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Spatial Point-pattern Analysis of a Population of Lodgepole Pine

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Abstract

Spatial point-patterns analyses were conducted to provide insight into the ecological process behind competition and mortality in two lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stands, one in the Lower Foothills, and the other in the Upper Foothills natural subregions in the boreal forest of Alberta, Canada. Spatial statistical tests were applied to live and dead trees and included Clark-Evans nearest neighbor statistic (R), nearest neighbor distribution function ($G(r)$), and a variant of Ripley's K function ($L(r)$). In both lodgepole pine plots, the results indicated that there was significant regularity in the spatial point-pattern of the surviving trees which indicates that competition has been a key driver of mortality and forest dynamics in these plots. Dead trees generally showed a clumping pattern in higher density patches. There were also significant bivariate relationships between live and dead trees, but the relationships differed by natural subregion. In the Lower Foothills plot there was significant attraction between live and dead tees which suggests mainly one-sided competition for light. In contrast, in the Upper Foothills plot, there was significant repulsion between live and dead trees which suggests two-sided competition for soil nutrients and soil moisture.

Key Words: boreal forest, competition, *Pinus contorta*, point-patterns, spatial statistics

Introduction

Competition and mortality are fundamental ecological processes of forest stand dynamics (Gray and He 2009). As forest stands thin over time due to competition for resources (e.g., light and soil moisture), it is expected that the surviving individuals will show a regular distribution rather than a random spatial arrangement of trees (He and Duncan 2000; Kreutz et al. 2015). While it is generally expected that mortality leads to an increasingly regular spatial distribution, there are relatively few empirical studies which conclusively support this notion. Some spatial point pattern analysis studies have supported this notion (Kenkel 1988; He and Duncan 2000; Gray and He 2009), while others have not or are inconclusive (Metasaranta and Lieffers 2010). Field sampling for quantifying localized spatial structure includes careful mapping of individuals in a stand and accounting for each of their fates and then examining whether the degree of regularity in surviving members of the population is more than is expected under the null hypothesis of random mortality. The random mortality hypothesis asserts that the distribution of surviving trees does not differ from what is expected if mortality is a completely random event.

Confounding factors such as environmental heterogeneity, an uneven aged distribution, and random regeneration, may affect the spatial pattern detected such that a regular pattern may not be observed (Kenkel 1988).

Failure to detect a regular spatial pattern is not indicative that competition is not present. Furthermore, in clonal populations that can reproduce asexually from a surviving plant organ (e.g., root suckers in trembling aspen (*Populus tremuloides* Michx.), detecting a regular pattern may be an artifact of poorly defining what an individual is since closely spaced individuals may be physiologically considered as one. For spatial studies, ideal species and site factors include a long-lived, non-clonal species which randomly disperses seed at initial high densities over a homogeneous soil substrate. Good preservation of the remains of dead trees increases the likelihood that dead trees are accounted for (He and Duncan 2000). While larger trees that died have a longer-term imprint at the site, it generally remains uncertain as to the extent of which small trees have completely decomposed. Consequently, the spatial distribution of trees generally does not fully account for initial sapling mortality.

Lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) is shade intolerant (Lotan and Critchfield 1990). It generally forms even-aged stands after a stand replacing fire and is regarded as a fire-maintained subclimax forest although in the absence of disturbances is usually succeeded by more shade tolerant competitors. Its semi-serotinous cones release a large amount of seed after fire to form high density stands of pure lodgepole pine. Lodgepole pine has a large ecological amplitude and grows well on a wide spectrum of site conditions although growth is optimal on moist, rich, well-aerated sites. Some areas in the Lower Foothills natural subregion of Alberta contain these site conditions while more extensive areas in the Upper Foothills subregion provide optimal site conditions (Alberta Environment Protection 1994). Lodgepole pine is known to form root grafts (Fraser et al. 2006).

The objective of this study is to examine the spatial point pattern of live and dead trees in lodgepole pine stands in relation to a baseline null hypothesis of complete spatial randomness. It is expected that the spatial pattern of live and dead trees will not deviate from that expected from complete spatial randomness because of the initial random input of seed to the site following a stand replacing fire. It is expected that the spatial distribution of live trees has a regular distribution than that expected under the null hypothesis of random mortality because of a zone of competitive influence around surviving trees and the thinning of trees in high density patches. It is expected that dead trees will show a clumped distribution than that expected under the null hypothesis of random mortality due to increased likelihood of predisposition to mortality of individuals in high density patches. Since lodgepole pine is shade intolerant and is known to form root grafts, it is expected that the second phase of competition for light will define the dominant form of competitive interrelationships between live and dead trees. Consequently, it is expected that there will be attraction in the bivariate spatial analyses than that expected under the null hypothesis of random mortality.

## Materials and Methods

Study area and site selection

In Alberta, lodgepole pine is the most common tree species in the Rocky mountains and adjacent foothills regions, and it is very important to Alberta's forest industry (Huang, 2000). One lodgepole pine stand was selected in each of the Lower Foothills and Upper Foothills natural subregions (Alberta Environmental Protection 1994) from the Alberta Forest Service (AFS) permanent sample plot (PSP) database (Alberta Land and Forest Service 1994). The two stands were formed following a stand replacing fire. To minimize the effect of confounding factors, the criteria for stand selection included that they must have a minimum stand age of at least 80 years, and be no older than 130 years to avoid selecting stands in natural decline. Furthermore, stands selected also showed no history of major disturbances (e.g., fire, disease, or insect damage).

The PSP program was initiated in the early 1960s with subsequent 5- to 10-year re-sampling intervals (Alberta Land and Forest Service 1994) (Table 1). The AFS PSP database includes historical censuses of mortality of individual trees. Although PSP plots were established in the early 1960s, it was not until 1984 that formal stem mapping occurred (Huang, personal communication). Consequently, for both PSP's it was not until 1991 (PSP092) and 1993 (PSP152) that stem mapped data were available. A further sampling restriction was that down dead trees were not mapped. For stem mapping, the locations of trees were originally recorded as distances and azimuth of each tree from the plot centre. For the current study, tree locations were re-expressed as x- and y-coordinates relative to the

Table 1. Site and stand characteristics of permanent sample plots (PSP) of lodgepole pine

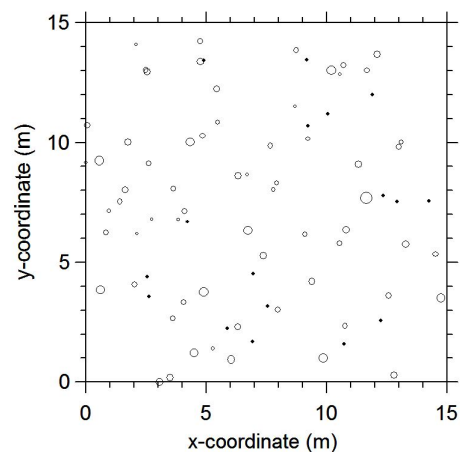| Descriptor	PSP092	PSP152
Natural Subregion	Lower Foothills	Upper Foothills
Elevation (m)	1070	1585
Slope percent (topography)	0 (flat)	45 (slope)
Aspect	N.a.	West
Soil drainage	Moderately well drained	Rapidly drained
Depth of organic matter to mineral soil (cm)	3	10
Sampling times	1962, 1968, 1981, 1991	1963, 1976, 1983, 1993
Stand origin date	~1897	~1905
Plot dimensions and area	30×30 m (900 m^2)	15×15 m (225 m^2)
No. of live trees (density[a], proportion[b])	85 (0.0944, 60.7)	65 (0.289, 64.4)
No. of standing dead trees (density, proportion)	26 (0.0289, 18.6)	17 (0.0667, 16.8)
No. of down dead trees (density, proportion)	29 (0.0322, 20.7)	19 (0.0844, 18.8)
No. of live and standing dead (density, proportion)	111 (0.123, 79.2)	82 (0.364, 81.2)
No. of live and all dead (density)	140 (0.156)	101 (0.449)
DBH of live trees (Mean+S.E.)	18.2+0.5 cm	12.9+0.5 cm

[a]density＝no. m^{-2}; [b]proportion (%) is relative to number of live and all dead.
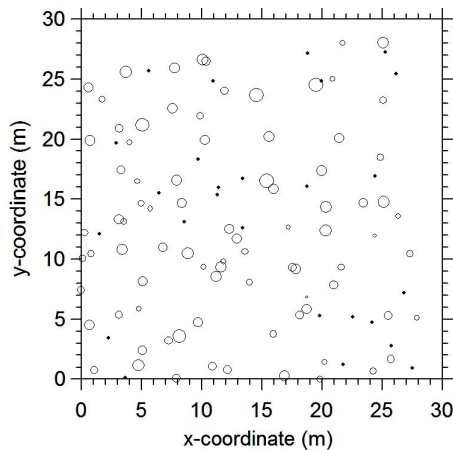
Fig. 1. Spatial point pattern distribution of lodgepole pine in permanent sample plot (PSP) 092 located in the Lower Foothills natural subregion. The symbol for live trees (open circle) is scaled to diameter at breast height (DBH) of live trees. Dead trees＝solid circle.

Fig. 2. Spatial point pattern distribution of lodgepole pine in permanent sample plot (PSP) 152 located in the Upper Foothills natural subregion. The symbol for live trees (open circle) is scaled to diameter at breast height (DBH) of live trees. Dead trees＝solid circle.

SW corner of the plot.

Further site and stand characteristics of the two plots are summarized in Table 1. PSP092 in the Lower Foothills is characteristically flat and moderately well drained and originated in the late 1890s. The total number of mapped live (85) and dead standing (26) trees in PSP092 was 111. PSP152 located in the Upper Foothills has a sloping topography with a western facing aspect, is rapidly drained and

originated in the early 1900s. The total number of mapped live (65) and dead standing (17) trees in PSP152 was 82. Regardless of what category of a tree is considered, PSP152 is noticeably much more dense than PSP092. Furthermore, concomitant with the higher density, the trees in PSP152 also had a lower DBH than trees in PSP092. The spatial point pattern distribution of live and standing dead trees in PSP092 and PSP152 are shown in Figs. 1 and 2, respectively.

Spatial statistical techniques to analyze marked spatial point patterns

There are a number of spatial statistical techniques to test the random mortality hypothesis. They can be generally grouped into two categories (Ripley 1981; Kenkel 1988; Cressie 1993; He and Duncan 2000; Baddeley and Turner 2004; Grey and He 2009; Law et al. 2009): 1) univariate, and 2) bivariate. Univariate analyses were applied to three data sets: (1) live and standing dead, (2) only live, and (3) only standing dead. In addition, bivariate analyses were also conducted to examine the spatial interrelationship between live and standing dead individuals. Most of the analysis of mapped point patterns requires the use of Monte Carlo simulations to examine the significance of any departure of the observed spatial pattern from complete spatial randomness (CSR) or random mortality. This is described further in the section on constructing random confidence envelopes.

Clark-Evans nearest neighbor statistic (R)

The first univariate analysis includes a modified version of Clark-Evans nearest neighbor statistic taking into account for edge effects (Clark and Evans 1954; Ripley 1981; Kenkel 1988; Cressie 1993). The nearest neighbor index (R) is defined as: $R = \dfrac{r_A}{r_E}$, where r_A is the average distance between randomly selected plants and their nearest neighbor, and r_E is the expected mean distance between nearest neighbors under the null hypothesis of CSR. Values of $R >$ 1 indicate a regular distribution, $R = 1$ indicates a random distribution, and $R < 1$ indicates an aggregated distribution

Univariate and bivariate nearest neighbor distribution function (G(r))

The second univariate method examines the cumulative distribution function of nearest neighbors ($G(r)$) which provides a more detailed analysis of nearest neighbor distances than that provided by the Clark-Evans statistic which can only provide summary information (Ripley 1981; Kenkel 1988; Cressie 1993; Baddeley and Turner 2004; He and Duncan 200). $G(r)$ is the probability that the distance of a randomly chosen plant to its nearest neighbor is equal to or less than r. $G(r)$ has the form of: $G(r)_{observed} =$

$\sum_{i=1}^{n} I(r_i \leq r)/n$, where r_i is the nearest neighbor distance from a randomly chosen plant i, n is the number of events, $I(r_i < r)$ is an indicator function such that $I(r_i < r) = 1$ if ($r_i < r$) is true, otherwise $I(r_i < r) = 0$. The univariate $G(r)$ function can be extended to the bivariate case to examine the probability that the distance from a typical point of live to nearest dead tree is equal to or less than r, and vice versa. Univariate (bivariate) $G(r) > 0$ indicates an aggregated distribution (attraction), $G(r) = 0$ indicates a random distribution (independence), and $G(r) < 0$ indicates a regular distribution (repulsion). In either the univariate or bivariate case of $G(r)$, whether the deviation of the observed pattern from CSR or random mortality is significant is assessed using Monte Carlo simulations.

Univariate and bivariate second-order statistic (L(r))

The third univariate technique involves the use of second-order spatial statistics which unlike the $G(r)$ function examines all plant-to-plant distances and thus provides further insight into the underlying spatial pattern. A commonly used function to analyze spatial point patterns is the K-function ($K(r)$) also known as Ripley's K-function (Ripley 1981; Kenkel 1988; Cressie 1993; He and Duncan 2000; Baddeley and Turner, 2004; Grey and He 2009; Law et al. 2009). $K(r)$ is also known as a second-moment measure since instead of the mean of the point pattern, the focus of analysis is the variation of the point-point distances. $K(r)$ is defined as as: $K(r) = \lambda^{-1} E$ (number of other events within a distance r of an arbitrary chosen event), where E is the expectation operator. $K(r)$ is usually expressed as $L(r)$: $L(r) = \sqrt{\dfrac{K(r)}{\pi}} - r$; since the square root transformation helps stabalize the variance. Under the null hypothesis of CSR: $E(L(r)) = 0$, such that $L(r) > 0$ suggests an aggregated pattern, $L(r) = 0$ suggests a random pattern, and $L(r) < 0$ suggests a regular spatial pattern.

The univariate K-function can be extended to the bivariate case by taking into account any marks of the point patterns. The bivariate K-function ($K_{12}(r)$) is defined as: $K_{12}(r) = \lambda_2^{-1} E$ (number of type 2 events within a distance r of an arbitrary event of type 1). $K_{12}(r)$ is usually expressed as $L_{12}(r) = \sqrt{\dfrac{\widehat{K_{12}(r)}}{\pi}} - r$. Under the null hypothesis of CSR:

$E(L_{12}(r))=0$, such that $L_{12}(r)>0$ suggests attraction, $L_{12}(r)=0$ suggests independence, and $L_{12}(r)<0$ suggests repulsion. In either the univariate or bivariate case of $L(r)$, whether the deviation of the observed pattern from CSR or random mortality is significant is assessed using Monte Carlo simulations.

Random confidence envelopes

Monte Carlo simulations with 25 iterations were conducted to determine whether the spatial patterns deviated from a pattern expected under two null hypotheses of spatial randomness (Goreaud and Pelissier 2003). The first null hypothesis (H_{o1}) is CSR. Using a uniform random number generator, random coordinates were generated for a number of points equivalent to the number of trees in the data set of interest (*i.e.*, both live and dead (univariate, bivariate cases), only live, and only dead). For each iteration of each random spatial point pattern, the spatial functions (*i.e.*, $G(r)$, $K(r)$, and $g(r)$) were calculated for each distance r. An approximate 95% confidence envelope was defined as the lowest and highest values of the simulations of the spatial functions at each distance r.

The second null hypothesis (H_{o2}) is random mortality which states that the pattern of surviving trees does not differ from what is expected if mortality is a random event. Again, using a uniform random number generator, a random number was applied to each tree in the data set of live and dead trees. The trees were subsequently ranked in ascending order according to their random numbers, and starting with the minimum ranked random number up to the number of points corresponding to the number of only live or only dead trees were retained. In the bivariate case, the data of live and dead trees was essentially randomly split to the first set of randomly ranked numbers to one category and the second set of randomly ranked numbers to another category. After the random selection of trees, the spatial functions were calculated. An approximate 95% confidence envelope was defined as the lowest and highest values of the simulations of the spatial functions at each distance r.

Implementation of spatial statistical techniques using r functions

The spatial data analysis was conducted in the R statistical environment (Venables et al. 2004) using the func-

tions developed by Baddeley and Turner (2004) in their "*spatstat*" library extension that includes: *clarkevans, Gest* (univariate $G(r)$), *Gmulti* (bivariate $G(r)$), *Kest* (univariate $K(r)$), and Kmulti (bivariate $K(r)$). $G(r)$ was estimated using the Kaplan-Meier estimator (Baddeley and Turner 2004). $K(r)$ was estimated using Ripley's isotropic edge correction (Baddeley and Turner 2004).

Results

Clark-evans nearest neighbor statistic (R)

For PSP092, the Clark-Evans nearest neighbor statistic (R) indicated that the distribution of both alive and dead trees was significantly regular (R=1.185, p=0.018) with a mean spacing between nearest neighbors of 1.571 m (Table 2). The distribution of only live trees was also significantly regular (R=1.196, p=0.022) with a mean spacing of 1.812 m. The distribution of dead trees did not deviate from CSR (R=1.248, p=0.153) with a mean spacing of 3.250 m.

For PSP152, the nearest neighbor index for both live and dead, only live, and only dead, did not deviate significantly from CSR. Live and dead trees had a mean spacing of 0.790 m, while only live trees had a mean spacing of 0.973 m, and only dead trees had a mean spacing of 1.566 m.

Nearest neighbor distribution function (G(r))

For PSP092, the cumulative distribution function of nearest neighbor distances for live and dead trees was significantly regular with respect to H_{o1} at distances of 1.0,

Table 2. Clark-Evans nearest neighbor index (R) statistics for lodgepole pine permanent sample plots

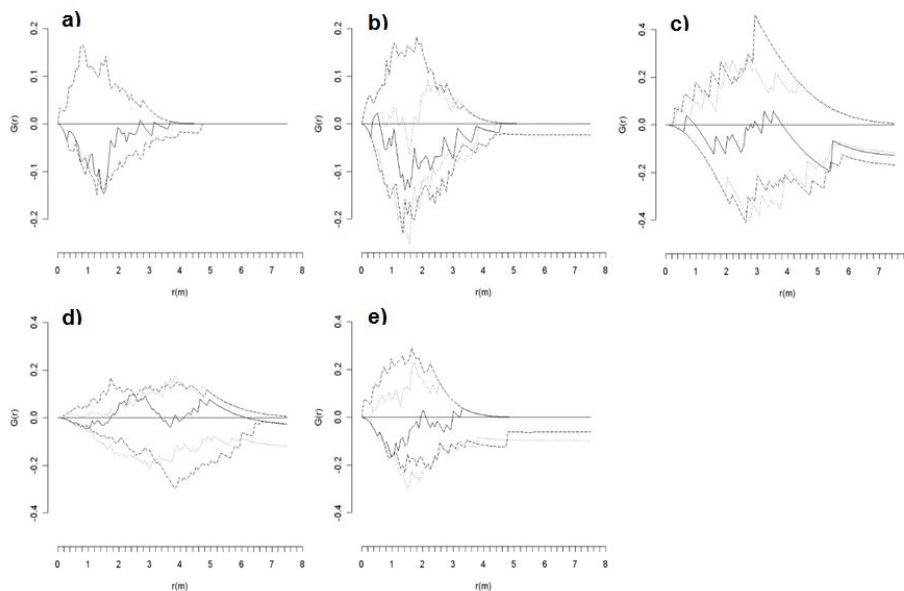| Plot	R	p-value	Mean Spacing (m)
PSP092 (Lower Foothills)			
Live and dead	1.185	0.018	1.571
Live	1.196	0.022	1.812
Dead	1.248	0.153	3.250
PSP152 (Upper Foothills)			
Live and dead	0.988	0.212	0.790
Live	1.084	0.237	0.973
Dead	1.096	0.136	1.566

and 1.5-1.6 m (Fig. 3a). Similarly, live trees had a random pattern according to H_{o1}, but were significantly regular than that expected under Ho_2 at 2.9-3.0 m and 3.8-4.5 m (Fig. 3b). Dead trees were also significantly regular compared to both H_{o1} at 5.4 m, and Ho_2 at 5.0-5.4 m and 5.7-7.5 m (Fig. 3c). The bivariate relationship of live to nearest dead tree was that of independence under H_{o1}, but that of significant attraction under Ho_2 at 2.2-2.7 m (Fig. 3d). The relationship of dead to nearest live tree was that of significant repulsion compared to both H_{o1} at 1.0 m and Ho_2 at 0.9-1.0 m (Fig. 3e).

For PSP152, $G(r)$ of live and dead trees did not differ significantly from that expected under H_{o1} (Fig. 4a). $G(r)$ of live trees was random under H_{o1}, but significantly regular compared to Ho_2 at 1.1-1.4 m (Fig. 4b). $G(r)$ of dead trees was random under H_{o1}, but significantly clumped than that expected under Ho_2 at 2.0-2.1 m (Fig. 4c). The bivariate relationship between live to nearest dead was that of independence under H_{o1}, but that of significant repulsion under Ho_2 at 2.5-2.6 m (Fig. 4d). The bivariate relationship of dead to nearest live tree did not deviate from that expected under either H_{o1} or Ho_2 (Fig. 4e).
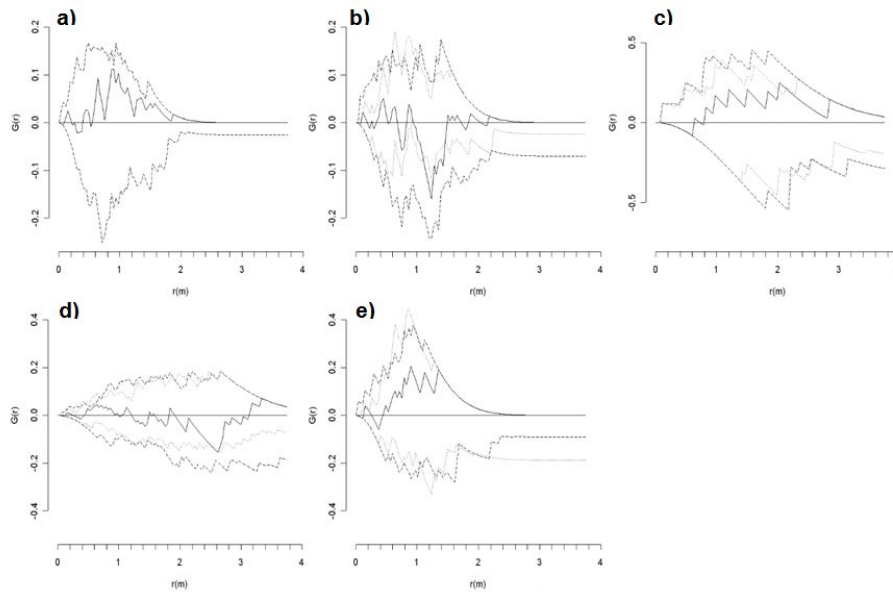
Second-order statistic (L(r))

For PSP092, the empirical second-order statistic ($L(r)$) of live and dead trees showed a significant regular distribution under H_{o1} at 0.8 m, but became significantly aggregated at distances of 4.9-5.2 m and 5.5-6.2 m (Fig. 5a). $L(r)$ of live trees showed a significant regular distribution for both H_{o1} at 1.6-1.7 m and 2.1-2.7 m, and Ho_2 at 2.4-3.2 m (Fig. 5b). $L(r)$ of dead trees was significantly clumped than expected under both H_{o1} at distances of 4.3-4.4 m and Ho_2 at distances of 4.5-4.7 m (Fig. 5c). The bivariate inter-relationship between live and dead trees showed that there was significant repulsion under H_{o1} at 0.8-1.0 m, and significant attraction than that expected under Ho_2 at 2.4-2.5 m (Fig. 5d).
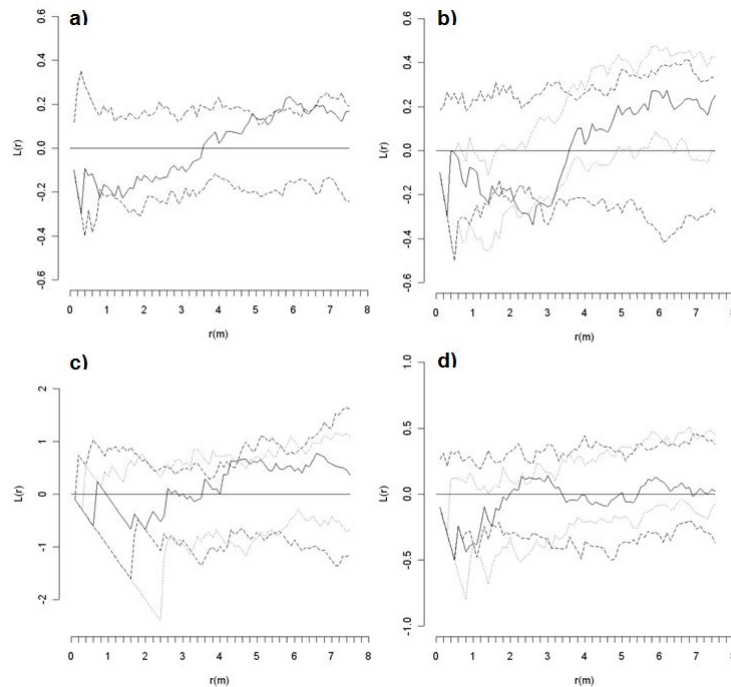
For PSP152, $L(r)$ of live and dead trees was within the confidence evelope defined by H_{o1} (Fig. 6a). $L(r)$ of live trees was significantly regular under H_{o1} at distances of 1.1-1.4 m, but was within the confidence envelope defined by Ho_2 (Fig. 6b). Dead trees were randomly distributed under H_{o1}, but significantly clumped than expected under Ho_2 at 2.0-2.1 m (Fig. 6c). The bivariate $L(r)$ of live and


Fig. 3. Plot 092 in Lower Foothills: Univariate nearest-neighbor distribution function ($G(r)=G(r)_{observed}-G(r)_{theoretical}$) for three data sets: (a) live and dead trees, (b) live trees, and (c) dead trees. Bivariate $G(r)$ measuring the distance (d) from a typical point of live to nearest dead tree, and (e) from dead to nearest live tree. Univariate (bivariate) $G(r) > 0$ indicates an aggregated distribution (attraction), $G(r) = 0$ indicates a random distribution (independence), and $G(r) < 0$ indicates a regular distribution (repulsion). Observed distribution (___) and confidence envelopes for 25 Monte Carlo simulations for the null hypothesis of complete spatial randomness (- - -) or random mortality (···).

Fig. 4. Plot 152 in Upper Foothills: Univariate nearest-neighbor distribution function $(G(r)=G(r)_{observed}-G(r)_{theoretical})$ for three data sets: (a) live and dead trees, (b) live trees, and (c) dead trees. Bivariate $G(r)$ measuring the distance (d) from a typical point of live to nearest dead tree, and (e) from dead to nearest live tree. Univariate (bivariate) $G(r)>0$ indicates an aggregated distribution (attraction), $G(r)=0$ indicates a random distribution (independence), and $G(r)<0$ indicates a regular distribution (repulsion). Observed distribution (___) and confidence envelopes for 25 Monte Carlo simulations for the null hypothesis of complete spatial randomness (- - -) or random mortality (⋯).

Fig. 5. Plot 092 in Lower Foothills: Univariate second-order statistic $(L(r))$ for three data sets: (a) live and dead trees, (b) live trees, and (c) dead trees. (d) Bivariate $L(r)$ measuring the relationship between live and dead trees. Univariate (bivariate) $L(r)>0$ indicates an aggregated distribution (attraction), $L(r)=0$ indicates a random distribution (independence), and $L(r)<0$ indicates a regular distribution (repulsion). Observed distribution (___) and confidence envelopes for 25 Monte Carlo simulations for the null hypothesis of complete spatial randomness (- - -) or random mortality (⋯).
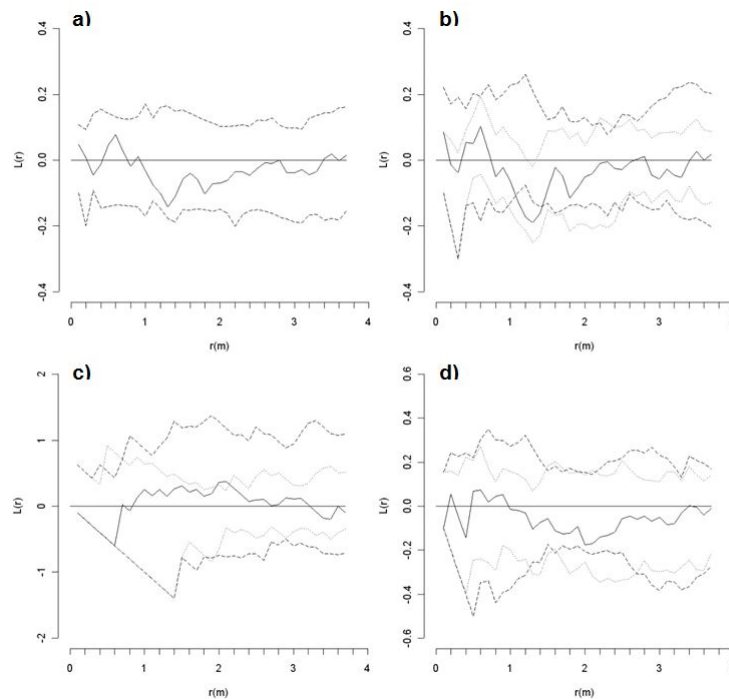
Fig. 6. Plot 152 in Upper Foothills: Univariate second-order statistic ($L(r)$) for three data sets: (a) live and dead trees, (b) live trees, and (c) dead trees. (d) Bivariate $L(r)$ measuring the relationship between live and dead trees (d). Univariate (bivariate) $L(r) > 0$ indicates an aggregated distribution (attraction), $L(r) = 0$ indicates a random distribution (independence), and $L(r) < 0$ indicates a regular distribution (repulsion). Observed distribution (___) and confidence envelopes for 25 Monte Carlo simulations for the null hypothesis of complete spatial randomness (- - -) or random mortality (···).

dead trees was within the confidence envelope defined by either H_{o1} or H_{o2}.

Discussion

In the Lower Foothills plot (PSP092) of the current study, there was evidence to suggest regularity in the live plus standing dead trees as indicated by Clark-Evans nearest neighbor index (R), the nearest neighbor distribution function ($G(r)$) and second-order cumulative distribution function ($L(r)$) at very local distances. In contrast, instances of clumping were shown by $L(r)$ at larger spatial scale. This regularity in the live plus dead trees was not expected. The results suggest that the stand was initially very regular but the regularity may also be an artifact of not accounting for the down dead trees in the forest inventory.

In the Lower Foothills plot (PSP092), despite the initial local regularity as indicated by $G(r)$ and $L(r)$ of live and dead trees, live trees also showed regularity but at larger spatial scales. Clark-Evans nearest neighbor index also in-

dicated regularity in the spatial pattern of live trees. Furthermore, in the case of $L(r)$, regularity was more than expected under both H_{o1} and H_{o2}. This indicates that there was some increase in the competitive influence zone of live trees from the initial distribution of live and dead trees. In PSP092, dead trees did not show an expected clumped pattern of nearest neighbor distances. Nonetheless, there was clumping observed according to $L(r)$ (for both H_{o1} and H_{o2}) suggesting increased mortality in high density patches.

In terms of the bivariate relationship of live and dead trees in PSP092, there was significant attraction according to $G(r)$ and $L(r)$ under H_{o2}. This supports the hypothesis that there is mainly one-sided competition for light in this stand. This was expected because of the shade intolerant nature of lodgepole pine as well as its tendency to form root grafts (Fraser et al. 2006).

In the Upper Foothills plot (PSP152), the initial distribution of live and dead trees was within random expectation according to $G(r)$ and $L(r)$. In contrast, live trees

were significantly regular under Ho_2 according to $G(r)$. According to $L(r)$, live trees were significantly regular under H_{o1}. There is thus some evidence to suggest that there is increased regularity in the surviving members of the stand due to competition. Under Ho_2, dead trees were significantly clumped according to $G(r)$ and $L(r)$ suggesting that dead trees experienced mortality in high density patches. The bivariate relationship between live and dead trees was mainly that of repulsion according to $G(r)$ under Ho_2, suggesting two-sided competition for soil nutrients and water in high density patches.

The general pattern of regularity observed in the two plots of lodgepole pine examined in this study has also been observed in other studies that have tested the random mortality hypothesis. This spatial pattern of regularity is more likely to occur in species that are shade intolerant. Shade intolerant, pioneer tree species undergo self-thinning which often leads to regularly spaced survivors. For instance, Kenkel (1988) examined a stand of shade intolerant jack pine (*Pinus banksiana* Lamb.) and reported that the initial distribution of live and dead trees was random while the distribution of surviving trees was significantly regular. The likelihood of regularity to be observed in the spatial pattern of forest stands appears to be also associated with older stands. For instance, both intraspecific and interspecific competition was observed to influence the spatial point-pattern of shade intolerant Douglas fir (*Pseudotsuga menziesii* Mirb.) in an old-growth forest stand in British Columbia, Canada (He and Duncan 2000). Density-dependent, intraspecific competition was the main driver of stand development at different successional stages in the boreal forest region of Alberta, Canada (Gray and He 2009). Furthermore, Gray and He (2009) observed that the effect of intraspecific competition was initially stronger for early successional species (i.e., trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*)) at the early successional stage and intraspecific competition was stronger for late successional species (i.e., white spruce) at the late successional stand stage. In a jack pine stand in Canada, the spatial pattern of live trees was initially clustered during the early phases of stand development and then showed very limited regularity at one site later on in stand development (Metsaranta and Lieffers 2008).

Nevertheless, not all studies have examined significant regularity in the spatial point-pattern of surviving trees. For instance, Kreutz et al. (2015) observed in the boreal forest of Fennoscandia that stands containing *Picea abies, Betula pubescens*, and *Betula pendula*, were either randomly distributed or clumped. Kruetz et al. (2015) attributed the clumped pattern to facilitative mechanisms related to nutrient availability and microclimatic moderation. Furthermore, Little (2002) reported no evidence of density-dependent spatial point-patterns in a boreal mixedwood site containing trembling aspen and jack pine but the lack of density dependence may be associated with the young (21-year old) stand that was investigated.

Spatially explicit studies of stands dominated by a single species have shown differences in the spatial pattern of mortality that appears to be influenced by species' shade tolerance, stand age, and disturbance regime. It is generally expected that shade intolerant, pioneer species experience higher mortality in high density patches. Mortality in lodgepole pine (a shade intolerant species) observed in the current study generally had a tendency towards a clumped spatial pattern. Furthermore, for another shade intolerant species of jack pine examined in western Canada, the spatial pattern of dead trees was initially clustered but over time as the stand aged, the pattern was randomly distributed (Metsaranta and Lieffers 2008). Metsaranta and Lieffers (2008) indicated that after the peak rate of mortality had passed, other factors besides competition were influencing forest dynamics. The likelihood of randomness observed in the spatial pattern of mortality appears to be more likely for tree species sampled in older stands. For instance, Aakala et al. (2012) found that mortality in an old-growth stand of red pine (*Pinus resinosa*, which is moderately shade tolerant) in northern Minnesota was spatially random using both Ripley's K-function and the pair correlation function. The spatial pattern of mortality events was also predominantly random in another old-growth stand (with stand ages up to 209 years) of red pine sampled in Minnesota (Silver et al. 2013). Silver et al. (2013) attributed mortality to multiple agents including windthrow, root-rot fungi, and infrequent droughts. In study and other studies examining shade intolerant tree species establishing after a stand-replacing fire(e.g., Metsaranta and Lieffers 2008), a clumped spatial pattern in mortality is more likely to occur in a stand replacement fire regime. In contrast, Aakala et al. (2012)

observed random mortality patterns in old growth red pine stands which generally experience a more variable pattern and intensity of repeated surface fires in an understory fire regime.

Conclusions

This study provides new insight and understanding of the underlying competitive processes driving forest stand dynamics of lodgepole pine derived from the analysis of spatial point-patterns. While other spatial ecology studies have devoted attention to other tree species (e.g., jack pine, red pine, trembling aspen), our study represents the first consideration of lodgepole pine. Additional analyses on other boreal tree species would be useful in providing further insight into the ecological process behind competition and mortality in boreal forests.

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