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Spatial Patterns of Tree Mortality in an Old-Growth *Abies*–*Pseudotsuga* Stand

Abstract

The processes that generate spatial patterns of organisms are often inferred from analysis of the patterns themselves. To test the reliability of such inferences, we examined spatial patterns of tree mortality over 16 years in a permanent 1-ha study area where causes of mortality are reasonably well known. The area is an old-growth stand in the Cascade Mountains of Oregon, dominated by *Abies amabilis* (60% of stems but only 12% of basal area), *Abies procera* (52% of basal area), and *Pseudotsuga menziesii* (22% of basal area). Mortality was dominated by the two *Abies* species. Dying *A. amabilis* occupied lower canopy strata and often had been suppressed or damaged by falling limbs or trees. Dying *A. procera* occupied upper canopy strata and often had been attacked by pathogens. The positions of dying trees and causes of mortality suggested that dying *A. amabilis* should be found near canopy trees and that dying *A. procera* should be aggregated. These hypotheses were tested by quadrat- and distance-based methods. On average, dying *A. amabilis* were not significantly closer to canopy trees than expected for a random distribution or closer than random selections of trees from the entire population of *A. amabilis*. Dying *A. procera* were aggregated at a scale of about 20 m; however, the degree of aggregation was not significant compared with the distribution of the entire population. The potential for large falling trees to strike other trees at some distance from their bases, and the underlying non-random distribution of some tree populations, may limit the extent to which causes of tree mortality can be inferred from spatial patterns.

Introduction

Understanding the causes of spatial patterns of organisms is a primary goal of ecology (Greig-Smith 1983, Ludwig and Reynolds 1988). Often, spatial patterns are analyzed to determine which processes generated the patterns. However, the degree to which pattern can be used to infer process is an open question, one requiring critical examination (Cale et al. 1989). One means of testing the proposition that pattern can be used to deduce process is to examine patterns generated by known processes. In this paper we examine spatial patterns of tree mortality in a permanent study area where the causes of mortality are reasonably well known.

The study area, a 1-ha portion of the H. J. Andrews Experimental Forest in western Oregon, provides an appropriate setting in which to test whether spatial patterns of tree mortality concur with predictions based on underlying processes. As described below (see Results), the two species accounting for most of the tree mortality, *Abies amabilis* (Pacific silver fir) and *A. procera* (noble fir), have contrasting causes of mortality, and dying trees occupy different canopy positions. Damage

from falling green trees or limbs and suppression are the predominant causes of *A. amabilis* mortality; nearly all dying trees occupy lower canopy strata. *A. procera* mortality is often caused by pathogens; most dying trees occupy upper canopy strata.

Because of these differences in mortality patterns, one would expect different spatial patterns for the two tree species. Falling trees often strike and kill other trees in mature and old-growth forest stands in the Pacific Northwest (Franklin et al. 1987). In multicohort or uneven-aged stands such as our study area, shading and suppression also lead to mortality of younger, smaller trees (Oliver and Larson 1990). Thus, small trees near canopy trees should be most likely to die. Large trees, on the other hand, are more likely to succumb to pathogens or wind (Franklin et al. 1987). Pathogens, in particular, may affect groups of trees within stands, especially when dispersal of the pathogens is limited (e.g., the root rot *Armillaria mellea*, which spreads through the soil (Manion 1981)). We therefore used the spatial data collected in the study area to test separate hypotheses for the two species:

- 1) Dying *Abies amabilis* trees are near canopy trees observed when the study began;
- 2) Dying *Abies procera* trees are aggregated.

Study Area

The study area is in an old-growth forest in the *Abies amabilis* zone (Dyrness et al. 1974), in the H. J. Andrews Experimental Forest near Blue River, Oregon (44° 16' N lat., 112° 8' W long.). The elevation is 1290 m, with a south-facing slope of 5 percent. Soils on the study area belong to the Haplumbrept great group and are moderately deep and stony; they developed in andesitic glacial till mixed with volcanic ash and pumice (C. T. Dyrness, pers. comm.).

The canopy is predominately of *A. procera* and *Pseudotsuga menziesii* (Douglas-fir). Other canopy species include *Abies amabilis*, *Tsuga heterophylla* (western hemlock), and *T. mertensiana* (mountain hemlock). The understory is dominated by *Xerophyllum tenax* (beargrass).

Methods

Field methods

The study area was established as a 1-ha square in 1977 by researchers from the Pacific Northwest Research Station and Oregon State University (Franklin and Van Pelt 1990). All trees ≥ 5 cm dbh were tagged and mapped in relation to a grid of string placed at 5-m intervals. Accuracy of this method of tree mapping is estimated to be ± 1 m (Hawk et al. 1978). Trees were remeasured in 1983, 1988, and 1993. The area was surveyed annually from 1978 to 1991 for tree mortality. During the 5-year remeasurements and annual surveys, conditions of newly dead trees and any obvious causes of mortality were recorded.

Analytical methods

To provide necessary background for tests of spatial hypotheses, we summarized stand structure and mortality by species. In preliminary analyses, we noted that a very few *A. amabilis* were also canopy trees. Because we were interested in the relationship between the canopy and the smaller *A. amabilis* trees, we excluded *A. amabilis* canopy trees from the *A. amabilis* population in the spatial analyses.

To test hypotheses, we used quadrat-based and distance-based methods. Quadrat-based methods

included 2 x 2 contingency tables (Sokal and Rohlf 1981; Greig-Smith 1983) and Morisita's index, I_d (Pielou 1977; Krebs 1989). Quadrat sizes ranging from 1 x 1 m to 20 x 20 m were used to test for pattern at a variety of spatial scales. The 2 x 2 contingency table method tests whether two populations (*i.e.*, dying *A. amabilis* and canopy trees) co-occur more or less often than would be expected from their respective densities (Greig-Smith 1983). Morisita's index, used to test aggregation of dying *A. procera*, is based on comparison of the probability that any two individuals drawn at random from the observed population will be from the same quadrat and the corresponding probability for a population with a random spatial pattern (Pielou 1977). Values of I_d greater than 1 indicate some degree of clumping; values less than 1 indicate a more regular distribution.

The quadrat-based statistical tests of spatial pattern compare observed patterns of dying trees with expectations under random distribution. The tests do not take into account the spatial patterns of all individuals of a species. However, if the underlying pattern of all individuals is ignored, it is possible to mistake patterns of dying trees for patterns intrinsic to a species. Therefore, in addition to testing patterns of dying trees relative to random distributions, we also performed randomization tests using the respective species' entire populations (Crowley 1992). For these tests, we repeatedly drew a random sample from the species' population equal in size to the number observed dying. For each random sample, the spatial statistic was computed and compared with the observed value of the statistic. The reported values of P are the fraction of times a value of the statistic at least as extreme as the observed value occurred in 1000 random samplings (Crowley 1992).

Distance-based methods included both univariate and bivariate combined count-distance statistics (Ripley's $K(t)$ function, Muer 1993; see also Kenkel 1988). Ripley's $K(t)$ takes into account the location of all individuals, not just nearest neighbors, to describe spatial patterns (Kenkel 1988). $K(t)$ is essentially a summation of all individuals within distance t of a target individual, averaged over all target individuals. Because some of the near neighbors of target individuals close to plot boundaries may lie outside of the plot, a correction is employed for edge effects (Muer 1993). The correction imposes a weighting that

is the inverse of the proportion within the plot of the circumference of a circle centered on the target tree and passing through the near neighbor. With the correction factor,

$$K(t) = A * \sum_{i=1}^n \sum_{j=1}^n w_{ij}(t)/n^2 \text{ for } i \neq j$$

for all pairs of trees with $t_{ij} \leq t$,

where $K(t)$ = Ripley's K for distance t ,

A = area of the plot,

n = the number of trees

$w_{ij}(t)$ = edge-correction weighting factor, and

t_{ij} = distance between trees i and j (Mouer 1993).

To assess spatial patterns at a range of scales comparable to those in the quadrat-based analyses, the combined count-distance statistics were computed for distances from 1 to 30 m.

To convert to a scale more convenient for assessing spatial pattern at a range of spatial scales, $K(t)$ is transformed as follows:

$$L(t) = t - (K(t) / \pi)^{1/2} \text{ (Kenkel 1988)}.$$

$L(t)$ has an expectation of zero for random patterns; values greater than zero indicate more regular patterns, and values less than zero indicate more aggregated patterns (Kenkel 1988). $K12(t)$ is a bivariate analog of $K(t)$ that allows assessment of attraction or repulsion between two species or other classes of trees (Kenkel 1988; Mouer 1993). The analogous transformation of $K12(t)$ to $L12(t)$ is used to facilitate examination of patterns at a range of spatial scales. Positive values of $L12(t)$ indicate repulsion between types; negative values indicate attraction.

Observed values of $L(t)$ and $L12(t)$ are compared with results from randomly generated sets of points to determine significance. Following Mouer (1993), we computed the statistics for 200 randomly drawn sets of points and generated one-sided 95 percent confidence envelopes. Since this technique does not take into account the spatial patterns of all individuals of a species, we also constructed "random mortality" confidence envelopes (see Kenkel 1988) by drawing 200 random samples from the initial populations of the species. The observed values of $L(t)$ and $L12(t)$ were compared with both the random and the random mortality 95 percent confidence envelopes.

Results

Stand structure

Abies amabilis accounted for 60 percent (393 stems) of the 651 stems in the 1-ha plot (Table 1). However, the total basal area of 86.8 m²/ha was dominated by *A. procera* (52% of total), and to a lesser extent, *P. menziesii* (22%) (Table 2). The size distribution of *A. amabilis* contrasted with that of the species dominating the canopy (Fig. 1). *Abies amabilis* had a reverse-J-shaped size distribution, with an overwhelming majority of small stems, whereas both *A. procera* and *P. menziesii* had very few small stems and large median stem sizes (82 and 88 cm, respectively).

TABLE 1. Decrease in number of stems due to tree mortality, by species, 1977-1993.

Species	Number in original population (1977)	Number dying, 1977-1993	% original population dying	% dying per annum ¹
<i>Abies amabilis</i>	393	40	10.2	0.7
<i>Abies procera</i>	82	38	46.3	3.8
<i>Pseudotsuga menziesii</i>	30	0	0	0
<i>Tsuga heterophylla</i>	83	5	6.0	0.4
<i>Tsuga mertensiana</i>	63	7	11.1	0.7
All species	651	90	13.8	0.9

¹Computed by the negative compound interest formula (Lorimer 1981) from percentage of original population dying.

TABLE 2. Decrease in basal area (m²/ha) due to tree mortality by species, 1977-1993.

Species	Basal area in original population (1977)	Basal area lost to mortality, 1977-1993	% original basal area lost	% per annum ¹
<i>Abies amabilis</i>	10.2	2.7	26.2	1.9
<i>Abies procera</i>	45.0	18.7	41.5	3.3
<i>Pseudotsuga menziesii</i>	19.0	0	0	0
<i>Tsuga heterophylla</i>	5.6	0.02	0.4	0.03
<i>Tsuga mertensiana</i>	7.0	0.7	9.5	0.6
All species	86.8	22.1	25.4	1.8

¹Computed by the negative compound interest formula (Lorimer 1981) from percentage of original population dying.

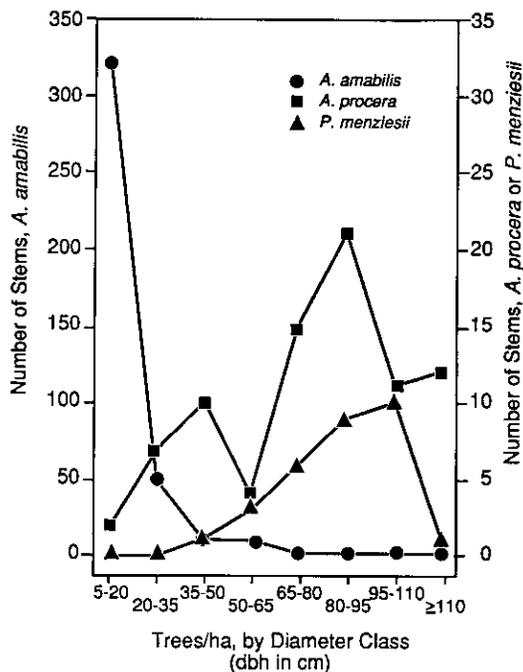


Figure 1. Diameter distribution in trees/ha for *Abies amabilis*, *A. procera*, and *Pseudotsuga menziesii* in 1977.

The most notable change between 1977 and 1993 was the decline of *A. procera* (Tables 1 and 2); the number of stems declined by 46.3 percent, and the basal area dropped by 41.5 percent. *A. amabilis* and *A. procera* accounted for most of the mortality (44% and 42% of dying stems, respectively, Table 1). Basal area lost to mortality was 7 times greater for *A. procera* than for *A. amabilis* (18.7 vs. 2.7 m²/ha, Table 2).

More than half of the *A. amabilis* mortality was attributed to suppression or damage from falling green trees or limbs (Fig. 2); many dying *A. amabilis* were relatively small trees, with a median diameter at breast height (dbh) of 15 cm. Nearly all (98%) dying *A. amabilis* occupied lower canopy strata (i.e., suppressed or intermediate trees (Daniel et al. 1979)). In contrast, almost 40 percent of the *A. procera* mortality was attributed to mistletoe or other pathogens (Fig. 2), more than to any other obvious cause. Eleven of the 13 trees with no recorded cause of mortality died standing, and it is likely that pathogens also contributed to the deaths of these trees. Most dying *A. procera* trees were relatively large (median dbh = 75 cm), and most (74%) occupied upper canopy strata (i.e., codominant or dominant trees (Daniel et al. 1979)).

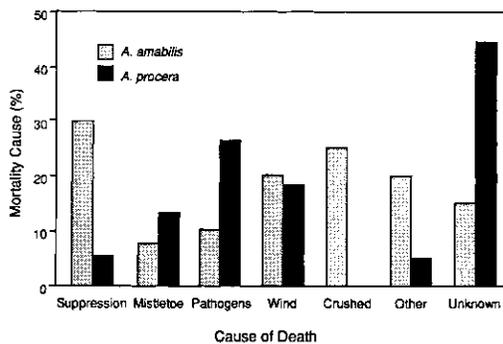


Figure 2. Causes of mortality for *Abies amabilis* and *A. procera* (1978–1993). Values displayed combine primary and secondary causes of mortality, and therefore add to more than 100% for each species.

Tests of Spatial Hypotheses

Neither quadrat- nor distance-based methods showed dying *Abies amabilis* to be significantly nearer to canopy trees than expected from a random distribution. Co-occurrence of dying *A. amabilis* and canopy trees alive in 1977 was not significantly different from random association at all quadrat sizes examined (Table 3). Furthermore, such co-occurrence was not unusually large in comparison with co-occurrence of the entire *A. amabilis* population and canopy trees (i.e., randomization tests in Table 3). The combined count-distance method indicated that dying *A. amabilis* were not closer to canopy trees than either a random selection from the entire population of *A. amabilis* or a random selection of points for spatial scales from 1 to 30 m (Fig. 3).

Dying *A. procera* trees were aggregated according to both quadrat and combined count-distance methods, at least in comparison with random selections of points. However, aggregation of dying *A. procera* was not significant compared with the pattern of the entire population. Morisita's index indicated significant aggregation in 20 x 20 m quadrats, but not for other quadrat sizes (Table 4). However, compared with random samples from the entire population, the observed aggregation was not extreme (i.e., $P = 0.20$ in randomization test, Table 4). The combined count-distance method indicated significant clumping at scales of 7, 8, 15–19, and 21 m in comparison with the random 95 percent confidence envelope (Fig. 4). However, in comparison with the random mortality 95 percent confidence envelope, dying *A. procera* were not aggregated at any scale from 1 to 30 m (Fig. 4).

TABLE 3. Tests of association between dying non-canopy *Abies amabilis* and canopy trees (all species) within quadrats of various sizes (2 x 2 contingency tables, tested with G-tests, except as noted).

Quadrat size (m)	G statistic	Adjusted G statistic	P	Randomization test ¹	
				Average value of G statistic	P
1 x 1	0.91	0.66	P > 0.25	0.86	P = 0.87
2 x 2	0.03	0.03	P > 0.75	1.29	P = 1.00
5 x 5	0.09	0.09	P > 0.75	1.41	P = 0.73
10 x 10	0.13	0.12	P > 0.5	1.17	P = 0.73
20 x 20	0.00	N/A ²	P = 1.0	0.00	P = 1.00

¹Results from 1000 random samples of population of non-canopy *Abies amabilis* alive in 1977; P value is fraction of samples for which G statistic was at least as large as observed value.

²Probability computed by Fisher's exact test.

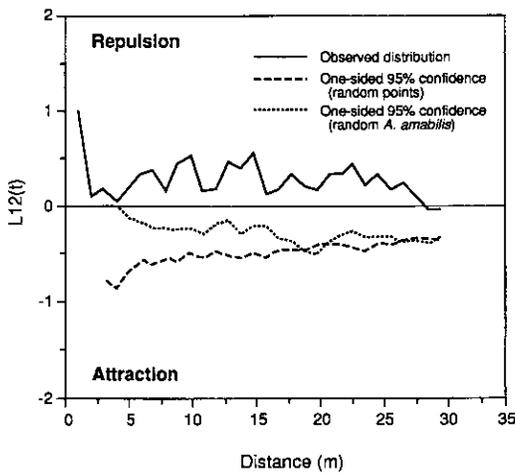


Figure 3. Bivariate combined count-distance analysis ($L_{12}(t)$ vs. t) for *Abies amabilis* dying between 1977 and 1993 and codominant and dominant trees in 1977. Solid line = observed distribution; dashed line = one-sided 95% confidence interval based on random selection of points ("random" confidence envelope); dotted line = one-sided 95% confidence interval based on random selection from initial population of *A. amabilis* ("random mortality" confidence envelope). Because of the discrete distribution of $L_{12}(t)$, neither confidence envelope could be computed for $t = 1$ or 2. Compared with both random sets of points and random selections from the initial population, $P \gg 0.05$ for $t = 1$ and 2.

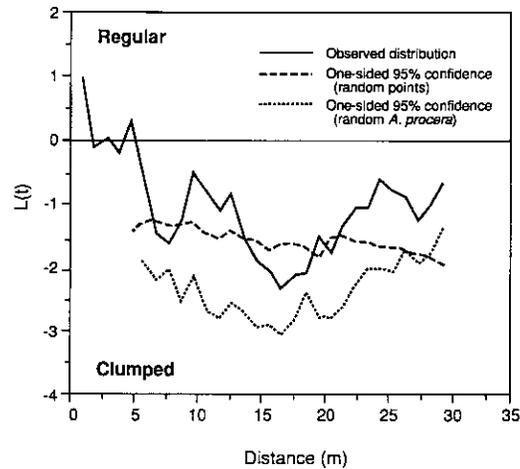


Figure 4. Combined count-distance analysis ($L(t)$ vs. t) for *Abies procera* dying between 1977 and 1993. Line types as in Fig. 3. Because of the discrete distribution of $L(t)$, the random and random mortality confidence envelopes could not be computed for $t < 5$ or 6, respectively. For all cases lacking 95% confidence envelope values, $P \gg 0.05$.

TABLE 4. Values of Morisita's index, I_d , a test of aggregation of dying *Abies procera*.

Quadrat size (m)	I_d	P (1-tailed)	Randomization test ¹	
			Average value of I_d	P
1 x 1	1.00	P = 1.0	0.00	P = 1.00
2 x 2	0.00	P = 1.00	1.67	P = 1.00
5 x 5	0.57	P = 1.00	0.49	P = 0.64
10 x 10	1.42	0.25 > P > 0.10	1.09	P = 0.22
20 x 20	1.35	P < 0.05	1.18	P = 0.20

¹Results from 1000 random samples of population of *Abies procera* alive in 1977; P value is fraction of samples for which I_d was at least as large as observed value.

Discussion

Mortality in this study affected populations of two species that contrast in autecology. *Abies amabilis* in this stand is a tolerant, climax species (Dyrness et al. 1974; Crawford and Oliver 1990), as illustrated by its size distribution (Daniel et al. 1979). On the other hand, the size distribution of *A. procera* is typical of even-aged populations of intolerant species (Daniel et al. 1979) and is consistent with its status as a seral species (Dyrness et al. 1974; Franklin 1990). The usual agents of mortality also are different for the two species—falling trees and limbs and suppression affect *A. amabilis*, and pathogens affect *A. procera*. Thus, different spatial patterns of mortality were hypothesized for the two species: dying *A. amabilis* would be close to canopy trees, and dying *A. procera* would be aggregated.

Dying *A. amabilis*, however, were not closer than *A. amabilis* in general to canopy trees standing in 1977. Because toppling canopy trees contribute to mortality of *A. amabilis*, canopy trees may kill trees of lower strata at some distance from themselves. Thus the spatial pattern of small dying trees may more strongly reflect underlying processes when suppression, rather than physical damage from canopy trees, is the predominant cause of mortality. It is also possible that death of small *A. amabilis* trees in the study area is due more to crowding by neighboring trees of all sizes than to proximity to canopy trees (see, e.g., Stohlgren 1993). The tendency of *A. amabilis* to establish in canopy gaps (Wilson 1991) could contribute to diminishing the influence of canopy trees on mortality of small *A. amabilis*. However, assessing the effects of crowding on small *A. amabilis* is beyond the scope of this study.

Although dying *A. procera* trees were aggregated at scale of about 20 m, dying trees were not more aggregated than the entire population. Death of adjacent *A. procera* may contribute to formation of large canopy gaps, but it is unclear whether proximity contributes to *A. procera* mortality. If patterns are to be definitively shown, future studies may need to encompass larger numbers

of trees to compensate for non-random spatial distributions of *A. procera* (possibly caused by limited seed dispersal distances; see Franklin 1990). Even with larger sample sizes, it is conceivable that no aggregation of dying *A. procera* will be found. Published observations of spatial distribution of mortality due to root diseases of *Pseudotsuga menziesii* and other conifers in the Pacific Northwest indicate that either clumped or dispersed mortality may occur (Filip and Goheen 1995; Thies and Sturrock 1995).

Although the observed spatial patterns correspond to those hypothesized for *A. procera*, they did not correspond to those suggested for *A. amabilis*. In addition, based on the spatial pattern of all *A. procera* trees, the pattern of dying trees was not markedly different from randomness. The inferences that can be drawn from these results are limited by the relatively small study area and a lack of information on how representative the study area may be of *Abies* forests in the Pacific Northwest or any larger set of forests. Within those limitations, our results do not definitively support the proposition that the processes causing tree mortality can be deduced from spatial patterns of dying trees (though cf. Stohlgren 1993). Furthermore, these results indicate that it is sometimes not possible to predict spatial patterns of dying trees even when mortality causes are known.

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