

Bivariate pattern analysis of jack pine - trembling aspen interaction

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Abstract. Interspecific interaction between jack pine and trembling aspen was investigated in a 70 x 70 m plot within an even-aged, mixed boreal forest stand in east-central Ontario. A total of $n = 621$ trees were mapped ($n_1 = 241$ trembling aspen, $n_2 = 380$ jack pine). This empirical spatial pattern was analyzed using Ripley's bivariate second-order spatial analysis, with confidence limits set by randomly relabelling species affinities of the 621 trees. The results indicate strong negative association between the two species at all spatial scales investigated (0 - 20 m radius). Some possible mechanisms for the development of a strong negative association between jack pine and trembling aspen are outlined.

Introduction

To the uninitiated, the North American boreal forest appears to be a relatively simple ecosystem. Mono-specific, even-aged forest stands are found over large areas, and it is generally assumed that there is a strong relationship between vegetation and substrate conditions (see Larsen 1980). Furthermore, boreal forest community structure is assumed to be relatively simple, since species richness is low. However, more detailed ecological investigations have revealed that the relative 'simplicity' of boreal ecosystems is largely illusory. For example, relatively fine-scale surveys have indicated that vegetation-environment relationships in both upland jack pine stands (Kenkel 1986) and boreal wetlands (Kenkel 1987) are surprisingly complex. The specific determinants of boreal forest vegetation composition include environmental factors (e.g. substrate conditions, drainage and drainage patterns), biotic processes (e.g. interspecific interactions such as competition, mutualism, and herbivory), stochastic factors (e.g. seed dispersal and plant establishment), and disturbance. Fire is a pervasive natural disturbance in upland boreal forest stands. The prevalence of extensive stands of pioneer, shade-in-

tolerant, pyric tree species such as jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*) is testament to the frequency and overall importance of fire in the boreal ecosystem. In wetland areas, changes in drainage and drainage patterns through both beaver activity and the accumulation of peat deposits (mainly from the genus *Sphagnum*) are also important. However, a number of fundamental questions regarding the determinants of vegetation structure and composition in the boreal forest have yet to be addressed. One of the greatest challenges facing boreal ecologists lies in elucidating and modelling the factors determining vegetation pattern and ecosystem processes at the landscape scale.

Moderately to excessively drained upland sites in the boreal forests of central and western North America are dominated by pure, even-aged jack pine or trembling aspen stands. Both are pioneer, highly shade-intolerant species that are very well adapted to fire. Jack pine produces serotinous cones that normally open to disperse their seed immediately following a fire. The post-fire environment offers ideal germination conditions: mineral soils are exposed, potential competitors are absent, and soil nutrient levels are comparatively

high. Since germination occurs immediately following a fire, interspecific competition is largely avoided at the establishment stage. It has even been suggested that jack pine has evolved features to increase site flammability. Trembling aspen has adapted to pyric ecosystems through its clonal habit. While fire kills the clonal ramets, the underground root systems remains unharmed in all but the most severe fires. Following the fire, this root system produces new, fast-growing sprouts (clonal 'suckers') at very high initial densities. As in jack pine, the strategy is to quickly recolonize the disturbed area.

Both jack pine and trembling aspen normally form monospecific stands, and it is rare to find these two species growing together. The most straightforward explanation for their non-overlapping distributions (negative association) is that these two species have different ecological requirements. Indeed, jack pine usually occurs on well to excessively drained sandy soils and rock outcrops, whereas trembling aspen is found primarily on well to moderately drained glacial till. This is only a partial explanation, however, as extensive stands of jack pine can also occur on moderately well drained glacial till. It is also important to recognize that observed distributional patterns are not necessarily indicative of ecological preferences, but may instead reflect historical factors and/or biotic interactions (e.g. Kenkel et al. 1991). Indeed, when not competing with other tree species, jack pine shows its best growth on sites that are not excessively drained (e.g. Fowells 1965). It is therefore not unreasonable to suggest that jack pine is restricted to excessively drained sites because it is outcompeted by trembling aspen elsewhere. However, because both species are long-lived, very few competition experiments have been performed to test this hypothesis (Peterson & Peterson 1992). A study of seedling competition between jack pine and trembling aspen indicated that trembling aspen is the superior competitor (Farmer et al. 1988). However, these authors emphasized that their experiment was performed under conditions "which provided excellent nutritional and moisture conditions for both species", and that jack pine would be expected to fare better under drier, more nutrient-limiting conditions. In northern Ontario stands dominated by jack pine, Mugasha (1989) noted that interspecific interactions between jack pine and trembling aspen appeared to be stronger than intraspecific interactions within jack pine. Both studies indicate that trembling aspen outcompetes jack pine in 'better' sites. Since both species are extremely shade-intolerant, we would intuitively expect there to be strong above-ground interspecific interactions between them.

Since long-term interspecific competition experiments are not feasible, an alternative approach to the study of interspecific interaction is to examine fine-scale spatial patterning in mixed stands. While it may be difficult to infer ecological processes from observed spatial patterns (Cale et al. 1989), pattern studies are nonetheless useful in generating hypotheses regarding probable causative processes. A positive association between species is suggestive of commensalism or amensalism, while a negative association is generally interpreted to mean that the two species are competing (or at least 'apparently competing', Goldberg 1990).

In this study, I examine the interaction between jack pine and trembling aspen in a boreal forest stand using bivariate spatial pattern analysis. The objective of the study is to determine the nature of spatial interaction (positive, negative, or no association) between these two boreal forest species, and to offer alternative explanations for the association observed.

Study area

The study site lies at 47°50'N, 80°30'W in east-central Ontario, ≈15 km north of the town of Elk Lake. This region occurs along the southern edge of the North American boreal forest as delineated by Rowe (1972). The terrain is flat to gently undulating, with the occasional rocky hill or outcrop. Surficial sand deposits dominate the flat areas, while finer silts and clays are found in rockier and hillier sites. Many poorly drained areas of organic peat occur in low-lying regions.

The climate of the area is continental, characterized by short, warm summers and long, cold winters. The following climate data summaries are for Indian Chute, 4 km from the study site: mean annual precipitation: 78 cm; mean annual temperature: 2°C; January mean: -17°C; July mean: 16°C.

A severe, extensive forest fire burned through the study area in the early 1920's, so that the upland forests in the region are relatively young and even-aged. This is typical of boreal forest as a whole (Larsen 1980).

The study region is characterized by a diversity of vegetation types. Upland sites are generally dominated by pure stands of jack pine or trembling aspen, or by a mixed forest of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), jack pine, trembling aspen and white birch (*Betula papyrifera*). Pure jack pine stands are generally restricted to well-drained, sandy sites (Kenkel 1986), while trembling aspen prefers well-drained glacial tills. The mixed forest stands generally occur on silt and clay deposits. Lowland sites are dominated by wetland types characteristic of the boreal forest (Kenkel 1987).

Study site

A preliminary examination of aerial photographs indicated that pure stands of jack pine are commonly encountered on the flat sandy plains north of Indian Chute, while trembling aspen stands dominate the more southern sites. Between these regions stands of jack pine intermixed with large clumps of trembling aspen were noted, and occasionally mixed stands were encountered. The 70 x 70 m² study site was located in one of these mixed stands. This stand gave way to a pure jack pine forest to the north, and pure trembling aspen to the south. The site chosen had relatively uniform topography and edaphic conditions, so that I could be certain that these factors would not confound the study of spatial interaction between the two species. The substrate was a well-drained fine sandy soil with some stones and boulders.

The stand was mapped in July 1987. Mean stand age at that time, as determined by coring jack pine and trembling aspen trees in the area, was ≈65 yrs. Mean tree sizes (DBH) were 22.4 cm for jack pine, and 19.6 cm for trembling aspen.

Species

Pinus banksiana Lamb. (jack pine)

Jack pine, a coniferous species, is a pioneer tree of well-drained sandy soils and rock outcrops throughout the southern and central portions of the North American boreal forest (excluding the far western portion, where it is replaced by the closely related *P. contorta*). It is a relatively short-lived, medium-sized tree, growing to 15 - 20 m in height and 20 - 30 cm in diameter in typical sites. Growth is greatest in the first 50 yrs, and virtually ceases after 80 yrs. The species is well adapted to fire, producing serotinous cones that open up immediately following a crown fire. Seeds normally germinate in the same year, and the seedlings undergo rapid initial growth. This results in extensive, even-aged and often monospecific stands of jack pine. Young stands are often heavily stocked, resulting in stand 'stagnation' for the first 20 yrs or so. Extensive density dependent mortality occurs between ages 25 and 35, with up to 95% of the individuals dying by the time the stand is 50 yrs in age (Bella & DeFranceschi 1974, Yarranton & Yarranton 1975). The species is highly shade intolerant, and is therefore considered to be a very poor competitor. The species forms well-developed mycorrhizal associations (Fowells 1965).

Populus tremuloides Michx. (trembling aspen)

Trembling aspen is a deciduous tree species found throughout the northern half of North America. In the

boreal forest, it is most commonly encountered on moderately to well-drained glacial till. Like jack pine, it is highly shade intolerant and therefore considered a poor competitor. It is a clonal species, forming an extensive and persistent lateral root system connecting members of the same genet (Graham et al. 1963, Tappeiner 1982). Following a fire, the lateral root system produces large numbers of 'sucker shoots'. These suckers grow quickly, and the stand undergoes substantial self-thinning in the early stages of establishment. Individual ramets are relatively short-lived and of medium size, averaging 15-25 m in height and 20 - 30 cm DBH in preferred sites by age 70. The species is susceptible to pathogen and herbivore attack, and little is known about its potential to form mycorrhizal associations (Peterson & Peterson 1992).

Methods

Measurement of trees

Within the 70 x 70 m study plot, the coordinates of all standing trees (alive or dead) were measured using the method described in Kenkel (1988). Trunk diameter at breast height (DBH) was also recorded. The plot contained mature jack pine and trembling aspen, and a few juveniles of white birch, black spruce and balsam fir were also present. A total of $n = 621$ trees were recorded ($n_1 = 241$ trembling aspen, $n_2 = 380$ jack pine).

Statistical analysis

Ripley's second-order spatial analysis. The spatial pattern of the trees was analyzed using bivariate second-order spatial pattern analysis, which is derived by reduction of second moments under the assumptions of point pattern homogeneity and isotropy (Ripley 1977, Cressie 1991). I will first consider the univariate form of Ripley's statistic. For n individuals distributed in an area A , the mean number of individuals per unit area is $\lambda = n/A$. Ripley suggested centering a circle of radius t on each individual and determining the number of neighbours within the circle. By varying the circle radius t , spatial pattern can be examined at various spatial scales.

The function $\lambda K(t)$ is the expected number of individuals within distance t of a randomly selected individual. If the spatial pattern is random at scale t , then $K(t) = \pi t^2$. However, the empirical function $\hat{K}(t)$ (the observed number of points within distance t of a randomly selected point) is biased unless an edge correction is implemented. Ripley (1977) suggested a toroidal edge correction:

$$\hat{K}(t) = A \sum \sum \frac{k(x,y)}{n^2}$$

where n is the number of individuals. For a circle centered on point x and passing through point y , $k(x,y)$ is defined as the inverse of the proportion of the circle's perimeter lying within the bounds of the study area. Thus $k(x,y)$ is inversely proportional to the probability of observing a point at a distance y from point x (Ripley 1981:159).

In practice, the analysis of point pattern involves plotting $\hat{L}(t)$ against t , where:

$$\hat{L}(t) = t - \left(\frac{\hat{K}(t)}{\pi} \right)^{1/2}$$

Like $K(t)$, the function $L(t)$ has zero expectation when the point pattern is random at scale t . For a given value of t , the degree to which $\hat{K}(t)$ deviates from πt^2 offers insight into the empirical point pattern at that spatial scale. Positive values of $\hat{L}(t)$ indicate spatial regularity, while negative values indicate clumping.

Bivariate second-order spatial analysis. The univariate second-order statistic $K(t)$ can be generalized to the bivariate case by considering the function $\lambda_1 K_{12}(t)$, where $\lambda_1 = n_1/A$ is the expected number of individuals of species 1 within a distance t of a randomly chosen individual of species 2. If two species are statistically independent at scale t , then $K_{12}(t) = \pi t^2$. The empirical function is calculated as

$$\hat{K}_{12}(t) = \frac{[n_2 \tilde{K}_{12}(t) + n_1 \tilde{K}_{21}(t)]}{(n_1 + n_2)}$$

where

$$\lambda_1 \tilde{K}_{12}(t) = \sum \sum \frac{k(x,y)}{n_2} \text{ and}$$

$$\lambda_2 \tilde{K}_{21}(t) = \sum \sum \frac{k(y,x)}{n_1}$$

The value $k(x,y)$ is defined as in the univariate version of the statistic. The function

$$\hat{L}_{12}(t) = t - \left(\frac{\hat{K}_{12}(t)}{\pi} \right)^{1/2}$$

has zero expectation given spatial independence at scale t . Thus a plot of $\hat{L}_{12}(t)$ vs. t can be used to examine spatial dependence of species 1 and 2 at various neighbour distances t . Positive values of $\hat{L}_{12}(t)$ indicate 'repulsion' (negative association) between species, while negative values indicate 'attraction' (positive association). If the species are spatially independent

($\hat{L}_{12}(t) = 0$), a lack of spatial interaction between species is indicated. Harkness & Isham (1983) were the first to use this method in biology. Kenkel (1988) used bivariate second-order spatial analysis to examine mortality patterns in jack pine, while Anderson (1992) discussed other potential applications of the method in the analysis of biotic interactions. Algorithms for computing these second order statistics are given in Fisher (1990).

Statistical significance. Monte Carlo simulation can be used to assess the significance of departures from spatial independence. In this study, the procedure would be: (a) generate $n = 621$ random points (Poisson forest), with $n_1 = 241$ randomly labelled species 1 (trembling aspen) and the remaining $n_2 = 380$ labelled species 2 (jack pine); (b) compute the bivariate second-order for this pattern; (c) repeating steps (a) and (b) a large number of times to generate a random simulation confidence envelope (Diggle 1983, Kenkel 1988). Portions of the empirical function exceeding the confidence envelope limits indicate spatial scales at which the bivariate pattern deviates significantly from spatial independence.

A drawback of the above strategy is that the observed spatial point pattern of trees is completely ignored. A more direct approach involves retaining the spatial coordinates of the $n = 621$ trees, while 'randomly reassigning' species identities to these coordinates in the same proportion as those observed ($n_1 = 241$, $n_2 = 380$). Repeating this random assignment a large number of times generates a simulation envelope under the assumption that the species are spatially independent given the spatial pattern observed. I used this more realistic approach, generating a confidence envelope based on 100 random reassignments.

Results

The empirical distribution is strongly suggestive of spatial dependence between jack pine and trembling aspen at the study site (Fig. 1). Specifically, statistical repulsion (i.e. negative association between the two species) is indicated at all local spatial scales examined (0 - 20 m). This was confirmed by the simulation envelope generated by random reassignment. The entire empirical distribution falls well outside the envelope, indicating strong negative association between the two species over all spatial scales examined.

The observation of statistical repulsion implies that an individual of a given species (say, jack pine) tends to have other individuals of the same species as its neighbours. Since statistical repulsion was observed at all

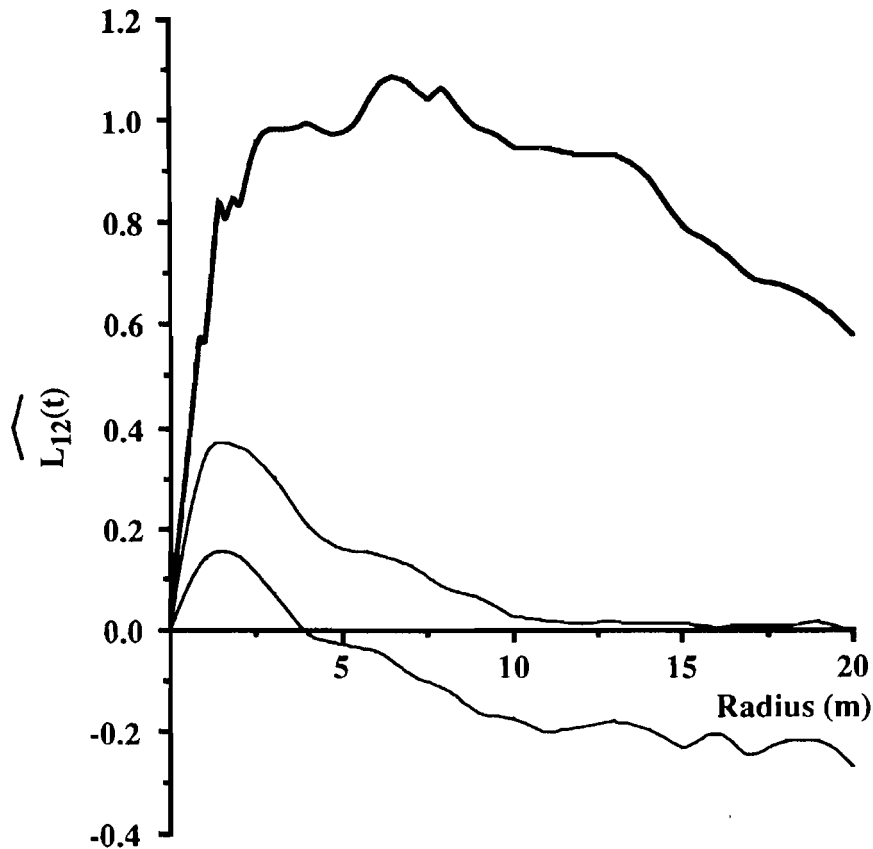


Figure 1. Bivariate (jack pine and trembling aspen) second-order spatial pattern analysis results. Thick line = observed (empirical) bivariate pattern. Thin lines = confidence envelope (100 simulations), random species reassignments of the empirical pattern.

spatial scales, strong within-species clumping is indicated.

Discussion

Observations in North American boreal forest suggest that both jack pine and trembling aspen usually occur in monospecific stands. This in part reflects habitat differences, since jack pine is more tolerant of drier, more nutrient-limiting conditions. Nonetheless, sites with apparently similar substrate conditions often support one or the other of these species, but rarely both. This suggests that habitat differences alone cannot explain spatial differentiation between jack pine and trembling aspen. The results of this study are important, since they indicate that strong negative spatial association also occurs between these species at local spatial scales. The mechanism leading to this negative association remains to be determined, but a number of possibilities exist.

(a) Local spatial variation in substrate conditions

The possibility that the observed spatial pattern simply reflects substrate patchiness cannot be entirely discounted. However, observations at the site indicated limited variation in substrate conditions, and there was no apparent relationship between local substrate conditions and tree species composition.

(b) Allelopathy

Allelopathic interactions, while difficult to demonstrate in the field, cannot be discounted. However, strong allelopathic effects have yet to be demonstrated in either jack pine or trembling aspen (Peterson & Peterson 1992). Another possibility is an 'indirect' allelopathic effect, whereby certain understory species produce chemicals detrimental to one of the tree species (e.g. Zhu & Mallik 1994). A chemical produced by a species characteristic of a jack pine understory, for example, may have detrimental effects on trembling aspen. Laboratory and field experiments

would be required to determine the importance of allelopathy in boreal forest ecosystems.

(c) Substrate alteration

Strong between-species differences in litter quality, and the rate and timing of litter production (coniferous vs. deciduous), may lead to small-scale substrate differentiation. Indeed, it is well known that the understory vegetation of jack pine and trembling aspen forests differs substantially, even in areas of similar parent material. Jack pine produces a flammable, acidic litter that is slow to decay, while aspen litter normally decomposes more quickly to produce a rich organic layer. A jack pine understory may therefore burn more severely during a fire, killing any aspen suckers that may be present. Less severe ground fires in areas dominated by aspen allows suckers to survive and perpetuate at the site, while seedling establishment by jack pine is favoured in more severely burned areas. In this scenario, site history (specifically, the forest composition over the long term) is important in determining local fire severity, which in turn determines relative species success. Since post-fire 'dispersal' is limited in both species (jack pine seeds from freshly-opened serotinous cones, trembling aspen from root systems already present in the soil), the development of patchiness in species distributions may in fact be amplified with each fire event.

(d) Intraspecific vs. interspecific interactions

Another possibility is that interspecific interactions between jack pine and trembling aspen are greater than intraspecific interactions. If this were the case, a strong negative association between the species would be expected. Formal observations of jack pine - trembling aspen stands indicate that trembling aspen has a greater effect on jack pine than jack pine has on itself (Mugasha 1989), supporting the notion that interspecific interactions are indeed stronger. Interspecific contacts are minimized when species are strongly negatively associated (i.e. forming highly clumped spatial patterns), and recent simulation studies have suggested that strong clumping in plants can promote species coexistence (Silvertown et al. 1992). A clumped spatial pattern, once established, would tend to be 'consolidated' following each disturbance event. A fire in a jack pine - trembling aspen stand will result in complete stand mortality, followed immediately by jack pine seed germination and the development of aspen root suckers. Assuming limited dispersability, the majority of jack pine seeds will germinate beneath the former jack pine canopy. Similarly, the majority of aspen suckers will arise from beneath the former trembling aspen canopy. If interspecific interactions are

stronger than intraspecific ones, a strongly clumped spatial pattern will develop as 'stray' individuals (e.g. a jack pine surrounded by aspen, or vice versa) are culled. In this way negative associations would be perpetuated in the long term.

In conclusion, this study has demonstrated that strong negative associations arise between jack pine and trembling aspen at local spatial scales. This in turn suggests that interspecific interactions between these species are mutually negative (i.e. interspecific competition). Further studies are required to determine the specific mechanisms and processes leading to this observed pattern. However, as Farmer et al. (1988) state, "no experimental studies of interspecific competition have been reported" between jack pine and aspen. Given the difficulty of performing long-term competition experiments in forest trees, empirical studies of naturally established stands can offer important insights into species interactions. Additional studies should be undertaken in a number of habitats, and consideration should be given to the role of pests and pathogens, mycorrhizae, understory species and herbivores in determining competitive outcome between jack pine and trembling aspen.

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