

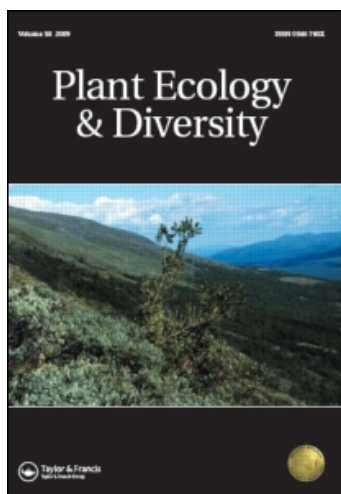
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Pattern reveals process: spatial organisation of a Kamchatkan stone birch forest

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Pattern reveals process: spatial organisation of a Kamchatkan stone birch forest

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Background: Spatial patterns within forests reflect their formative processes. In Kamchatka, the dominant stone birch (*Betula ermanii*) forest exists in a primeval state. *Betula* species can reproduce via clonally produced ramets, leading to a clustered distribution of stems, or from seed on open ground, although subsequent mortality may obscure initial establishment patterns.

Methods: Spatial patterns of all trees and regenerating stems in a fully mapped 0.25 ha plot were analysed using the $g(r)$ function and the pattern of trees modelled using a Matérn cluster process. Mark correlation analysis was used to detect patterns in stem sizes.

Results: Clustering of trees at scales up to 3 m occurred, with model parameters indicating a density of 180 clusters ha^{-1} , each containing on average three stems >1 cm diameter at breast height (DBH) within a 1.6 m radius. Stem size compensation was detected, with nearby trees smaller than expected by chance. Regenerating stems were strongly clustered at scales below 3.5 m and from 5–8 m, and were aggregated around small trees (<10 cm DBH) but not large trees (≥ 10 cm DBH), or in gaps.

Conclusions: These patterns are consistent with clonal reproduction followed by competition as the processes determining spatial structure in old-growth stone birch forests.

Keywords: *Betula ermanii*; boreal forest; Far Eastern Russia; Kamchatka; mark correlation; Matérn cluster process; pair correlation function; spatial point pattern analysis

Introduction

Ecological processes often reveal themselves through their spatial signatures (Watt 1947). The recent development of sophisticated methods for statistical description of spatial point patterns has opened the potential to conduct spatially explicit hypothesis tests of the patterns that may be formed by particular processes (Ripley 1977; Diggle 2003; Perry et al. 2006; Illian et al. 2008; Law et al. 2009), though patterns present within populations are likely to be complicated by multiple processes acting at different spatial and temporal scales (Murrell 2009). This will be especially true in old-growth forests, where the spatial patterns generated during early development can be modified by later competition. The simplest model is of an initially clustered (or random) distribution of individuals which becomes regularly dispersed as a result of mortality caused by competition (Laesele 1965; Ford 1975; Sterner et al. 1986; Moeur 1993), though there are conceivable circumstances in which this may not occur, dependent on the species involved (e.g. Peterson and Squiers 1995) and the scales at which processes operate (Murrell 2009). Boreal forests provide an ideal study system for investigating spatial patterning of tree populations, as they contain relatively few tree species and have simple dynamics (Brassard and Chen 2006), reducing their complexity relative to temperate or tropical forests.

The Kamchatka Peninsula lies on the extreme eastern fringe of Russia. Due to its remoteness and the strict controls on entry applied to both Russian nationals and

foreigners for most of the past century, its vegetation has been little modified by human impacts. The peninsula is 88% forested (Newell 2004), of which the majority is dominated by *Betula ermanii* Cham., covering an estimated 5781.6 M ha (Krestov 2003). Within the peninsula these forests are remarkably homogeneous in structure and composition and characterised by small gaps (Kojima 1994). Fire cycles are little-known, though tree cores suggest that mature *B. ermanii* stands are at least 200 years old (see below and Doležal et al. 2010), making them suitable for studying the natural spatial patterning of old-growth forests.

A range of potential spatial patterns might be predicted in forests composed of birch trees (*Betula* spp.). They have the capacity to reproduce either by seed (genets) or through the production of clonal offshoots (ramets) which subsequently become independent trees (Perala and Alm 1990). Since *Betula* species are strongly light-demanding, their seeds germinate poorly in understorey conditions. They therefore depend on fire or other stand-replacing disturbance events for successful regeneration, typically those which open up bare ground (Perala and Alm 1990). Despite their intolerance of shade, forest gaps are also likely to be a relatively hostile environment for *Betula* seedlings in Kamchatka due to tall herbaceous growth (particularly *Chamaenerion angustifolium* (L.) Scop.) and deep winter snow. By contrast, adult trees routinely produce clonal ramets from the root collar following stem damage (Hou et al. 2004; Doležal et al. 2006), often leading to a naturally coppiced form in heavily

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disturbed areas. This is especially true of *B. ermanii* in Kamchatka, where stems are frequently broken by heavy snow-loading in winter (Hultén 1927–30), which is likely to affect individual trees rather than impacting whole stands.

The spatial structures of mono-dominant forests with the potential for regeneration from both seed and vegetative sources have seldom been investigated. In this paper I characterise the spatial structure of tree regeneration in an old-growth *Betula ermanii* forest in central Kamchatka and use spatial point process models to infer the dominant mode of regeneration. Given the proposed modes of reproduction and light competition among birch trees, a set of predictions can be made about the possible spatial signatures that might remain in the pattern of trees. Spatially restricted reproduction through production of ramets would lead to clustering at small scales, consistent with the sizes of adult trees (canopies of c. 2 m radius). Competition among stems would lead to size compensation among nearby stems. An alternative explanation for such a clustered pattern of trees might be that gaps formed by tree deaths become filled by a cluster of regenerating and competing stems (Shimatani and Kubota 2004). The two hypotheses can be separated by the pattern of regenerating stems within the plot. If the majority are ramets, they will be predominantly aggregated around adult trees, whereas if gap dynamics and regeneration through seed determine the spatial pattern, regenerating stems will be predominantly associated with canopy gaps.

Though some authors have questioned whether past processes can be deduced from static patterns (Lepš 1990), the application of clear a priori hypotheses enables valid inferences to be drawn from analyses (McIntire and Fajardo 2009). Of the emerging techniques in spatial statistics, the most informative descriptor of pattern structure is the neighbourhood density function $g(r)$ (Perry et al. 2006; Law et al. 2009) which describes the plant's-eye perspective (sensu Turkington and Harper 1979) of neighbourhood density at an increasing distance r around any focal plant, averaged across the population sampled. Since the distribution of stem sizes may also indicate interactions among them, these can be analysed by the little-used mark correlation function (Stoyan and Penttinen 2000).

The hypotheses that regeneration would be either via ramets and clustered around adults, or via seed and concentrated in canopy gaps, were tested in an old-growth *Betula ermanii* forest in central Kamchatka in which a plot was established in 2008, with all individual stems mapped. Detailed spatial analyses were used to describe the spatial organisation of this tree population, and the pattern was modelled to extract the parameters of the inferred processes giving rise to the observed structure.

Materials and methods

Study species

Betula ermanii is found throughout north-east Asia in areas with an even distribution of precipitation throughout

the year (Krestov et al. 2008). It is typically a montane, treeline or coastal species, and tolerant of extreme cold in the winter, including rapid chills and burial in snow (Gansert et al. 1999; Gansert 2002), perhaps due to its greater investment in roots than other *Betula* species (Koike et al. 2003); it grows poorly in areas with hot summer temperatures (Takahashi et al. 2003). At lower altitudes with wider temperature amplitudes it is replaced by the more strongly competitive *B. platyphylla* Sukacz., which has a broader range of tolerances (Koike et al. 2003). Although *B. ermanii* tends to form monodominant stands in Kamchatka, it is reported to form mixed stands with *Picea ajanensis* (Lindl. ex Gord.) Fisch. ex Carr. in the northern part of its range and near the treeline (Krestov 2003), and also in the Sikhote Alin range, or with *Abies veitchii* Lindl. in Honshu, Japan (Nakamura and Krestov 2005). It also forms mixed forests in Japan where it is considered to be an early successional species (Hara et al. 1991).

Study site

The site (co-ordinates 55° 52.532' N, 158° 37.789' E) was chosen as being representative of local *B. ermanii* forest, following extensive reconnaissance within central Kamchatka (see Eichhorn 2010). A 0.25 ha (50 × 50 m) plot was selected using random co-ordinates within a block of homogeneous forest over 1 km² in size. It was situated on a south-east-facing slope (155°) with a gradient of 15° at 700 m above sea level. The lower boundary was perpendicular to the slope. A grid of posts at 10-m intervals was made and distances to all tree stems and stumps were measured from the lower two posts of each 100 m² subplot at a height of 1.3 m, unless nearby stems or thickets of *P. pumila* prevented measurement, in which case the upper posts were used. Measurements were converted to x and y co-ordinates (see Newton 2007). Diameter at breast height (DBH; 1.3 m) for all stems above 1 cm was recorded using a graded tape following Newton (2007). Regenerating stems were defined as those having a DBH below 1 cm, and their height to uppermost growing bud was recorded. It was not possible to distinguish ramets from genets in the field without excavation of stems; this was not attempted as future surveys of survival are anticipated. The location of each regenerating stem was recorded (forest floor, raised ground, fallen log or base of adult tree).

Betula ermanii was the only species of tree present in the plot, although *Salix caprea* L. occurred infrequently at the site, and *Pinus pumila* (Pall.) Regel occurred as a sub-canopy shrub, covering 6% of the plot. The average height of *B. ermanii* was 10.4 ± 0.97 m (mean ± SE, $n = 24$), with the tallest measured tree at 18.75 m. The soils had a pH of 5.65 with 43.5 mg kg⁻¹ oxidised N (NO_x), 31.3 mg kg⁻¹ ammonium N (NH₄) and 0.86 mg kg⁻¹ phosphate (PO₄³⁺) (see Eichhorn 2010 for details). Tree cores were not taken as the plot is intended for long-term study; however, cores taken from *B. ermanii* trees ($n = 68$) in a nearby stand recorded a maximum age of 271 years with evidence of continuous recruitment throughout the cohort

(J.B.G. Hesketh, unpublished data). The understorey was dominated by *Chamaenerion angustifolium* and *Carex pallida* C.A. Mey. For further descriptive information see Eichhorn (2010).

Statistical methods

The analysis of spatial point patterns follows techniques derived from Ripley's K function $K(r)$ (Ripley 1977). This is typically estimated within a spatial window, i.e. a plot, as

$$\hat{K}(r) = \frac{\sum_{i=1}^n \sum_{j=1}^{n-1} I_{ij}(r)}{n \hat{\lambda}} \quad (1)$$

where r is the radius from each event i (in this case each tree), $I_{ij}(r)$ is 1 for each event j within r of i and otherwise 0, n is the number of events within the sample window, and $\hat{\lambda}$ is an estimate of the expected number of events per unit area. When applied to a completely spatially random (CSR) point pattern, $K(r) = \pi r^2$. Since $K(r)$ is a cumulative function, in order to assess effects at specific distances it is recommended to examine the related function $g(r)$, otherwise known as the pair correlation function (Illian et al. 2008; Law et al. 2009):

$$\hat{g}(r) = \frac{\hat{K}'(r)}{2\pi r} \quad (2)$$

where $\hat{K}'(r)$ is the first derivative of $\hat{K}(r)$. If densities are independent at a given distance, $g(r) \sim 1$. When $g(r) > 1$, pairs of plants are more abundant than the spatial average, while $g(r) < 1$ means they are less abundant. Current opinion regards $g(r)$ to be the most informative statistic for the description of spatial patterns (Law et al. 2009). Following Baddeley and Turner (2005), $g(r)$ was estimated at distances of up to 25% of the plot extent, i.e. 12.5 m. A weighted edge correction (Ripley 1977) and Epanechnikov smoothing kernel (Illian et al. 2008) were applied to the curves.

Detection of spatial patterns that differ significantly from CSR expectations requires the construction of envelopes based on null model simulations. For descriptive analyses, envelopes were calculated based on the fifth highest and lowest of 999 Monte Carlo CSR simulations, corresponding to a two-tailed test with $\alpha \approx 0.01$ (Diggle 2003). Though not a formal significance test (Loosmore and Ford 2006), the approach is strongly supported by most authors (Illian et al. 2008).

Modelling of tree spatial patterns compared the Thomas process (Thomas 1949) and the Matérn cluster process (Matérn 1960). The former has three parameters: K determines the intensity of a Poisson process which generates parent points that become cluster centres, σ determines the standard deviation of the displacement of

daughter points from cluster centres under a Gaussian distribution, while μ gives the Poisson mean number of daughter points per cluster. The Matérn cluster process is similar, except that daughter points are distributed uniformly and randomly within a distance R from parent points. Both processes can be fit to a point pattern using the method of minimum contrast (Diggle 2003). Their relative efficacy was assessed by comparing the sum of squared deviation of the observed pattern from the mean of 999 Monte Carlo simulated patterns based on the fitted parameters (Loosmore and Ford 2006):

$$u_i = \sum_{t_k=t_{\min}}^{t_{\max}} [\hat{H}_i(t_k) - \bar{H}_i(t_k)]^2 \delta t_k \quad (3)$$

where t_k is distance, $t_{\min}$ and $t_{\max}$ are the lower and upper limits of the range of distances over which the index is to be calculated (here $t_{\min} = 0$, $t_{\max} = 12.5$), $\hat{H}_i(t_k)$ is the empirical result of the $g(r)$ test statistic for pattern i , $\bar{H}_i(t_k)$ is the mean result computed for all Monte Carlo simulated patterns excluding i , and $\delta t_k = (t_{k+1} - t_k)$ is the width of the distance interval between points at which the difference between empirical and mean functions was assessed (here $\delta t_k = 0.0244$ m).

Marked point patterns combine the spatial positions of individuals with additional variables, which may be continuous (e.g. size) or ordinal (e.g. tree or seedling). Careful choice of null models is essential to ensure adequate tests of spatial patterning hypotheses (Wiegand and Moloney 2004). Patterns in DBH of trees were analysed using the mark correlation function $g_{mm}(r)$ (Stoyan and Penttinen 2000; Law et al. 2009), which calculates the product of marks between all pairs of points occurring up to $r = 12.5$ m. Values of $g_{mm}(r) > 0$ indicate facilitation (i.e. the product of marks is greater than expected by chance given the spatial positions of trees), whereas $g_{mm}(r) < 0$ signifies inhibition, and can be used to detect the effects of competition. A null hypothesis of random labelling of points with observed DBH values was applied.

Bivariate analyses assessed whether interactions among regenerating stems and large trees (≥ 10 cm DBH) or small trees (< 10 cm DBH) occurred under a null hypothesis of spatial independence (Goreaud and Pélissier 2003) whereby the positions of trees were kept fixed while the positions of regenerating stems were shifted using a random toroidal transformation. This tested whether trees and regenerating stems were independently distributed while maintaining their inherent spatial patterns. In all cases envelopes were calculated as above.

To test whether forest structure influenced the distribution of regeneration, an inhomogeneous Poisson process was fit using log-likelihood to the distribution of regenerating stems (Baddeley and Turner 2005). The null hypothesis of a homogeneous Poisson process was compared with models incorporating spatial covariates. The first of these was the distribution of live tree biomass, represented

as a smoothed surface, produced by Gaussian kernel weighting (bandwidth $k = 5$ m) of tree DBH. The second covariate was distance to the nearest live tree, which indicated the presence of gaps. Significance of spatial covariates was assessed by both deviance change (Δd) and Akaike's Information Criterion (AIC). All analyses were conducted by using the spatstat package (Baddeley and Turner 2005) in R.2.9.0 (R Development Core Team 2009).

Results

The plot contained 126 live *B. ermanii* trees with a mean DBH of 15.8 ± 1.18 cm (Figure 1). This equates to 504 stems ha^{-1} and a total basal area of $16.94 \text{ m}^2 \text{ ha}^{-1}$. The average nearest-neighbour distance was 1.85 ± 0.15 m. There were 16 dead trees (mean DBH 28.5 ± 3.57 cm, basal area $5.44 \text{ m}^2 \text{ ha}^{-1}$), four stumps and 56 regenerating stems (either genets or ramets) of *B. ermanii* with a mean height of 1.16 ± 0.08 m. Two regenerating stems of *Salix caprea* were found; however, as there were no adult trees within the plot they were not considered further. The majority of regenerating stems of *B. ermanii* were found on raised mounds (71%) or elsewhere on the forest floor (14%) with relatively few on fallen logs or stumps (9%) or directly at the base of an adult tree (5%).

Pattern of trees

The pair correlation function $g(r)$ indicated that significant clustering of stems occurred at scales up to 3 m; stems were distributed randomly thereafter (Figure 2(a)). The Thomas and Matérn cluster processes were fitted to the observed pattern, and the sum of squared deviance of the empirical $g(r)$ function was compared with the mean of 999 simulations of the fitted model. The Thomas cluster process ($u_i = 1.62$) was out-performed by the Matérn cluster

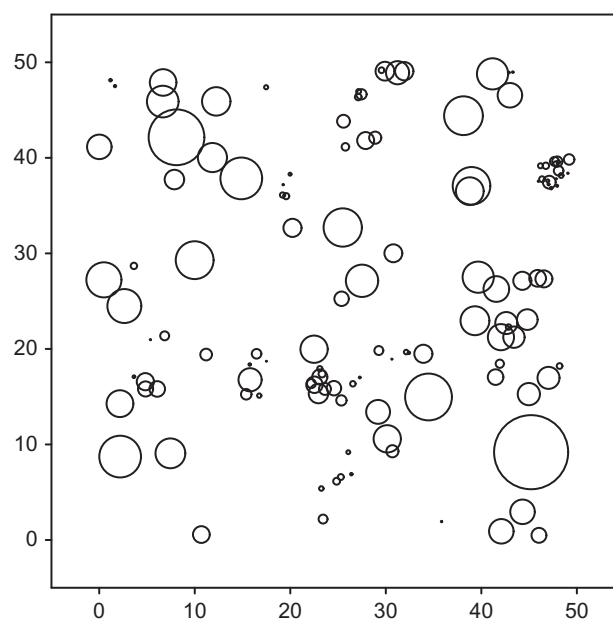


Figure 1. Positions of live *B. ermanii* stems >1 cm DBH in a 0.25 ha plot in central Kamchatka. Axis scale in metres, circle size is an arbitrary scale representing DBH.

process ($u_i = 1.41$). The parameters indicated that stem clusters were distributed according to a Poisson process with unit intensity $\kappa = 0.018$, equating to a density of 180 clusters ha^{-1} . An expected mean number of $\mu = 2.84$ stems were distributed around cluster centres within a radius $R = 1.59$ m. This gave an approximate cluster diameter of 3.18 m, corresponding closely to the clustering detected by the $g(r)$ function. Envelopes generated from 999 simulations of the Matérn cluster process using these parameters closely matched the observed data (Figure 2(b)), and the Matérn cluster process is therefore a reasonable statistical description of the observed pattern.

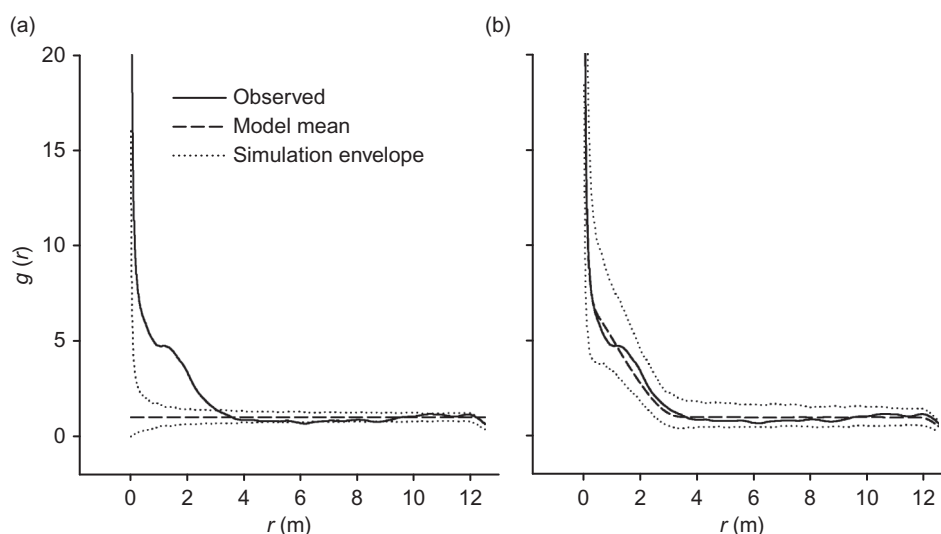


Figure 2. Spatial pattern analysis of *Betula ermanii* stems >1 cm DBH. Data assessed against fifth highest and lowest of 999 null model simulations ($\alpha \approx 0.01$). Pair correlation function $g(r)$ for all stems against (a) null model of complete spatial randomness, (b) Matérn cluster process (see text for details).

The mark correlation function $g_{mm}(r)$, assessed against a null model of random labelling of fixed tree positions, indicated that at scales below 3 m there was a significant negative correlation of stem sizes (Figure 3). This suggests that competition within tree clusters leads to a compensation effect whereby stems less than 3 m apart are smaller than would be expected by chance.

Pattern of regeneration

Regenerating stems were significantly aggregated at scales below 3.5 m and between 5 and 8 m, and less abundant than expected at scales between 8.5 and 11.5 m (Figure 4(a)). The distribution of live tree biomass, as represented by a spatial smoothing function, was strongly negatively correlated with the distribution of regenerating stems ($\Delta d = 186.9$, $df = 1$, $P < 0.001$). Compared with a null model of random distribution of regenerating stems, the AIC value fell from 539.5 to 354.6 when the distribution of live tree biomass was added as a covariate. In contrast, when analysing the distribution of regenerating stems with respect to the distances to live trees, there was a negative correlation (AIC = 412.6, $\Delta d = 128.8$, $df = 1$, $P < 0.001$), indicating that regenerating stems were found close to trees rather than in gaps. This apparent paradox was resolved by dividing the live trees into large (>10 cm DBH, $n = 72$) and small (<10 cm DBH, $n = 54$) size classes and comparing the distribution of regenerating stems using the bivariate form of $g(r)$. Large trees were on average 13.0 ± 1.2 m in height ($n = 16$), while small trees were 5.2 ± 0.9 m tall ($n = 8$). There was no indication that regenerating stems were clustered around large trees (Figure 4(b)), but were

significantly aggregated at distances up to 3 m from small trees (Figure 4(c)).

Discussion

The analysis of the spatial structure of this old-growth *B. ermanii* forest plot suggests that small-scale aggregation of stems up to 3 m occurs, after which the structure does not differ from random expectations. This is consistent with regeneration occurring through the production of clonal ramets, as is known to occur in *Betula* species (Hou et al. 2004; Doležal et al. 2006), and which in Kamchatka has been implicated as the main form of regeneration for burnt *B. platyphylla* (Homma et al. 2003). Although the stand investigated here was old-growth, a signature of post-fire recovery by resprouting might be retained, perhaps indefinitely. Similar patterns have been seen in young regenerating stands of clonally resprouting tree species following fire (Doležal et al. 2004) or logging (Doležal et al. 2009), and clonal species may even increase their degree of clustering over time (Peterson and Squiers 1995). Excavation of roots may indicate where stems are linked below ground, or genetic techniques could identify whether clusters correspond to clones. Beyond these clusters, there is no evidence of regularity in structure, though this is not always expected to occur, even in mature stands (Murrell 2009).

The mark correlation function $g_{mm}(r)$ indicates that there is a negative correlation between the sizes of stems at scales below 3 m. Intriguingly, this matches the observed scale of clustering within the plot, and suggests that negative size compensation occurs within clusters. If the model of reproduction via ramets is correct, the indication is that related stems compete against each other for growth, and the size structure of stems will therefore be influenced by this process. Beyond 3 m, the distribution of stem sizes is consistent with random expectations. This is in accord with the major cause of tree mortality in the forest, which is believed to be stem breakage due to snow loading (Hultén 1927–30), and which is likely to lead to disturbance on the scale of individual trees. The potential impacts of volcanic tephra deposition on forest structure are unknown (Doležal et al. 2010).

A Matérn cluster process provided a close statistical fit to the pattern of *B. ermanii* stems, with its parameters suggesting that clusters occurred at a density of 180 ha^{-1} , each containing c. 3 stems within a radius of 1.6 m. It must be noted that the fit of a spatial point pattern process does not imply that the process is responsible for generating the observed pattern; similar caveats apply as with conventional linear statistical models. Nevertheless, such an exploratory analysis can allow parameters to be estimated that define meaningful spatial structures within the population. Cluster processes have been used previously in modelling the spatial distributions of trees, though more commonly the Thomas process is employed to capture the signal of dispersal limitation in population structure (Plotkin et al. 2000; Yu et al. 2009). In the case of *B. ermanii*,

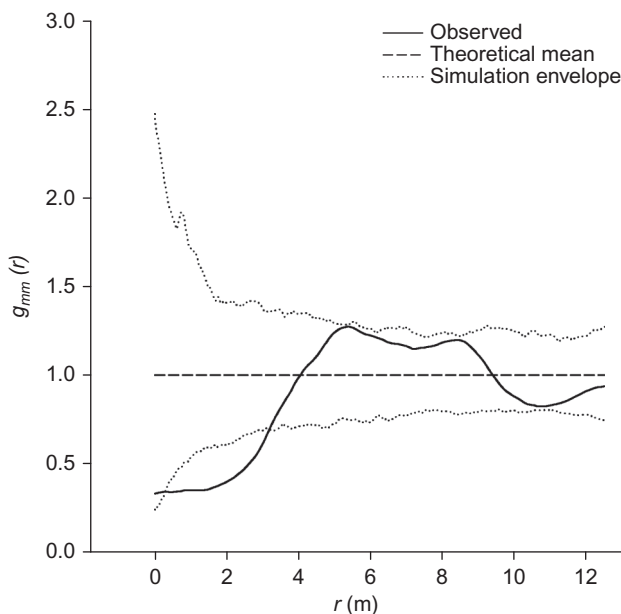


Figure 3. Mark correlation function $g_{mm}(r)$ based on a null hypothesis of random labelling of DBH values across fixed tree positions. Data assessed against fifth highest and lowest of 999 null model simulations ($\alpha \approx 0.01$).

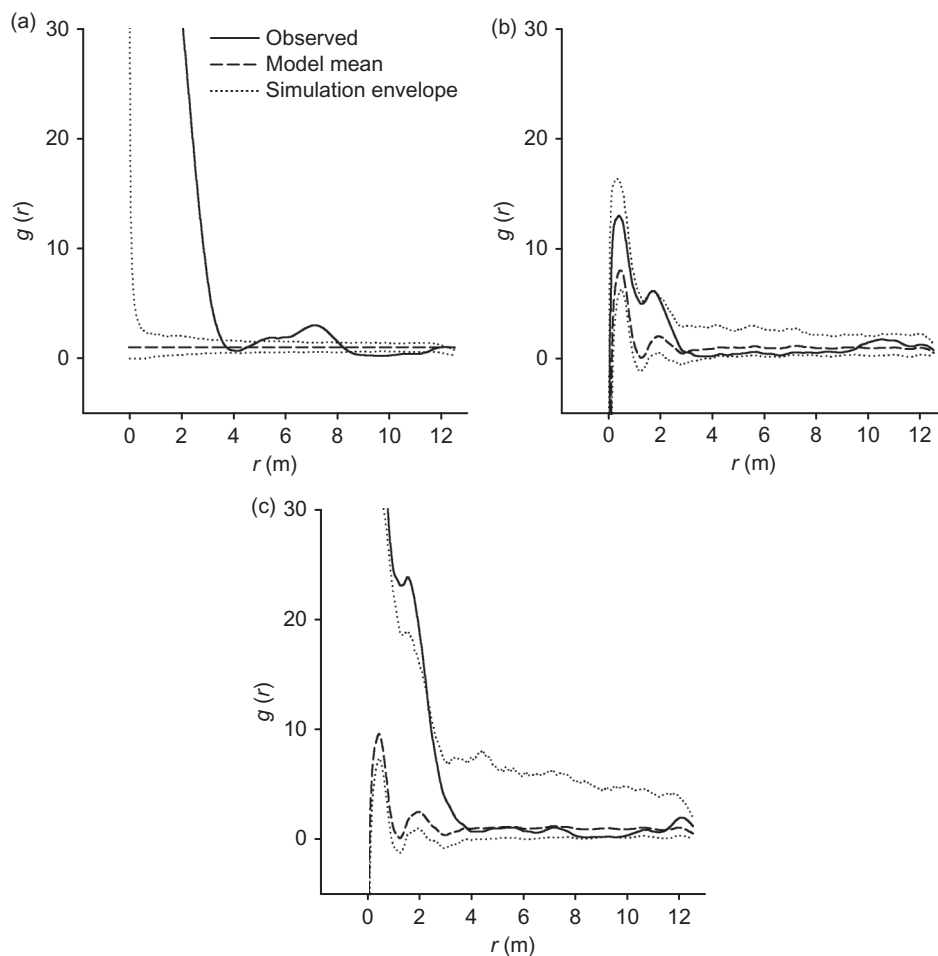


Figure 4. Spatial pattern analysis of regenerating stems of *Betula ermanii*. Data assessed against the fifth highest and lowest of 999 null model simulations ($\alpha \approx 0.01$). (a) Pair correlation function $g(r)$ for all regenerating stems against null model of complete spatial randomness. Bivariate functions for regenerating stems compared to the patterns of (b) live trees >10 cm DBH and (c) live trees <10 cm DBH against null models generated via toroidal shifts of the pattern of regenerating stems relative to trees.

this is probably not the cause of clusters, since birch trees produce immense numbers of wind-dispersed seeds (Perala and Alm 1990), which are unlikely to lead to recruits being aggregated around parent trees.

The distribution of regenerating stems also suggests clonal reproduction via ramets rather than gap-phase regeneration. Regenerating stems were aggregated at scales up to 3.5 m and from 5 to 8 m, though also less abundant than expected at distances between 8.5 and 11.5 m, indicating a complex spatial distribution within the plot. The distribution of regenerating stems was significantly negatively correlated with live tree biomass within the plot. Nevertheless, there was also a negative correlation with distance to live stems. This can be explained by the close association of regenerating stems with live trees under 10 cm DBH. Since there was no evidence that regeneration occurred in gaps, gap-phase dynamics are unlikely to be a major process in this forest. Moreover, the dense herbaceous understorey and deep winter snowfall in gaps are likely to impede growth of regenerating stems which have no shelter from adult trees. Gap dynamics in boreal forests differ from those at lower latitudes (Bartemucci et al. 2002), as the combination

of later snow melt in gaps, as opposed to earlier melt around canopy trees, can lead to a tree-island regeneration pattern (Brett and Klinka 1998). The lack of association between regenerating stems and large trees suggests a reduction in the incidence of clonal reproduction around larger stems.

The above analyses allow a narrative of the regeneration processes in this forest to be derived, with parameters derived from spatial analyses consistent with the expected pattern. Trees that are damaged by snow loading, volcanic ash or fire may resprout from the roots, leading to a tightly clustered distribution of stems. These stems compete with each other, such that large trees will tend to monopolise space and prevent the regeneration of conspecifics. Regeneration is concentrated around smaller trees, where reduced competition and support from maternal trees allows them to survive despite the dense herbaceous understorey. Little regeneration is found in gaps, likely due to a combination of snowfall, competition from understorey plants and the limited ability of *Betula* species to colonise areas without bare ground. Gaps will therefore be filled by vegetative reproduction of surrounding trees or otherwise only following stand-replacing disturbance.

Continuous regeneration through ramets will therefore maintain the spatial structure of this old-growth forest, at least until the next stand-replacing disturbance event, which may occur only every few centuries.

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