Spatially random mortality in old-growth red pine forests of northern Minnesota

Tuomas Aakala, Shawn Fraver, Brian J. Palik, and Anthony W. D'Amato

Abstract: Characterizing the spatial distribution of tree mortality is critical to understanding forest dynamics, but empirical studies on these patterns under old-growth conditions are rare. This rarity is due in part to low mortality rates in old-growth forests, the study of which necessitates long observation periods, and the confounding influence of tree in-growth during such time spans. Here, we studied mortality of red pine (*Pinus resinosa* Ait.) in five old-growth stands in Minnesota, USA, demonstrating the use of preexisting information of cohort age structures to account for in-growth after the most recent cohort establishment. Analyses of spatial point patterns, using both Ripley's K-function and the pair correlation function, showed that tree mortality was essentially a random process, without evidence of contagious mortality patterns that are often expected for old-growth forests. Our analyses further demonstrated in practice that the distribution of dead trees may differ from that of the tree mortality events, which are constrained to occur within the initial distribution, and how mortality patterns can shape the spatial distribution of mature living trees, often attributed to aggregated regeneration patterns. These findings emphasize the need to disentangle the influence of the initial distribution of trees from that of actual tree mortality events.

Résumé : La caractérisation de la distribution spatiale des arbres morts est importante pour comprendre la dynamique forestière, mais les études empiriques portant sur ces patrons ont rarement été réalisées dans de vieilles forêts. Cette rareté est en partie attribuable aux faibles taux de mortalité dans les vieilles forêts dont l'étude requiert de longues périodes d'observation ainsi qu'à la confusion qu'engendre le recrutement d'arbres sur de telles périodes de temps. La présente étude porte sur la mortalité de pin rouge (*Pinus resinosa* Ait.) dans cinq vieux peuplements du Minnesota, aux États-Unis, et démontre l'utilité de l'information préexistante sur la structure d'âge des cohortes d'arbre pour tenir compte du recrutement à la suite de l'établissement de la plus récente cohorte. L'analyse des patrons de points, à l'aide de la fonction K de Ripley et de la fonction de corrélation par paires, a montré que la mortalité des arbres était un processus essentiellement aléatoire, sans indice de patrons de mortalité contagieuse qui sont souvent anticipés dans les vieilles forêts. En pratique, nos analyses ont aussi démontré que la distribution des arbres morts peut être différente de celle des épisodes de mortalité, qui sont contraints de survenir dans la distribution initiale, et comment les patrons de mortalité peuvent modeler la distribution spatiale des arbres vivants dominants, qui est souvent attribuée à des patrons regroupés de régénération. Ces résultats soulignent le besoin de dissocier l'influence de la distribution initiale des arbres de celle des épisodes réels de mortalité.

[Traduit par la Rédaction]

Introduction

Death of mature trees is a fundamental process driving old-growth forest dynamics, and its spatial distribution strongly influences the dynamics of forest structure and composition. Tree mortality changes the distribution of living (i. e., surviving) trees, determines the distribution of regeneration substrates (such as deadwood and soil pits and mounds), and alters the allocation of growing space within and among populations (Franklin et al. 1987). Spatial and temporal patterns in the release of growing space determine which species have the potential to establish and grow and thus regulate tree species composition. However, despite its fundamental importance to natural forest development, the spatial distribution of tree mortality has only rarely been studied in the

mature tree populations occurring in old-growth forests. Such information is needed for interpreting historical forest stand dynamics (Fraver and White 2005; Aakala et al. 2007), for determining forest restoration targets (Larson and Churchill 2008), for developing templates for the application of ecological forestry practices (Palik and Pederson 1996), and for refining, calibrating, and testing forest simulation models (Coates et al. 2003).

The spatial distribution of tree mortality is determined essentially by two factors: the distribution of living trees and the distribution of the tree mortality events among those trees. The initial distribution of living trees provides the matrix within which tree mortality occurs and thus limits the extent and spatial pattern of tree mortality (Little 2002; Aakala et al. 2007). Within these limits, the spatial distribution of

T. Aakala[*] **and A.W. D'Amato.** Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA.
S. Fraver and B.J. Palik. USDA Forest Service, Northern Research Station, Grand Rapids, MN 55744, USA.

Corresponding author: Tuomas Aakala (e-mail: tuomas.aakala@helsinki.fi).

[*]Present address: Department of Forest Sciences, P.O. Box 27, FI-00014 University of Helsinki, Finland.

tree mortality is then influenced by a number of factors, including the characteristics of mortality agents and the varying predisposition of trees to these agents (Manion 1991). Exogenous disturbances are often considered to be important drivers of forest stand dynamics. Many such disturbance agents occur in contagious spatial patterns (Harmon et al. 1986), owing to the agents' biology (e.g., the spread of pathogenic fungi or insects from an epicenter) or their physical nature (e.g., storm downbursts). However, it is known that in many forest types, background mortality, i.e., mortality that occurs outside distinct disturbance events, can be a more important process structuring old-growth forests (Franklin et al. 1987). Rigorous empirical evidence documenting the spatial patterns of tree mortality in old-growth forests is scarce, and these hypotheses remain largely untested.

Background mortality occurs at a very low rate. Therefore, long time spans are needed to elucidate its patterns, but at such time scales, tree in-growth (the gradual accrual of newly established trees) can confound the interpretation of the initial living tree distribution, thus undermining proper analyses. However, if in-growth can be accounted for, spatial patterns of tree mortality can be analyzed following the random mortality hypothesis testing approach, which entails an analysis of the spatial distribution of tree mortality events within a fixed initial distribution of trees (Kenkel 1988). This approach provides stronger inferences regarding tree mortality than those derived from comparisons of the contemporary living tree distribution with the dead tree distribution (Goreaud and Pelissier 2003), which is a less powerful, yet more commonly taken approach.

In this study, we used preexisting information on tree age structures to overcome the limitation of tree in-growth to produce more rigorous analyses of spatial patterns of tree mortality. We applied this approach in five old-growth red pine (*Pinus resinosa* Ait.) dominated stands in northern Minnesota, USA. Red pines on these sites form distinct age cohorts, which have most likely established following dated wildfires (Fraver and Palik 2012). This allowed us to rule out the confounding effects of in-growth after the establishment of the most recent cohort. We further assessed the patterns of living and dead trees to demonstrate how tree mortality had changed the spatial distribution of living trees and the resulting spatial distribution of dead trees. In doing so, we compared two commonly used methods of spatial point pattern analysis, Ripley's *K*-function (Ripley 1977) and the pair correlation function.

Material and methods

Study sites

The data employed in this study were derived from Fraver and Palik (2012), which addresses cohort age structure in seven remnant old-growth red pine forests in Minnesota. We excluded two of the seven sites because of insufficient numbers of dead red pines for analysis. Exploratory analyses revealed that a minimum sample size of 30 dead trees (i.e., mortality records) was necessary; smaller sample sizes produced only trivial changes to the spatial distributions of surviving trees. The five sites employed in the current study were Lac La Croix Research Natural Area, Ramshead Lake, Voyageurs Island, Pine Point Research Natural Area, and

Table 1. Number of living and dead red pines (*Pinus resinosa*) and the number of age cohorts (from Fraver and Palik 2012) in each plot included in the analyses.

Study site	Living	Dead	Cohorts
Lac La Croix	39	66	2
Pine Point	85	57	2
Ramshead Lake	49	55	2
Sunken Lake	91	113	3
Voyageurs Island	34	68	2

Sunken Lake Research Natural Area (Table 1). These five sites are located in two ecological sections following the national hierarchical framework of ecological units (Cleland et al. 1997): Lac La Croix, Ramshead Lake, and Voyageurs Island are located in the Northern Superior Uplands, while Pine Point and Sunken Lake are located in the Northern Minnesota Drift and Lake Plains. The former section is characterized by glacially scoured bedrock overlain by thin, coarse loamy tills; the latter section is characterized by complex juxtapositions of ice-contact, fluvioglacial, and lacustrine deposits, with soils typically deeper than those of the former section. In addition to these substrate differences, sites on the Northern Superior Uplands were subjected to a severe windstorm in 1999. Taken together, these differences likely influence tree spatial distributions, and they contribute to site–site variability.

All five sites show distinct two- or three-cohort red pine age structures (Fraver and Palik 2012), with cohort establishment mainly following dated wildfires. No additional red pine in-growth has occurred following the most recent cohort establishment 104–213 years ago (depending on site). Sites are dominated by red pine, although other species, particularly eastern white pine (*Pinus strobus* L.), also occupy main canopy positions.

Field data collection

At each site, we established one 70.7 m × 70.7 m plot (0.5 ha) placed in the geographic center of the stand to avoid edge effects and subjectivity in plot placement. Within each plot, we recorded diameter at breast height (1.37 m), species, and *X* and *Y* coordinates for all living and standing dead trees (stems ≥10 cm diameter at breast height). Similarly, for down woody debris pieces greater than 10 cm diameter, we recorded species (when possible), diameters at large and small ends, length, and *X* and *Y* coordinates (pines only, recording the former rooted location). For both living and dead pines (when possible), we extracted one increment core near the base to estimate age. Cores from dead pines were cross-dated against the living tree chronology to arrive at establishment dates.

Statistical analyses

Stem maps with locations for all living and dead red pines on the five plots allowed us to analyze tree spatial distributions in these old-growth stands. To this end, we used the widely applied Ripley's *K*-function (Ripley 1977) and complemented it with the pair correlation function $g(r)$ (Stoyan and Stoyan 1994). The empirical *K*-function quantifies a spatial point pattern by giving an expected number of individu-

als within a given distance r from a randomly chosen individual (for details, see Goreaud and Pelissier 2003). In our analyses, we used the L-function, which is a square root transformation of the K-function that stabilizes its variance and equals zero under complete spatial randomness (Goreaud and Pelissier 2003). $L(r)$ suffers from a caveat associated with its cumulative nature: inferences about the patterns at specific scales can be biased (Perry et al. 2006). Thus, we complemented $L(r)$ with the pair correlation function $g(r)$, which can be interpreted as a noncumulative version of $L(r)$. It has the potential to more accurately determine the exact scales at which deviations from the null pattern occur (Perry et al. 2006). In computing $g(r)$, we relied on the implementation by Baddeley and Turner (2005) in which an estimate of $g(r)$ is computed using smoothing splines to approximate the derivative of the L-function at specific distances (for details, see Baddeley and Turner 2005).

Using both the $L(r)$ and $g(r)$, we first analyzed the univariate spatial distributions of current living trees, $L_{live}(r)$ and $g_{live}(r)$, the distribution of current dead trees, $L_{dead}(r)$ and $g_{dead}(r)$, and the initial distribution of living trees (current living and dead trees combined), $L_{initial}(r)$ and $g_{initial}(r)$. Second, we quantified the spatial distribution of tree mortality events by calculating the difference between the univariate functions $L_{initial}(r) - L_{live}(r)$ and $g_{initial}(r) - g_{live}(r)$. Any shift in the distribution in living trees without in-growth is essentially a thinning process. It can be shown that under randomly occurring tree mortality, $L_{live}(r) = L_{initial}(r)$, i.e., the difference between the two is zero (Goreaud and Pelissier 2003). Positive deviations from zero, i.e., $L_{initial}(r) > L_{live}(r)$, would indicate that there are fewer living trees within distance r (current distribution of living trees) than in the original distribution $L_{initial}(r)$, which would result from aggregated tree mortality. Negative deviations would indicate repulsion, i.e., that tree mortality was less likely to occur within distance r from another tree mortality event. The same applies to the g-function, as it is essentially a noncumulative version of the L-function.

In addition to quantifying the global spatial pattern of tree mortality (sensu Fortin and Dale 2005) on each site, we computed local versions of the L-function for tree mortality. Earlier studies have shown that global patterns can contain heterogeneous internal regions (Perry et al. 2006; Larson and Churchill 2012). The local version can thus be used to detect within-stand pattern variation, to reveal spatial trends in the data, and, when aggregation is detected, to show the distribution of clusters within the stand. We thus complemented the global pattern analysis $L_{initial}(r) - L_{live}(r)$ with its localized version (denoted here as $L_{initial}(d) - L_{live}(d)$) following the approach by Getis and Franklin (1987). In this analysis, $L(d)$ is computed separately for each tree, which can also be considered as the individual summands for the global L-function (Baddeley and Turner 2005). We displayed the results as a map, which aims to reveal specific regions of variation in the pattern within the stand. In analyzing patterns of mortality, the intensity λ (number of points per area) of the initial distribution differs from the current living tree distribution (fewer points in the same area). The local L-functions for the current living tree distributions were thus scaled so that under random mortality, the expectation would be $L_{initial}(d) - L_{live}(d) = 0$. This scaling was done to make the interpretation

similar to that of the global $L(r)$. The scaling factor was the ratio of the intensity of the two patterns, i.e., $\lambda_{live}/\lambda_{initial}$. Hence, for the local analysis, the expected value under random mortality of $L_{initial}(d) - L_{live}(d) \times \lambda_{live}/\lambda_{initial}$ is zero.

In the following sections, it is important to note the distinction between the spatial distribution of dead trees (i.e., the location of structural elements within the stand) and the spatial distribution of tree mortality events, which refers to the arrangement of dead trees within the joined distribution of all living and dead trees within the fixed population of trees (i.e., the spatial occurrence of the mortality process within the initial population).

In the first three analyses (i.e., analyses for the living, dead, and initial tree distributions) for both the $L(r)$ and the $g(r)$, we tested the statistical significance of deviations from complete spatial randomness, created with Monte Carlo simulations (i.e., to test if the observed distribution could be the result of a random processes). For the distribution of tree mortality events, we tested for the departures from random occurrence within a fixed population using the random labeling approach. For this, the location of all trees (the initial distribution) was held constant, the events (number of dead trees) were randomly reassigned to these fixed locations, and the functions were calculated for that data set (Goreaud and Pelissier 2003). In all cases, the significance of the departures from random was then assessed in 3 m distance classes (1–4, 4–7, 7–10, 10–13, and 13–16 m) using the goodness-of-fit statistic developed by Loosmore and Ford (2006). Due to multiple tests, we used Bonferroni-corrected significance levels (five comparisons in each five sites, significance limit $p = 0.002$). In contrast, most earlier studies have based statistical tests on the critical bands from the Monte Carlo simulations, which can inflate type I error rates (Loosmore and Ford 2006). We instead based our interpretations on the goodness-of-fit statistics, but nevertheless also present the critical bands to aid in interpretation of the results and for comparisons with earlier studies.

The exact p value in the goodness-of-fit statistic of Loosmore and Ford (2006) is subject to uncertainty, with the amount of uncertainty decreasing with increasing number of simulations. To confine this uncertainty so that the actual p value of the test statistic lies within an arbitrarily defined 0.0005 unit (95% confidence limits) of our p value of 0.002, we simulated the random patterns 30 671 times (see Loosmore and Ford (2006) for the number of simulations needed to reach a desired level of uncertainty). Hence, with this number of simulations, the actual p value can be assumed to lie between 0.0015 and 0.0025.

All analyses were done using R (R Development Core Team 2011). The global and local versions of the L-functions, the pair correlation functions, as well as the Monte Carlo simulations were computed using the spatstat package in R (Baddeley and Turner (2005) following Baddeley (2008)).

Results

Red pine mortality events were spatially random in all five sites; that is, the change in the pattern $L(r)$ of living (i.e., surviving) trees did not differ from that expected from a random occurrence of mortality in the initial population (p values

Fig. 1. Spatial distribution of red pine (*Pinus resinosa*) mortality events as a function of distance *r* in five old-growth forests, quantified with both *L*- and *g*-functions, showing random patterns at all sites. Statistical significance of deviations from random, computed using goodness-of-fit statistics, are shown as circles along the *x*-axis. Critical bands from the Monte Carlo simulations are shaded and shown for comparison with earlier studies; however, the goodness-of-fit statistics, not the critical bands, were used for statistical inference (see text).
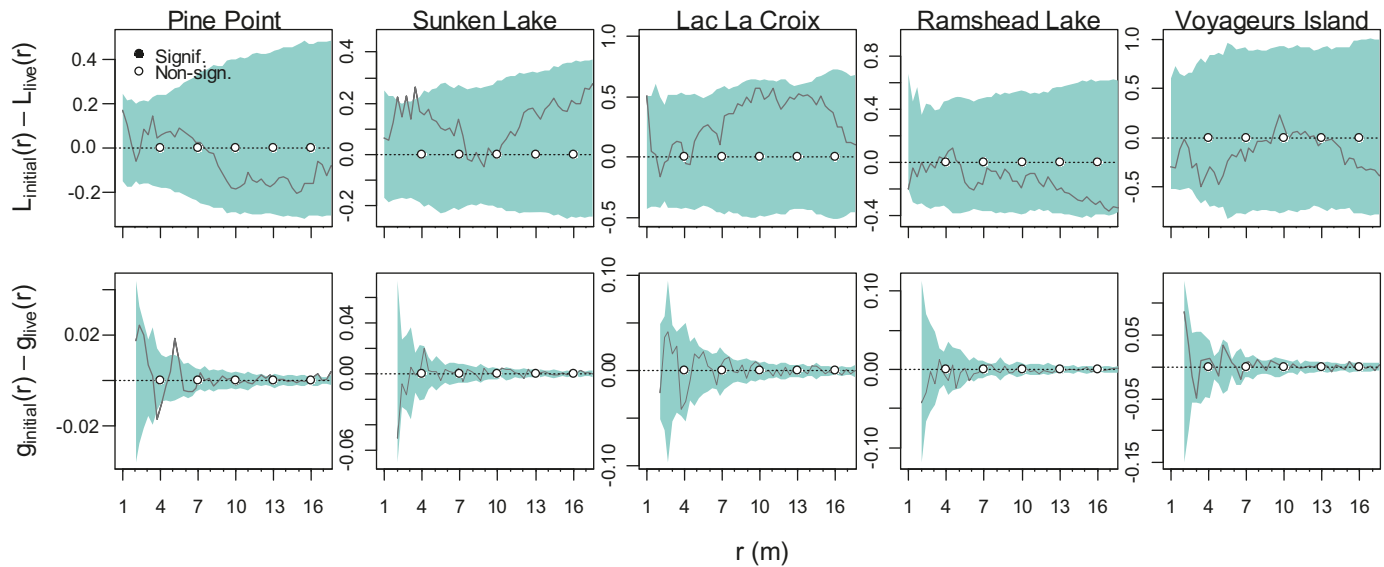
ranging between 0.06 and 0.99) (Fig. 1). The results from the $g(r)$ yielded findings similar to $L(r)$ analysis, with p values ranging from 0.04 to 0.99 (Fig. 1).

The local version of the L-function values for the distribution of tree mortality (i.e., the change in the pattern from initial to current living trees) was used to complement the global pattern analysis. It was evident that the intensity of change in the pattern was distributed across the plots, supporting the random mortality patterns detected in the global analysis (Fig. 2). At the smallest scale tested (intertree distance = 3 m), there were several regions visible with stronger change, indicative of within-site spatial variability. However, these were not confined to specific portions of the study area but were scattered throughout the distribution of initial red pines across the plots. The patterns were similar also on the larger scales (distances of 9 and 15 m).

Importantly, red pine mortality had occurred over a wide range of diameters (Fig. 3). Although on several sites, tree mortality appeared to be more prevalent in smaller diameter classes, in none of the sites did the diameter distributions of dead versus living trees differ significantly (Kolmogorov–Smirnov two-sample test, $p \gg 0.05$ in all cases). This finding also justifies testing the observed distributions using random labeling, as primarily competition-driven mortality of smaller understory trees would have warranted an alternative null hypothesis and analytical procedure (e.g., Das et al. 2011).

The spatial patterns of dead trees within sites showed more variability than the patterns of tree mortality events (Fig. 4). Dead trees at Pine Point, Ramshead Lake, and Voyageurs Island showed no significant deviations from random patterns (p values between 0.32 and 0.67). On the other two sites, dead trees were more aggregated than expected ($p < 0.002$) at larger intertree distances: at Sunken Lake from 10 m onwards and at Lac La Croix from 7 m onwards. The results from $g(r)$ corroborated the $L(r)$ results of dead tree aggrega-

tion but also revealed that this aggregation was limited to the 10–13 m distance class at Sunken Lake and the 7–10 m distance class at Lac La Croix.

The $L(r)$ of the initial distribution (living plus dead) showed significant aggregation on all sites (Fig. 5). At Pine Point, this occurred throughout the analyzed distance classes (from 1 to 16 m) and at Voyageurs Island from 1 to 13 m. Sunken Lake, Lac La Croix, and Ramshead Lake showed aggregation over larger distances, from 7 to 16, 7 to 16, and 10 to 16 m, respectively. Findings from the $g(r)$ analysis were similar to the $L(r)$ results for Pine Point, whereas $g(r)$ implied no specific scales of aggregation for Ramshead Lake. For Sunken Lake, aggregation was observed at intermediate distance classes (from 7 to 13 m), and at Lac La Croix, aggregation was significant at the 7–10 m distance class. Voyageurs Island, on the other hand, showed an aggregated initial distribution only at the smallest analyzed distance class.

The $L(r)$ of the currently living trees showed significant deviations from random on all distance classes at Pine Point and on the smallest distance class for Voyageurs Island (Fig. 5). For Ramshead Lake, the deviations were significant at the greatest distance class analyzed, whereas the pattern did not differ from random at the Sunken Lake and Lac La Croix sites. The pair correlation function $g(r)$ showed significant deviations from random at all distance classes at Pine Point and at the smallest distance class for Voyageurs Island. On the three remaining sites, the patterns did not deviate significantly from random.

As could be expected from random mortality, the changes in the patterns from the initial to current distribution of living trees were relatively minor (Fig. 5). The only exception was at small distances for Voyageurs Island where the current living tree distribution differed greatly from the initial distribution at small intertree distances. Despite these seemingly minor differences between the initial and current patterns,

Fig. 2. Stem maps and the results of the local version of the *L*-function analysis showing that the intensity of change in red pine (*Pinus resinosa*) mortality pattern varies spatially within the plots. The darker the color, the larger the change from initial to current pattern. Results are shown for three intertree distances, 3, 9, and 15 m. Note the relatively uniform change in the pattern where trees exist; the areas where the local *L* values have not changed (white) are primarily on a portion of the plot without red pine in the initial distribution.
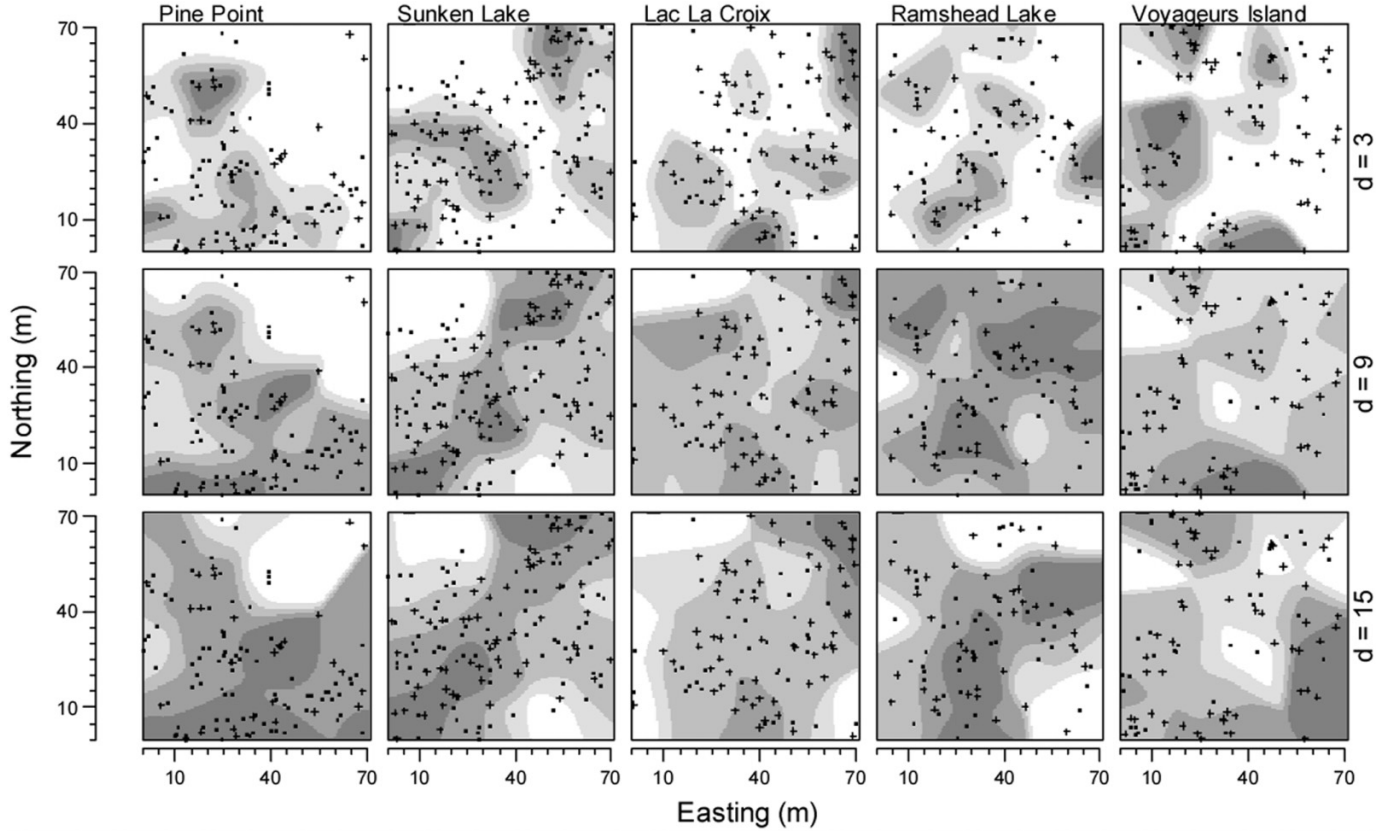

Fig. 3. Diameter distributions of dead (solid bars) and currently living (open bars) red pine (*Pinus resinosa*) suggesting that mortality was not from self-thinning.
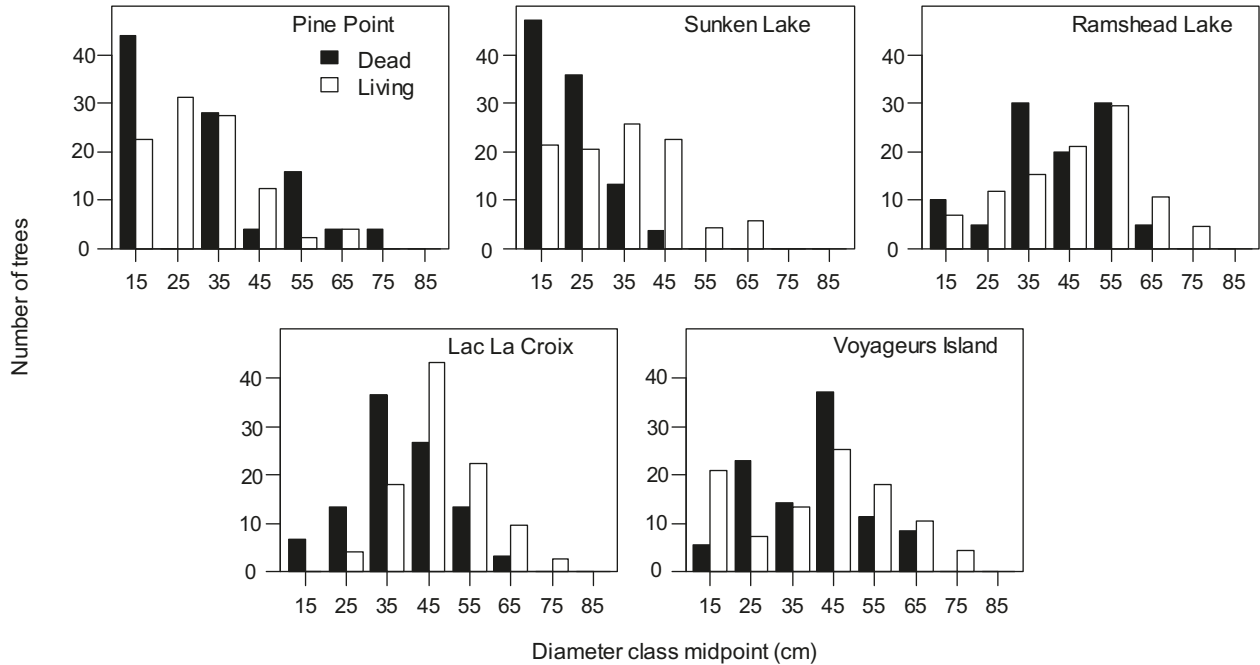
Fig. 4. Spatial distribution of dead red pines (*Pinus resinosa*) as a function of distance *r*, quantified with *L*- and *g*-functions, showing aggregation at several sites in contrast with the finding of random locations of mortality events (Fig. 1) within the initial populations. Symbols as in Fig. 1.
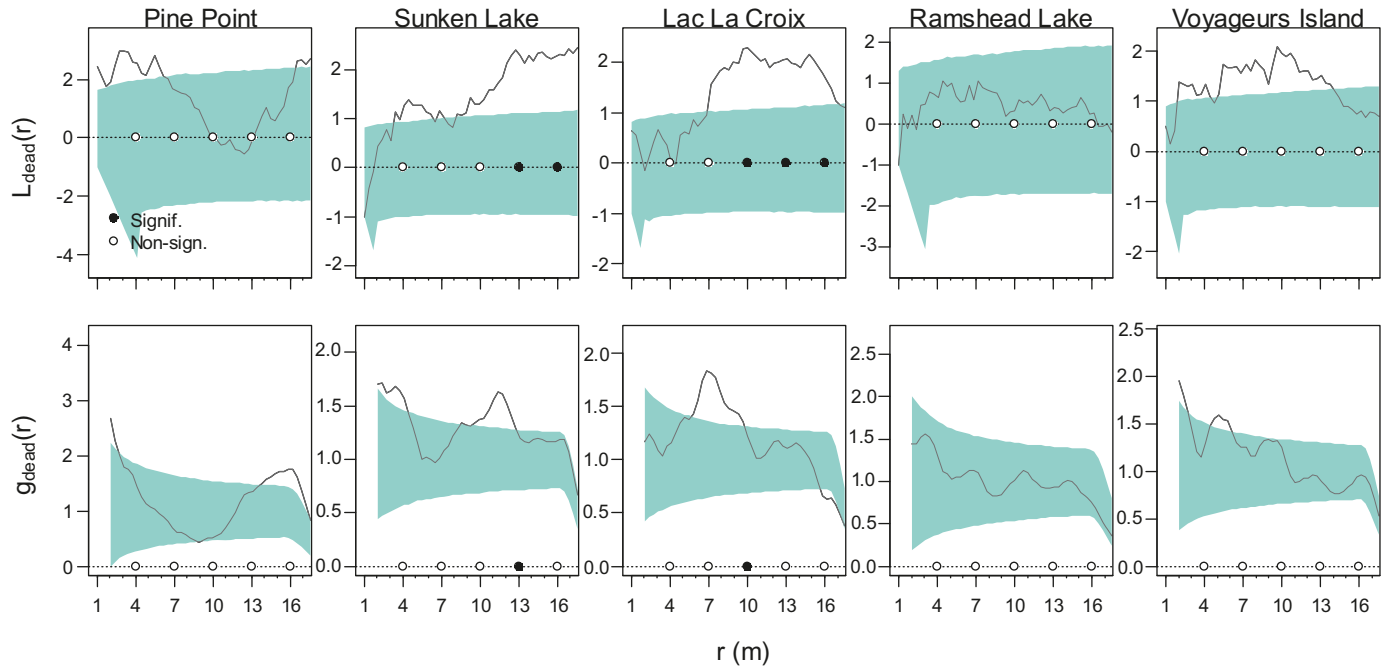
Fig. 5. Spatial distribution of initial and current living red pines (*Pinus resinosa*) in each of the five sites as a function of distance *r* quantified using the *L*- and *g*-functions. Solid circles represent the 95% distribution limits for complete spatial randomness for the initial distribution and open circles those for the current living trees. Statistical significances for specific distance classes (see text), computed with goodness-of-fit statistics, are shown for both the initial distribution and current living tree distributions.
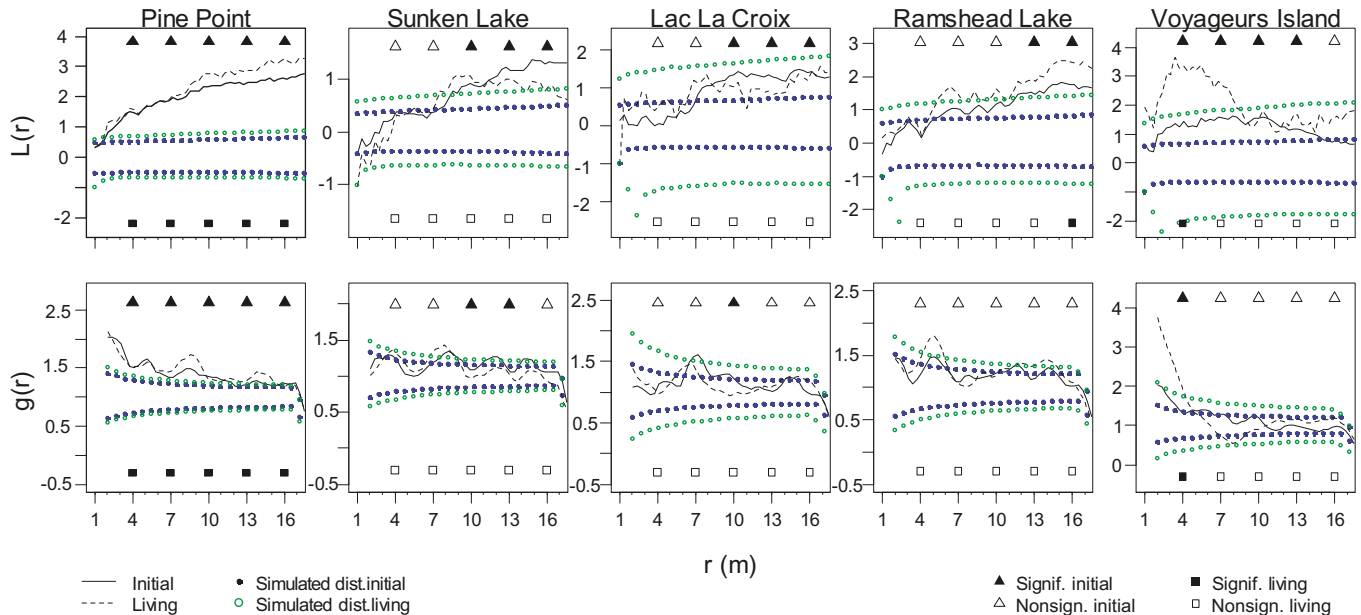
the deviations from random were more often significant for the initial distribution than for the current living distribution (Fig. 5).

Discussion

In the mature red pine populations from old-growth stands examined in this study, mortality events have occurred ran-domly. This finding was consistent in all five sites analyzed as well as between the two different methods applied, the *L*- and the pair correlation functions. Importantly, using preex-isting information on red pine cohort age structure, we were able to disentangle the spatial pattern of the tree mortality events from the initial (living and dead) tree spatial pattern. That is, an aggregated distribution of dead trees was detected on several sites, despite the random patterns of tree mortality.

Although it facilitates ecologically meaningful interpretations, the random labeling approach is rarely used, probably due to strict data requirements, namely the need to control for tree in-growth (the accrual of newly established trees). As a result, the interpretations of the detected mortality patterns have often remained weak relative to the strong potential of point pattern analyses (e.g., see Kenkel 1988; Svoboda et al. 2010; Das et al. 2011). To overcome this limitation, the most obvious way to control for in-growth would be remeasuring of permanent plots; however, long-term measurements from natural populations are scarce. On our study sites, the cohort age structures (Fraver and Palik 2012) allowed us to rule out the influence of in-growth. It should be noted that these analyses relied on the assumption that the initial distribution (i.e., the joined distribution of living and dead trees as mapped in the field) represents the distribution of living trees after the establishment of the last cohort and the tree mortality events have occurred within this fixed population. There are two potential sources of uncertainty here. First, it is possible that some of the dead trees had died prior to the establishment of the last cohort. However, in all stands, the majority of the trees belonged to the latest cohort, and thus this influence was likely small. Second, although care was taken to map all dead trees, it is likely that some trees, particularly smaller ones, had decayed beyond recognition and hence went undetected. We assumed that such trees had died mainly from competition-driven mortality early in stand development and therefore were not part of our study population of mature, established red pines.

Recent studies have shown that these cohort-like age structures, often resulting from low-intensity fires, are more common than has traditionally been considered (Kuuluvainen and Aakala 2011), thus permitting the use of the methods employed here. As such, the methods applied in this work for detecting spatial patterns of mortality are widely applicable to other regions and forest types where similar age structures and disturbance regimes predominate.

Rigorous knowledge of spatial patterns of tree mortality can potentially provide insight into the relative importance of the various mortality agents that drive forest dynamics. In pine forests of Minnesota, previous research has documented wind storms as an important cause of tree death (Bergman 1924; Frelich and Reich 1995), and there is also evidence (largely anecdotal) suggesting that fungi in the *Armillaria* genus can cause considerable tree mortality (see also McLaughlin 2001). If these agents were the dominant causes of mortality in the past, current forest dynamics theory would suggest aggregated mortality patterns (Nagel and Diaci (2006), but see Filip and Goheen (1995) for evidence of spatially random *Armillaria*-caused mortality). Our findings thus suggest that tree mortality patterns have been more complex than expected. There is a number of additional potential causes of tree death that could have resulted in the detected random mortality; these include surface fires that can be patchy and variable in intensity even at these small scales (Thomas and McAlpine 2010). As an example, van Mantgem et al. (2011) reported random patterns of mortality after a prescribed fire in their study areas in Sierra Nevada. Nevertheless, our results were somewhat unexpected, given the expectation of aggregated tree mortality in old-growth forests (Franklin and Van Pelt 2004). Yet, the results were consistent

with those of Getzin et al. (2006) and Das et al. (2011), who observed random patterns of background mortality in conifer stands in western North America. Although those studies used different approaches to elucidate mortality patterns (such as tagged trees in permanent plots in Das et al. (2011) instead of cohort age structures), this range of findings underscores the need for more studies on the relationship between mortality agents and resulting spatial patterns.

The detected patterns of red pine mortality were surprisingly consistent across the two ecological sections, particularly given the pronounced differences in edaphic conditions and recent disturbance histories between these regions. In particular, the thin soils and small-scale patchy rock outcrops in the Northern Superior Upland sites (Lac La Croix, Ramshead Lake, and Voyageurs Island) no doubt influenced the initial tree distributions, as such heterogeneity has been shown to influence tree spatial patterns and demographics (Getzin et al. 2008). While the 1999 windthrow around these sites may have been responsible for a number of tree deaths within these populations, the event did not result in the expected aggregated pattern of wind-induced mortality (Nagel and Diaci 2006). Despite being consistently random across the sites, it is noteworthy that the shape of the global *L*-function did differ among the sites (as did the local *L*-function within the sites). This type of variability in process and structure is often expected in natural old-growth forests (Spies 2004).

Living tree distributions deviated from complete spatial randomness, with a tendency towards aggregation. These deviations were significant at variable distances, depending on the site. Similar to the findings here, both random and aggregated living tree distributions have been reported for other old-growth conifer forests (Dobbertin et al. 2001; Aakala et al. 2007). Partially, in contrast with our findings, in cases where aggregation of living trees has been observed, it has primarily been associated with aggregated patterns of tree establishment (Sterner et al. 1986; Silla et al. 2002). However, the pattern shifts, such as those seen at Voyageurs Island (i. e., that the current living tree distribution was more aggregated than the initial distribution (Fig. 5)) suggests that an aggregated distribution of living trees can also be the direct result of the spatial distribution of tree mortality.

An important point regarding the comparisons of initial versus current living tree distributions was that although tree mortality was random and the changes in the patterns therefore minor, there were somewhat dramatic differences in the statistical significance of the function values when comparing the initial and current living tree distributions. Plotting the simulated distribution limits revealed that changes in statistical significance were associated more with a decrease in statistical power resulting from decreases in the number of points in the patterns than with actual changes in the distributions: the critical distribution limits changed more than the observed empirical distributions (Fig. 5). Thus, although the simulated limits should not be used directly for inference (Loosmore and Ford 2006), plotting them can provide information useful for interpreting the findings.

Contrary to mortality events, the spatial distribution of dead trees varied between aggregated and random. This finding demonstrates the importance of knowing the initial distribution of living trees, particularly how random mortality can

give rise to aggregation of dead trees. Importantly, as our study clearly demonstrates, without knowledge of the initial tree distribution, aggregated patterns of dead trees can erroneously be attributed to aggregated mortality events. Because tree mortality had occurred randomly, it is evident that the processes governing the initial population spatial structure (environmental heterogeneity, regeneration pattern, and competition-induced mortality: Silla et al. 2002; Getzin et al. 2008; Das et al. 2011) have a long-lasting influence on the spatial structure of the sites. Both types of dead tree distributions, i.e., random and aggregated, have been previously reported (e.g., Parish et al. 1999; Aakala et al. 2007), yet they have rarely been evaluated with respect to the initial distribution of live trees.

Visualizations of the results of the univariate analyses (Figs. 4 and 5) clearly exemplified the differences in the $L(r)$ and $g(r)$ methods, which results from the cumulative nature of $L(r)$ (Perry et al. 2006). Aggregation in the initial and dead tree distributions at the Sunken Lake and Lac La Croix sites was detected with both methods but persisted at greater distances only in the $L(r)$, while the $g(r)$ implied that the deviations were in fact constrained to only one of the intervals analyzed. On the other hand, on several sites, the $g(r)$ was unable to detect aggregation that was not pronounced at a specific distance but more a result of a gradual accrual of a higher than expected numbers of trees (under complete spatial randomness). In the light of these results, we support Perry et al.'s (2006) recommendation of using both functions in a complementary manner in quantifying spatial point patterns.

Finally, we note that our conclusions about the distributions of live and dead trees would have been different had we employed the critical bands from the Monte Carlo simulations as the basis for inference (Figs. 4 and 5); however, the conclusions regarding the spatial distribution of tree mortality events would have been similar, as random distributions prevailed also in the less conservative approaches (i.e., the observed distribution of tree mortality was within the critical bands). If anything, using the critical bands for inference would have strengthened our conclusions about randomly occurring background mortality, specifically demonstrating that an aggregated initial distribution can lead to aggregated dead tree distributions due to spatially random mortality.

Acknowledgments

References

Aakala, T., Kuuluvainen, T., De Grandpré, L., and Gauthier, S. 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. Can. J. For. Res. **37**(1): 50–61. doi:10.1139/x06-201.

Baddeley, A. 2008. Analysing spatial point patterns in R. Workshop notes, version 3. Available from http://www.csiro.au/resources/Spatial-Point-Patterns-in-R.

Baddeley, A., and Turner, R. 2005. spatstat: an R package for analyzing spatial point patterns. J. Stat. Softw. **12**: 1–42.

Bergman, H.F. 1924. The composition of climax plant formations in Minnesota. Pap. Mich. Acad. Sci. Arts Lett. **3**: 51–60.

Cleland, D.T., Avers, P.E., McNab, W.H., Jensen, M.E., Bailey, R.G., King, T., and Russell, W.E. 1997. National hierarchical framework of ecological units. *In* Ecosystem management applications for sustainable forest and wildlife resources. Yale University Press, New Haven, Conn. pp. 181–200.

Coates, D.K., Canham, C., Beaudet, M., Sachs, D.L., and Messier, C. 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. For. Ecol. Manage. **186**(1–3): 297–310. doi:10.1016/S0378-1127(03)00301-3.

Das, A., Battles, J., Stephenson, N.L., and van Mantgem, P.J. 2011. The contribution of competition to tree mortality in old-growth coniferous forests. For. Ecol. Manage. **261**(7): 1203–1213. doi:10.1016/j.foreco.2010.12.035.

Dobbertin, M., Baltensweiler, A., and Rigling, D. 2001. Tree mortality in an unmanaged mountain pine (*Pinus mugo* var. *uncinata*) stand in the Swiss National Park impacted by root rot fungi. For. Ecol. Manage. **145**(1–2): 79–89. doi:10.1016/S0378-1127(00)00576-4.

Filip, G.M., and Goheen, D.J. 1995. Precommercial thinning in *Pseudotsuga*, *Tsuga*, and *Abies* stands affected by armillaria root disease: 10-year results. Can. J. For. Res. **25**(5): 817–832. doi:10.1139/x95-089.

Fortin, M.-J., and Dale, M. 2005. Spatial analysis — a guide for ecologists. Cambridge University Press, Cambridge, U.K.

Franklin, J.F., and Van Pelt, R. 2004. Spatial aspects of structural complexity in old-growth forests. J. For. **102**: 22–28.

Franklin, J.F., Shugart, H.H., and Harmon, M.E. 1987. Tree death as an ecological process. Bioscience, **37**(8): 550–556. doi:10.2307/1310665.

Fraver, S., and Palik, B.J. 2012. Stand and cohort structures of old-growth *Pinus resinosa*-dominated forests of northern Minnesota, USA. J. Veg. Sci. **23**(2): 249–259. doi:10.1111/j.1654-1103.2011.01348.x.

Fraver, S., and White, A.S. 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. J. Veg. Sci. **16**: 597–610.

Frelich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. Ecol. Monogr. **65**(3): 325–346. doi:10.2307/2937063.

Getis, A., and Franklin, J. 1987. Second-order neighbourhood analysis of mapped point data patterns. Ecology, **68**(3): 473–477. doi:10.2307/1938452.

Getzin, S., Dean, C., He, F., Trofymow, J.A., Wiegand, K., and Wiegand, T. 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. Ecography, **29**: 671–682. doi:10.1111/j.2006.0906-7590.04675.x.

Getzin, S., Wiegand, T., Wiegand, K., and He, F. 2008. Heterogeneity influences spatial patterns and demographics in forest stands. J. Ecol. **96**(4): 807–820. doi:10.1111/j.1365-2745.2008.01377.x.

Goreaud, F., and Pelissier, R. 2003. Avoiding misinterpretation of biotic interactions with the intertype K12-function: population independence vs. random labelling hypotheses. J. Veg. Sci. **14**: 681–692.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr, and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. **15**: 133–302. doi:10.1016/S0065-2504(08)60121-X.

Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology, **69**(4): 1017–1024. doi:10.2307/1941257.

Kuuluvainen, T., and Aakala, T. 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. Silva Fenn. **45**: 823–841.

Larson, A.J., and Churchill, D. 2008. Spatial patterns of overstory trees in late-successional conifer forests. Can. J. For. Res. **38**(11): 2814–2825. doi:10.1139/X08-123.

Larson, A.J., and Churchill, D. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. For. Ecol. Manage. **267**: 74–92. doi:10.1016/j.foreco.2011.11.038.

Little, L.R. 2002. Investigating competitive interactions from spatial patterns of trees in multispecies boreal forests: the random mortality hypothesis revisited. Can. J. Bot. **80**(1): 93–100. doi:10.1139/b01-141.

Loosmore, N.B., and Ford, E.D. 2006. Statistical inference using the G or K point pattern spatial statistics. Ecology, **87**(8): 1925–1931. doi:10.1890/0012-9658(2006)87[1925:SIUTGO]2.0.CO;2. PMID: 16937629.

Manion, P.D. 1991. Tree disease concepts. Prentice Hall, Englewood Cliffs, N.J.

McLaughlin, J.A. 2001. Impact of Armillaria root disease on succession in red pine plantations in southern Ontario. For. Chron. **77**: 519–524.

Nagel, T.A., and Diaci, J. 2006. Intermediate wind disturbance in an old-growth beech–fir forest in southeastern Slovenia. Can. J. For. Res. **36**(3): 629–638. doi:10.1139/x05-263.

Palik, B.J., and Pederson, N. 1996. Overstory mortality and canopy disturbances in longleaf pine ecosystems. Can. J. For. Res. **26**(11): 2035–2047. doi:10.1139/x26-229.

Parish, R., Antos, J.A., and Fortin, M.J. 1999. Stand development in an old-growth subalpine forest in southern interior British Columbia. Can. J. For. Res. **29**(9): 1347–1356. doi:10.1139/x99-080.

Perry, G.L.W., Miller, B.P., and Enright, N.J. 2006. A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. Plant Ecol. **187**(1): 59–82. doi:10.1007/s11258-006-9133-4.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/.

Ripley, B.D. 1977. Modelling spatial patterns. J. R. Stat. Soc. B. Methodol. **39**: 172–212.

Silla, F., Fraver, S., Lara, A., Allnutt, T.R., and Newton, A. 2002. Regeneration and stand dynamics of *Fitzroya cupressoides* (Cupressaceae) forests of southern Chile's Central Depression. For. Ecol. Manage. **165**(1–3): 213–224. doi:10.1016/S0378-1127 (01)00619-3.

Spies, T.A. 2004. Ecological concepts and diversity of old-growth forests. J. For. **102**: 14–20.

Sterner, R.W., Ribic, C.A., and Schatz, G.E. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. J. Ecol. **74**(3): 621–633. doi:10.2307/2260386.

Stoyan, D., and Stoyan, H. 1994. Fractals, random shapes and point fields: methods of geometrical statistics. John Wiley & Sons, Chichester, U.K.

Svoboda, M., Fraver, S., Janda, P., Bače, R., and Zenáhlíková, J. 2010. Natural development and regeneration of a Central European montane spruce forest. For. Ecol. Manage. **260**(5): 707–714. doi:10.1016/j.foreco.2010.05.027.

Thomas, P.A., and McAlpine, R.S. 2010. Fire in the forest. Cambridge University Press, Cambridge, U.K.

van Mantgem, P.J., Stephenson, N.L., Knapp, E., Battles, J., and Keeley, J.E. 2011. Long-term effects of prescribed fire on mixed conifer forest structure in the Sierra Nevada, California. For. Ecol. Manage. **261**(6): 989–994. doi:10.1016/j.foreco.2010.12.013.