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Effects of Variable-Density Thinning on Understory Diversity and Heterogeneity in Young Douglas-fir Forests

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Abstract

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Nine years after variable-density thinning (VDT) on the Forest Ecosystem Study, we examined low understory vegetation in 60 plots of eight stands (four pairs of VDT and control). We compared native, exotic, ruderal, and nonforest species richness among the stands. We used clustering, ordination, and indicator species analysis to look for distinctive patches of plant associations. Native, exotic, ruderal, and nonforest plant species diversity were higher in VDT stands compared to control stands for both forests. Differentiation of the understory into multiple distinct vegetation patches was not definitive, but there were trends toward greater heterogeneity in VDT stands.

Keywords: Biodiversity, forest management, indicator species, ordination, plant communities.

Summary

Conserving biological diversity, maintaining ecological services, and restoring characteristics of natural, late-seral forests are increasingly important objectives in managing second-growth forests. Variable-density thinning (VDT) is a silvicultural technique intended to promote biological diversity and structural heterogeneity (biocomplexity) characteristic of old-growth forests, by inducing fine-scale variation in homogeneous second-growth forest canopies. The Forest Ecosystem Study, in the Puget Trough of Washington, USA is an experiment designed to test the efficacy of VDT for accelerating development of biocomplexity. Nine years after VDT, we examined low understory vegetation in 60 plots of eight stands (four pairs of VDT and control). Half of the stands were in forests where legacies had been retained during logging of old growth, but which had not been manipulated since. The rest of the stands were in a forest where legacies were removed and homogeneity emphasized during two conventional commercial thinnings prior to the experiment. We compared native, exotic, ruderal (pioneer), and nonforest species richness among the stands. We used clustering, ordination, and indicator species analysis to look for distinctive patches of plant associations. Native, exotic, ruderal, and nonforest plant species diversities were higher in VDT stands compared to control stands for both forests. Differentiation of the understory into multiple

distinct vegetation patches was not definitive, but there were trends toward greater heterogeneity in VDT stands. Managers considering VDT for forest stands should carefully evaluate the objectives of the thinning, past management history, local environmental conditions, and landscape context of the stands. Many of the hypothesized benefits of VDT are expected to take many years to develop.

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Introduction

Old forests (forests >150 years) are valued for their aesthetic qualities, biodiversity, and ecological services. Most old forests worldwide have been lost to logging or human development, and there is a recognized need to restore second-growth forests to naturalistic late-seral forests (Gardiner et al. 2003, Roberts and Gilliam 1995). The public has a growing interest in maintaining the ecological services and biological diversity that old, complex forests formerly provided (Bengtsson et al. 2000).

Old forests in the Pacific Northwest of North America developed over the course of 250 to 750 years (Franklin et al. 2002). They are characterized by legacies of species and structural elements from the preceding forest, heterogeneity in horizontal and vertical structure, and in physical properties such as frequency and duration of sun flecks, microclimate, and nitrogen availability (Canham et al. 1990, Chen and Franklin 1997, Franklin et al. 2002). Mosaics of dense canopy patches, thin canopy patches, and canopy gaps produce simple and complex foliage height profiles, accumulations of woody debris, and a wide range of understory light and microhabitat conditions suitable for a diversity of understory plants, animals, and fungi (Carey et al. 1999a, Franklin et al. 2002). In natural Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests, diversity of understory plant species and structural spatial heterogeneity are lowest in young, closed-canopy stands and increase with the age of the forest (Franklin et al. 2002). Young, managed forests are even simpler than young unmanaged forests, lacking legacies and native species (Carey et al. 1999a, 1999b).

The process of development from a low-diversity, closed-canopy monoculture into a forest with high biocomplexity may take hundreds of years, if it occurs at all (Franklin et al. 2002). Variability in forest canopies accrues slowly in natural forests as a result of patchy, multispecies regeneration, the influence of legacies of large live and dead trees on regeneration and growth, self-thinning of dense patches, and density-independent mortality and gap formation in the older tree cohort (Franklin et al. 2002). Regeneration after clearcutting is usually dense, uniform, and monospecific. Thus, the crown-class differentiation that promotes self-thinning may be absent, leading to intense competition in which trees may become unstable owing to greater height than diameter growth and reduced crown depth; the stand may become vulnerable to disturbance (Wilson and Oliver 2000). Desire to restore ecological services, resilience, and biological diversity to natural levels has spurred development of management techniques and land use planning

specifically designed to benefit wildlife, protect riparian corridors, and to enhance biological diversity and forest functions in second-growth forests (Bengtsson et al. 2000, Carey 2003).

Variable-density thinning (VDT) is a technique that has emerged as a potentially promising tool in promoting forest biocomplexity by restoring canopy heterogeneity (Carey 1995, 2003, Muir et al. 2002). Variable-density thinning consists of thinning a forest stand at different intensities in patches at a scale of approximately 0.1 to 0.5 ha, mimicking the scale of patchiness found in old growth (Carey et al. 1999a) and creating a mosaic of overstory tree densities. It is intended to create spatial heterogeneity in canopies that will promote heterogeneity in understory composition and structure and, thus, hasten the development of the structural and functional characteristics of late-seral forests (Carey et al. 1999b). Spatial heterogeneity and environmental variability are critical in promoting plant species and plant growth-form diversity. It is this variability that underlies “preinteractive niche differentiation”—the basis for maintaining high biological diversity in small areas (Hutchinson 1978). Thus, in theory, VDT is expected to increase understory plant community heterogeneity and plant species diversity, and to promote differentiation of habitat for other organisms (e.g., fungi, invertebrates, and vertebrates).

Development of a restored ecosystem with full ecological function and aesthetic appeal requires species composition, spatial heterogeneity, and biocomplexity similar to that in natural reference systems (Carey 2003, Franklin et al. 2002). Carey et al. (1999a) found mosaics of 0.1- to 0.5-ha patches of 6 to 12 plant patch types differing in taxonomic and growth form composition in old-growth Douglas-fir forests of about 20 ha. The diversity of the mosaic (its habitat breadth) proved to be a prime determinant of the diversity and abundance of vertebrates (Carey 2003, Carey et al. 1999a). Younger, managed forest exhibited far less spatial heterogeneity, fewer plant patch types, and less diverse vertebrate communities.

The Forest Ecosystem Study (FES) was initiated in 1991 to test the feasibility of management to accelerate forest development with VDT and underplanting tree seedlings (to restore lost tree species diversity) to promote biocomplexity (Carey et al. 1999b). Because the effects of any management intervention vary with time and many of the benefits expected of VDT are only expected to develop over more than 20 years, long-term monitoring of system responses is necessary to evaluate the effectiveness of the attempted restoration. This study is part of the long-term monitoring effort of this management experiment designed to examine the early and midterm effects of VDT on understory vascular plant communities and diversity.

In summer 2002 (9 years after VDT), we assessed understory vegetation in one pair of stands in each of the four blocks in the study area. We were particularly

interested in whether or not VDT resulted in (1) increases in understory plant community heterogeneity, defined as development of a mosaic of 6 to 12 patch types; (2) marked increases in native plant species diversity; and (3) increases or decreases in exotic plant diversities.

Study Area

The FES was established on the Fort Lewis Military Reservation (N 46° 55'42", W 122° 40') approximately 30 km east of Olympia, Washington, USA in the Puget Trough Physiographic Province in forests of the *Pseudotsuga menziesii/Holodiscus discolor* association of the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973). The area is at the terminus of the Vashon glaciation, 100 to 200 m above sea level, underlain by well-drained glacial outwash sandy loams, with gentle to rolling terrain; slopes range from 0 to 50 percent (Carey et al. 1999b). The area was previously an industrial forest managed for timber production before being acquired as a training area by the U.S. Army during World War II. We chose four blocks of forests, two each in two tracts that had different management histories. The first tract, called the commercial forest (Farley and Hill blocks), was clearcut in 1925, planted, and conventionally thinned in 1972 and again between 1979 and 1989; all salvageable dead wood was removed during thinning operations. The result was a Douglas-fir monoculture with trees averaging 54 cm diameter at breast height (d.b.h.) and 225 stems/ha. The second tract, called the legacy forest (Star and Stellar blocks), was clearcut in 1937, with some large, live Douglas-fir trees, some large, dead Douglas-fir, and substantial coarse woody debris retained; natural regeneration produced a dense Douglas-fir monoculture with trees averaging 34 cm d.b.h. and 600 stems/ha. No other management was done prior to our experiment.

Variable-Density Thinning

The FES has a complete randomized block design, with two blocks in each forest and four 13-ha stands in each block, consisting of two untreated stands and two VDT stands underplanted with shade-tolerant tree seedlings (*Abies grandis* (Dougl. ex D. Don) Lindl., *Alnus rubra* (Bong.), *Pinus monticola* (Dougl. ex D. Don), and *Thuja plicata* (Donn. ex D. Don)). The VDT was implemented in 1993 with four density subtreatments randomly applied to 0.2-ha grid squares within the stand. Density subtreatments were designed to reduce intertree competition to various degrees. As the measure of competition, we used Curtis' (1982) relative density (RD) for Douglas-fir (scale of 1 to 14, with 14 representing a theoretical biological maximum density and 7 the level at which excessive crown restriction occurs). The subtreatments were no thin (RD >6.75), light thin (RD 4.75 to 6.75), heavy

thin (RD 3.25 to 4.75), and open cut (RD <3.25) (Carey et al. 1999b). The general proportion of 2:1, light thin:heavy thin, was based on the ratio found in old growth; the open-cut subtreatment was applied to 15 percent of the stand area and the no-thin subtreatment was from patches left unharvested during logging operations and averaged 13 percent of stand area (Carey et al. 1999a, 1999b). Immediately before our experiment, commercial stands averaged an RD of 6.5 (crowns had closed after thinnings) and legacy stands averaged 7.2 (extensive suppression mortality had occurred and crowns were restricted in diameter and depth). Because the experiment was specifically intended to replicate actual management practice that one would find in a typical thinning operation, roads were included in the forest stands. Both VDT and control stands had small to medium-sized dirt and gravel roads going through them.

The commercial forest had high understory plant cover and higher plant species richness, but was dominated by clonal natives and had 19 exotic species detected in pretreatment sampling; the legacy forest had a sparse, species-poor understory and two exotic species (Thysell and Carey 2000). In the first 3 years after VDT, native plant species diversity increased 150 percent on average, but ruderal (pioneer) species also invaded areas with disturbed soils (Thysell and Carey 2001).

Methods

We assessed understory vegetation in 8 of the 16 stands. These constituted one pair of VDT and untreated stands in each block. We refer to untreated stands as controls, but these stands were subject to continuing forest development and to natural disturbance, including root-rot (*Phellinus weirii*) mortality, windthrow, and ice-storm damage to large tree branches and tree tops. In each stand, 60 vegetation sampling points were located randomly, subject to the constraint that they were >10 m apart to ensure independence of observations. The same arrangement of 60 points was used for all stands.

Data Collection

At each of the 60 sampling points, we assessed the vegetation in two nested plots. We visually estimated the cover of all vascular plants, each plant species, and bryophytes in a 1.0-m² plot. We used the octave scale (< 0.5, 0.5 to 1, 1 to 2, 2 to 4, 4 to 8, 8 to 16, 16 to 32, 32 to 64, > 64) for visual estimation of cover values (Gauch 1982). In a larger 2.0-m fixed-radius (~12.5-m²) circular plot centered at the same point, we recorded the presence of additional vascular plant species that had not been found in the smaller plot. We also recorded slope (percent), aspect (degrees), and overstory canopy density. We described tree and canopy density with two

methods. We counted trees by using a 3-m basal area prism, and estimated canopy cover with “moosehorn” densiometer readings (Robinson 1947) taken at four points 1 m apart along two perpendicular north-south, east-west lines centered on the center point for a total of 17 points for each sample location.

Data Analysis

Plant species were classified as exotic or native, forest or nonforest, and ruderal or nonruderal according to Pojar and MacKinnon (1994), Hitchcock and Cronquist (1991), the USDA Plants Database (USDA 2004) and in consultation with local experts. The nonforest and ruderal species classifications were fairly redundant, with 37 species classified as both. All plant species recorded in the larger plot were used in estimates of species diversity and for constructing species accumulation curves. We calculated Whittaker’s (1972) three kinds of diversity for each stand. We calculated alpha diversity as the average species richness per sample plot. We calculated gamma diversity as the number of species in each stand. We estimated beta diversity, a measure of heterogeneity, as the ratio of the total number of species to the average number of species : $\beta = (\gamma / \alpha) - 1$ (McCune and Grace 2002, Whittaker 1972). We compared beta diversity using Wilcoxon Signed Rank tests. We also calculated the species richness of the classified subsets of species (i.e., exotic, ruderal, etc.) and compared mean richness per plot using analysis of variance (ANOVA). Species accumulation curves were generated for VDT and control stands for each forest. For this analysis, stands from the same treatment in the two blocks in each forest were combined (i.e., the species accumulation curve for VDT in the legacy stand includes the VDT stand from the Star and the Stellar blocks for a total of 120 sample points). In this routine, the number of species per sample unit was based on the average number of species from subsampling up to 500 times (McCune and Mefford 1999).

To assess whether various distinct vegetation patches had developed in the low understory of vascular plants, we used classification, ordination, and indicator species analysis using cover data from the small plot. Although bryophytes are not vascular plants, moss cover (not identified to species) is included as a species because it was an important component of ground cover that is often indicative of dense canopy cover and low vegetative structural diversity, and in some cases the only plant cover in a plot. Data were not relativized because we felt that the species abundances and total plant cover were important components of the patches.

We performed nonmetric multidimensional scaling (NMS) ordination, with Sørensen distances and varimax rotation. We used random starting configurations for 40 runs with real data and 50 runs with randomized data. The instability

criterion for accepting a solution was 0.00001 or 400 iterations. Dimensionality was assessed by adding dimensions that reduced the final stress by ≥ 5 if $P < 0.05$, for the Monte Carlo test. We classified plant communities using a flexible beta linkage with Sørensen distances and beta = -0.25 (Legendre and Legendre 1998, McCune and Grace 2002). We identified indicator species for each of the groups identified in the classification procedure by using the indicator value method (Dufrêne and Legendre 1997). The statistical significance of the maximum indicator value for each group was evaluated using a Monte Carlo randomization method with 25,000 permutations and $\alpha = 0.05$, and we used a threshold of 25 for significant indicator values.

As measures of heterogeneity, we calculated coefficients of variation (CV; ratio of standard deviation:mean) for each NMS axis for each stand. We also assessed the diversity of vegetation groups in each stand at the eight-groups level, using Shannon's diversity index. We calculated Shannon's index as

$$H' = - \sum_i^s p_i \log p_i$$

where p_i is the proportion of each group (i) relative to the total number of groups and s is number of species. We compared CV and Shannon's index using Wilcoxon Signed Rank tests.

Multivariate analysis was done using PC-ORD software (Version 4.0, McCune and Mefford 1999); other analyses were done using JMPIN software version 4.0 (SAS Institute, Cary, NC).

Results

Species Diversity

We recorded 136 species of vascular plants; 125 species were found in the commercial forest (22, or 17.6 percent of species, were exotic) and 91 species were found in the legacy forest (8, or 8.9 percent of species, exotic). Overall, there were more ruderal and nonforest species in the commercial forest than in the legacy forest (table 1). For all blocks, VDT stands had more native, more ruderal, more nonforest, and more exotic species than control stands (table 1). Within blocks, exotic species accounted for 10 to 40 percent of the increase in species richness in VDT stands, ruderal species accounted for 37 to 60 percent, and nonforest species for 47 to 74 percent. Within blocks there was an increase in VDT compared to control stands of 16 to 50 percent, or five to six species, that were native, nonruderal, forest species. Species richness per sample plot was higher in VDT stands than in control stands in

Table 1—Diversity (alpha, beta, and gamma) and numbers of understory plant species in stands from four forest blocks with different management history and thinning treatment in Puget Trough, Washington, summer, 2002

Forest	Block	Treatment	Number of species					
			Total species or gamma (alpha) diversity	Beta diversity	Native	Exotic	Ruderal	Nonforest
Commercial	Farley	VDT	95 (16.4 + 0.7) ^a	4.8	77 (15.1 + 0.5)	18 (1.3 + 0.2)	28 (2.9 + 0.3)	37 (3.5 + 0.4)
Commercial	Farley	C	64 (14.1 + 0.4)	3.5	57 (13.9 + 0.4)	7 (0.2 + 0.1)	12 (1.5 + 0.2)	14 (1.9 + 0.2)
Commercial	Hill	VDT	96 (16.3 + 0.8)	4.9	76 (15.1 + 0.6)	20 (1.2 + 0.2)	32 (3.7 + 0.4)	35 (3.6 + 0.4)
Commercial	Hill	C	81 (13.5 ± 0.6)	5.0	67 (13.0 ± 0.5)	14 (0.4 ± 0.2)	23 (1.6 ± 0.3)	28 (2.0 ± 0.3)
Legacy	Star	VDT	60 (10.5 ± 0.3)	4.7	54 (10.3 ± 0.3)	6 (0.3 ± 0.1)	11 (1.2 ± 0.1)	15 (1.8 ± 0.1)
Legacy	Star	C	50 (9.5 ± 0.4)	4.3	47 (9.3 ± 0.4)	3 (0.2 ± 0.1)	6 (1.0 ± 0.1)	9 (1.2 ± 0.1)
Legacy	Stellar	VDT	69 (14.3 ± 0.5)	3.8	64 (13.8 ± 0.4)	5 (0.4 ± 0.1)	13 (1.9 ± 0.2)	17 (2.5 ± 0.2)
Legacy	Stellar	C	50 (12.2 ± 0.3)	3.1	47 (12.0 ± 0.3)	3 (0.2 ± 0.1)	6 (1.0 ± 0.1)	7 (1.0 ± 0.1)
Total			136	113	113	23	41	53

^aNumbers in parentheses are mean and standard error of species found in 60 vegetation plots. VDT = variable density thinning, C = control (unmanipulated)

both forests (two-way ANOVA, $F = 52.6$, $DF = 1, 1$, $N = 479$, $P < 0.0001$; fig. 1), as were exotic species richness (two-way ANOVA, $F = 23.9$, $DF = 1, 1$, 1[interaction term], $N = 479$, $P < 0.0001$), ruderal richness ($F = 40.8$, $DF = 1, 1$, 1[interaction term], $N = 479$, $P < 0.0001$), and nonforest species richness ($F = 46.5$, $DF = 1, 1$, $N = 479$, $P < 0.0001$). We found no difference in β -diversity (range = 3.1 to 5.0) between commercial and legacy forests (Wilcoxon Signed Rank $T^+ = 23$, $DF = 1$, $P = 0.19$), but we found a trend toward higher β -diversity in VDT compared to control stands (Wilcoxon Signed Rank $T^+ = 25$, $DF = 1$, $P = 0.061$, block centered).

Most species were rare; a few species dominated the understory. Approximately 66 percent of all species, or 90 species, were found in <5 percent of sample plots. Only 15 species were present in >25 percent of the samples. On the other hand, three shrubs and two perennial ferns were found in ≥ 73 percent of the sample plots. These five dominant species were *Gaultheria shallon* Pursh, *Rubus ursinus* Cham. and Schlecht, *Mahonia nervosa* (Pursh) Nutt., *Polystichum munitum* (Kaulfuss) K. Presl, and *Pteridium aquilinum* (L.) Kuhn. These five species also had the highest total and average covers, whereas most species had low cover. For each stand, 39 to

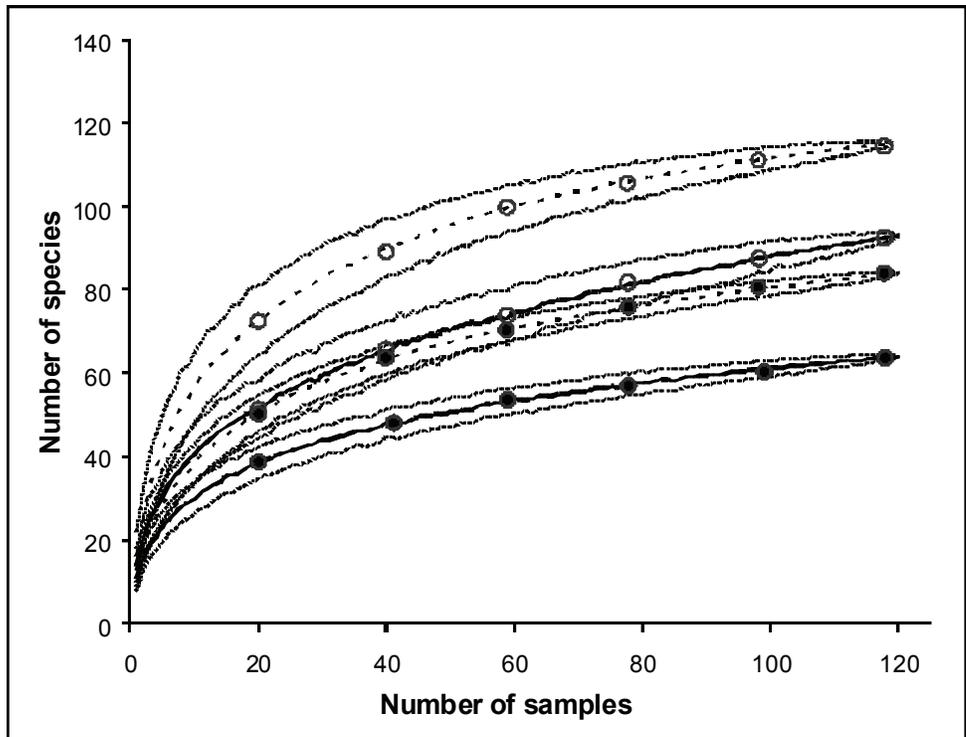


Figure 1—Species accumulation curves with standard deviation envelopes for commercial forest (open circles) and legacy forest (filled circles). Dashed lines indicate variable-density thinning stands and solid lines indicate control stands. The number of species per unit area was based on the average number of species from subsampling all samples up to 500 times.

59 percent of species were found in ≤ 5 percent of sample plots (one to three plots), and the 5 dominant species were always among the 10 most common and highest cover species.

Patch Analysis

Total understory vegetation cover was negatively correlated with bryophyte cover ($r^2 = 0.33$, $F = 237.1$, $P < 0.0001$, $N = 479$). Total plant cover was significantly higher and bryophyte cover lower in the commercial forest than in the legacy forest (plant cover: $t = 8.55$, bryophyte cover: $t = -17.1$, $P < 0.0001$, $N = 479$).

Indicator species analysis of the groups derived from the clustering procedure produced one or more indicator species for clustering levels of two through eight groups. With more than eight groups, not all groups had an indicator species. For this reason we discuss the ordination at the eight-groups clustering level. The first level of the clustering procedure separated plots dominated by bryophytes from those with a high cover of dominant perennials. Bryophyte cover had its maximum indicator value (IV) (Max IV = 88.4) with two groups. Bryophyte cover was broadly indicative of low vascular plant cover. At the eight-groups clustering level, indicator species for each group were the following: bryophytes group (IV = 47.7, made up of 157 plots), *Linnaea borealis* L. group (IV = 89.7, 28 plots), *P. munitum* group (IV = 46.7, 37 plots), *Vancouveria hexandra* (Hook.) Morr. and Dcne. group (IV = 27.9, 48 plots), *G. shallon* (IV = 38.9, 80 plots), *Corylus cornuta* Marsh. (IV = 82.9, 30 plots), *P. aquilinum* (IV = 31.4, 79 plots), *Holodiscus discolor* (Pursh) Maxim.-R. *ursinus* group (*H. discolor* IV = 34.9, *R. ursinus* IV = 32.6, 20 plots).

The best NMS solution was three-dimensional (stress = 17.4, instability = 0.012). The correlation between ordination distances and the distances in the original n -dimensional space was highest for axis 3 ($r^2 = 0.43$), followed by axis 1 ($r^2 = 0.19$), and axis 2 ($r^2 = 0.17$). Axis 3 was positively correlated with *P. munitum* cover ($r^2 = 0.73$) and negatively correlated with *G. shallon* ($r^2 = 0.37$) and bryophyte cover ($r^2 = 0.25$). Axis 1 was positively correlated with bryophyte cover ($r^2 = 0.69$) and negatively correlated with *G. shallon* ($r^2 = 0.19$) and *P. aquilinum* ($r^2 = 0.10$). Axis 2 was positively correlated with *P. aquilinum* ($r^2 = 0.30$) and *R. ursinus* ($r^2 = 0.18$) and negatively correlated with bryophyte cover ($r^2 = 0.301$) and *Corylus cornuta* ($r^2 = 0.13$). Correlations for other species were < 0.10 . However, none of the axes were correlated with either the densiometer or prism measure of directly overhead overstory cover, aspect, or slope. Lack of correlation of all axes with overstory and topographic variables is likely due to low sun angles and light from off-plot canopy openings and relatively flat-to-rolling, low-lying topography (Canham et al. 1990).

Of the a priori groups (forest, block, treatment), only the legacy control group was at all discrete in ordination space (fig. 2). Some of the clustering-derived groups were aggregated within the ordination space, and these were related to the correlations of the indicator species that define the groups. At the eight-groups clustering level, the bryophyte, *G. shallon*, *P. munitum* and, to a lesser extent, *C. cornuta* groups appeared the most discrete in ordination space (fig. 3). The *G. shallon* and bryophyte groups were overlapping on axes 2 and 3 and distinct from each other on axis 1. The *P. munitum* group overlapped these groups on axis 2,

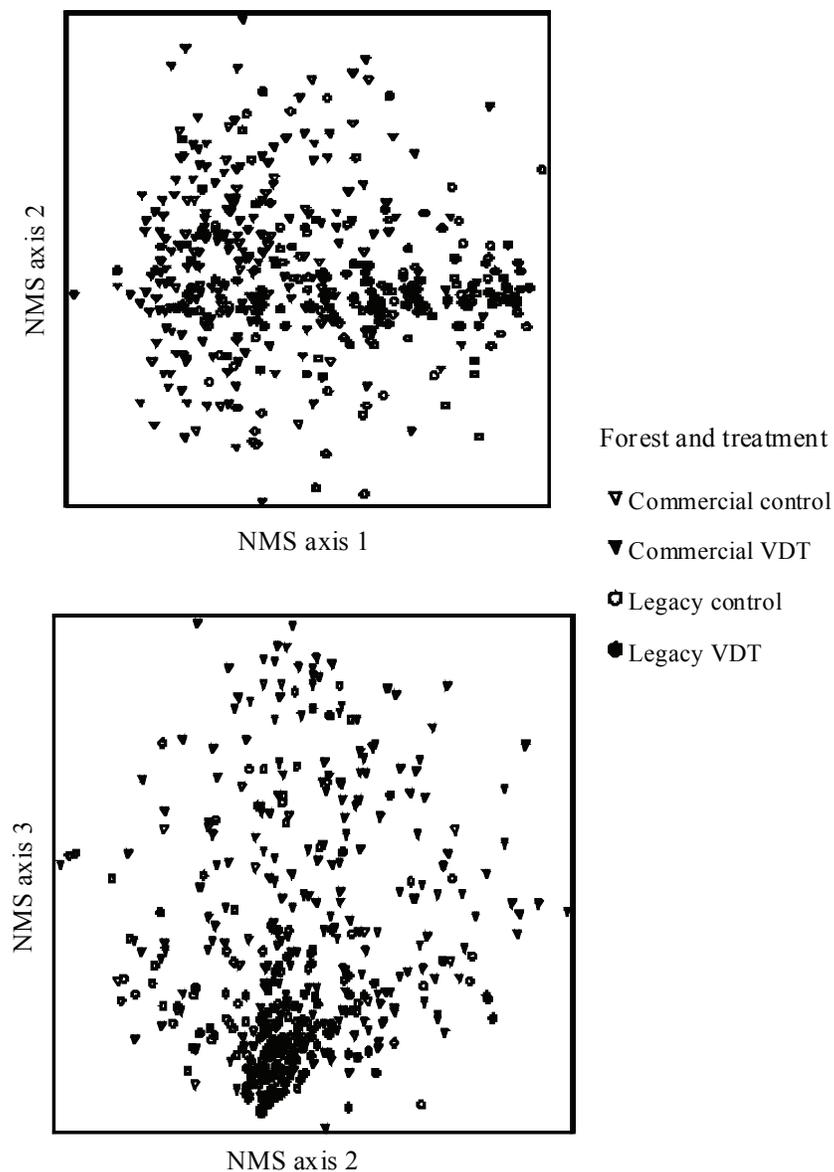


Figure 2—Sample points in nonmetric multidimensional scaling (NMS) ordination space for three axes. Symbols indicate the four forest-by-treatment combinations. VDT = variable-density thinning.

was discrete from them on axis 3, and fell between them on axis 1. The *C. cornuta* group was discrete along axes 1 and 2, but was widely distributed along axis 1. The *P. aquilinum*, *H. discolor-R. ursinus*, *V. hexandra*, and *L. borealis* groups were widespread in ordination space. The *L. borealis* group was not found along the central *G. shallon*-bryophyte-*P. munitum* band on axis 2.

The CV of values along NMS axis 1 was higher for the legacy forest than the commercial forest (Wilcoxon Signed Rank $T^+ = 26$, $DF = 1$, $P = 0.03$), but there was no difference on axis 2 or 3. In addition, CV of values on NMS axis 3 were

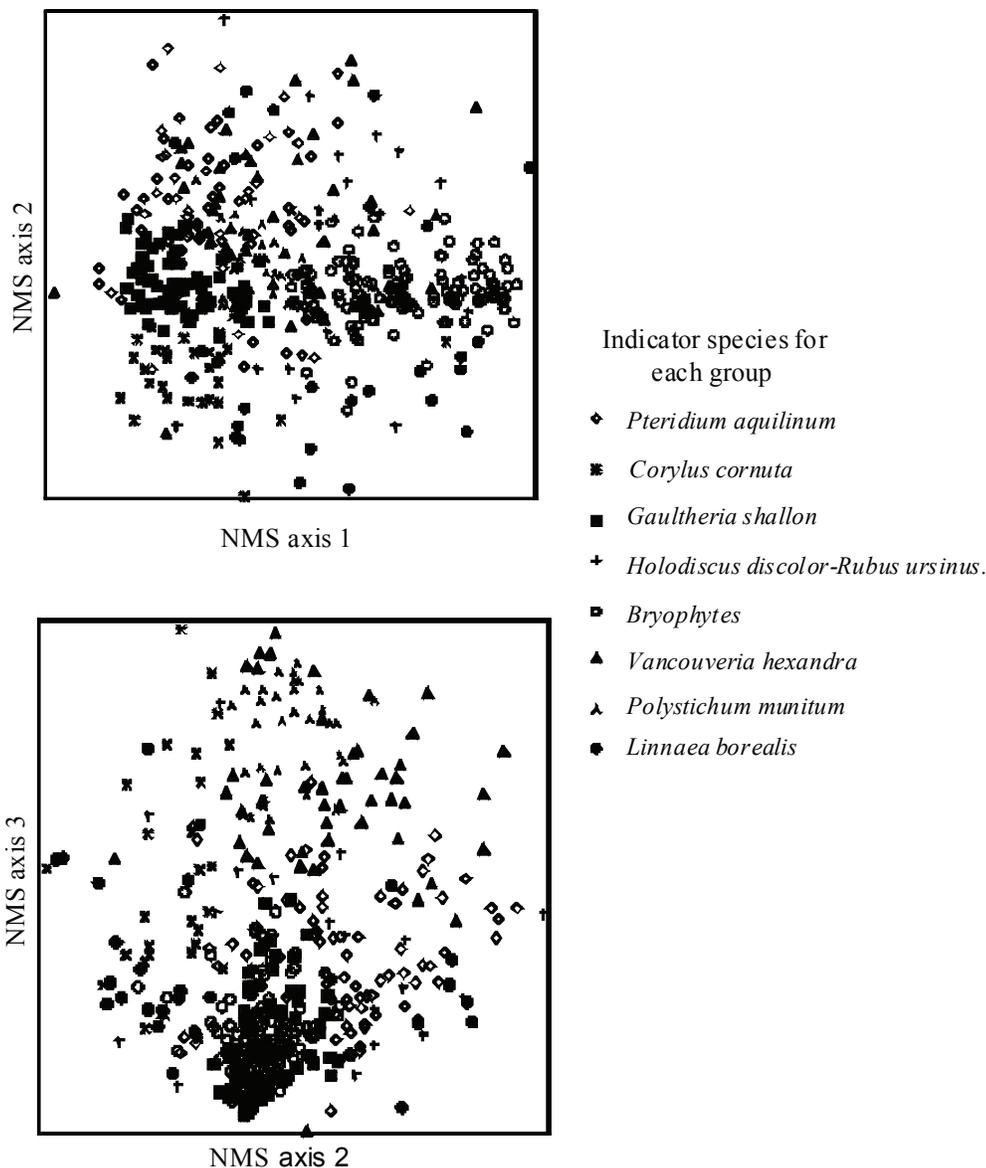


Figure 3—Sample points in nonmetric multidimensional scaling (NMS) ordination space for three axes. Symbols indicate clustering derived groupings for eight groups. Legend indicates corresponding indicator species.

greater for VDT than control stands (Wilcoxon Signed Rank $T^+ = 26$, $DF = 1$, $P = 0.03$, block centered) and there was a trend toward greater CV on axis 1 in VDT stands (Wilcoxon Signed Rank $T^+ = 25$, $DF = 1$, $P = 0.061$, block centered). The commercial forest had a greater diversity (Shannon's diversity index) of patch types than the legacy forest at the eight-groups level (Wilcoxon Signed Rank $T^+ = 26$, $DF = 1$, $P = 0.03$). We found a difference in Shannon's diversity index of patch types by treatment—VDT stands had a lower diversity than control stands (Wilcoxon Signed Rank $T^+ = 26$, $DF = 1$, $P = 0.03$, block centered), but there was no difference in the number of groups represented in the two forest types.

Discussion

Species Diversity and Understory Cover

Understory native plant species diversity was higher in stands with VDT-induced canopy heterogeneity in both forest tracts despite their markedly different management and prior disturbance histories. Thus the prediction of increased native species diversity was upheld. However, most species were relatively rare and the community was dominated by a few natives: perennial clonals (*G. shallon*, *R. ursinus*), a nonclonal perennial shrub (*M. nervosa*), and perennial ferns (*P. aquilinum*, *P. munitum*). Understory vegetation cover was greater in the commercial forest than in the legacy forest, and we found no effect of VDT on total understory cover. Our results are similar to the 3-year responses of the vegetation to VDT (Thysell and Carey 2000, 2001), except that reduction in understory cover owing to mechanical destruction during thinning was evident at 3 years; the understory has since regrown. Clonal natives are an important component of Pacific Northwest forests of all stages of development (Bailey and Tappeiner 1998, Bailey et al. 1998, Carey and Johnson 1995), but excessive dominance by these species can reduce vegetation patch diversity by creating a homogeneous understory and impeding regeneration of shade-tolerant trees (Huffman et al. 1994, Tappeiner et al. 2001, Thysell and Carey 2001). At present, understory cover of shrubs and ferns exceeds the goals set forth for the experiment (Carey et al. 1999b). Development of a midstory will be required to increase patchiness in understory cover.

Although we found higher numbers of native-nonruderal-forest species in VDT stands than in control stands, exotic, ruderal, and nonforest species diversity were also greater in VDT. Although we cannot directly compare our results with Thysell and Carey (2001) because of differences in sampling methods, our data do not support their prediction that exotic species would decrease in number in VDT stands over time, at least in the 6 years since their study. Instead, we found

increased numbers of both native and exotic species associated with increased number of thinnings a stand had undergone. The never-thinned legacy stands and the once-VDT-thinned legacy stands had few exotics, as was predicted. The twice-conventionally-thinned commercial controls and thrice-thinned (two conventional and one VDT) commercial stands had numerous exotics (7 to 20). We found the same pattern for ruderal and nonforest species. Exotic species richness typically increases with overall species richness, and exotic species are typically associated with disturbance (Fine 2002); it appears widespread homogeneous intermediate disturbance is especially pernicious in regard to increasing ruderal and certain exotic species. In no case, however, did exotics or ruderals appear to be assuming dominance and displacing native species; like most species, they remained relatively rare. We must continue to monitor changes in species diversity over time.

Many communities and plant species are believed to be dispersal-limited (Dalling et al. 2002, Ehrlén and Eriksson 2000, Hubbell 2001, Vellend 2003, Verheyen and Hermy 2001). In fact, studies suggest that dispersal limitation is a primary factor driving the recovery of forest herb diversity in young forests (Flinn and Vellend 2005, Peterken and Game 1984, Vellend 2003). In addition, landscape context can be important to colonization by forest species. Vellend (2003) found that diversity of forest herb species in recent forests increased as the proportion of ancient forests in the landscape increased. The theory behind VDT, however, assumes that communities in the Pacific Northwest are niche structured and that fine-scale environmental heterogeneity is necessary for maximal species diversity; practically no vascular plant species in the Pacific Northwest are confined to ancient forests (Franklin and Dyrness 1973).

Our study was in an extensively disturbed landscape of secondary forest, grasslands, agricultural lands, and suburbs; vehicular traffic was heavy. Thus, the increase in plant diversity that we observed following VDT included increases in ruderal or nonforest species. We saw an average increase of only five native-nonruderal-forest species in the VDT stands compared to the control stands. Still, native forest plant diversity was high (113 species). We did see a trend toward greater β -diversity in VDT stands, but it is not yet clear that this is biologically significant. Thus, niche diversity has not yet exerted a strong influence on community assembly. It may be that dispersal limitation may be an important factor limiting colonization by forest species in these stands. Research on a sister study showed that second-growth forests that persist in a dense, closed-canopy condition for decades have few native plants in the soil seed bank but retain seeds of numerous weeds that invaded after clearcutting (Halpern et al. 1999). It also may be that niche diversity depends on a longer term process of developing a

midstory of shade-tolerant species (Carey et al. 1999a, Franklin et al. 2002). But our study suggests that moderate homogeneous thinning can also lead to large increases in weedy species that may be sustained by subsequent patchy disturbance. Similarly, Decocq et al. (2004, 2005) found that a selective-cutting (frequent, low-intensity disturbance) silvicultural regime, in contrast to a coppice-with-standards (infrequent, high-severity disturbance) system, benefitted ruderal species while negatively impacting true forest species.

Patch Diversity and Heterogeneity

The lack of robust differentiation in the clustering of sample sites by species composition suggests that time and conditions have not been sufficient to develop repeating patterns of a diverse set of vegetation patches (Carey et al. 1999a). Still, we observed 8 patch types, with 6 to 12 types predicted. The principal difference between the patches we observed and those Carey et al. (1999a) reported lies with development of both deciduous and coniferous tall-shrub and shade-tolerant tree midstories. The comparisons of beta diversity and CV of NMS values suggested that VDT stands were becoming more heterogeneous than control stands, but the diversity of community groups did not support this. Thus, contrary to our predictions, VDT stands are, at best, moving very slowly toward having a greater diversity of patch types or environmental conditions than the control stands. This is supported by Aukema (unpublished manuscript on file with author) who found a lack of differentiation in microclimate (air and soil temperature and relative humidity) between the two types of stands in a complementary study.

We propose four nonexclusive explanations for the failure of VDT to bring about patchiness in vegetation composition in the understory after 9 years. First, time since treatment has not been sufficient to allow differentiation, especially differentiation that depends on development of a midstory shade-tolerant conifer and deciduous layer. Second, VDT initially disproportionately benefits two groups of species: ephemeral ruderal species and clonal natives (Thysell and Carey 2001). Third, history of management that established dense clonal native species populations in the commercial forest and a sparse, species-poor understory in the legacy forest puts stands on a trajectory that is difficult to overcome (essentially a stable-state alternative to naturally diverse forests). And fourth, natural disturbances that occurred in the stands since treatment (an ice storm, a windstorm, and root-rot spread) are opening the canopy. This may have reduced the effects of VDT on the vascular plant communities as opposed to the control (in other words, there has been gradually increasing light in all stands) (Carey 2003). It remains to be seen if the heterogeneity induced by VDT in the FES will translate into differentiation

in understory and midstory with time. The regeneration of shade-tolerant tree species post-VDT suggests further differentiation will occur (Aukema and Carey, unpublished manuscript on file with the authors). Finally, it is possible that we were simply unable to detect vegetation compositional heterogeneity owing to insufficient sampling. However, we believe the sampling was sufficient to capture strong effects of VDT on heterogeneity of herbaceous and shrub layer vegetation.

Management Implications

Variable-density thinning was first suggested as a way to restore biocomplexity in managed forests in 1991, based on comparative studies of natural and managed forest (Carey 1995, Carey and Johnson 1995, Carey et al. 1999b). The FES is the first experimental application of VDT and only 10 years have passed since its implementation. Many of the hypothesized benefits of VDT for biodiversity have emerged (Carey 2003), but the full development of forest complexity is not expected to emerge for years or decades to come.

Managers considering VDT for forest stands should (1) formulate site-specific objectives based on biogeography, site factors, and stand conditions; (2) evaluate the need for thinning and other treatments (underplanting, seeding, coarse woody debris augmentation, and snag creation); and (3) consider past management history, location in the landscape relative to wind and ice storms, and landscape context as it relates to seed sources of forest plants, invasion by plant predators, such as deer and elk (*Cervidae*), and roads. If VDT is agreed upon, leaving unthinned patches of 0.1 to 0.5 ha within VDT stands would be wise (Colgan et al. 1999, Thysell and Carey 2001). Unthinned patches are very useful for protecting biological legacies, headwater seeps and streams, and colluvial soils. Variable-density thinning will not be appropriate for all stands or situations, and in some cases, the potential short-term negative effects of disturbance—including increased ruderal species and short-term reduction of mycorrhizal sporocarps and some mammals (Colgan et al. 1999)—may argue against extensive, simultaneous thinning, especially where spotted owls (*Strix occidentalis*) depend on northern flying squirrels (*Glaucomys sabrinus*), which depend on mycorrhizal sporocarps. Managers should also be aware of the ecological time-scale for restoration and should not expect to see dramatic universal benefits immediately after VDT.

Given the wide appeal of using silvicultural systems that attempt to replicate natural disturbance regimes or natural forest structure to enhance biodiversity and ecosystem services while providing forest products (Bengtsson et al. 2000, Franklin 1989, Mitchell et al. 2002, Roberts and Gilliam 1995), it is important to continue to monitor different management practices to evaluate how well they are

meeting their objectives. Additional studies comparing VDT forests with commercially thinned forests and with old-growth forests would be useful to better understand how well VDT achieves its goals and how it compares to other management techniques that have been proposed to have some of the same benefits, such as increased plant species diversity and shrub layer development (Bailey and Tappeiner 1998, Bailey et al. 1998, Muir et al. 2002).

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English Equivalents

If you know:	Multiply by:	To find:
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Square meters (m ²)	10.76	Square feet
Kilometers (km)	0.621	Miles
Hectares (ha)	2.47	Acres
Stems per hectare (stems/ha)	0.405	Stems per acre

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