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Long-term mortality rates and spatial patterns in an old-growth *Pinus resinosa* forest

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Abstract: Understanding natural mortality patterns and processes of forest tree species is increasingly important given projected changes in mortality owing to global change. With this need in mind, the rate and spatial pattern of mortality was assessed over an 89-year period in a natural-origin *Pinus resinosa* (Aiton)-dominated system to assess these processes through advanced stages of stand development (stand age 120–209 years). Average annual mortality rates fluctuated through time, yet were within the range reported in other studies (0.60%–3.88% depending on species and sampling interval). Tree mortality was attributed to multiple agents, including the senescence of the short-lived *Pinus banksiana* Lamb., windthrow, root-rot fungi (*Armillaria ostoyae* (Romagn.) Herink), and perhaps infrequent droughts. Despite the often contagious nature of many disturbance agents, the overall spatial pattern of mortality events (the arrangement of dead trees within the fixed initial population of live trees) was random at all scales tested. Similarly, the current spatial pattern of dead trees was predominantly random, despite clustering at small scales (2–4 m). These findings underscore the importance of studying mortality rates, agents, and spatial patterns over long time periods to avoid misinterpreting stochastic mortality events, and their influence on longer term stand structure and development.

Résumé : Il de plus en plus important de comprendre les patrons et les processus de mortalité naturelle chez les espèces d'arbres forestiers étant donné l'impact prévu des changements globaux sur la mortalité. Avec cette préoccupation en tête, le taux de mortalité et sa configuration spatiale ont été étudiés sur une période de 89 ans dans un écosystème d'origine naturelle, dominé par *Pinus resinosa* Aiton, dans le but d'évaluer ces processus au cours des stades avancés de développement des peuplements (peuplements âgés de 120 à 209 ans). Le taux annuel moyen de mortalité fluctuait avec le temps mais restait à l'intérieur de l'étendue rapportée dans d'autres études (0,60 % à 3,88 %) selon l'espèce et l'intervalle d'échantillonnage. La mortalité des arbres était due à plusieurs agents incluant la sénescence du *Pinus banksiana* Lamb. qui a une brève durée de vie, au chablis, aux champignons de carie de racines (*Armillaria ostoyae* (Romagn.) Herink) et peut-être à des sécheresses peu fréquentes. Malgré la nature souvent contagieuse de plusieurs agents de perturbation, la configuration spatiale générale des épisodes de mortalité (la distribution des arbres morts parmi la population initiale fixe d'arbres vivants) était aléatoire à toutes les échelles testées. De la même façon, la configuration spatiale actuelle des arbres morts était essentiellement aléatoire malgré la présence de regroupements à grande échelle (2–4 m). Ces résultats soulignent l'importance d'étudier le taux, les agents responsables et la configuration spatiale de la mortalité sur de longues périodes pour éviter de mal interpréter les épisodes de mortalité stochastiques et leur influence sur la structure et le développement à plus long terme des peuplements. [Traduit par la Rédaction]

Introduction

Tree mortality is a fundamental process in forest development, influencing resource availability, tree regeneration, stand structure, and stand-level productivity (Franklin et al. 1987). Mortality can occur as a widespread disturbance, replacing entire forest stands, or more locally, forming large or small canopy gaps. Natural mortality rates and processes provide historical context against which current forest processes can be compared (D'Amato et al. 2008). Establishing these natural benchmarks is becoming increasingly important given the projected increases in mortality rates for forest ecosystems because of global change (van Mantgem et al. 2009); in fact, tree mortality may be increasing worldwide, from boreal systems (Peng et al. 2011) to the tropics (Lewis et al. 2009).

Tree mortality may occur stochastically or episodically, the result of various mortality agents. This temporal variability is evident in low-level background mortality (Franklin et al. 1987), and in virtually all disturbances that cause partial stand mortality, such as moderate-severity windstorms (Hanson and Lorimer 2007) and insect outbreaks (Swetnam and Lynch 1993). As such,

mortality rates and trends are best determined from long-term studies, which provide the temporal extent necessary to properly characterize tree mortality and forest disturbance.

In addition to temporal variability, tree mortality may exhibit strong spatial variability. In general, tree spatial information improves mortality predictions by strengthening measures of competition (Das et al. 2008), provides inferences about past disturbance agents (Fraver and Palik 2012), and can illuminate community-level responses to changes in composition and climate (Pacala and Deutschman 1995). Despite its importance in structuring forest communities, spatial patterning of mortality has been rarely studied in natural-origin, late-successional forests (but see Aakala et al. (2012)). These studies are rare in part because the repeatedly sampled stem-mapped plots ideal for addressing this issue are uncommon in these systems. Yet this information is critical for a full understanding of stand development and forest dynamics, because the spatial patterning of mortality may change over time, even in advanced stages of development (Castagneri et al. 2010). Studies that have examined spatial patterns of

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mortality in natural forest systems have rarely exceeded 30 years (e.g., Das et al. 2011), hampering our ability to predict long-term spatial dynamics within forest systems. In the absence of such long-term studies, analyses of mortality patterns are typically limited to comparisons of current live versus dead tree distributions, which can lead to erroneous conclusions (Goreaud and Pelissier 2003). For example, Aakala et al. (2012) demonstrated that an aggregated initial (combined live and dead trees) distribution can lead to an apparent aggregation of dead trees, even when mortality events occurred randomly, simply because the mortality events were constrained by the initial aggregated pattern.

A recently revived long-term study, including mapped locations of all trees, allowed us to overcome some of the limitations enumerated previously. This study, the longest for natural-origin red pine (*Pinus resinosa* Aiton) to our knowledge, includes nine re-inventories between 1923 and 2010. It consists of a 2-ha plot with 1129 trees (initially) individually tagged, mapped, and measured. At the time of plot establishment in 1923, stand age was 120 years, having established following an 1803 fire. The stand was never harvested, which allows us to rule out direct human influence, thereby focusing on natural mortality processes inherent to late-successional red pine forests.

Red pine has an extensive natural range in north-central and northeastern North America. In the northern Great Lakes region, it is one of the principal commercial timber species, and it occupies a significant proportion of protected natural areas. Despite its regional importance, much remains unknown regarding natural dynamics, including patterns of natural mortality. To fill these knowledge gaps, the objectives of the present study were to (1) examine long-term mortality rates for natural red pine systems, (2) quantify spatial patterning of individual tree mortality events, and (3) assess the relative importance of mortality agents potentially affecting this system based in part on the spatial patterns found under objective 2. Based on the results of Aakala et al. (2012) and similar spatial-pattern literature, we expected to find variability in the patterns, either clustering owing to root-rot fungi and insect disturbance or regularity owing to self-thinning. This study of natural tree mortality, including spatial patterning, sheds much light on the natural history of this forest type and can be used to guide forest management aimed at increasing structural diversity in ways that emulate the outcomes of natural disturbance (Larson and Churchill 2012) or confer resilience to future environmental conditions (Churchill et al. 2013).

Methods

Study area

The study site is located in a natural (i.e., unharvested), 209-year-old (at the time of our final sampling), fire-origin red pine stand within the Scientific and Natural Area of Itasca State Park, Minnesota, USA (47°13′N, 95°14′ W). Stand age was determined by dendrochronological analyses, with tree age estimates refined following methods outlined in Fraver et al. (2011), and corroborated by a documented 1803 fire in Itasca State Park (Frissell 1973). Mean site elevation is approximately 462 m a.s.l., with undulating slopes of 5%–10%. Soils are well-drained sandy loams and loamy sands derived from glacial outwash. Average annual temperatures range from −20 °C (January) to 25.4 °C (July), and average annual precipitation is 653 mm. Prescribed surface fires were applied in 1998, 2000, and 2003, and known drought periods occurred in the late 1960s and late 1980s (R. Marty (personal communication, 2012)); however, there was no mortality to the mature pines under study owing to the prescribed burns. The stand is currently dominated by red pine with a lesser component of white pine (*Pinus strobus* L.) and white spruce (*Picea glauca* (Moench) Voss). Historically, the early-successional jack pine (*Pinus banksiana* Lamb.) comprised a significant component of the stand, but had experienced complete mortality by the time of our recent sampling (see the

Table 1. Structural characteristics of living trees within the sampled old-growth red pine stand located in Itasca State Park, Minnesota.

Structural characteristic	Stand age (years)	
	120	207
Basal area (m²/ha)	30.4	38.0
Mean DBH (cm)	26.0	38.3
DBH range (cm)	8.0–61.0	10.0–64.0
Density (stems/ha)	517	298
Composition (% basal area)		
Pinus resinosa	69.0	86.0
Pinus banksiana	23.0	NA
Pinus strobus	6.3	7.5
Picea glauca	1.4	1.8
Betula papyrifera	NA	1.4
Unknown	0.3	NA
Other	NA	2.2

Note: Stand ages refer to plot establishment (1923, age 120 years) and a recent sampling (2010, age 207 years). NA, not applicable.

following). Historical logging activities are well-documented for the park, but no history of logging is recorded for this particular stand; however, we noted 23 apparently cut stumps in scattered locations, but the reason for the cutting is not known. Table 1 provides structural and compositional characteristics of the stand at plot establishment (1923) and a recent sampling (2010).

Long-term permanent plot sampling

The research plot on which this study is based was established in 1923 by J.H. Allison (University of Minnesota) to characterize tree growth and productivity (Fig. 1). The plot was laid out such that the southeast corner coincided with a Public Land Survey section corner, and it extended five chains (1 chain = 66 ft or 20.1 m) to the west and 10 chains to the north, that is, roughly 100 m × 200 m. At establishment, all trees greater than 3 in. (7.8 cm; *N* = 1129 trees) diameter at breast height (DBH) were tagged, and DBH and height (subset of trees) were measured. The plot had been re-inventoried in 1928, 1933, 1938, 1943, 1948, 1952, 1957, and 1963, recording DBH and noting status as dead, in which case DBH was no longer recorded. In 1948, 1952, and 1963, tree locations were hand-drawn on a map within 1-chain grid cells (approximately 20 m × 20 m).

Field and laboratory methods

We re-inventoried the plot from 2010 to 2012, recording DBH and live versus dead status of each tree in 2010. During this inventory, we realized that the hand-drawn tree locations from early maps lacked the precision needed for spatial pattern analyses. We thus remapped locations of all living and dead trees in 2012. For this purpose, the plot was divided into twenty 10 m × 100 m transects, and *X* and *Y* coordinates were recorded (to the nearest dm), using tapes and electronic measuring devices, within each transect. Most trees still had tags, presumably from intermediate inventories. Tags on fallen trees, many in advanced stages of decay, were located with a metal detector, and the former rooted center of each was mapped. Nevertheless, using these methods we were unable to locate and map 32% of the initial trees recorded in 1923, owing to their death and advanced decay. For these trees we relied on digitized locations from the 1952 map, after adjustments (i.e., shifted coordinates). These adjustments were based on discrepancies between known tree locations (2012) and hand-drawn mapped (1952) locations of those same trees, which showed a bias that increased slightly from south to north within the plot. To account for this nonstationary bias, we made adjustments separately for each 20 m × 20 m grid cell. Adjustments were based on probability distributions of discrepancies unique to each cell. The "sn" package in R (Azzalini 2011) was then used to simulate shifted

Fig. 1. (*a*) Example of a recent and an original tree tag found on a *Pinus resinosa* individual in the Allison plot. (*b*) Example of typical stand structure within the Allison plot in 2010.

locations for each tree without a 2012 location, based on this distribution of mapping discrepancies.

In an effort to better characterize past mortality agents, we searched historical records and published literature for mention of local windstorms, fires, insect outbreaks, drought, or the occurrence of root rot. To shed light on wind as a mortality agent, we recorded the fall direction of windthrown trees (those with uprooting mounds), and tested for uniform directionality using Rayleigh's test for circular uniformity (Rayleigh 1919). We collected fungal tissue samples (mycelial fans or fruiting bodies) from six trees with declining vigor apparently from root rot fungi. Samples were identified by DNA extraction and sequencing followed by a Basic Local Alignment Search Tool (BLAST) to search for similar sequences in GenBank (Altschul et al. 1997). Trees of declining vigor were common within the plot, and considerable mortality presumably from this same agent was visible in locations throughout the larger stand.

Data analysis

Mortality rates were calculated for pooled species initially present, as well as for red pine and jack pine separately, for each sampling interval. Rates were calculated as

$$1 - [1 - (M_1/N_0)]^{1/t}$$

where M_1 is the total number of stems that died during the sampling period, N_0 is the total number of live stems in the previous sampling, and t is the number of years between sampling periods (Sheil and May 1996). Rates were not calculated for jack pine in the two most recent inventories because fewer than 20 living trees were present. The 23 cut trees (mentioned previously) were not included in our calculation of natural mortality rates.

Currently, the most common approach to ecological spatial point pattern analysis is Ripley's K and associated transformations (Ripley 1976). However, because the method is based on the cumulative sum of points within ever-increasing radii, it may not accurately detect the distance at which deviations from spatial randomness occur (Perry et al. 2006). A newer method, the pairwise correlation function (PCF), also known as $g(r)$, is a first-order derivative of the K function that overcomes this cumulative distance limitation by measuring the rate of change in the K function (Stoyan and Stoyan 1994). We analyzed the spatial patterns of mortality using the PCF, which captures the "average" pattern across a given study area (Getis and Franklin 1987). Our null hypothesis for all spatial analyses was complete spatial randomness based on the Poisson distribution (Goreaud and Pelissier 2003). All analyses included isotropic edge corrections (Ripley 1976).

We calculated the PCF statistic for each of the following four spatial point patterns at 1-m distance classes: (1) univariate pattern of live pines in 1923 (g_{1923}); (2) univariate pattern of dead pines in 2012 (g_{2012}); (3) bivariate pattern of mortality ($g_{1963} - g_{1923}$),

1923–1963; and (4) bivariate pattern of mortality ($g_{2012} - g_{1964}$), 1964–2012. For a completely random univariate (Poisson) process, the PCF equals one. PCF values greater than one suggest a clustered pattern, whereas values less than one suggest a uniform pattern (Stoyan and Penttinen 2000). Under randomly occurring mortality, the bivariate pattern ($g_{current} - g_{initial}$) equals zero. Positive deviations from zero ($g_{initial} > g_{current}$) suggest a clustered pattern, whereas negative deviations ($g_{initial} < g_{current}$) suggest a uniform pattern (Stoyan and Stoyan 1994). The two selected time periods split the complete sampling period roughly in half and were chosen because the number of tree deaths using shorter time periods was too low for robust statistical tests.

Finally, the bivariate PCFs (patterns 3 and 4) were used to test the null hypotheses of spatially random mortality events using the random-labeling approach (Goreaud and Pelissier 2003), which assesses differences in the initial (live and dead trees) and current (live trees) distributions. Dead trees were randomly assigned locations within the initial fixed distribution, and PCF simulations were used to test if the observed pattern matched those resulting from random assignments. This procedure was necessary because the spatial pattern of mortality events is necessarily constrained by the fixed initial pattern of all trees (Aakala et al. 2012). For all analyses we removed in-growth species (non-pines established after the initial pine cohort; the stand had no pine regeneration) from the analysis to avoid confounding pine mortality patterns (Aakala et al. 2012). We calculated 999 global Monte Carlo simulation envelopes for all patterns to test for deviations from the null hypothesis using a 95% confidence level. These tests were conducted using all pine species present in the initial inventory. To further explore species influence in spatial patterning, red pine (being most abundant) was analyzed separately for each of these point patterns, resulting in four additional analyses. Jack pine could not be similarly isolated because of small sample size in the later 1964–2012 period. Spatial analyses were conducted with the "spatstat" package in R (Baddeley and Turner 2005) using the variation for inference and formal hypothesis testing described in Baddeley (2008). Lastly, for each simulation, the coordinates of trees with uncertain locations (32% of trees; see Field and laboratory methods) were shifted randomly 1000 times within their probability density kernels to determine if the error associated with the uncertain locations would change the results and subsequent interpretation. Ultimately, results were not changed by the error associated with the shifted locations.

Results

During the 89-year sampling period (1923–2012), 664 (61%) of the initially mapped trees died. Average annual mortality rates, calculated for each sampling interval, fluctuated over time, with jack pine showing a general increase through stand development (Table 2). The average rate for red pine was 0.76% over the entire sampling period, ranging from 0.15% to 3.54% depending on

Table 2. Annual mortality rates (%) for each of the nine sampling periods following study initiation in 1923 (at stand age 120 years), for an old-growth red-pine-dominated stand in Itasca State Park, Minnesota.

Species	Sample period ending date								
	1928	1933	1938	1943	1948	1952	1957	1963	2012
Red pine	0.28	0.43	0.47	0.15	0.45	0.35	0.72	3.54	0.50
Jack pine	5.45	4.25	4.66	4.88	9.94	8.26	10.99	—	—
Species pooled	1.44	1.16	1.14	0.70	1.27	0.87	1.19	3.88	0.60

Note: Rates determined only when 20 or more trees were available for calculation.

sampling interval (Table 2). Average annual mortality for jack pine during this time was 6.92%, ranging from 4.25% to 10.99% (Table 2). Jack pine had experienced complete mortality by 2012. Average annual mortality rates for all species (pines and spruce) pooled was 1.36%, ranging from 0.60% to 3.88% depending on the sampling interval (Table 2). Despite persistent mortality, basal area increased over time (Table 1).

In addition to the documented historical disturbances (see Discussion), our work identified several biotic and abiotic mortality agents affecting the plot. Fungal tissue cultures obtained from six dying red pine trees in the plot used for DNA extraction and sequencing showed a BLAST match of 100% to *Armillaria ostoyae* (Romagn.) Herink when compared to GenBank sequences, and one representative sequence was submitted to GenBank with the sequence number JX174637. Although *A. ostoyae* was isolated from just these six poor-vigor trees, many others were likely infected (E.J. Silver (personal observation, 2012)). Windthrown trees (11% of the originally mapped trees) spanning a range of decay states had significant uniform fall directions, but with high variance (mean azimuth, 89.9°; Rayleigh's p value, 0.00; $n = 127$; circular SD = 78.2°), implicating westerly winds as the cause.

The initial univariate spatial patterns for living trees (1923, with species pooled or red pine treated separately) did not deviate significantly from random (Figs. 2 and 3). Similarly, the bivariate test for both time periods (from 1923 to 1963 and 1964 to 2010) indicate random mortality events for the three pine species pooled and for red pine separately (Fig. 3). The final dead tree univariate pattern (with species pooled and red pine treated separately) were found to be clustered at small scales (2–4 m), but were random at all distances beyond 2–4 m (Fig. 3).

Discussion

These long-term data provide a rare look at the mortality processes and spatial patterns through the advanced stages of development (stand age 120–207 years) of a natural-origin red pine stand, allowing us to document temporal changes that would likely go undetected in short-term studies. Results suggest that the spatial pattern of tree mortality events was random for both analyzed time periods. However, the pattern of dead trees in 2012 indicated spatial aggregation at small intertree distances (2–4 m), with random patterning at all larger scales. Mortality rates fluctuated through time, a finding that also underscores the value of examining these patterns over the extended periods of development as represented in this data set. The mortality agents responsible for these variable temporal and spatial patterns were difficult to assign; however, self-thinning, drought, windthrow, *Armillaria* root-rot fungi, and senescence of the short-lived *P. banksiana* likely played a significant role, singly or through interactions, during stand development.

Mortality rates

Annual mortality rates differed by species, suggesting differential mortality risks or agents. Rates also fluctuated over time, with jack pine showing a general increase in mortality rate through stand development (Table 2). The average annual mortality rate for red pine (0.76%, averaged over nine inventory periods), the first reported for natural stands of this species, was similar to

studies of managed red pine (Powers et al. 2010). The rate for jack pine was considerably higher (6.87%), reflecting the advanced stand developmental stage and the maximum longevity of this species: 230 years, compared with 400 years for red pine (Burns and Honkala 1990). All jack pines had died by the time of our recent inventory. The spike in mortality seen during the 1963 census (Table 2) likely reflects stress from a well-documented 1961 drought.

The annual mortality rate for pooled species (1.36%) documented here was somewhat higher than rates found in other temperate old-growth coniferous forests (Franklin and DeBell 1988; Stephens and Gill 2005; Larson and Franklin 2010), again reflecting the high rate from the shorter lived jack pine. When the overall annual mortality rate for red pine (0.76%) is considered separately, it is more in line with these previous studies. Interestingly, the pooled-species mortality rate was similar to that of old-growth temperate hardwood forests (Lorimer et al. 2001; Runkle 2013), perhaps pointing to the generally higher mortality rates expected in hardwood forests (Stephenson and van Mantgem 2005). Our results also corroborate previous studies documenting that mortality rates vary by species (Lutz and Halpern 2006; Larson and Franklin 2010). This differential mortality caused a shift in species' relative abundance through time, ultimately favoring red pine, given its lower mortality rate. Finally, the nonconstant mortality rates reported here reinforce conclusions from Lutz and Halpern (2006) that stand-development models that do not account for such fluctuations may be overly simplistic.

Mortality agents

Our results allow us to make inferences regarding past mortality agents; however, definitive conclusions regarding the relative importance of various agents were difficult to draw. The six trees on which *Armillaria* was isolated are still living, but of very poor vigor, and many other plot trees show equally poor vigor. The current role of *Armillaria* in this plot may have been to weaken structural integrity and exacerbate damage from windstorms, as has been shown for other wood-decay fungi (Edman et al. 2007). In fact, windstorms are rather common in this region, with documented storms occurring in 1941, 1983, and 1995 (Webb 1988), and in 2012 after the conclusion of the current study. Mortality risk from windstorms in Itasca State Park historically depended on tree species, tree size, and presence of wood-decaying fungi (Webb 1989). Finally, although fire can potentially lead to patchy tree mortality in red pine systems (Fraver and Palik 2012), the three prescribed fires that occurred during our study period did not cause mortality of mature pines (note the relatively low mortality rate in the most recent survey interval; Table 2), nor did they appear to increase mortality from bark beetles (*Ips* spp.), an interaction that has been found elsewhere in Itasca State Park (Santoro et al. 2001).

Because of inconsistent measurement intervals, as well as the focus of the early data collection on surviving trees, we could not assign actual causes of mortality to individual trees; however, the agents previously discussed likely affected the plot throughout the study period. In addition to the agents we documented, it is likely that physical damage from neighboring tree fall was prevalent, but we lack the annual resolution to confirm this. The role

Fig. 2. Map of Allison plot stem locations by species as the plot appeared at the first sampling in 1923, stand age 120 years (left panel) and a map of mortality events from 1923 to 2012 (right panel). Plot dimensions are in metres.
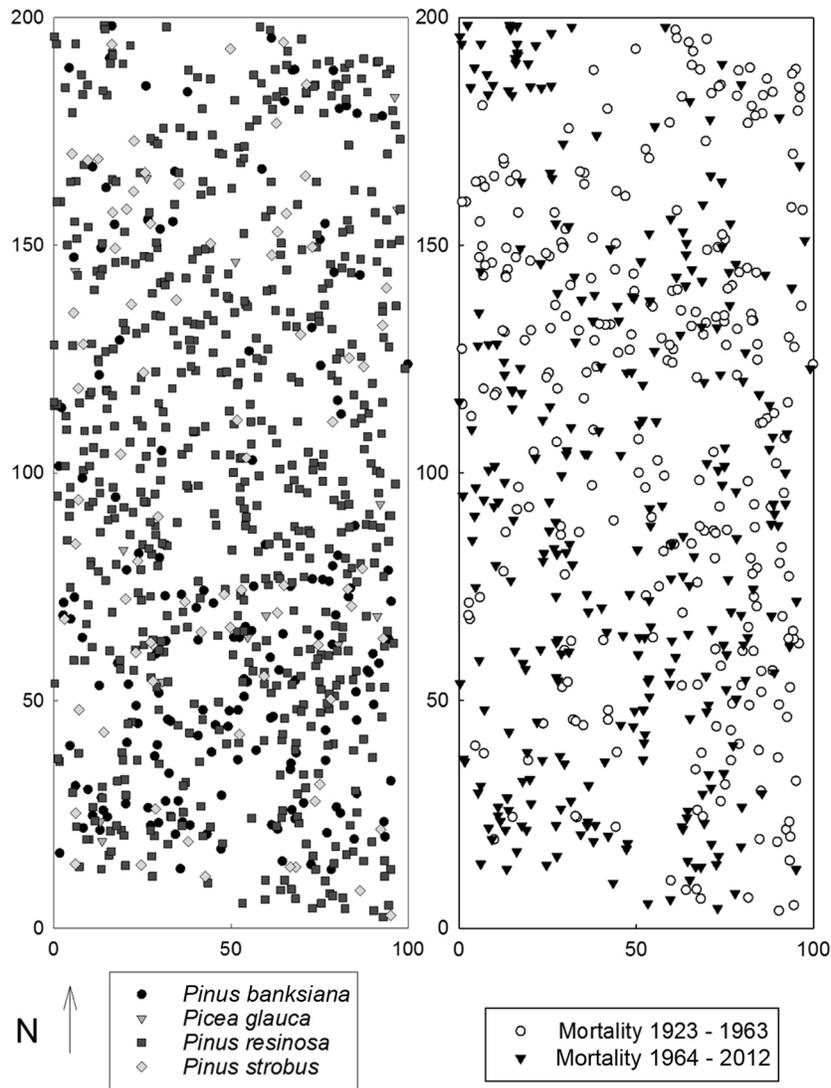
of physical damage has been well-documented in other temperate coniferous forests (Larson and Franklin 2010; Holzwarth et al. 2013). Further, the weakening of standing trees from fungal pathogens, insect disturbance, or drought may have exacerbated mortality from windstorms or physical damage, which has been shown in similar forest types worldwide (Worrall et al. 2005; Allen et al. 2010).

Spatial pattern of mortality

Throughout the advanced stages of stand development documented in this study (stand ages 120–209 years), the spatial pattern of mortality events (the arrangement of dead trees within the fixed initial population of live trees) was random at all scales tested, a finding consistent with that of Aakala et al. (2012). However, the current spatial pattern of dead trees was found to be clustered at small scales (2–4 m). This small-scale clustering may be explained in part by the recent infection of trees by *Armillaria*, creating small nascent patches of dead trees. *Armillaria* root-rot typically leads to clustered red pine mortality at much larger scales (up to 50 m in diameter; Ostry et al. 2012), but it did not do so here, likely because it has not been present on the plot long enough to have caused substantial mortality. Although windthrown trees showed weak evidence of spatial clustering (not

shown), they were likely too few to have influenced the clustered pattern seen at small scales. Clustered tree mortality has been previously reported (however, at scales larger than those found here) and attributed to insect damage (Hurst et al. 2012), and possibly the interaction of root-rot fungi and insect damage (Metsaranta and Lieffers 2008). Where clustering of dead trees has been reported at similarly small scales, it was attributed to differential mortality within higher density patches that existed prior to mortality events (Kenkel 1988; Aakala et al. 2007).

Beyond these small scales in the current pattern of dead trees, mortality events were randomly spaced, a finding corroborated by Aakala et al. (2012), also working with red pine. Similarly, Das et al. (2011) documented spatially random mortality of canopy trees in western US conifer forests, a pattern also documented in a review of mortality patterns and processes in fire-dependent forests in western North America (Larson and Churchill 2012).

A number of factors, acting singly or in combination, may have contributed to the predominantly random spatial mortality seen here. Principle among those is drought, which is suggested to cause spatially heterogeneous mortality of canopy trees (Ganey and Vojta 2011). Documented droughts occurred in this region of Minnesota in the 1930s, 1961, 1988, and 2006. Drought is also

Fig. 3. Pairwise correlation functions (PCF) computed for the bivariate pattern of mortality events (1923–1963, 1964–2010, and all species), the initial univariate pattern of living trees (species pooled, *Pinus resinosa* separately), and the final univariate pattern of dead trees (species pooled, *P. resinosa* separately). No significant clustering (upper envelope) or regularity (lower envelope) was detected, aside from clustering at small scales for dead trees. The solid grey lines are the PCF, which equals 1 under complete spatial randomness. The dotted lines and solid grey bands are the confidence intervals as generated from 999 Monte Carlo simulations.
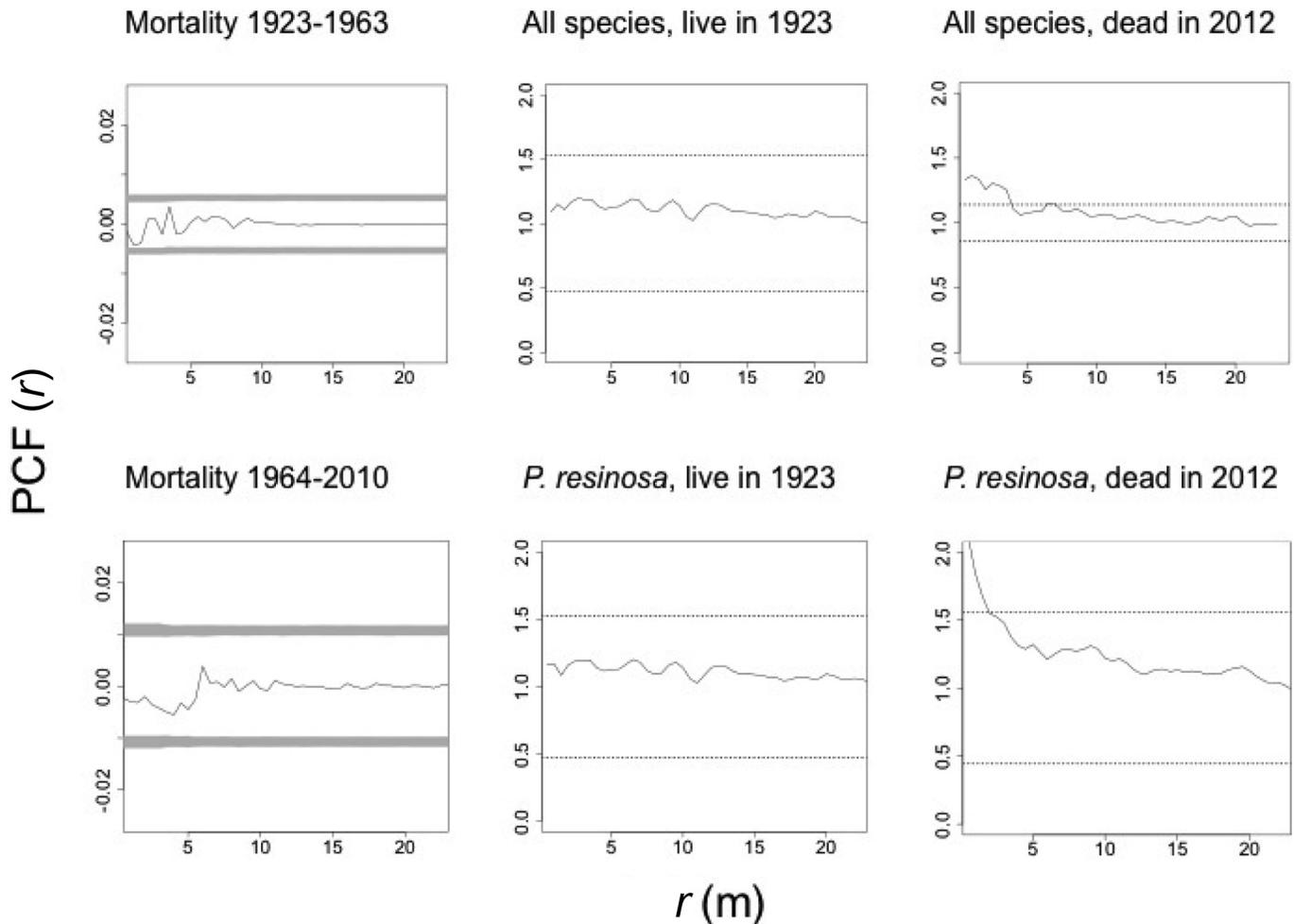
known to interact with *Armillaria* to increase the mortality risk of red pine (Mclaughlin et al. 2011). In addition, given its large size, the plot necessarily includes substrate and topographic heterogeneity (Spurr and Allison 1956), which influences drought-mediated mortality and has been shown to influence the spatial patterns of mortality in other conifer forests (Getzin et al. 2006).

The random mortality seen in these advanced stages of development may also have been constrained by the initial (1923) random pattern of living trees. This initial pattern may have resulted from early post-establishment density-dependent competition acting on an initially clumped distribution (Lepš and Kindlmann 1987), or it may have been perpetuated from an initial random distribution (Kent and Dress 1979). Simulation studies have shown that random patterns remain random over time when mortality is not dependent on neighboring trees (Kent and Dress 1979). This finding suggests that tree mortality events were not strongly dependent on neighbor competition, a finding also reported for mature pine stands in central Canada (Metsaranta and Lieffers 2008). The variability in spatial patterns at different scales further demonstrates the importance of comparing univariate dead tree patterns with bivariate mortality-event patterns over long periods of time.

Conclusions and management implications

Long-term demographic data from old-growth forests, such as the one we studied, are rare and invaluable resources for documenting processes and population dynamics in natural systems (Franklin et al. 1987). These data are needed to parameterize growth models (e.g., FORET and SORTIE), which can then be used to address potential long-term consequences of biotic and abiotic changes on forest ecosystems in ways that are impractical with field studies. Moreover, monitoring mortality rates and spatial patterns over long time periods can provide critical benchmarks for assessing the influence of global change on tree populations in natural forest systems.

A more applied use of such data are as reference benchmarks of population demographics and forest structural dynamics against which to compare similar parameters in managed forests. Globally, there is increasing interest in managing forests for greater structural heterogeneity, in ways that emulate natural disturbance and stand-development processes (Larson and Churchill 2012); long-term studies in old-growth forests are critical for developing these management approaches.

Commercial tree species are often managed to promote simplicity of structure and composition (Schönau and Coetzee 1989; Fox et al. 2007). Moreover, through planting and thinning efforts,

the spatial pattern is pushed deliberately towards uniformity (Gilmore and Palik 2006) for operational efficiency and because of the prevailing belief that natural systems of this forest type displayed similar characteristics (Palik and Zasada 2002). Our results provide information that can be used to manage these systems in ways that better reflect the more heterogeneous structure and underlying spatially random dynamics of this forest type.

Specifically, the spatially random tree distribution we documented (at stand age 120 years) suggests that variable density thinning (VDT) might be a useful intermediate treatment early in stand development if a goal is to restore old-growth structure or manage for more heterogeneous conditions. In short, VDT is an approach to thinning that emulates the natural variation in small-scale canopy disturbances and competition-based mortality (Carey 2001) and results in much greater spatial variability in stand densities and, consequently, greater structural heterogeneity than does standard thinning (Franklin et al. 2007).

Variable density thinning later in stand development also has been suggested as a way to sustain heterogeneity in managed old-growth systems (Curtis and Carey 1996; O'Hara et al. 2010; Larson et al. 2012). For red pine forests, VDT could be used to emulate the spatially random mortality events we documented after stand age 120 years. Moreover, thinning methods (i.e, thinning from above or below) could also vary among tree removal locations to emulate the patterns of mortality across different size classes.

Our results can serve as a template for developing VDT approaches in red pine forests, where there is great need and interest in managing for more heterogeneous structure. They also may be useful for developing such approaches in similarly structured fire-adapted pine and (other) conifer ecosystems around the world.

Acknowledgements

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