Spatial patterns of overstory trees in late-successional conifer forests

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Abstract: We analyzed spatial patterns of overstory trees in late-successional *Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes forests and late-successional *Pseudotsuga menziesii* (Mirb.) Franco forests to establish reference spatial patterns for restoration thinning treatments, and to determine whether thinning treatments with minimum intertree spacing rules result in spatial patterns characteristic of late-successional forests. On average, 32.7% of overstory trees in *Abies* plots and 26.3% of overstory trees in *Pseudotsuga* plots occurred as members of multitree clusters (groups of trees in which trees are spaced within a specified minimum distance of each other) at a distance of 3.0 and 4.0 m, respectively. Multitree clusters occurred throughout the three *Abies* plots; the distribution of multitree clusters within the two *Pseudotsuga* plots was variable. Spatial patterns of overstory trees in late-successional forests were significantly different from those created by simulated restoration thinning treatments. Restoration thinning treatments that release both individual trees and multitree clusters promote characteristic late-successional tree spatial patterns at the within-patch scale (<0.04 ha). This formulation of restoration thinning highlights conservation of existing small-scale (<0.04 ha) spatial heterogeneity within the treatment area, elaborating on current practices that emphasize introduction of spatial heterogeneity at scales of 0.04 ha to 1.0 ha.

Résumé : Nous avons étudié la répartition des arbres formant la canopée de forêts dominées par des espèces de fin de succession, soit *Abies amabilis* (Dougl. ex Loud.) Dougl. ex Forbes et *Pseudotsuga menziesii* (Mirb.) Franco, afin d'établir des répartitions pouvant servir de référence pour les traitements d'éclaircie de restauration et de déterminer si les traitements d'éclaircie basés sur des règles minimales d'espacement entre les arbres produisent des répartitions caractéristiques des forêts de fin de succession. En moyenne, 32,7 % des arbres de la canopée des placettes dominées par *Abies* et 26,3 % des arbres de la canopée dominée par *Pseudotsuga* font partie de groupes de plusieurs arbres (groupes d'arbres espacés les uns des autres d'une distance minimale spécifiée) distants les uns des autres de respectivement 3,0 et 4,0 m. Des groupes de plusieurs arbres étaient présents dans les trois placettes dominées par *Abies* alors que la distribution des groupes de plusieurs arbres dans les deux placettes de *Pseudotsuga* était variable. La répartition des arbres de la canopée des forêts de fin de succession était significativement différente de celle qui a été engendrée par des traitements simulés d'éclaircie de restauration. Les traitements d'éclaircie de restauration, qui libèrent des arbres individuels et des groupes de plusieurs arbres, produisent les caractéristiques de la répartition des arbres de fin de succession à l'échelle de la placette (<0,04 ha). Cette forme d'éclaircie de restauration met en évidence la conservation de l'hétérogénéité spatiale qui existe à petite échelle (<0,04 ha) dans la superficie traitée, ce qui explique les opérations courantes qui visent à créer une hétérogénéité spatiale à des échelles variant de 0,04 à 1,0 ha.

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Introduction

Restoring late-successional conditions in previously harvested or otherwise anthropogenically modified forests is an increasingly common forest management objective (e.g., USDA and USDI 1994; City of Seattle 2000). Forest density management with thinning is the primary silvicultural intervention used to increase the rate of forest structural development (Carey 2003), and to promote development of characteristic late-successional forest structure and composi-

tion, including understory plant communities and wildlife habitat, in previously harvested mesic conifer forests (Wilson and Puettmann 2007). These objectives represent a major departure from the traditional primary objective of thinning, which is to optimize the yield of merchantable timber volume and financial return (Smith et al. 1997). Traditional thinning treatments typically include tree spacing guidelines (e.g., Curtis 2006) to optimize the use of available growing space. One outcome, by definition, of spacing-based thinning treatments is uniform tree spatial patterns at scales up to the specified spacing distance; this outcome is most strongly expressed when thinning treatments include a minimum intertree spacing rule. It is currently not known whether spacing-based thinning treatments result in tree spatial patterns characteristic of late-successional forests.

Any thinning treatment imposes a spatial pattern on the arrangement of trees in the treated forest stand; silviculturalists have the opportunity to specify particular tree spatial patterns to be retained or introduced. In mesic Pacific Coast conifer forests Carey (2003; A. Carey, personal communica-

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tion, 10 February 2008) recommends creating patches at the 0.1 to 0.5 ha scale with a 2:1 ratio of light to heavier thinnings. These recommendation are based on spatial patterns of forest structure in late-successional forests capable of supporting populations of northern spotted owls (Carey et al. 1999*a*) and results from the Forest Ecosystem Study (Carey et al. 1999*b*). This method is known as variable density thinning (VDT) (Carey 2003) and is a specific case of "free" thinning (Tappeiner et al. 2007). In free thinning, the size and species of trees designated for removal and retention vary across the treatment area and are determined by the relative priority for retention and by the frequency of occurrence of different tree species and size classes (Tappeiner et al. 2007). Other recommendations for restoration thinning treatments in mesic Pacific Coast conifer forests include leaving unthinned "skips" and creating open "gaps" or heavily thinned patches at scales ranging from 0.04 to 0.3 ha (Carey and Harrington 2001; Roberts et al. 2007) up to 1.0 ha (Wilson and Puettmann 2007). Skips and gaps together usually occupy 10% to 25% of the treatment area (e.g., Roberts et al. 2007) and are embedded in the remaining 75% to 90% of the treatment area. This remaining area is thinned to one or sometimes two target densities using traditional spacing-based method (Roberts et al. 2007; Wilson and Puettmann 2007).

The recommended scale (0.04 to 1.0 ha) for introducing spatial heterogeneity with restoration or VDT thinning (Carey and Harrington 2001; Carey 2003; Roberts et al. 2007; Wilson and Puettmann 2007) appears to approximate patch-scale spatial patterns found in mesic late-successional conifer forests in Washington (Chen et al. 2004; Larson and Franklin 2006) and Oregon (Bradshaw and Spies 1992). However, guidance for restoration thinning treatments with respect to tree spatial patterns at the within-patch scale (i.e., less than ~0.04 ha, or a radius of about 11 m) is lacking.

Characterization and analysis of tree spatial patterns are carried out with stem-map data (Moeur 1993): tree locations are surveyed in the field and then represented as points on a plane, with the spatial point pattern subjected to statistical or descriptive analysis. One popular method for analyzing tree spatial patterns is the family of distance-based spatial point pattern statistics (Loosmore and Ford 2006); Ripley's K statistic is an example of this type of analysis. However, translating results from analyses with spatial point pattern statistics into management recommendations is extremely difficult and, in many cases, operationally infeasible. Silvicultural prescriptions are often written and implemented in terms of specific forest structural elements such as individual trees or patches (e.g., "thin to a residual density of 150 trees/ha" or "leave one, 0.1 ha unthinned skip per hectare"). Thus, a method of characterizing spatial patterns in terms of discrete groups of trees, rather than frequency distributions of intertree spacing or departure from a null spatial model, should be useful in the design of restoration thinning prescriptions.

In this study we examine the spatial patterns of overstory trees in several mesic late-successional conifer forests of the Pacific Northwest. Residual trees left following restoration thinning treatments in these forests are intended to become the initial cohort of overstory trees in the target late-successional (restored) stand structure. Thus, information about

spatial patterns of overstory trees in late-successional forests will help managers ensure that restoration thinning prescriptions achieve their intended result. Our study proceeds in two stages. First, we characterize patterns of overstory tree spacing in five late-successional forests using the clustering algorithm of Plotkin et al. (2002). Second, we determine whether the spatial pattern of residual trees created by spacing-based restoration thinning treatments differs significantly from the spatial pattern of overstory trees in late-successional forests. Specifically, we test the null hypothesis that spatial patterns of overstory trees in five different mesic late-successional conifer forests are not significantly different from those created by simulated restoration thinning prescriptions that include a minimum intertree spacing rule. For sites characterized by the presence of the long-lived early-seral-dominant *Pseudotsuga menziesii* (Mirb.) Franco we repeated these analyses using only overstory *Pseudotsuga* stems to examine the spatial patterns of an overstory species that does not typically self-replace in late-successional forests.

Methods

Study area

The study sites are situated within *Tsuga heterophylla* Zone and *Abies amabilis* Zone forests in the western Washington Cascade Range. None of the study forests have experienced silvicultural manipulations. The *Tsuga heterophylla* Zone is the most extensive forest vegetation type in western Washington and Oregon, occurring on mesic, temperate sites below about 1000 m (Franklin and Dyrness 1988). Total precipitation ranges from about 1500 to 3000 mm, falling primarily as winter rains with transient snowfall. Mean annual temperatures are about 8 to 11 °C. *Tsuga heterophylla* Zone forests are equivalently termed *Pseudotsuga* forests, reflecting the early-seral dominance and long-lasting presence of *P. menziesii* in these forests (Franklin et al. 2002). The *Abies amabilis* Zone, where *Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes occurs as the principal late-successional species, occupies middle- and upper-slope sites (about 1000 to 1500 m) in the western Cascade Range (Franklin and Dyrness 1988). Environmental conditions within the *Abies amabilis* Zone are characterized by cool temperatures (mean annual temperature of about 5 to 6 °C) and heavy precipitation (2000 to 2500 mm annually), with much precipitation falling as winter snow and accumulating to depths of 1000 to 3000 mm (Franklin and Dyrness 1988). We refer to the *Abies amabilis* Zone and *Tsuga heterophylla* Zone as *Abies* forests and *Pseudotsuga* forests, respectively.

We used previously published data sets to generate maps of overstory tree locations in two late-successional *Pseudotsuga* forests and three late-successional *Abies* forests (Table 1). Overstory trees were defined as those trees ≥25 m tall in the *Abies* plots (Larson and Franklin 2006). We defined overstory trees in the Canopy Crane plot as trees ≥40 m tall based on inspection of tree height distribution. A complete inventory of tree heights was not available for the Yellowjacket Creek plot. However, maximum tree height (~65m) and diameter (190 cm) in the Yellowjacket Creek plot (Winter et al. 2002*a*) were similar to max-

Table 1. Summary of site characteristics for the study plots.

Site	Forest Zone[a]	Age (years)	Elevation (m)	Plot dimensions or size	Source
Sutton Lake	*Abies amabilis*	∼300	1160	100 m × 100 m	Larson and Franklin 2006
Sister Rocks	*Abies amabilis*	∼600	1200	100 m × 100 m	Larson and Franklin 2006
Mosquito Lake	*Abies amabilis*	∼300	1110	100 m × 200 m	Larson and Franklin 2006
Canopy Crane	*Tsuga heterophylla*	∼500	370	200 m × 200 m	Shaw et al. 2004
Yellowjacket Creek	*Tsuga heterophylla*	∼500	700	3.3 ha irregular polygon	Winter et al. 2002b

[a]According to Franklin and Dyrness (1988).

imum tree height (64.6 m) and diameter (182.5 cm) in the Canopy Crane plot. Thus, we assumed that the overstory canopy stratum and height–diameter relationships in the Yellowjacket Creek plot could be adequately represented by those of the Canopy Crane plot and defined overstory trees in the Yellowjacket Creek plot as all trees with a diameter at breast height (DBH) >45 cm, which is the smallest overstory tree DBH in the Canopy Crane plot. Site characteristics, field sampling methods, and stand structure for the study sites have been reported elsewhere (Winter et al. 2002a, 2002b; Shaw et al. 2004; Larson and Franklin 2006). Overstory tree species composition ranged from two to six conifer species per plot, and overstory density ranged from 81.5 to 215.0 trees/ha (Table 2).

Cluster analysis

The clustering algorithm is very straightforward. Trees are members of the same cluster if they are within distance t of each other. At any value of t the data set is partitioned into a set of unique clusters. In the case of $t = 0$ the number of clusters will equal the number of trees in the pattern. All trees are members of the same single cluster when t exceeds the maximum nearest neighbor distance in the pattern.

Clusters coalesce and grow in a pairwise fashion: not all trees within the cluster need be within t of each other; however, all trees in the cluster must link to at least one neighbor within t. For example, if tree I and J are within t of each other, they are in the same cluster. If tree K is greater than t from either tree I or J, it forms a separate cluster. However, if a fourth tree is introduced, H, which is within t of tree J and tree K, the cluster grows to a size of four and now contains trees H, I, J, and K. Refer to Fig. 1 in Plotkin et al. (2002) for a graphical example. There are no constraints on the spatial configuration of the cluster: clusters may take any form as long as a chain of pairwise linkages ≤t is maintained among the cluster members.

Variation in cluster characteristics and demographics vary with respect to t provides the basis for spatial pattern characterization at multiple scales. For a given t, the data set will be portioned into m distinct clusters, with the size of the individual clusters represented as $c_1, c_2, \ldots, c_m$. The total number of points in the pattern is then denoted as

$$n = \sum c_i$$

Mean cluster size (Plotkin et al. 2002) is then:

$$\bar{c} = \frac{1}{n} \sum_{i=1}^{m} c_i^2$$

The normalized mean cluster size $\hat{c}$, which is useful for comparing results across patterns of different n, is calculated as:

$$\hat{c} = \bar{c}/n$$

The cluster size distribution at various scales is particularly useful, as it provides a quantitative, yet intuitive characterization of spatial heterogeneity.

Statistical analysis

The G and K spatial point pattern statistics (Diggle 2003) were used to test the null hypothesis of no difference between the spatial patterns of overstory trees (all species pooled) in natural late-successional *Abies* forests and *Pseudotsuga* forests and the spatial patterns of trees created by spacing-based restoration thinning in young forests. Statistical analysis of spatial point patterns is based on comparing an empirical test statistic calculated from interpoint distances of the observed pattern to a null distribution of test statistics derived from a set of s Monte Carlo (MC) simulated spatial point patterns, where point-to-point distances are considered up to some maximum distance t_{max} (Diggle 2003). Traditionally, inference is made using a method known as the simulation envelope approach and a null model of complete spatial randomness (CSR; e.g., Kenkel 1988). Unfortunately, the simulation envelope method leads to sharply inflated type-I error rates (Loosmore and Ford 2006), rendering it inappropriate as a method of inference about pattern and scale. Loosmore and Ford (2006) developed a goodness-of-fit test for the G and K statistics that provides the expected type-I error performance; their method for inference is used in this present analysis. Briefly, the values of the spatial statistic of interest (G or K) over the range of scales examined are reduced to a single summary test statistic, u_i (eq. 3 in Loosmore and Ford (2006)). Test statistics (u) are calculated for the observed pattern (u_1) and each of the MC simulated patterns (u_i; $i = 2, \ldots, s$). A statistical test can then be performed by ranking u_1 against the test statistics for the s MC simulated patterns.

The nature of our hypothesis required that a null model other than CSR be used, because spacing-based thinning treatments by definition do not create CSR tree patterns. Postrestoration thinning tree spatial patterns in young forests were modeled with a hard-core inhibition spatial point process (simple sequential inhibition, Diggle 2003): locations of points (i.e., trees) are constrained such that no points occur within a specified distance t_{thin} of each other. This method mimics operational guidelines and contract language for minimum spacing requirements in spacing-based restoration thinning prescriptions (Hunter 2001); e.g., "remove all trees

Table 2. Overstory tree species composition in the study plots.

| Species | Density (trees/ha) | | | | |
	Sutton Lake	Sister Rocks	Mosquito Lake	Canopy Crane	Yellowjacket Creek
Abies amabilis	77.0	171.0	181.0	1.0	—
Abies grandis	—	—	—	3.0	—
Abies procera	6.0	—	—	0.3	—
Pseudotsuga menziesii	3.0	—	1.0	34.0	13.9
Thuja plicata	—	—	—	11.0	9.1
Tsuga heterophylla	78.0	21.0	8.0	32.3	63.6
Tsuga mertensiana	51.0	—	35.0	—	—
Total	215.0	192.0	225.0	81.5	86.7

Note: Overstory trees are defined as trees ≥25 m tall for the Sutton Lake, Sister Rocks, and Mosquito Lake sites (Larson and Franklin 2006); trees ≥40 m tall for the Canopy Crane site; and trees ≥45 cm DBH for the Yellowjacket Creek site. See Methods for further explanation.

Fig. 1. Normalized mean cluster size of overstory trees (all species pooled) plotted as a function of distance for the three *Abies* plots. All trees belong to the same cluster when normalized mean cluster size = 1. The inflection point marks t_{crit}, the "percolation threshold" (Plotkin et al. 2002), which is the scale at which trees transition from being arranged primarily in many small clusters to a single large cluster. In all three *Abies* plots t_{crit} = 7 to 8 m. See Methods for additional detail.

Abies amabilis zone plots
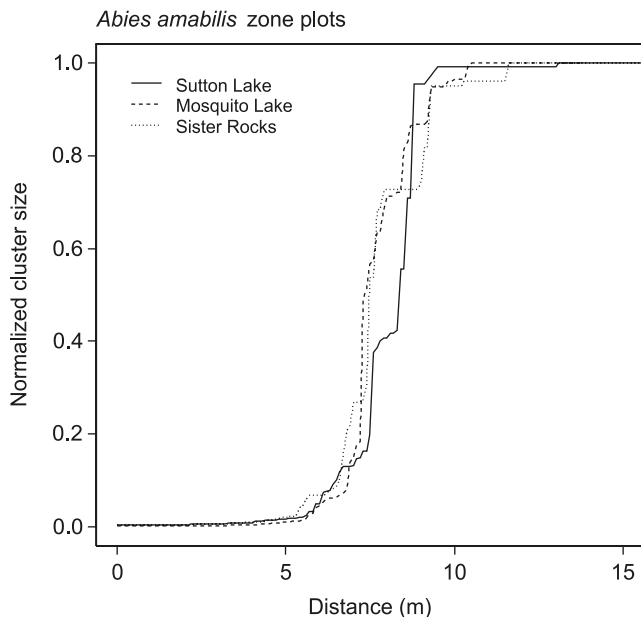
within 3.5 m of the target tree". The value of t_{thin} was set to 3.0 m for *Abies* plots and 4.0 m for *Pseudotsuga* plots; these values are conservative representations (i.e., more closely spaced) of tree spacing created by typical restoration thinning treatments in both merchantable and nonmerchantable stands of these respective forest types (e.g., Curtis et al. 2000; Curtis 2006). Tree spacing was implemented using pith-to-pith distances in simulations, which is also conservative; tree spacing in actual thinning treatments is usually between the outer radii of tree boles. The number of points in a simulated pattern was set equal to the number of overstory trees in the plot being tested. A null distribution of n = 1999 Monte Carlo simulated patterns was used for each test. Edge

correction was carried out using the reduced sample method (Loosmore and Ford 2006): points are excluded from the sample when a neighbor point does not occur within a search radius less than the distance to the nearest plot boundary. The 2 ha Mosquito Lake study plot (Table 1) was subdivided into two, 1 ha plots (Mosquito Lake west and Mosquito Lake east) to reduce computation time and memory requirements, which were prohibitively large. Statistical analysis was not conducted for the Yellowjacket Creek plot because the method used (Loosmore and Ford 2006) does not accommodate plots with irregular boundaries.

The value of t_{max} is user specified based on the spatial scale of the null process to which the observed pattern is compared (see eq. 3 and associated discussion in Loosmore and Ford (2006)). Initially, tests were conducted with t_{max} = t_{thin}, the scale at which the process of interest — restoration thinning — occurs. Tests were repeated with t_{max} = 13.0 m, the best estimate available for the maximum expected scale of competitive interactions — the ecological process that causes natural self-thinning in *Pseudotsuga* (Franklin et al. 2002) and *Abies* (Oliver et al. 1985) forests, and for which restoration thinning is a surrogate — among trees in mesic Pacific Coast conifer forests (Canham et al. 2004). Setting t_{max} = 13.0 m allowed comparisons of tree spatial patterns over the range of scales at which competition and, presumably, natural self-thinning occur.

A second test was conducted in which only *Pseudotsuga* trees were considered in the Canopy Crane plot. Limiting the analysis to only *Pseudotsuga* stems provided a more conservative test of the null hypothesis: *Pseudotsuga* does not self-replace in the absence of major disturbance (Franklin et al. 2002). The shade-tolerant conifers *Abies amabilis*, *Tsuga heterophylla* (Raf.) Sarg., and *Thuja plicata* Donn ex. D. Don, and the moderately shade tolerant species *Abies grandis* (Dougl. ex D. Don) Lindl. and *Abies procera* Rehd. can occupy canopy positions in natural late-successional *Pseudotsuga* forests (Table 2). Closely spaced overstory trees are less likely to be detected when these species are excluded from the analysis.

All analysis was carried out in the statistical program and language R (R Core Development Team, http://cran.r-project.org). We used R source code supplied as an online supplement to Loosmore and Ford (2006) for hypothesis

testing with the *G* and *K* point pattern statistics. We developed R source code to implement the cluster algorithm and provide it as a supplement to this present article.[3]
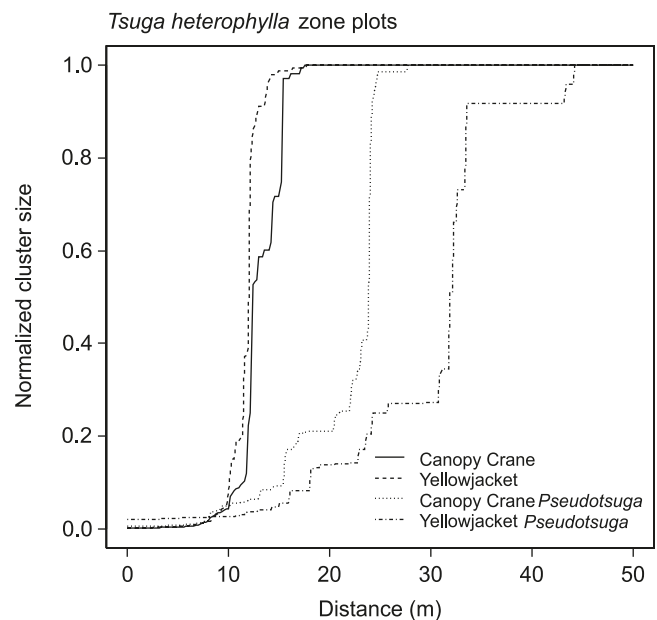
Results

Cluster analysis

The shape of the normalized mean cluster size curve was similar among the three *Abies* plots (Fig. 1): normalized mean cluster size was very small up to about $t = 5$ m. From 5 to 10 m, however, the mean cluster size rose sharply, approaching the maximum cluster size. This transition marks the critical distance (t_{crit}) known as the "percolation threshold" (Plotkin et al. 2002), which is the scale at which trees transition from being primarily arranged in many small clusters to one single large cluster. This transition occurred consistently at about 7 to 8 m in the *Abies* plots. In other words, the majority of overstory trees had multiple neighbors within about 8 m, such that the trees formed a single or few large cluster(s).

Normalized mean overstory tree (all species pooled) cluster size increased with distance in the *Pseudotsuga* plots, but the scale of pattern differed from that observed in the *Abies* plots. Overstory trees in the both the Canopy Crane and Yellowjacket Creek plots were arranged such that t_{crit} was relative larger than that in the *Abies* plots, about 13 m, and the transition from many small to a few large clusters occurred at larger distances and over a greater range, from about 8 to 15 m (Fig. 2). When only *P. menziesii* trees were considered in the Canopy Crane and Yellowjacket Creek plots, the transition from many small clusters to a single large cluster occurred over an even wider range of distances, from about 7 to 43 m (Fig. 2). Conspecific *P. menziesii* clusters coalesced and grew relatively slowly until t_{crit} was reached at about 24 m in the Canopy Crane plot and 33 m in the Yellowjacket Creek plot (Fig. 2). The larger t_{crit} in the Yellowjacket Creek plot likely reflects the relatively lower density of *P. menziesii* trees in the Yellowjacket Creek plot (13.9 trees/ha) compared with that in the Canopy Crane plot (34.0 trees/ha): on average, *P. menziesii* trees should be spaced further apart in the Yellowjacket Creek plot.

The distribution of trees among clusters of different sizes at a given distance (Tables 3 and 4) is perhaps of greatest relevance to informing the design of restoration thinning treatments. In the three *Abies* plots 64.9% to 71.9% of overstory trees occurred in single-tree clusters at a distance of t_{thin} (3.0 m). However, multitree clusters were present at scales as small as 1 m in the Mosquito Lake plot and 2 m in the Sutton Lake and Sister Rocks plots (Table 3). Overstory trees occurred in clusters of three to six or more trees at a distance of t_{thin} in the *Abies* plots (Table 3). Similarly, only 73.3% of overstory trees in the Canopy Crane plot and 74.1% of overstory trees in the Yellowjacket Creek plot occurred in single-tree clusters at t_{thin} (4.0 m), and clusters as large as four trees were observed at t_{thin} (Table 4). *Pseudotsuga menziesii* trees were less likely to

Fig. 2. Normalized mean cluster size of overstory trees (all species pooled) and *Pseudotsuga menziesii* trees only plotted as a function of distance for the two *Pseudotsuga* plots. All trees belong to the same cluster when normalized mean cluster size = 1. The inflection point marks t_{crit}, the "percolation threshold" (Plotkin et al. 2002), which is the scale at which trees transition from being arranged primarily in many small clusters to single large cluster. When all species were included t_{crit} was reached at about 13 m in both the Canopy Crane and Yellowjacket Creek plots. However, when only *P. menziesii* trees were considered t_{crit} increased to about 24 m in the Canopy Crane plot and 33 m in the Yellowjacket Creek plot. The larger t_{crit} for *P. menziesii* trees in the Yellowjacket Creek plot likely reflects the relatively lower density of *P. menziesii* trees in the Yellowjacket Creek plot (13.9 trees/ha) compared with that in the Canopy Crane plot (34.0 trees/ha): on average, *P. menziesii* trees should be spaced further apart in the Yellowjacket Creek plot. See Methods for additional detail.

Tsuga heterophylla zone plots

belong to conspecific multitree clusters at t_{thin}; however, 8.8% and 4.3% of *P. menziesii* trees belonged to a conspecific cluster of size = 2 (i.e., composed of two trees) (Table 4).

The prevalence of multitree clusters at scales $\leq t_{thin}$ explains the results from the statistical tests. Spacing-based thinning treatments eliminate multitree clusters at scales $\leq t_{thin}$.

Multitree clusters at t_{thin} exhibited variable spatial patterns in terms of distribution of clusters across the plot area in the intensively studied stands (Fig. 3). Multitree clusters at t_{thin} were distributed throughout the plot area in all three *Abies* plots (Figs. 3b–d). Considerable heterogeneity was apparent in the distribution of multitree clusters in the Canopy Crane plot: a patch of approximately 1 ha lacked multitree clusters (Fig. 3a). Multitree clusters were distributed throughout the Yellowjacket Creek plot (data not shown).

Table 3. Number per hectare (with percentages in parentheses) of overstory trees (all species pooled) in *Abies amabilis* Zone stands occurring in clusters of different sizes at various spatial scales.

Scale (m)	Cluster size (trees/cluster)					
	1	2	3	4	5	≥6
Sutton Lake						
1	215.0 (100.0)	—	—	—	—	—
2	177.0 (82.3)	16.0 (14.9)	2.0 (2.8)	—	—	—
3	140.0 (65.1)	26.0 (24.2)	6.0 (8.4)	—	1.0 (2.3)	—
4	92.0 (42.8)	29.0 (27.0)	11.0 (15.3)	4.0 (7.4)	2.0 (4.7)	1.0 (2.8)
5	62.0 (28.8)	14.0 (13.0)	12.0 (16.7)	5.0 (9.3)	2.0 (4.7)	8.0 (27.5)
6	35.0 (16.3)	7.0 (6.5)	5.0 (7.0)	5.0 (3.7)	6.0 (14.0)	10.0 (52.5)
7	15.0 (7.0)	3.0 (2.8)	—	1.0 (1.9)	3.0 (7.0)	9.0 (81.3)
8	5.0 (2.3)	2.0 (1.9)	—	—	—	6.0 (95.8)
9	5.0 (2.3)	—	—	—	—	1.0 (97.7)
10	1.0 (0.5)	—	—	—	—	1.0 (99.5)
Sister Rocks						
1	192.0 (100.0)	—	—	—	—	—
2	180.0 (93.8)	6.0 (6.2)	—	—	—	—
3	138.0 (71.9)	21.0 (21.9)	4.0 (6.2)	—	—	—
4	92.0 (47.9)	24.0 (25.0)	12.0 (18.8)	2.0 (4.2)	—	1.0 (4.1)
5	48.0 (25.0)	17.0 (17.7)	9.0 (14.1)	5.0 (10.4)	2.0 (5.2)	6.0 (27.6)
6	25.0 (13.0)	8.0 (8.3)	5.0 (7.8)	4.0 (8.3)	2.0 (5.2)	8.0 (57.4)
7	11.0 (5.7)	3.0 (3.1)	3.0 (4.7)	1.0 (2.1)	1.0 (2.6)	5.0 (81.8)
8	3.0 (1.6)	1.0 (1.0)	1.0 (1.6)	1.0 (2.1)	1.0 (2.6)	2.0 (91.1)
9	1.0 (0.5)	—	—	2.0 (4.2)	1.0 (2.6)	2.0 (92.7)
10	1.0 (0.5)	—	—	1.0 (2.1)	—	1.0 (97.4)
Mosquito Lake						
1	222.0 (98.7)	1.5 (1.3)	—	—	—	—
2	183.5 (81.6)	18.5 (16.4)	1.5 (2.0)	—	—	—
3	146.0 (64.9)	28.5 (25.3)	4.0 (5.3)	0.5 (0.9)	1.0 (2.2)	0.5 (1.4)
4	80.5 (35.8)	34.5 (30.7)	10.5 (14.0)	4.0 (7.1)	2.0 (4.4)	2.5 (8.0)
5	39.0 (17.3)	21.0 (18.7)	7.5 (10.0)	5.5 (9.8)	5.5 (12.2)	9.0 (32.0)
6	20.5 (9.1)	8.0 (7.1)	5.0 (6.7)	3.5 (6.2)	3.5 (7.8)	9.0 (63.1)
7	9.5 (4.2)	2.0 (1.8)	1.5 (2.0)	1.0 (1.8)	0.5 (1.1)	7.0 (89.1)
8	4.0 (1.8)	1.5 (1.3)	0.5 (0.7)	1.0 (1.8)	0.5 (1.1)	2.0 (93.3)
9	1.5 (0.7)	—	0.5 (0.7)	0.5 (0.9)	—	1.5 (97.7)
10	0.5 (0.2)	—	—	—	—	1.0 (99.8)

Statistical analysis

The spatial pattern created by simulated spacing-based restoration thinning prescriptions was statistically different from the spatial pattern of overstory trees (all species pooled) in the three *Abies* plots and the Canopy Crane *Pseudotsuga* plots at spatial scales of 0 to 3.0 m and 0 to 4.0 m, respectively. The null hypothesis was rejected ($P \leq 0.009$) when $t_{thin} = t_{max}$ with both the G and K spatial statistics (Table 5). The spatial patterns of trees created by simulated spacing-based restoration thinning treatments remained significantly different from the spatial pattern of overstory trees in all plots when tests were repeated with $t_{max} = 13.0$ m ($P \leq 0.014$).

The spatial pattern trees in the Canopy Crane plot remained statistically different from patterns created by simulated spacing-based restoration thinning prescriptions when only *P. menziesii* trees were considered (Table 5). The null hypothesis was rejected with both the G and K spatial statistics ($P \leq 0.001$) when $t_{thin} = t_{max}$, and again when $t_{max} = 13.0$ m ($P \leq 0.003$).

Discussion

Development and detection of spatial structure within forest patches

Plant population ecology theory predicts that self-thinning in plant populations due to competitive mortality may lead to the development of spatial uniformity (or, equivalently, spatial regularity) in the distribution of plants surviving the self-thinning process (Greig-Smith 1957; Pielou 1962). Spatial uniformity is rare in natural plant populations (Greig-Smith 1957; Adler 1996), although some empirical studies have found that self-thinning leads to the development of modest spatial regularity in the arrangement of the trees surviving competitive mortality (e.g., Kenkel 1988).

Natural stand development often includes a self-thinning phase in *Pseudotsuga* (Oliver and Larson 1996; Franklin et al. 2002) and *Abies* forests (Oliver et al. 1985). A tendency towards spatial regularity in the distribution of overstory trees has been observed in mesic conifer forests of the Pacific Coast region (Stewart 1986; He and Duncan 2000;

Table 4. Number per hectare (with percentages in parentheses) of overstory trees (all species pooled) and *Pseudotsuga menziesii* trees only in *Tsuga heterophylla* Zone stands occurring in clusters of different sizes at various spatial scales.

Scale (m)	Cluster size (trees/cluster)					
	1	2	3	4	5	≥6
Canopy Crane						
1	81.5 (100.0)	—	—	—	—	—
2	77.0 (94.5)	2.3 (5.5)	—	—	—	—
3	70.0 (85.9)	5.0 (12.3)	0.5 (1.8)	—	—	—
4	59.8 (73.3)	7.0 (17.2)	2.3 (8.3)	0.3 (1.2)	—	—
5	50.8 (62.3)	9.5 (23.3)	2.5 (9.2)	0.8 (3.7)	0.3 (1.5)	—
6	37.8 (46.3)	10.8 (26.4)	3.8 (13.8)	1.8 (8.6)	0.5 (3.1)	0.3 (1.8)
7	29.0 (35.6)	9.5 (23.3)	4.5 (16.6)	1.0 (4.9)	1.3 (7.7)	1.5 (11.9)
8	20.0 (24.5)	8.3 (20.2)	3.5 (12.9)	1.5 (7.4)	0.8 (4.6)	2.3 (30.4)
9	13.3 (16.3)	5.8 (14.1)	2.8 (10.1)	0.8 (3.7)	1.5 (9.2)	2.5 (46.6)
10	8.5 (10.4)	3.8 (9.2)	2.5 (9.2)	0.8 (3.7)	1.5 (9.2)	3.3 (58.3)
Yellowjacket Creek						
1	86.7 (100.0)	—	—	—	—	—
2	83.0 (95.8)	1.8 (4.2)	—	—	—	—
3	77.0 (88.8)	4.8 (11.2)	—	—	—	—
4	64.2 (74.1)	10.3 (23.8)	0.6 (2.1)	—	—	—
5	54.2 (62.6)	10.9 (25.2)	2.1 (7.3)	0.3 (1.4)	0.6 (3.5)	—
6	40.9 (47.2)	12.1 (28.0)	3.0 (10.5)	0.9 (4.2)	0.6 (3.5)	0.9 (6.6)
7	27.9 (32.2)	7.9 (18.2)	5.5 (18.9)	1.5 (7.0)	1.5 (8.7)	1.8 (15.0)
8	18.5 (21.3)	7.3 (16.8)	3.6 (12.6)	2.1 (9.8)	1.2 (7.0)	3.3 (32.5)
9	10.3 (11.9)	6.7 (15.4)	1.8 (6.3)	1.2 (5.6)	1.2 (7.0)	3.6 (53.8)
10	5.5 (6.3)	4.2 (9.8)	1.8 (6.3)	0.9 (4.2)	1.2 (7.0)	2.7 (66.4)
Canopy Crane *P. menziesii*						
1	34.0 (100.0)	—	—	—	—	—
2	34.0 (100.0)	—	—	—	—	—
3	33.5 (98.5)	0.3 (1.5)	—	—	—	—
4	31.0 (91.2)	1.5 (8.8)	—	—	—	—
5	28.0 (82.4)	3.0 (17.6)	—	—	—	—
6	23.3 (68.4)	3.8 (22.1)	0.8 (6.6)	0.3 (2.9)	—	—
7	21.3 (62.5)	3.5 (20.6)	0.8 (6.6)	0.5 (5.9)	—	0.3 (4.4)
8	15.5 (45.6)	4.0 (23. 5)	0.8 (6.6)	1.5 (17.6)	—	0.3 (6.7)
9	12.8 (37.5)	2.8 (16.2)	1.5 (13.2)	0.8 (8.8)	0.3 (3.7)	0.5 (20.6)
10	11.3 (33.1)	1.8 (10.3)	2.0 (17.6)	0.5 (5.9)	0.3 (3.7)	0.8 (29.4)
Yellowjacket Creek *P. menziesii*						
1	13.9 (100.0)	—	—	—	—	—
2	13.9 (100.0)	—	—	—	—	—
3	13.9 (100.0)	—	—	—	—	—
4	13.3 (95.7)	0.3 (4.3)	—	—	—	—
5	12.7 (91.3)	0.6 (8.7)	—	—	—	—
6	12.1 (87.0)	0.9 (13.0)	—	—	—	—
7	12.1 (87.0)	0.9 (13.0)	—	—	—	—
8	10.9 (78.3)	1.5 (21.7)	—	—	—	—
9	9.7 (69.6)	2.1 (30.4)	—	—	—	—
10	9.7 (69.6)	2.1 (30.4)	—	—	—	—

Van Pelt and Franklin 2000; Zenner 2004) as well as in other forest types (e.g., Kenkel 1988; Oliver and Larson 1996). In a previous study of the Canopy Crane plot, trees ≥76 cm DBH were more regularly spaced than expected at distances of 0 to 15 m based on a null model of spatial randomness (North et al. 2004).

These earlier findings seem to contrast with results from the statistical tests (Table 5) reported in this present study, which indicate that overstory tree spatial patterns in the study plots are not regular. What might explain this apparent discrepancy? It is critical to note that the prior studies and this present study did not use similar spatial null models. The previous studies demonstrated that the spatial pattern of overstory trees in their study plots departed from (rejection of) a null model of spatial randomness, i.e., the patterns observed in these studies were more spatially uniform than the random expectation. However, the authors did not confirm strict regular (i.e., hard-core inhibition) tree spatial patterns.

Fig. 3. Locations of overstory trees (all species) belonging to clusters of size >1 (black symbols) and clusters of size = 1 (i.e., single trees; gray symbols) in the Canopy Crane (*a*), Sutton Lake (*b*), Sister Rocks (*c*), and Mosquito Lake (*d*) study plots. A tree belongs to a multitree cluster if it has a neighboring tree within a distance of t_{thin}. In this figure, t_{thin} = 4.0 m for the Canopy Crane plot (*a*) and t_{thin} = 3.0 m for the Sutton Lake (*b*), Sister Rocks (*c*), and Mosquito Lake (*d*) study plots. Refer to Table 3 (Sutton Lake, Sister Rocks, and Mosquito Lake) and Table 4 (Canopy Crane) for additional detail on cluster demographics at t_{thin}.
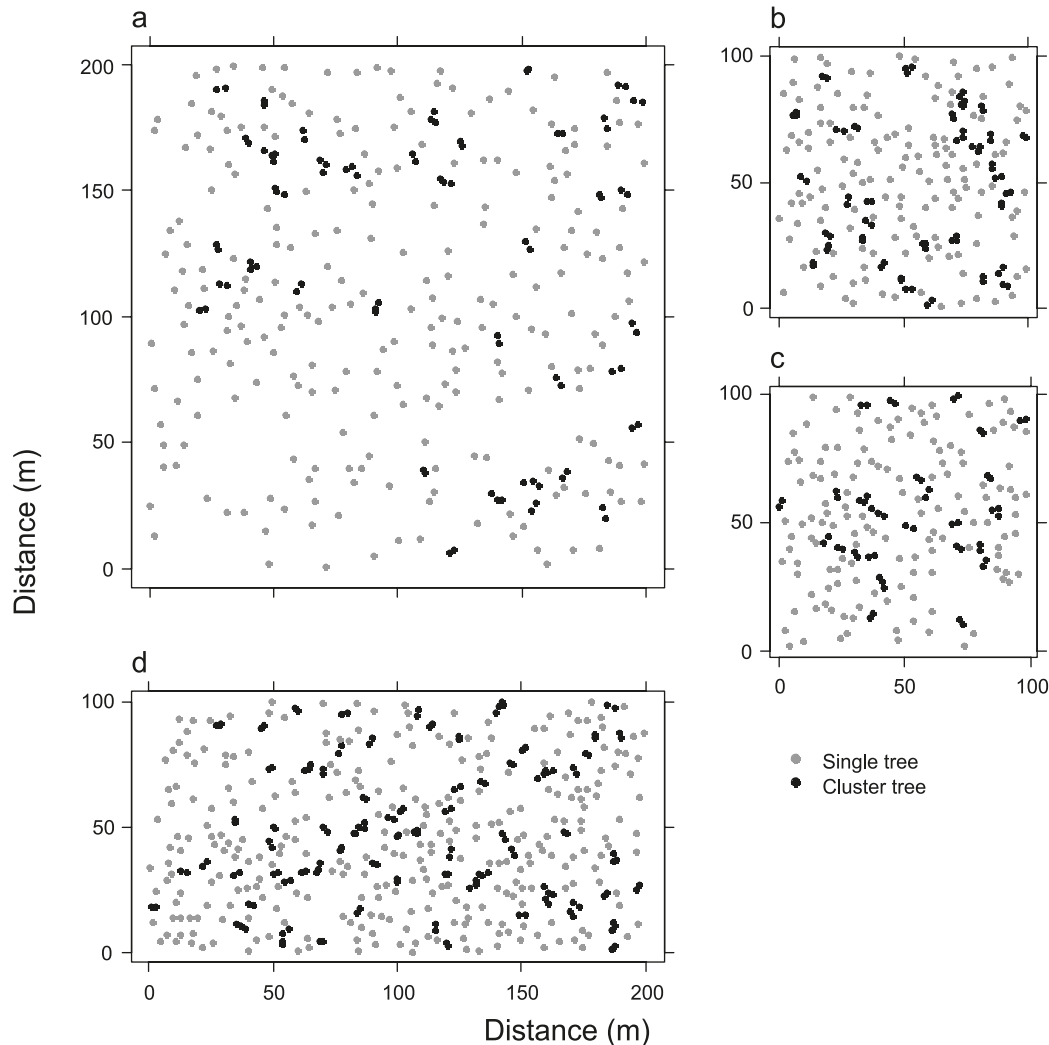
By using a null model of hard-core inhibition we were able to test, and reject (Table 5), the upper limit on the degree of spatial regularity potentially present in the tree patterns (at a scale of t_{thin}). However, the cluster analysis indicates that some spatial regularity is apparent in the spatial distribution of overstory trees (Tables 3 and 4). Between 65% and 72% of overstory trees in *Abies* forests occurred as single trees (cluster size = 1) at a scale of 3 m. *Pseudotsuga* forests exhibited a slightly greater degree of regularity: 73% to 74% of overstory trees occurred as single trees at 4 m. Our results from both forest types, in combination with those of past studies, provide a more precise characterization of the spatial structure of overstory trees. Overstory tree spatial patterns appear to be best characterized by the gradient between spatial randomness and hard-core inhibition. This type of pattern is known as soft-core inhibition (Diggle 2003). Future studies that parameterize soft-core inhibition spatial point process models, such as the Strauss inhibition process, may allow for even more precise characterization

of pattern intensity and scale (see Kenkel (1993) for an ecological application of the Strauss process).

Our results and those of past studies in similar forests are strong evidence that competition and subsequent nonrandom mortality influence the spatial distribution of overstory trees (Kenkel 1988). However, the results from the cluster analysis indicate that the intensity of the past self-thinning was not so great as to create a strict uniform pattern, the type of pattern created by spacing-based thinning treatments. Approximately one-third and one-quarter of overstory trees in *Abies* and *Pseudotsuga* forests, respectively, occur in multitree clusters at t_{thin}. We cannot determine the precise cause of this heterogeneity. Several factors, such as favorable microsites or edaphic conditions; initial tree spacing or density; localized disturbance that released tree clusters from other neighboring competitors; or even resource sharing via root grafting or common mycorrhizal networks (Simard et al. 1997), are potential causes of the observed heterogeneity. Our results support the idea that natural forest development

Table 5. Characteristics of statistical tests (goodness-of-fit test) with the G and K spatial point pattern statistics.

Site	n_{points}[a]	t_{thin} (m)[b]	t_{max} (m)[c]	P_G[d]	P_K[e]
Sutton Lake	215	3.0	3.0	<0.001	<0.001
	215	3.0	13.0	<0.001	<0.001
Sister Rocks	192	3.0	3.0	<0.001	<0.001
	192	3.0	13.0	<0.001	<0.001
Mosquito Lake West	212	3.0	3.0	0.009	0.001
	212	3.0	13.0	0.014	0.001
Mosquito Lake East	238	3.0	3.0	0.002	<0.001
	238	3.0	13.0	0.003	<0.001
Canopy Crane	326	4.0	3.0	<0.001	<0.001
	326	4.0	13.0	0.003	<0.001
Canopy Crane *P. menziesii*	145	4.0	4.0	<0.001	<0.001
	145	4.0	13.0	0.003	<0.001

Note: Results shown are for tests of the null hypothesis of no difference between tree spatial patterns created by simulated spacing-based restoration thinning treatments (see Methods) and observed spatial patterns of overstory trees in late-successional conifer forests. The small P values for tests conducted with both the G and K statistics indicate that the null hypothesis can be rejected.

[a]Number of points in the pattern.

[b]Minimum spacing distance between points in the simulated thinning patterns.

[c]Maximum scale considered for the goodness-of-fit tests.

[d]P value of the goodness-of-fit test with the G statistic.

[e]P value of the goodness-of-fit test with the K statistic.

and the resultant tree spatial patterns integrate the relatively deterministic process of competitive self-thinning, which drives the development of spatial uniformity, and other stochastic factors that provide for the retention of spatial heterogeneity in the form of tree clusters at small spatial scales.

What causes some forests to have many multitree clusters of overstory trees at small scales, while others have relatively few? While the *Abies* and *Pseudotsuga* forests we studied exhibited similar general trends, there are some conspicuous differences in the results. The percolation threshold was reached at smaller scales in *Abies* forests (Fig. 1) than in *Pseudotsuga* forests (Fig. 2). The difference in scale between the *Pseudotsuga* and *Abies* plots is likely due to the relatively larger stature of the trees in the overstory of the *Pseudotsuga* plots (Van Pelt and North 1996; Winter et al. 2002a, 2002b; Shaw et al. 2004; Larson and Franklin 2006). Additionally, more overstory trees occurred as members of multitree clusters at t_{thin} in *Abies* forests than in *Pseudotsuga* forests (Tables 3 and 4). One possible explanation for this difference is that there may be relatively less intense competition and less complete self-thinning — leaving more small scale aggregation — in the *Abies* forests. However, this explanation does not seem likely because developing *Abies* stands have characteristically high stem densities and a protracted (100–300 years) self-thinning stage (Long 1976; Packee et al. 1982; Oliver et al. 1985). A more likely explanation for the higher degree of clustering in the *Abies* forests is the high degree of crown-level morphological plasticity of *A. amabilis*, which allows for asymmetrical crown development and increased tree survival under highly aggregated initial tree spatial patterns (Sorrensen-Cothern, et al. 1993).

Because natural self-thinning influences spatial patterns at small scales (Kenkel 1988), it follows that stands with different initial densities should exhibit divergent patterns of clustering at scales $\leq t_{thin}$. On a relative frequency (i.e., percentage) basis, one would expect multitree clusters at small scales to be more common in stands that developed at low initial densities than in stands that developed at high initial density. However, our analysis indicates that high initial stand density does not necessarily lead to the elimination of multitree clusters; the Yellowjacket Creek *Pseudotsuga* plot had a high initial density and formed a closed canopy by stand age 40 years (Winter et al. 2002a). Yet, 14.3% of *P. menziesii* stems in the Yellowjacket Creek stand had their nearest conspecific neighbor within 4.0 m at stand age 500 years. It is also necessary to determine how non-stand-replacing disturbances influence the spatial distribution of overstory trees. The Yellowjacket stand experienced multiple canopy-thinning disturbances during its 500 year life (Winter et al. 2002b). Partial fire disturbance is known to influence the spatial structure of *Pseudotsuga* forests (Goslin 1997); however, the influence of non-stand-replacing fire on the formation and persistence of multitree clusters at small scales has not been studied. Future studies that incorporate permanent-plot and stand-reconstruction techniques will be necessary for identifying specific mechanisms of spatial pattern formation throughout natural forest stand development.

Restoration thinning treatments in *Abies* and *Pseudotsuga* forests

Spacing-based thinning prescriptions eliminate pairs and groups of closely spaced overstory trees (i.e., the solid black symbols in Fig. 3), components of natural forest structure (Fig. 4) that are not quickly replaced via stand development processes. Spacing between residual post-thinning overstory trees will increase through time as members of the overstory cohort die. New trees must successfully establish and recruit into the overstory to redevelop closely spaced pairs and

Fig. 4. An example of a cluster of three codominant overstory *Pseudotsuga menziesii* trees (i.e., cluster size = 3 in Tables 3 and 4) in a ca. 300-year-old *Pseudotsuga* forest in the Gifford Pinchot National Forest, Washington, USA. (Photo by A.J. Larson.)

groups of overstory trees in stands treated with spacing-based restoration thinning treatments.

Coastal *P. menziesii* does not readily regenerate under closed-canopy conditions (Herman and Lavender 1990). Recovery of closely spaced *P. menziesii* trees thus requires a stand-replacing or partial stand disturbance, allowing the establishment of a new cohort (e.g., Larson and Franklin 2005) and successful recruitment into the overstory, a process that requires many decades or centuries of forest development (Churchill 2005; Zenner 2005).

Abies amabilis and the associated species *Tsuga heterophylla* and *Tsuga mertensiana* (Bong.) Carrière are shade tolerant and capable of regeneration in the absence of significant overstory disturbance (Lertzman 1992). Seedlings of shade-tolerant tree species may establish and then persist in a suppressed state with virtually no height growth for several decades (Antos et al. 2005). Recruitment into the canopy occurs in canopy gaps (Lertzman 1992; Parish and Antos 2004): seedlings respond to small-scale disturbance by increasing height (Van Pelt and Franklin 1999) and diameter (Winter et al. 2002*a*) growth. However, understory and midstory trees are spatially segregated from overstory trees in old-growth *Abies* forests (Larson and Franklin 2006), suggesting that recruitment from subordinate height classes into the overstory class is not likely to occur in locations near established overstory trees. Consequently, redevelopment of closely spaced pairs and groups of overstory trees in *Abies* forests will likely proceed via gap-phase regeneration, a process that also requires many decades or centuries.

Restoration thinning treatments in both commercial and precommercial stands will be more effective at creating the fine-scale spatial patterns characteristic of late-successional forest structure if they are modified to allow for the retention of closely spaced clusters of trees. Multitree clusters occurred throughout the study plots (Fig. 3), indicating that the fine-scale spatial patterns characteristic of late-successional overstory trees cannot be achieved by leaving one or less unthinned skip per hectare (e.g., Roberts et al. 2007); retention of closely spaced tree clusters within thinned areas will be necessary. On average, 32.7% of overstory trees in *Abies* plots and 26.3% of overstory trees in *Pseudotsuga* plots occurred as members of multitree clusters at scales of 3.0 and 4.0 m, respectively. The data presented in Tables 3 and 4 can be used as a rough guideline for how many clusters of different sizes to retain per hectare in *Abies* and *Pseudotsuga* forests, respectively, if site-specific data on spatial patterns of late-successional overstory trees are not available.

Restoration thinning treatments that release individual trees as well as multitree clusters promote characteristic late-successional tree spatial patterns at the within-patch scale. This formulation of restoration thinning explicitly incorporates conservation of existing small-scale spatial heterogeneity within the treatment area as a core element of the silvicultural design process. This approach extends current restoration thinning practices that emphasize introduction of patch-scale spatial heterogeneity with "skips", "gaps", and variable thinning densities throughout the stand. Restoration thinning prescriptions will be most effective at creating desired spatial patterns when they do not include minimum tree spacing guidelines, and when they contain clear, operationally meaningful descriptions of the desired spatial patterns.

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