural layer and plant community dynamics between treatments with and without manual vegetation removal for different relative aspects, indicative of moderate (eastern exposure) and harsh (western exposure) site conditions.

Methods

Study location

Southwestern Oregon has a mixed severity fire regime with average fire return intervals ranging between 5 and 75 yr (Sensenig 2002). The climate is generally characterized by mild, wet winters and warm, dry summers. Topography is often steep (slopes > 25%) with volcanic bedrocks and elevations between 800 and 1000 m.

In 2002, the Timbered Rock fire burned 11 000 ha in the Western Cascades physiographic province of southwestern Oregon. The area lies within the *Abies concolor* and mixed conifer forest zones (Franklin & Dyrness 1973) and federal lands within the fire have been designated for management to maintain or enhance late-seral forest characteristics (USDA & USDI 1994). Before the fire, *Pseudotsuga menziesii* (Douglas-fir) plantations less than 35 yr old occupied approximately 40% of the burned area. The study was conducted in five such plantations selected based on fire severity (moderate to high, using fire severity maps derived from Landsat 7 satellite imagery), size (> 3 ha), and determined to be a high priority for reforestation.

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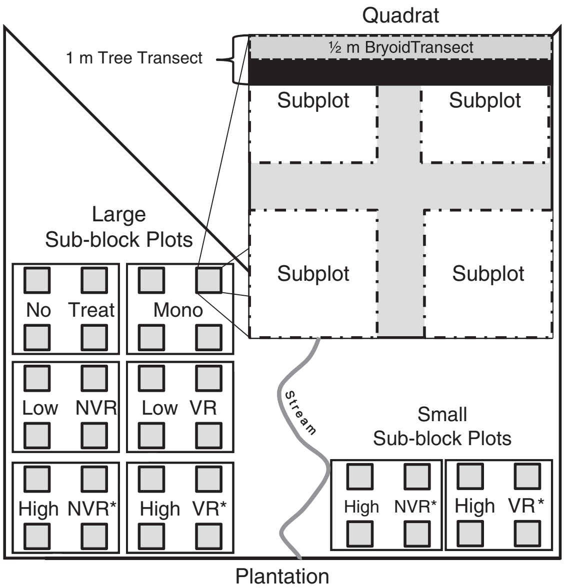
The pre-fire plantations averaged 280 planted *P. menziesii* stems per hectare (sph). Plantations ranged in age from 17 to 37 yr old when burned. In addition to the dominant *P. menziesii*, the plantations had smaller components of *A. concolor* (average 50 sph), *Pinus ponderosa* (average 42 sph), *Pinus lambertiana* (average 10 sph), and *Calocedrus decurrens* (average 11 sph). Hardwoods, including *Arbutus menziesii, Acer macrophyllum* and *Quercus chrysolepis,* were abundant in plantations before the fire with a combined average density of 500 sph. See Kayes et al. (2010) for full plantation descriptions.

Research design

Within each plantation, six 0.25 ha (slope corrected) square plots were established on one generally uniform aspect (referred to as a large sub-block) 2 yr post-fire (Fig. 1). Six treatments representing a range of management objectives were used: (1) 'Untreated' – unplanted without vegetation removal; (2) 'Low-density NVR' – mixed species (see below) planted at 470 sph (low density) without vegetation removal (NVR); (3) 'High-density NVR' – mixed species planted at 1075 sph (high density) without vegetation removal; (4) 'Low-density VR' – mixed species planted at 470 sph with vegetation removal (VR); (5) 'High-density VR' – mixed species planted at 1075 sph with vegetation removal; and (6) 'Monoculture' – *P. menziesii* planted at 1075 sph with vegetation removal (typical of historical US federal land management). Treatments were randomly assigned to plots.

To reflect surrounding forest composition and account for expected mortality, mixed-species treatments were planted with 40% *P. menziesii* and 20% of each *P. lambertiana*, *P. ponderosa*, and *C. decurrens*. Vegetation removal consisted of manually cutting vegetation (targeting tall shrubs and hardwood trees but including surrounding forbs and graminoids) taller than approximately 30 cm over the entire plot each summer in years 2–4 post-fire and scraping (scalping) all vegetation down to mineral soil in an approximate 0.75 m radius around planted conifer seedlings in year 3 post-fire (year 2 post-planting). Average area scalped ranged from 0% to 22% of a given plot in year 3 with $<8\%$ remaining disturbed in year 4 post-fire. In one plantation, the high-density NVR plot on a harsh aspect was accidentally scalped.

Two additional plots were established on a contrasting aspect (referred to as a small sub-block) within each plantation. A subset of treatments (high-density mixed species plantings with and without vegetation removal) was randomly assigned to small sub-block plots. High-density plantings were assumed to have a greater impact on vegetation than low-density plantings and therefore were considered more sensitive to affects on contrasting aspects. Sub-blocks on contrasting aspects were designated as relatively 'harsh' or 'moderate' within a plantation based on azimuth, to reflect solar radiation and temperature patterns. Harsh aspects ranged from 220° to 360° and moderate aspects ranged from 44° to 160°. During the summer, steep west-facing slopes aspects receive maximum radiation during the hottest time of the day (i.e. afternoon). In contrast, east-facing slopes aspects receive maximum radiation early in the morning, when it is cooler (Gates 1972). One plantation had the large sub-block on the moderate aspect whereas the other four plantations had the large sub-block on the harsh aspect as a result of available area and plantation orientation.



Treatment Component	No Treat	Low NVR	High NVR*	Low VR	High VR*	Mono
Species	-	Mixed	Mixed	Mixed	Mixed	PSME
Veg Removal	-	NVR	NVR	VR	VR	VR
Density	-	Low	High	Low	High	High
Subblock	Large only	Large only	Both	Large only	Both	Large only

Fig. 1. Schematic of experimental and sampling design within one plantation and table of different treatment components. The large sub-block was on the harsh relative aspects for four plantations and on the moderate aspect for one plantation. Tall shrubs and trees were sampled in four quadrats (10 m × 10 m, encompassing subplots and transects) within each plot. Low shrubs and herbs were sampled in four 3 m × 3 m subplots within each quadrat. Bryoids were sampled in 1/2 m bryoid transect. Tree seedlings were sampled in the 1/2 m bryoid transect and an additional 1/2 m to make a 1 m tree transect. NVR, no vegetation removal; VR, vegetation removal; High, high-density or 1075 stems per hectare (sph); Low, low-density or 470 sph; Mixed, species mixture of *Pseudotsuga menziesii*, *Pinus ponderosa*, *Pinus lambertiana*, and *Calocedrus decurrens*. Mono, *Pseudotsuga menziesii* (PSME) monoculture planted at 1075 sph with vegetation removal, *indicates treatments represented on both contrasting aspects (i.e. both sub-blocks).

Data collection

Cover (per cent of area) of vascular plant species was recorded for three summers (years 2–4 post-fire, or

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treatment years 1 through 3). Within each plot, we established four permanently marked 10 m × 10 m quadrats, each randomly dispersed within one quadrant of the plot (Fig. 1). Both small hardwood trees (resprouting hardwood trees < 5 cm DBH) and shrubs ≥ 1.3 m tall were termed tall shrubs because post-fire sprouting growth forms occupy the same structural layer. Individual tall shrub per cent cover was measured as [canopy area (width × length: cm^2)/quadrat area (cm^2)] 100. Length was measured along the longest axis of each tall shrub in a quadrat and width was measured perpendicular to the long axis at a variable observer chosen point. Cover (to nearest 1%) of all other vascular plants, including shrubs < 1.3 m tall (low shrubs), was visually estimated by species in 16 3 m × 3 m subplots, one at each quadrat corner (Fig. 1). Species with < 1% cover were recorded as present. Total layer cover (maximum 100% per layer) of tall shrubs per quadrat and low shrubs and herbs per subplot was visually estimated. Naturally regenerated tree seedlings were counted in a 1 m × 10 m transect on the upslope quadrat edge (Fig. 1) for inclusion in multivariate analyses.

Bryoid layer (i.e. terrestrial bryophytes, lichens and fungi) cover data were collected in 20 contiguous subplots (0.5 m × 0.5 m) along 0.5 m × 10 m transects across the upslope quadrat edge (Fig. 1) in the third and fourth summer post-fire. Bryoid layer species and the total bryoid layer across taxa were assigned cover classes adapted from McCune et al. (1997). Cover classes were coded as follows: (1) < 3 shoots present; (2) 4–10 shoots present; (3) > 10 shoots present but < 25% cover; (4) 25–50% cover; (5) 51–80% cover; and (6) 81–100% cover. Including the abundance count at a fine scale weights species with small populations more heavily and simplifies quantifying dispersed populations. On this scale, the average value approximates average log (abundance) and is not transformable to an arithmetic scale. The bryoid layer was included because it has been shown to respond differently from vascular plants to disturbance and environmental factors (McCune & Antos 1981; Penman et al. 2008; Turner & Kirkpatrick 2009). In addition, the bryoid layer is a major component of early-seral vegetation biomass and diversity (Cremer & Mount 1965; Wang & Kemball 2005) that is often excluded from ecological studies because of logistical constraints, such as difficult identification.

Plants were determined to the species level when possible, otherwise to the genus level or species groups. Fungi were not identified. To characterize changes in plant community composition, life-history trait groups (traits) were defined based on Lawton (1971), Vitt et al. (1988), Spies (1991), Hickman (1993), Wang & Kemball (2005), USDA (2006, 2007), and personal experience. Vascular traits were based on fire response (invader – highly dispersive pioneer species; avoider – shade tolerant, slow colonizers; evader – seed banking species; or endurer – sprouting species) as defined by Rowe (1983), herbaceous life form (forb, graminoid, or fern), growth form (annual or perennial herb, woody sub-shrub species, or deciduous or evergreen shrubs), successional status (early- or late-seral), nitrogen-fixer association (fixer) and origin (exotic or native). The bryoid layer traits were based on fire response (invader – highly dispersive pioneers, sexual reproduction or residual – likely present before fire, asexual reproduction), longevity [short (< 5 years) or long (5+yr) – lived], and growth form (acrocarpous or pleurocarpous moss, leafy or thalloid liverwort, lichen, or fungi). See the Supporting Information for full list of species and life-history traits.

Data analysis

We examined dynamics of structural layers using analysis of variance (ANOVA) and dynamics of plant community composition using multivariate techniques: non-metric multidimensional scaling (NMS), blocked multi-response permutation procedure (MRBP) and indicator species analysis (ISA). Because of the incomplete block design, data was analysed using two subsets of treatments (Fig. 1). We first examined differences in vegetation dynamics in reforestation treatments over time using the six treatments (four mixed-species treatments, untreated and monoculture) on the large sub-block. For structural layers and plant community composition, we examined differences in variables between (1) individual reforestation treatments and untreated areas; (2) treatments with and without vegetation removal; and (3) treatments planted at high and low densities on the large sub-block. The large sub-block analyses were not influenced by removal of the single large sub-block that occurred on a relatively moderate aspect (data not shown). The influence of aspect on the impacts of vegetation removal on structural layers and plant community composition was tested using the mixed species high-density reforestation treatments, with and without vegetation removal, on both aspects.

Structural layers

Effects of reforestation treatments on cover of individual structural layers (bryoids, herbs, and low and tall shrubs) over time were evaluated using a mixed model ANOVA using SAS (version 9.1; SAS Institute Inc., Cary, NC, USA) PROC Mixed. Treatment (four mixed-species treatments, untreated and monoculture in the large sub-block) was a fixed effect and plantation was a random effect. Plots served as subjects for repeated measurements (2 yr for

 Doi: 10.1111/j.1654-109X.2011.01129.x

bryoids and 3 yr for vascular plants). All model assumptions were met. The one accidentally scalped plot was removed from year 3 and 4 analyses. Multiple comparisons, corrected using a Dunnett (1955) adjustment, examined differences in cover of each structural layer between untreated and treated areas. A priori contrasts were used to assess differences in structural layer cover between areas with vegetation removal (Low-density and High-density VR treatments) versus without vegetation removal (Low-density and High-density NVR treatments) and areas planted at low density (Low-density VR and NVR) versus high density (High-density VR and NVR) in individual years.

To examine the influence of contrasting aspect on vegetation removal effects for structural layer responses, we applied a mixed model ANOVA as described above. In this model, explanatory variables were vegetation removal (vegetation removal or no vegetation removal), year and the addition of aspect (harsh or moderate) modeled as a split plot factor because of restriction of plot location. Contrasts assessed differences in structural layer covers between areas with and without vegetation removal on moderate and harsh aspects.

Community composition

Before analysis of community composition, species cover per plot was relativized by species maximum to standardize for different measures of cover and large variation in magnitudes of cover between different species (McCune & Grace 2002). Species occurring in $< 5\%$ of plots in all years (33% or 63 vascular and 47% or 20 bryoid species) were deleted to reduce dataset noise (McCune & Grace 2002).

Effects of reforestation treatments on vascular plant and bryoid community dynamics were determined by NMS (Kruskal 1964) ordination (PC-ORD version 6.1; MjM Software, Gleneden Beach, OR, USA) using autopilot 'slow-and-thorough' setting with Sørenson distance, random starting configurations and 250 runs of real data (McCune & Grace 2002). Three-dimensional solutions had a final instability of < 0.00001. To control for large differences among plantations and years (see Kayes et al. 2010), differences in plant communities between areas (1) with and without reforestation treatments, (2) with and without vegetation removal, and (3) planted at low density and high density were discerned graphically from the length and direction of NMS vectors connecting values for the untreated area to treated area values within each plantation and year. Differences in community composition between planted areas with and without vegetation removal were further discerned by examining successional trajectories of plots remeasured over time and rotating the tails of successional vectors to the origin (McCune & Grace 2002). We graphically examined difference in plot scores between areas with and without vegetation removal on contrasting aspects.

Possible associations of the functional attributes of plant community composition with the occurrence of vegetation removal were assessed by Pearson's correlation coefficients between trait abundance and NMS plot scores following rotation of ordination axes to maximize the influence of vegetation removal. Functional attribute associations for the vascular communities were assessed by individual year because of the strong impact of time since fire (Kayes et al. 2010). Specific trait dominance for vascular communities in areas with and without vegetation removal was determined using a blocked ISA (Dufrêne & Legendre 1973) applied to each combination of year and vegetation removal status. For the bryoid communities, the blocked ISA for trait abundance was run for vegetation removal status in years 3 and 4 combined.

To support graphical results from NMS, differences in vascular plant and bryoid community composition between untreated areas and all other treated areas were examined with Bonferroni-corrected (Miller 1981) pairwise comparisons from MRBP (Mielke & Berry 2001; McCune & Grace 2002). The MRBP was also used to examine differences in vascular plant and bryoid community composition between areas (1) with and without vegetation removal, (2) with low-density versus high-density planting and (3) with and without vegetation removal on contrasting aspects in individual years. For MRBP analyses, treatment medians were converted to non-parametric ranks and aligned to zero within plantations (which requires Euclidean distance) to focus on the within-plantation differences (McCune & Grace 2002).

Results

Structural layers

Structural layer covers, with the exception of low shrubs, were altered by reforestation treatments (Table 1). Average tall shrub cover was higher in untreated areas than those with vegetation removal (Table 1). Herb coverage was, on average, 20% higher (95% CI 4%, 36%) in areas planted at low density with vegetation removal than in untreated areas (Table 1). Bryoid layer cover class was lower in areas planted at high density with vegetation removal (95% CI 2.32, 3.48) than in untreated areas (95% CI 3.12, 4.28; Table 1).

Structural layer covers differed in areas with and without vegetation removal (Fig. 2) but not in areas planted at different densities (data not shown). Tall shrub cover was lower in areas with vegetation removal than in areas without vegetation removal and differences in tall shrub

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Table 1. ANOVA *F*-statistics and *P*-values (a) and contrast results (b) of structural layer coverage for differences between areas with different reforestation treatments and untreated areas on the large sub-block. *P*-values and contrast values that were significant at $P \leq 0.05$ are in bold type. Per cent (%) and cover class are the average difference in per cent cover and bryoid cover class between the untreated and specified treatment. Denominator df = 66 for tall shrubs, low shrubs and herb and denominator *df* = 42 for bryoids. High-density = mixed species planting at 1075 stems per hectare (sph), low-density = mixed species planting at 470 sph, monoculture = *Pseudotsuga menziesii* planting at 1075 sph with vegetation removal, NVR = no vegetation removal, VR = vegetation removal, SE = Standard error from contrasts, *F* = ANOVA *F*-statistics, *P* = ANOVA *P*-value and df = numerator degrees of freedom.

ANOVA results	Tall shrubs			Low shrubs		Herbs		Bryoids		
	df	*F*	*P*	*F*	*P*	*F*	*P*	df	*F*	*P*
(a)										
Treatment	5	8.5	< **0.0001**	1.51	0.2	2.5	**0.043**	5	3.4	**0.01**
Year	2	44	< **0.0001**	194	< **0.0001**	131	< **0.0001**	2	8.9	**0.005**
Treatment × year	10	9.5	< **0.0001**	1.09	0.39	0.47	0.9	10	1.2	0.34

Difference from untreated	Tall shrubs		Low shrubs	Herbs	Bryoids
	Year 2	Year 4			
Treatment	% (SE)	% (SE)	% (SE)	% (SE)	Cover Class (SE)
(b)					
Low-density NVR	1.5 (4.2)	3.5 (4.2)	− 1.9 (5.1)	3.9 (6.2)	0.1 (0.26)
High-density NVR	2.9 (4.2)	4.3 (4.2)	9.9 (5.3)	8.8 (6.2)	0.15 (0.28)
Low-density VR	**9.0 (4.2)**	**25.8 (4.2)**	4.4 (5.1)	**20.0 (6.2)**	− 0.1 (0.26)
High-density VR	**9.1 (4.2)**	**25.8 (4.2)**	− 1.5 (5.1)	4.8 (6.2)	**− 0.8 (0.26)**
Monoculture	**9.1 (4.2)**	**25.8 (4.2)**	− 0.3 (5.1)	8.6 (6.2)	− 0.1 (0.26)

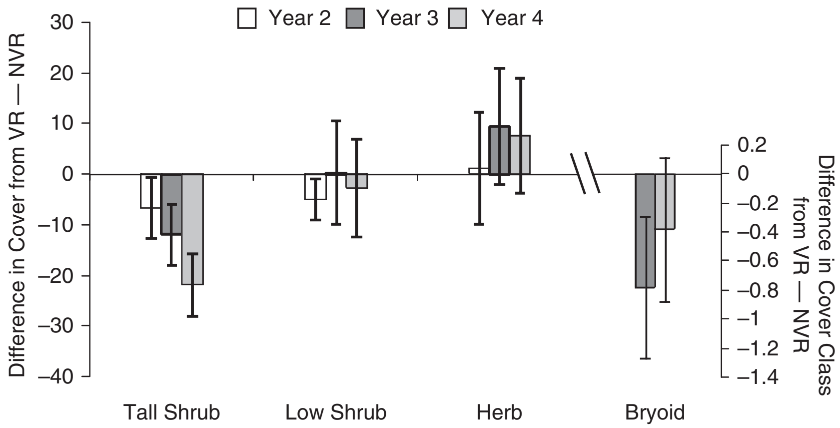

Fig. 2. Average difference in structural layer coverage (%: left axis) and bryoid layer coverage class (right axis) between areas with and without vegetation removal over time on the large sub-block. Numbers are average difference between areas with and without vegetation removal and 95% CIs. Differences with CIs that do not encompass zero were significantly different from zero at $P \leq 0.05$. NVR, mixed species planting without vegetation removal and VR, mixed species planting with vegetation removal.

cover became more pronounced over time (Fig. 2). Vegetation removal decreased low shrub and bryoid layer cover at the time of initial sampling (Fig. 2). By the fourth year post-fire, the impacts of vegetation removal on low shrub and bryoid layer cover were not discernible (Fig. 2). Vegetation removal had no effect on herb cover throughout the study (Fig. 2). Planting density of mixed-species conifers had no discernable impact on vegetation cover for any structural layer in any year (data not shown).

Aspect influence on vegetation response to vegetation removal was limited to the low shrub structural layer (Table 2). Vegetation removal decreased low shrub cover by 16% (95% CI − 26%, − 6%) on moderate aspects, but had no effect on harsh aspects (95% CI − 13%, 7%). Aspect did not influence responses to vegetation removal by tall shrub, herbaceous and bryoid layers (Table 2).

Community composition

Vascular plant communities differed between all treated, regardless of treatments, and untreated areas within plantations based on NMS (Fig. 3). However, MRBP did

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Table 2. ANOVA results of structural layer per cent cover and cover class for differences in areas with and without vegetation removal on contrasting aspects over time. Results are for high-density mixed species plantings with and without vegetation removal in large and small sub-blocks. Significant *P*-values ($\leq$ 0.05) are in bold type. N = numerator df, D = denominator *df*, F = ANOVA *F*-statistic, *P* = ANOVA *P*-value.

ANOVA results	*df*		Tall shrubs		Low shrubs		Herbs		Bryoids			
	N	D	*F*	*P*	*F*	*P*	*F*	*P*	N	D	*F*	*P*
Vegetation removal	1	38	804.7	< **0.0001**	13.03	**0.0009**	0.19	0.67	1	22	20.92	**0.0001**
Aspect	1	4	0.24	0.65	2.08	0.22	2.74	0.17	1	4	2.3	0.2
Vegetation removal × aspect	1	38	0.24	0.63	6.16	**0.02**	0.01	0.93	1	22	0.23	0.64
Year	2	38	46.32	< **0.0001**	250.85	< **0.0001**	81.6	< **0.0001**	1	22	13.4	**0.001**
Vegetation removal × year	2	38	46.32	< **0.0001**	0.47	0.63	1.9	0.16	1	22	8.43	**0.008**
Aspect × year	2	38	0.84	0.44	0.76	0.47	0.44	0.64	1	22	0.08	0.78
Vegetation removal × aspect × year	2	38	0.84	0.44	1.7	0.12	0.41	0.67	1	22	0.97	0.34

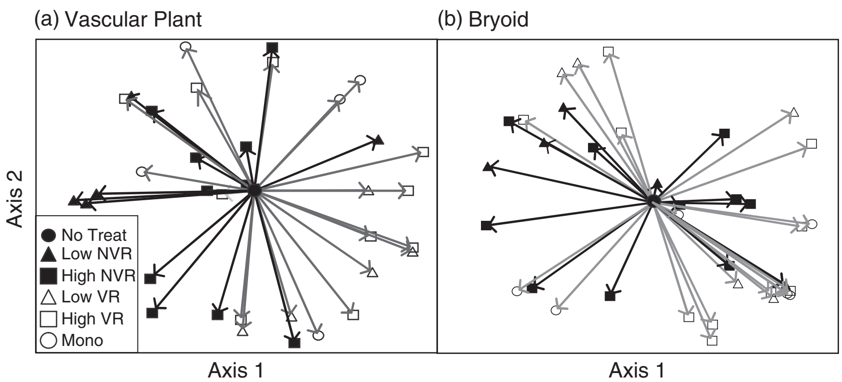

Fig. 3. Change in community composition (indicated by tinted arrows for areas with vegetation removal and black arrows for areas without vegetation removal) between areas with mixed-species reforestation treatments and untreated areas (centroid) in year 4 for vascular plants (**a**) and bryoids (**b**) within plantations from three-dimensional non-metric multidimensional scaling (NMS) ordinations. No Treat, untreated; NVR, no vegetation removal; VR, vegetation removal; High, mixed species planting at 1075 stems per hectare (sph); Low, mixed species planting at 470 sph; Mono, *P. menziesii* monoculture planted at 1075 sph with vegetation removal.

not confirm differences in vascular plant community composition between treated and untreated areas (Table 3). In general, differences in vascular plant community composition among years (Fig. 4) and plantations (data not shown) were greater than differences among treatments. The change in vascular plant community composition between year 2 and year 3 was similar in all treated areas (associated with increased herb coverage and scalp area) based on NMS successional trajectories (Fig. 4a).

Although only slight differences were evident among treatments, when singled out, vegetation removal practices resulted in altered vascular plant community composition. Differences in composition owing to vegetation removal increased with time since treatment. These findings are based on four results. First, community composition of areas planted with and without vegetation removal differed in the direction of change from untreated areas shown in NMS (Fig. 3a). Second, the community compositions of areas with and without vegetation removal were significantly different by year 4 based on MRBP (Table 3). Third, correlation between vascular plant NMS community composition scores and an indicator of vegetation removal status increased over time (Table 4). Finally, changes in vascular plant community composition from year 3 to year 4 diverged between areas with and without vegetation removal based on NMS successional trajectories (Fig. 4b).

Vegetation removal resulted in a shift in dominance of vascular plant trait groups over time. Vascular plant NMS scores for plots with vegetation removal were correlated with cover of perennials in year 2 and cover of annuals, exotics and graminoids in year 4 (Table 4). Vascular plant NMS scores for areas without vegetation removal were correlated with evergreen shrub coverage in year 2 and with cover of deciduous shrubs, evaders and natives in year 4 (Table 4). Similarly, based on ISA, annuals, exotics and invaders were indicators of areas with vegetation removal in year 3; graminoids were indicators in year 4 (Table 4). In year 4, areas without vegetation removal had many indicator traits, including those that were correlated above and evergreen shrubs, endurers, sub-shrubs, early-seral species and perennials (Table 4).

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Table 3. A-statistics (A) and *P*-values (*P*) for differences in vascular plant and bryoid community composition between areas with different treatment combinations on the large sub-block from a blocked multi-response permutation procedure (MRBP). Significant *P*-values ($\leq$ 0.05) are in bold type. Plantation with accidentally scalped plot was included because of no change in results. Multiple comparison *P*-values (treatment versus untreated) are corrected using a Bonferroni correction. NVR = No vegetation removal, VR = vegetation removal.

Comparison	Treatment 1	Treatment 2	Vascular				Bryoid layer			
			Year 2		Year 4		Year 3		Year 4	
			A	*P*	A	*P*	A	*P*	A	*P*
Treatment versus untreated	Untreated	Low-density NVR	– 0.02	1	– 0.02	1	0.02	0.2	0.02	0.75
	Untreated	High-density NVR	– 0.02	1	– 0.02	1	0.01	1	– 0.05	1
	Untreated	Low-density VR	0.01	0.45	0.04	0.1	0.04	0.6	0.01	1.7
	Untreated	High-density VR	– 0.001	1	0.01	0.95	0.03	1	– 0.01	1
	Untreated	Monoculture	– 0.005	1	0.001	1	0.02	1	– 0.005	1
NVR versus VR	High-density NVR	High-density VR	0.02	0.12	0.04	**0.04**	0.05	**0.04**	0.04	0.22
	Low-density NVR	Low-density VR	0.03	**0.04**	0.04	**0.04**	0.05	**0.04**	0.03	0.44
Low density versus high density	Low-density NVR	High-density NVR	– 0.006	1	– 0.01	1	0.03	0.14	– 0.004	1
	Low-density VR	High-density VR	0.0009	0.96	– 0.02	1	0.02	0.4	– 0.02	1

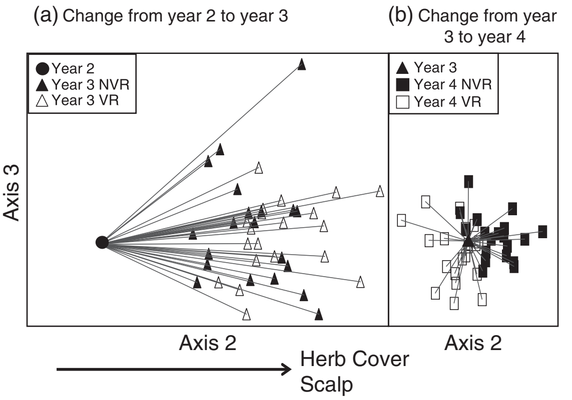

Fig. 4. Successional trajectories (tinted lines) of vascular plant communities in reforestation treatments in the large sub-block at both densities with and without vegetation removal between year 2 and 3 (**a**) and year 3 and 4 (**b**). The centroid represents year 2 (**a**: circle) and year 3 (**b**: triangle). The black arrow below ordination indicates direction of correlated coverage variables ($R^2 \geq 0.2$).

Differences in bryoid community composition between areas with and without vegetation removal were greater than among all reforestation treatments, years or plantations based on NMS (Fig. 5). Bryoid community composition differed between treated and untreated areas within plantations in NMS (Fig. 3b). However, MRBP did not confirm differences in bryoid community composition between treated and untreated areas (Table 3). The MRBP indicated that the bryoid community composition differed between areas with and without vegetation removal in year 3 but not year 4 (Table 3), contrary to the vascular plant community. However, based on NMS, bryoid community composition was consistent across areas with and without vegetation removal regardless of plantation and year (Fig. 5). All bryoid layer traits were negatively associated with vegetation removal (Fig. 5, Table 4). The presence of thalloid liverworts, acrocarpous mosses, and invading and short- and long-lived bryoid species was indicative of areas without vegetation removal (Table 4).

Regardless of time since fire, the effects of vegetation removal on bryoid community composition were more evident on moderate aspects than on harsh aspects, as demonstrated by the separation of areas with and without vegetation removal on moderate aspects in NMS (Fig. 6) and MRBP (Table 5). Aspect did not influence the response of vascular plant community composition to vegetation removal (Table 5).

Discussion

These reforestation activities, primarily vegetation removal, altered structural layers and community composition, and shifted dominant trait groups directly (decreased shrubs and hardwood trees and bryoid layer) and indirectly (increased herb layer, annuals and exotics) in ways that may affect future forest structure and the development of late successional forests.

Structural layers

Dramatic decreases in hardwood trees immediately following manual cutting are expected and have been previously documented (Bell et al. 1997; Canadell & Lopez-Soria 1998; Lindgren & Sullivan 2001). Rapid recovery of sprouting shrubs and hardwood trees limits the effect duration of a single application of manual vegetation removal (Hobbs et al. 1992; Tesch et al. 1992; Canadell & Lopez-Soria 1998; Lindgren & Sullivan 2001). Repeated manual vegetation removal, however, was successful at reducing canopy cover of tall shrubs and hardwood trees for the 4-yr period of observation. While long-term direct

 Doi: 10.1111/j.1654-109X.2011.01129.x

Table 4. Trait indicator values (IV) and Pearson's correlations (*r*) with large sub-block vascular plant (years 2 and 3 individually) and bryoid (years 3 and 4 combined) species composition scores of non-metric multidimensional scaling ordination (NMS) axis rotated to maximize vegetation removal (See Fig. 5 for bryoid community, vascular community not shown). Traits are sorted by direction and strength of correlation in year 4. Strong negative correlations are sensitive to vegetation removal. Strong positive correlations are favored by removal of vegetation. Correlations > 0.40 are in bold type. Indicator traits are from blocked indicator species analysis (ISA) with $P \leq 0.05$. NVR = no vegetation removal and VR = vegetation removal.

Vascular Plants					Bryoid			
Variable	Year 2	Year 4	IV	Indicator Group (year)	Variable	*r*	IV	Indicator Group (year)
	r	*r*						
Traits								
Vegetation Removal	0.190	**0.47**			Vegetation Removal	**0.507**		
Annuals	0.391	**0.556**	29.7	VR (3)	Leafy Liverworts	– 0.272		
Exotics	– 0.147	**0.467**	26.9	VR (3)	Lichens	– 0.309		
Graminoids	– 0.134	**0.406**	27.6	VR(4)	Thalloid Liverworts	– **0.482**	38.5	NVR (3)
Sub-shrubs	0.198	0.181	25.3	NVR (4)	Fungi	– **0.507**		
Avoiders	– 0.093	0.143			Pleurocarpous Mosses	– **0.588**		
Invaders	– 0.155	0.142	23.8	VR (3)	Short-lived	– **0.594**	27.4	NVR (4)
Evergreen Shrubs	– **0.641**	0.02	23.9	NVR (4)	Residuals	– **0.669**		
Perennial Forbs	**0.413**	– 0.062	21.3	NVR (4)	Acrocarpous Mosses	– **0.723**	28.3	NVR (3)
Ferns	0.221	– 0.215			Invaders	– **0.730**	28.2	NVR (3)
Early-Seral	0.137	– 0.290	24.8	NVR (4)	Long-lived	– **0.781**	32	NVR (3)
Endurers	0.224	– 0.335	23.5	NVR (4)				
Nitrogen Fixers	– 0.372	– 0.355	36.4	NVR (4)				
Late-Seral	0.332	– 0.361	24.8	NVR (4)				
Deciduous Shrubs	0.180	– **0.402**	28.7	NVR (4)				
Evaders	0.298	– **0.462**	26.5	NVR (4)				
Natives	0.147	– **0.467**	22.9	NVR (3)				

effects of the vegetation removal on sprouting tall shrub and hardwood tree cover are unlikely (Haeussler et al. 2004), depletion of carbohydrate reserves below ground may occur (Canadell & Lopez-Soria 1998). Potentially because of this depletion of carbohydrate reserves, shrub and hardwood tree biomass has been shown to decrease with repeated disturbance (Trabaud 1991; Delitti et al. 2005; Donato et al. 2009) and repeated cutting (Riba 1998). The reduction of tall shrubs and hardwood trees may alter the structure of late-successional forests because many of these species, if present initially following disturbance, normally persist in forest understories following canopy closure (Halpern 1988; Spies 1991; Puettmann & Berger 2006; Donato et al. 2009). Early-seral woody species may also facilitate the development of late-seral woody species by inhibiting other early successional species (Walker et al. 2010) or by increasing soil nutrients (Chapin et al. 1994). However, shrub cover generally decreases as canopies close (Puettmann & Berger 2006; Garcia et al. 2007) and the removal of vegetation presumably speeds up the process of shrub cover decline.

Bell et al. (1997) also found a negative response of the low shrub layer to removal of upper structural layers as seen on moderate aspects. Other studies found a lack of response from the shrub layer on a range of site conditions (Lindgren & Sullivan 2001; Simard et al. 2004; Nagai & Yoshida 2006), while we found this trend only on harsh aspects. Slash from cut tall shrubs and hardwood trees may damage and/or impede growth of low shrubs. However, plantations in the Acadian forest had greater sub-shrub cover than natural forests (Ramovs & Roberts 2005). While decreases in cover of the low shrub layer did not appear to persist throughout our study, this may reflect the shifting of tall shrub and hardwood tree cover contributions to the low shrub layer as a result of the manual cutting (personal observation). As sprouting tall shrubs and hardwood trees grow, reduction of the low shrub layer may become evident in the future. Many low shrubs are disturbance-responding species that reproduce by seed (i.e. *Rubus* sp. and *Ceanothus* sp.). These species are unlikely to recover over time if there are no microsites available for seed germination and seedling establishment or mature plants to produce seeds. However, many low shrubs persist under forest canopies to the exclusion of other vegetation (Young & Peffer 2010).

Manual vegetation removal may facilitate herb establishment because of increases in light and moisture availability and ground disturbance. Increases in herb cover have also been documented following thinning (Bailey et al. 1998), removal of woody species (Walker et al. 2010) and repeated fires (Delitti et al. 2005; Donato et al. 2009). In contrast, other studies have documented limited or negative response of the herbaceous layer to removal of upper structural layers in a wide variety of forest

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ecosystems (Halpern 1988; Bell et al. 1997; Lindgren & Sullivan 2001; Simard et al. 2004; Nagai & Yoshida 2006; Newmaster et al. 2007). However, these studies did not include a scalping treatment that directly affected the herb and shrub layer. Continued increases in herbaceous cover are possible if the shrub cover remains low in the near-term. Long-term herbaceous cover will probably decline or shift species composition as the canopy closes (Cremer & Mount 1965; Schoonmaker & McKee 1988; Puettmann & Berger 2006; Aubin et al. 2008).

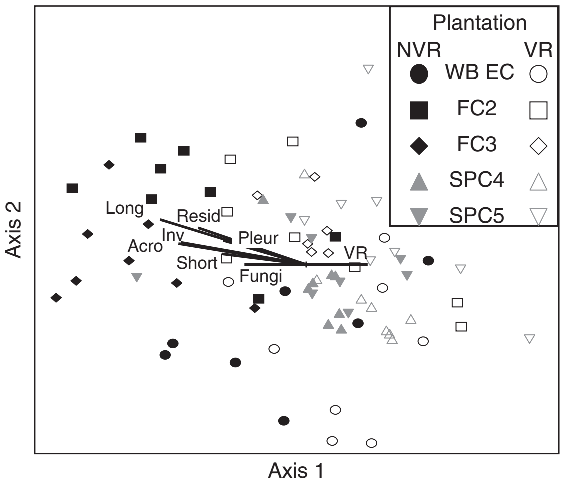

Fig. 5. Plot of areas with and without vegetation removal by plantation (WBEC, FC2, FC3, SPC4 and SPC5) on two axes of non-metric multi-dimensional scaling (NMS) ordination for bryoid community composition. All years are shown and ordination was rigidly rotated by vegetation removal status. Joint plot lines (black) indicate the direction and magnitude of correlated trait variables and a vegetation removal indicator (VR: $R^2 > 0.25$). VR, vegetation removal; NVR, no vegetation removal; Long, long-lived species; Short, short-lived species; Pleur, pleurocarpous mosses; Acro, acrocarpous mosses; Resid, residual species; and Inv, invading species.

Decreased bryoid coverage in association with vegetation removal has been attributed to direct removal (e.g. scalping) and desiccation in several forest types (Fenton et al. 2003; Nelson & Halpern 2005; Davis & Puettmann 2009). Our observed changes (decreases) in bryoid cover coincided with the soil disturbance caused by the scalping treatment. Long-term effects of vegetation removal on the bryoid layer are unlikely because of rapid re-establishment of disturbance adapted species as observed for other disturbed sites (Cremer & Mount 1965; de las Heras et al. 1994; Haeussler et al. 1999; Newmaster et al. 2007). Late-seral bryoid species will also likely colonize over time as canopy conditions change (de las Heras et al. 1994; Kayes et al. 2010).

Community composition

The combination of the direct impact of tree planting (i.e. ground disturbance from planting and planting crew

Table 5. A-statistics and *P*-values for differences in plant community composition between high-density mixed species planting with vegetation removal (VR) versus no vegetation removal (NVR) on two aspects (harsh and moderate) from a blocked multi-response permutation procedure (MRBP). The plantation with the accidentally scalped plot was included because it did not alter the results. Significant *P*-values ($\leq$ 0.05) and relatively strong A-statistics ($>$ 0.1) are in bold type. *P*-values are corrected for multiple comparisons using a Bonferroni correction.

Year	Aspect	Vascular plant		Bryoid	
		A	*P*	A	*P*
Two/three	Harsh	– 0.01	1.0	0.08	0.06
	Moderate	0.02	0.19	**0.15**	**0.05**
Four	Harsh	0.04	**0.03**	0.0005	0.94
	Moderate	0.04	**0.05**	**0.17**	**0.04**

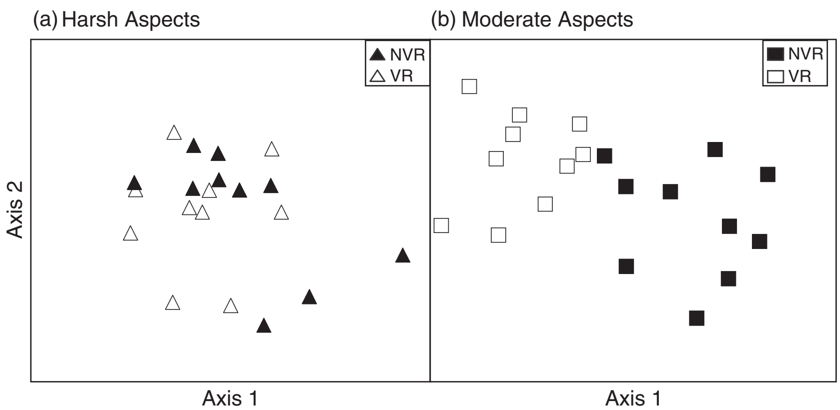

Fig. 6. Bryoid community composition in high-density mixed species treatments with and without vegetation removal on harsh (**a**) and moderate (**b**) aspects from three-dimensional non-metric multidimensional scaling (NMS) ordination. VR, vegetation removal, NVR, no vegetation removal.

 Doi: 10.1111/j.1654-109X.2011.01129.x

traffic) and subsequent increased competition for soil resources by seedlings (Maestre & Cortina 2004; Aubin et al. 2008) created only subtle changes in plant community composition. The relatively weak differences in community composition detected in our study may reflect low power of the experimental design. The difference may be more pronounced with greater replication or higher sampling intensity, or in areas with more homogeneous plant communities. Differences in plant community composition between areas with and without vegetation removal are caused by direct removal of shrubs and impacts of disturbance in herbaceous and bryoid vegetation (Halpern 1988; Bell et al. 1997; Aubin et al. 2008). Similar to our results, Bell et al. (1997) found that removal of the shrub layer shifted in community composition in the boreal forest. Changes in bryoid composition may result from increased harshness of moderate aspects, as less shrub cover results in higher solar radiation and lower surface boundary layer. Plantations have been shown to have altered vascular plant (Schoonmaker & McKee 1988; Loumeto & Huttel 1997; Ramovs & Roberts 2005; Aubin et al. 2008) and bryoid (Haeussler et al. 1999; Fenton et al. 2003; Nelson & Halpern 2005; Newmaster et al. 2007) species composition compared with natural forests in multiple ecosystems, suggesting potential long-term effects of reforestation activities on community composition.

Increased resource availability in conjunction with disturbances (Blumenthal 2005), such as reforestation and vegetation removal, potentially allows for increased cover of exotic and annual species. Increased exotic and annual species cover has occurred with vegetation removal in boreal (Haeussler et al. 2004; Aubin et al. 2008) and tropical forests (Loumeto & Huttel 1997), during plantation establishment (Maestre & Cortina 2004) and following thinning and/or burning in multiple forest types (Bailey et al. 1998; Thysell & Carey 2001). As the forests in our study progress towards canopy closure, cover of exotic species should decrease (Bailey et al. 1998; Ares et al. 2010). However, short-term concern over exotic persistence or spread is warranted as several exotic species were invasive noxious weeds (e.g. *Bromus tectorum*, *Cirsium arvense* and *Cirsium vulgare*). The long-term consequences for exotic species on these plantations are uncertain given existing seed sources and potential interactions with native species, planted conifers and future disturbances. As a result of this uncertainty, exotic species should be monitored during the removal of vegetation, particularly in areas with resident exotic populations nearby (Davis & Puettmann 2009).

Reforestation activities need to be tailored to site conditions even at small spatial scales, such as different aspects within stands. Site conditions, such as aspect, should be evaluated before implementation of post-fire reforestation. Differing site conditions influence vegetation recovery following disturbances, including removal of vegetation (as seen here), plantation establishment (Halpern 1988; Keenan et al. 1997; Haeussler et al. 1999) and wildfire (Turner et al. 1997). For example, long-term effects of mechanical site preparation on vegetation vary according to moisture status, with herbaceous species dominating on moist sites and woody species dominating on drier sites (Haeussler et al. 1999). In contrast, vegetation removal homogenized low shrub cover and bryoid community composition across aspects in the current study and during early plantation development in the other communities of the Pacific Northwest (Halpern 1988).

Our goal was not to assess these reforestation treatments for tree establishment and growth. However, successful vegetation removal treatments have been shown repeatedly to result in quicker conifer establishment (Pabst et al. 1990; Hobbs et al. 1992). Rapid conifer establishment would alter short-term successional trajectories and decrease the amount of time to return to closed canopy forest. However, conifers often survive under abundant shrub layers (Lopez-Ortiz 2007) and over time may become the dominant canopy layer with or without reforestation activities (Shatford et al. 2007). The long-term effects of manual vegetation removal in the absence of salvage logging on structural layers and plant communities are unknown, but the short-term nature of the effects of reforestation activities leaves the potential for many native species to recover over time. Although there is a growing body of literature on the effects of forest management activities on forest plant communities, the early-seral communities have been largely ignored until very recently (Swanson et al. 2010). The effects of shortening the early-seral stage by accelerating canopy closure through planting on processes and species associated with early-seral forests is largely unknown in both managed and unmanaged forest. Further research is needed to determine the long-term impacts of forest management that alters early-seral communities and structures on forest processes, communities, and species.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Vascular plant and bryoid layer species list and trait group designations.

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