

Spatial organisation of a bimodal forest stand

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Abstract Many populations have a bimodal size distribution, even when composed of a single cohort. In developing forest stands, this pattern is usually attributed to asymmetric competition at canopy closure among trees which have access to the upper canopy and those which have failed to reach it. Nevertheless, alternative explanations for bimodality exist, and in sessile organisms spatial pattern analysis can be used to compare their predictions. A 0.25-ha plot was created in a maturing stand of Asiatic white birch (*Betula platyphylla* Sukacz.) in Central Kamchatka. All stems >1 cm diameter at breast height (DBH) were fully mapped. Mark correlation analysis revealed size compensation among stems up to 3.5 m apart, providing evidence that competition affected the distribution of stem sizes. The spatial pattern of trees was analysed using the pair correlation function $g(r)$. Large trees (>20 cm DBH) had a dispersed distribution to which a Strauss soft-core Gibbs process model was fitted. This suggested that large trees interacted at scales up to 4.16 m. Small trees (1–20 cm DBH) were distributed randomly, but a cross-pair correlation analysis revealed a greater likelihood of occurrence beginning at 4.3 m from large trees, closely matching the modelled interaction distance. These results are consistent with the hypothesis that asymmetric competition is structuring this bimodal cohort of trees: large stems tend towards a dispersed pattern, exerting competitive effects at scales up to approximately 4 m, whereas

smaller stems are more commonly found in the interstices within the pattern of large trees.

Keywords Birch · Gibbs process · Kamchatka · Marked point-pattern · Size distribution

Introduction

In developing populations of plants it is common for a bimodal size distribution to develop, even if all individuals began at approximately the same size (Ford 1975; Rabinowitz 1979; Huston and DeAngelis 1987). Within a single cohort this can sometimes be attributed to the effects of competition, though similar patterns can be generated by a range of mechanisms (Huston and DeAngelis 1987). A major consequence of size bimodality is that competition among individuals is likely to become asymmetric (Weiner 1986; Bauer et al. 2004), meaning that small individuals are subject to competition from both large and small neighbours, whereas larger individuals compete solely with each other. The larger individuals are expected to have positive growth rates, while those of the smaller are suppressed by competition, reinforcing the bimodal distribution (Ford 1975; Rabinowitz 1979; Weiner 1986). Bimodality can be generated in stand development models as a response to shortage of resources (Gates 1978; Aikman and Watkinson 1980; Franc 2001), with the transition from a unimodal to a bimodal distribution likened to the process of interface roughening between physical media, from which analogous models can be derived (Franc 2001). The outcome of such interactions between plants is likely to leave a characteristic spatial signature in the distribution of large and small stems, though this has not previously been investigated.

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Recent developments in the statistical description and modelling of spatial point patterns have unlocked the potential to interpret the spatial organisation of natural communities (Perry et al. 2006; Illian et al. 2008; Law et al. 2009). The pair correlation function $g(r)$ is a robust means of describing the fine-scale structure of patterns (Law et al. 2009), corresponding to the “plant’s-eye view” of local plant neighbourhood interactions envisaged by Turkington and Harper (1979). Given a particular pattern of stems, their relative sizes can indicate patterns of facilitation or competition among them. Evidence for such processes can be derived from the little-used mark correlation function (Stoyan and Penttinen 2000; Law et al. 2009), which indicates whether the distribution of tree sizes differs from random expectations. Finally, Gibbs processes are statistical models which can be fit to observed spatial patterns, providing a versatile framework for modelling their structures, estimating biologically meaningful parameters, and gaining insights into their fundamental processes (Illian et al. 2008; Grabarnik and Särkkä 2009). The potential of these techniques has yet to be fully exploited in ecological studies, and there are no known studies which have combined them in the analysis of a single forest stand.

The phenomenon of size bimodality in populations has been relatively neglected since the landmark review by Huston and DeAngelis (1987). In this paper I investigate the spatial organisation of a birch stand with a bimodal size structure, utilising recently developed statistical techniques to disentangle the relationship between size classes. Because this is a developing stand, we would expect to see evidence of competition amongst stems, although this is likely to be asymmetric, with larger stems competing exclusively with each other whereas smaller stems exhibit signs of competition from both larger and similar-sized stems. This should lead to a spatial structure in which large stems are relatively dispersed within the stand, and smaller stems are preferentially located in the interstices formed by the pattern of large stems.

Alternative hypotheses should be considered simultaneously in order to strengthen the inferences that can be drawn from static spatial patterns (McIntire and Fajardo 2009). There are multiple mechanisms by which a bimodal distribution may arise (Huston and DeAngelis 1987), which would be expected to exhibit different spatial structures. If bimodality is caused by abiotic heterogeneity, we would expect large and small stem sizes to occur in separate clusters. If two different-aged cohorts are present, the two size classes should be relatively evenly mixed, representing the ability of a second cohort to form beneath the first. Under an assumption of symmetric competition, no spatial interaction would be found between the patterns of large and small stems.

These predictions were tested in a developing *Betula platyphylla* Sukacz. stand in Central Kamchatka in which a fully mapped plot was established in 2008. *B. platyphylla* is a widespread species in Northeast Asia, though it occurs in a relatively small proportion of Kamchatkan forests (641.7 Mha) compared with the cold-tolerant *B. ermanii* Cham. (Krestov 2003). In Japan *B. platyphylla* is the stronger competitor, limited in its altitudinal range only by winter cold (Koike et al. 2003). Because of the remoteness of Kamchatka, human impacts upon its forests have been remarkably limited, and therefore it provides an ideal location for studying natural patterns of forest assembly.

Materials and methods

Study area

The study site was an area of *B. platyphylla* forest close to the Kamchatka River in the Central Depression of Kamchatka. Both *Larix cajanderi* Mayr and *Salix* spp. form minor elements within the forest. The even distribution of stem sizes was indicative of a developing stand, with no evidence of recent fire or ash in the soil profile. It was entirely flat in topography. It is therefore presumed that inundation from the river was the most likely cause of the stand-replacing disturbance which allowed this forest to form. The plot location was selected by choosing random co-ordinates within a block of homogeneous forest over 1 km² in size (55°48′036N, 159°33′091E). Average tree height was 15.0 ± 1.2 m ($n = 25$), with the tallest measured tree at 24.0 m. Soils were pH 6.10 with 64 ± 6.5 mg kg⁻¹ N and 600 ± 90 mg kg⁻¹ P. The understorey was dominated by *Equisetum* spp. and *Calamagrostis purpurea* Trin.

A 10 m grid of posts was created within a square 0.25-ha plot. Distances to all trees and stumps were measured from two posts of each 100 m² subplot at a height of 1.3 m. Measurements were converted to Cartesian co-ordinates to map the spatial pattern of stems (Newton 2007), a method which minimises positioning errors on scales relevant to spatial analysis (Freeman and Ford 2002). Diameter at breast height (DBH; 1.3 m) for all stems above 1 cm was recorded using a graded tape, following Newton (2007), and converted to basal area. Four trees had two live stems at 1.3 m and their basal area was therefore summed. A map of all stems is included as Appendix A (in the electronic supplementary material).

Size structure analysis

The size distribution of stems was confirmed as bimodal by comparing the fit of a unimodal normal distribution to a

bimodal distribution formed by two superimposed normal distributions. Maximum likelihood estimates for each model were obtained using the mle function in R2.9.0 (R Development Core Team 2009) and model fit was assessed by the lowest estimate of $-2 \log$ likelihood ($-2LL$).

Spatial pattern analysis

Exploratory spatial pattern analysis employed the pair correlation function $g(r)$, which is regarded as the most robust descriptive statistic (Illian et al. 2008; Law et al. 2009). It is calculated as the first derivative of Ripley’s K function $K(r)$ (Ripley 1977), which gives the expected number of points within distance r of an arbitrary point, summed across all points in the pattern and divided by the pattern intensity λ . For a stationary and isotropic pattern, $K(r)$ can therefore be estimated as:

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

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 total number of events within the sample window, and λ is the expected number of events per unit area (the pattern intensity). Because $K(r)$ is cumulative, to determine the scales at which pattern structure is present it is best converted into the dimensionless function $g(r) = K'(r)/(2\pi r)$. When applied to a completely spatially random (CSR) point pattern, $K(r) \approx \pi r^2$ and $g(r) \approx 1$, implying that points are independently distributed at distance r . When $g(r) > 1$ there are more pairs of points at distance r than expected from a CSR pattern, implying clustering at this distance, whereas $g(r) < 1$ implies regularity. Following Baddeley and Turner (2005), $g(r)$ is estimated up to distances of one quarter of the minimum plot dimension, i.e. 12.5 m. A weighted edge correction (Ripley 1977) and Epanechnikov smoothing kernel (Illian et al. 2008) were applied to the curves. Detecting spatial patterns which differ significantly from CSR assumptions requires the construction of envelopes based on simulations of the null model. For descriptive analyses, envelopes were calculated on the basis of the 5th highest and lowest of 999 Monte Carlo simulations of a CSR distribution with equal intensity, corresponding to a two-tailed test with $\alpha \approx 0.01$ (Diggle 2003). Although not a formal significance test (Loosmore and Ford 2006), the approach is strongly supported by most authors (Illian et al. 2008), and $\alpha \approx 0.01$ is a relatively conservative level within the spatial statistical literature.

Marked point patterns combine the spatial positions of events with additional linked variables, which may be continuous (e.g. size) or ordinal (e.g. alive or dead). Null models must be chosen carefully to ensure adequate

hypothesis tests (Wiegand and Moloney 2004). Patterns in basal area of trees were analysed using the mark correlation function $g_{mm}(r)$ (Stoyan and Penttinen 2000; Law et al. 2009):

$$\hat{g}_{mm}(r) = E(i, j) \left[\frac{m_i m_j}{E(mm')} \right]$$

where $E(i, j)$ denotes the conditional expectation given that there are points at the locations i and j separated by distance r , and where m_i and m_j denote the marks attached to the two points. E is the null expectation when m and m' are random marks drawn independently from the marginal distribution of marks. Values of $g_{mm}(r) > 1$ indicate facilitation (the product of marks is greater than expected by chance given the spatial positions of trees), whereas $g_{mm}(r) < 1$ signifies inhibition, and can be used to detect the effects of competition. Two sets of bivariate $g_{12}(r)$ analyses were also conducted, between large and small trees and between live and dead trees, to assess their spatial interactions. Both were analysed assuming a null hypothesis of random labelling, in which tree positions were kept constant but randomly assigned to either category, keeping the overall frequency of each type constant. In all cases envelopes were calculated as above, following 999 Monte Carlo simulations of the null model.

Gibbs processes are spatial point process models defined by means of a probability density function which introduces interdependence among points (Baddeley and Turner 2005; Illian et al. 2008). Following (Strauss 1975), a process can be defined containing an interaction parameter which equals γ when $r \leq r_1$ but 0 when $r > r_1$. This assumes that points only interact with other points within a radius r_1 . The density of points is then given by the function:

$$f(x) = \alpha \lambda^{n(x)} \gamma^{s(x)}$$

in which α acts as a normalising constant, $\lambda^{n(x)}$ is a homogeneous Poisson process with intensity λ , and $s(x)$ is the number of pairs of points in x closer than r_1 apart, with γ determining the strength of interactions among points. It is necessary that $\gamma < 1$ for the process to be well-defined. When $\gamma = 0$, no two points can be closer than r_1 apart, known as a hard core process. When $\gamma = 1$, the model reduces to a CSR pattern with intensity λ . For $0 < \gamma < 1$, partial inhibition of points occurs within r_1 , leading to segregation in space.

In order to fit the Strauss process to the pattern of stems, the interaction radius r was estimated using profile pseudo-likelihood across a range of plausible values with a step of 0.01 m. The remaining parameters were fit using the Huang–Ogata one-step approximation to maximum likelihood (Huang and Ogata 1999). Model fit was assessed by

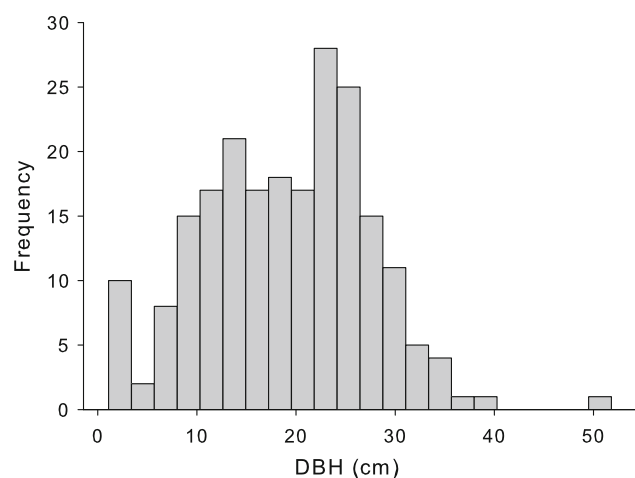


Fig. 1 Histogram of *B. platyphylla* trees (≥ 1 cm DBH) within 2.5 cm classes

comparison of the empirical $g(r)$ function to 999 Monte Carlo simulations of the fitted model with envelopes calculated as above. All spatial analyses were conducted using the spatstat package (Baddeley and Turner 2005) in R.2.9.0 (R Development Core Team 2009).

Results

A total of 216 *B. platyphylla* trees greater than 1 cm DBH were recorded, with an average DBH of 19.0 ± 0.6 cm (Fig. 1). A bimodal distribution composed of two overlaid normal distributions proved a better fit to the data than a unimodal normal distribution ($-2LL$ bimodal = 1524.8, unimodal = 1530.84). There were 13 standing dead *B. platyphylla* trees (mean DBH 11.2 ± 2.2 cm) and 50 stumps. A single large *Larix cajanderi* (DBH 59.1 cm, height 24.0 m) and two dead *Salix* sp., one stem and one stump, were also present. These were excluded from the analyses presented below.

The $g(r)$ function, when applied to all live *B. platyphylla* trees, indicated that significant clustering occurred at scales from 4.2 to 4.9 m (not shown). To look for evidence of spatial structure in the size distribution of stems, the mark correlation function was applied to all live trees using a null hypothesis of random labelling of basal area values among stems. This indicated that significant size compensation occurred at scales up to 3.5 m (Fig. 2), a signal of competition. Further analyses split the stand into two approximately even-sized sections to account for the bimodal distribution, with large trees having a DBH > 20 cm and small trees with DBH 1–20 cm.

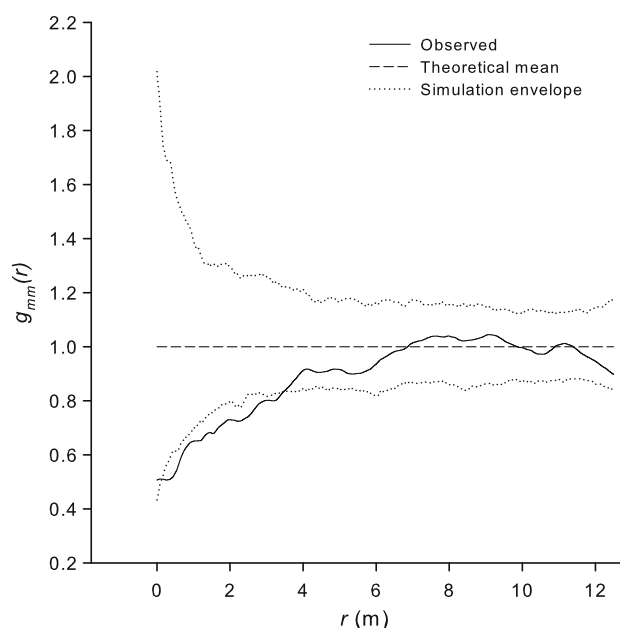


Fig. 2 Mark correlation function $g_{mm}(r)$ for DBH of live *B. platyphylla* trees

Large trees

A total of 104 *B. platyphylla* stems were in this category, distributed approximately evenly across the plot (Fig. 3a). The $g(r)$ function indicated significant dispersion in the pattern at scales up to 3.6 m (Fig. 3b). This was therefore modelled using a Strauss process. The initial starting parameters were determined based on the intensity of the observed pattern of stems ($\lambda = 0.0416 \text{ m}^{-2}$), the minimum observed distance between stems ($r = 1$ m) and the strength of the competitive interaction among stems was estimated at $\gamma = 0.2$ (range 0–1). The estimate of r was refined using profile pseudo-likelihood (range 0–5 m), which yielded a best estimate of $r = 4.16$ m. The remaining parameters were then refined using the Huang–Ogata estimation technique to obtain values of $\lambda = 0.186$ and $\gamma = 0.422$. A diagnostic $g(r)$ plot based on 999 Monte Carlo simulations of the Strauss process using these parameters confirmed that the model was an effective description of the observed pattern (Appendix B in the electronic supplementary material).

Small trees

There were 112 stems with DBH 1–20 cm distributed throughout the plot (Fig. 3c). These were effectively randomly distributed, satisfying the assumptions of a CSR pattern with intensity $\lambda = 0.0448 \text{ m}^{-2}$ (Fig. 3d). The cross-pair correlation function $g_{12}(r)$ with a null hypothesis

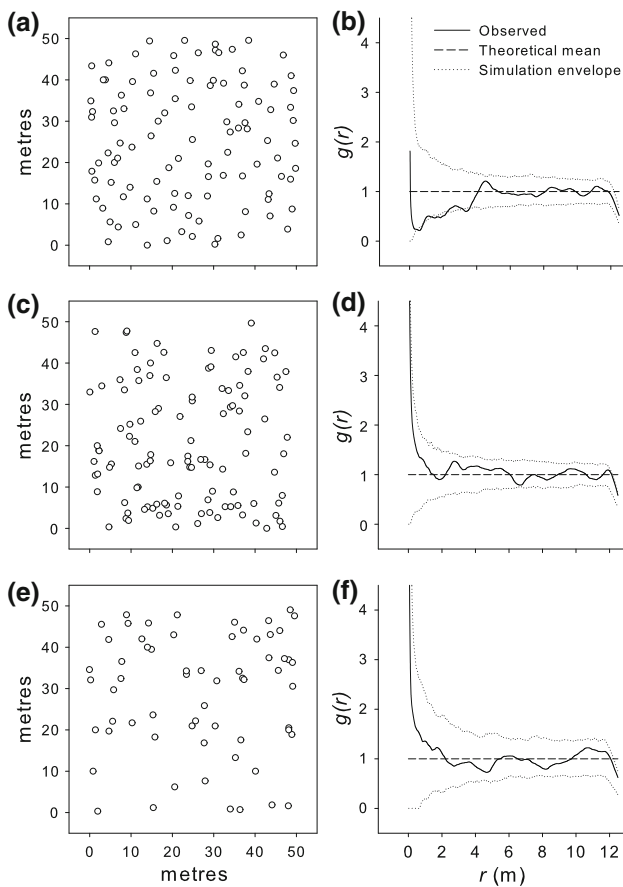


Fig. 3 **a** Positions of large *B. platyphylla* trees (DBH > 20 cm) with **b** pair correlation function $g(r)$ against simulation envelopes for a CSR null model, **b**, **d** small trees (1–20 cm DBH), and **e**, **f** dead trees and stumps

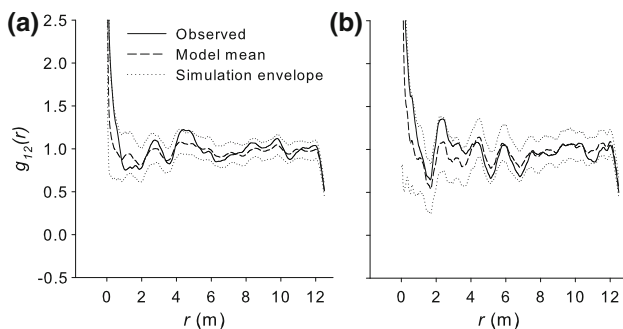


Fig. 4 Cross-pair correlation functions $g_{12}(r)$ for **a** large (>20 cm DBH) and small (1–20 cm DBH), and **b** live and dead *B. platyphylla* trees

of random labelling of stems indicated a greater probability of finding small stems at a distance around 4.3–4.8 m from large stems, although they were otherwise randomly distributed (Fig. 4a).

Dead trees

A total of 63 dead trees and stumps were present (Fig. 3e), satisfying the assumptions of a CSR pattern with intensity $\lambda = 0.0252 \text{ m}^{-2}$ (Fig. 3f). The cross-pair correlation function $g_{12}(r)$ with a null hypothesis of random labelling of stems indicated that dead stems were a random subset of all stems present in the plot (Fig. 4b), although a non-significant tendency was found for dead stems to be more common between 2 and 4 m from live stems. There were no differences when the pattern of dead stems was related to either large or small live stems (analysis not presented).

Discussion

The spatial organisation of this *B. platyphylla* forest is consistent with the hypothesis that asymmetric competition is responsible for the observed bimodal size structure (Fig. 1). Ecological processes often leave characteristic spatial signatures (Watt 1947), and by forming predictions based on rival hypotheses, a static pattern can be interpreted to ascertain the most plausible process responsible for its formation (McIntire and Fajardo 2009). Although the potential for bimodality to arise from competitive interactions is well-known from simulation models (Gates 1978; Aikman and Watkinson 1980), the parameter range over which this might occur is restricted, and therefore it is considered to be the least likely cause of bimodality in natural size distributions (Huston and DeAngelis 1987). Several lines of evidence drawn from the spatial organisation of the stand support its application here.

The first comes from the mark correlation function, which indicates size compensation of stems up to 3.5 m apart, a clear indication of competition among nearby stems (Fig. 2). Second, the patterns formed by large and small stems were markedly different, with large stems being significantly dispersed at scales up to 3.6 m whereas small stems were effectively randomly distributed (Fig. 3a–d). This implies that competition is stronger among large stems than smaller. The fitted Strauss process suggested that interactions among large stems occur up to 4.16 m, with a moderate strength of competitive effects within this range ($\gamma = 0.422$; complete exclusion would yield $\gamma = 0$). In stands with trees of mixed size, variable interactions can confound interpretation of spatial patterns, and it is therefore prudent to split trees into separate size classes for analysis if the dynamics of the whole stand are to be understood (Moravie and Robert 2003). A similar approach should be taken in analysing the patterns of bimodally size-structured plant populations elsewhere.

The tendency for large stems to show greater regularity than small stems is expected to occur as the age of a stand

increases (Laesele 1965; Ford 1975; Sterner et al. 1986; Moeur 1993), and was detected in a *Pinus sylvestris* L. stand by Grabarnik and Särkkä (2009), although in some cases multiple processes acting at different scales may obscure the pattern (Murrell 2009). It is therefore interesting that the overall pattern of stems remained clustered, which may be a relic of colonisation processes. Birch trees produce immense numbers of wind-dispersed seeds, which rapidly colonise bare ground (Perala and Alm 1990; Seiwa and Kikuzawa 1996), though it is unknown whether any initial spatial structure is introduced at this stage.

Finally, the pattern of small stems is not independent of the large stems. There was an increased probability of finding small stems at a distance around 4.3–4.8 m from large stems (Fig. 4a), which is slightly greater than the predicted range of competition among large stems. This suggests that large stems have an effect on the distribution of the smaller ones. However, it should be acknowledged that there is no evidence that small stems were less likely to be found close to large ones, which would be expected if large trees were causing their mortality.

This latter point is also made by the pattern of dead stems and stumps, which are effectively randomly distributed (Fig. 3e–f) and a random subset of all stems in the plot, albeit marginally more common at 2–4 m from live stems (Fig. 4b). There is therefore little evidence of recent competitive thinning, although the decay of dead *Betula* stems may make this difficult to detect. The number or proportion of dead stems is not itself a reliable means of inferring the state of development of a forest (Ferguson and Archibald 2002; Brassard and Chen 2006), and repeat surveys are a more powerful means of assessing patterns in mortality. Dead stems were still smaller than live, whereas in mature stands a switch occurs, with greater mortality of stems in large size classes (Coomes and Allen 2007).

Several plausible hypotheses for the existence of a bimodal size structure can also be assessed (Huston and DeAngelis 1987). The effect of spatial heterogeneity in resources can be rejected as an explanation, because the two size classes are distributed throughout the plot rather than independently clustered in space. Symmetric competition can also be rejected, because there is clear evidence that the spatial patterns of large and small stems differ, and that the pattern of small stems is affected by that of the large. The final possibility is that these might be separate cohorts. *Betula* species are light-demanding, seldom germinating beneath the canopies of other trees, and are therefore dependent on stand-replacing disturbance for regeneration (Perala and Alm 1990). *B. platyphylla*, being small-seeded, does not tolerate litter and establishes best on mineral soil in canopy gaps (Seiwa and Kikuzawa 1996). In Central Kamchatka it can be seen to colonise recently burnt

areas in very large numbers, often forming a dense carpet on landslides or other bare ground, whereas in closed forest it regenerates largely through ramets (Homma et al. 2003, and personal observation). This in itself makes an interpretation based on different-aged cohorts unlikely, unless the cohorts formed relatively close together in time. In this case we would expect greater mixing of the two cohorts. The scale of interactions among stems (c. 4 m) is more consistent with competition between tree canopies than seedlings.

Few comparable studies exist against which this stand can be compared. Of those which are known, all have considered post-fire stands in mixed forests, where the contribution of resprouts from *Betula* stools leads to a dense stand with a very different size structure (Takahashi et al. 2001; Homma et al. 2003; Doležal et al. 2004). There was no indication in this stand that stools had contributed to its regeneration, and all evidence suggested that it had arisen de novo following large-scale disturbance. In Central Kamchatka it is likely that a cohort of *B. platyphylla* can occupy a site for at least 150 years, although when seed sources are available it becomes out-competed by *Picea ajanensis* (Lindl. ex Gord.) Fisch. ex Carr. (Krestov 2003).

Conclusions

Spatial analyses within this plot suggest that a bimodal size distribution can arise through the action of asymmetric competition among stems, with such interactions leading to the formation of predictable spatial patterns by the stems within each size class. The trees which constitute the upper canopy are dispersed in space, with smaller stems preferentially found beyond the competitive ranges of larger stems. The lack of any spatial pattern in the distribution of dead stems implies that the process of self-thinning through competition is weakening as the stand approaches maturity. The potential for Gibbs process models to describe and interpret spatial patterns within natural systems has barely been exploited to date (Illian et al. 2008; Grabarnik and Särkkä 2009), with most examples being confined to the statistical literature. These powerful and versatile tools will play an important role in advancing our understanding of spatial organisation in nature, and in interpreting the causes of observed size distributions in both managed and natural forests.

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