

Heterogeneity influences spatial patterns and demographics in forest stands

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Summary

1. The spatial pattern of tree species retains signatures of factors and processes such as dispersal, available resource patches for establishment, competition and demographics. Comparison of the spatial pattern of different size classes can thus help to reveal the importance and characteristics of the underlying processes. However, tree dynamics may be masked by large-scale heterogeneous site conditions, e.g. when the restricting size of regeneration sites superimposes emergent patterns.

2. Here we ask how environmental heterogeneity may influence the spatial dynamics of plant communities. We compared the spatial patterns and demographics of western hemlock in a homogeneous and a heterogeneous site of old-growth Douglas-fir forests on Vancouver Island using recent techniques of point pattern analysis. We used homogeneous and inhomogeneous *K*- and pair-correlation functions, and case-control studies to quantify the change in spatial distribution for different size classes of western hemlock.

3. Our comparative analyses show that biological processes interacted with spatial heterogeneity, leading to qualitatively different population dynamics at the two sites. Population structure, survival and size structure of western hemlock were different in the heterogeneous stand in such a way that, compared to the homogeneous stand, seedlings were more clustered, seedling densities higher, seedling mortality lower, adult growth faster and adult mortality higher. Under homogeneous site conditions, seedling survival was mainly abiotically determined by random arrival in small gaps with limiting light. At the heterogeneous site, seedling densities and initial survival were much higher, leading to strong density-dependent mortality and selection for faster growing individuals in larger size classes. We hypothesise that the dynamics of the heterogeneous stand were faster due to asymmetric competition with disproportionate benefit to taller plants.

4. Synthesis. Our study supports the hypothesis that successional dynamics are intensified in heterogeneous forest stands with strong spatial structures and outlines the importance of spatial heterogeneity as a determinant of plant population dynamics and pattern formation.

Key-words: case-control, dispersal strategies, inhomogeneous pair-correlation function, large-scale heterogeneity, point pattern analysis, succession, western hemlock

Introduction

Dispersal strategies of species have a profound influence on their survivorship in different environments (Dieckmann *et al.* 1999; Hovestadt *et al.* 2000; Hille Ris Lambers & Clark 2003). Some species may follow a generalist dispersal strategy with a widespread but low density distribution of seeds that enable them to colonize new suitable sites, while others may specialize in local regeneration to form distinct clusters (He & Duncan 2000; Wiegand *et al.* 2007b). These contrasting

strategies reflect a trade-off with *r*-selected species relying on a combination of colonization and exploitation, while *K*-selected species rely on maintenance (Bolker & Pacala 1999). The dispersal strategy should leave a signature in the spatial pattern of the species, both in the spatial seedling – adult association (Ribbens *et al.* 1994) and in the clustering of seedlings. However, different spatial patterns may also reflect differential abilities of species to survive intra and inter-specific competition during succession (Getzin *et al.* 2006). The effects of density-dependent mortality may be revealed by comparing the change in spatial pattern of different life-history stages (Moeur 1997; Plotkin *et al.* 2002).

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Spatial pattern analysis becomes more complicated when large-scale environmental heterogeneity masks the dispersal and demographic behaviour of a given species, for example, by forcing it to aggregate in restricted regeneration sites (He *et al.* 1997; Coomes *et al.* 1999). A patchy distribution of limiting resources may then influence demographic processes and the emerging species patterns. Consequently, population dynamics and ecological feedbacks may interact in a complex manner (Clark *et al.* 1998; Dieckmann *et al.* 1999; Condit *et al.* 2000).

For this reason, gaining an understanding of the effects of environmental variation in space remains a major challenge in spatial ecology (Amarasekare 2003; Gratzner *et al.* 2004; Ronce *et al.* 2005). The problem at hand is to separate the effects of direct plant–plant interaction on the spatial pattern (so called ‘second-order effects’) from effects resulting from large-scale variation in habitat quality (so called ‘first-order effects’) because both may lead to similar spatial patterns (Coomes *et al.* 1999; Lancaster 2006; Wiegand *et al.* 2007a). For example, the effects of density-dependent thinning on the pattern of large adult trees need to be separated from the effects of habitat-induced thinning. However, contrasting environmental conditions may also cause feedbacks between spatial structure and demographics by qualitatively changing key processes such as regeneration due to different gap sizes or competition due to heterogeneous resource distribution (Colasanti & Hunt 1997), or may result in indirect effects (e.g. pathogen transmission) on spatial patterns in communities.

A rarely used but important approach to study such cascade effects of environmental heterogeneity is to compare plots within the same type of plant community but contrasting environmental variability. Although the importance of heterogeneity has been recognized (e.g. Spieth 1979), comparisons of differential population response to homogeneous and heterogeneous site conditions have been mostly limited to artificial research designs (Hartgerink & Bazzaz 1984; Blair 2001; Neatrou *et al.* 2007). However, there is need for detailed comparisons under field conditions because environmental variability is the rule rather than the exception in nature (Hewitt *et al.* 2007).

One approach to exploring spatial plant dynamics is to use point pattern analysis of fully mapped plant locations using, for example tree–trunk or tree–crown positions (Getzin & Wiegand 2007). Spatial statistics such as Ripley’s *K*-function (Ripley 1976, 1981), the pair-correlation function (Stoyan & Stoyan 1994; Illian *et al.* 2008), or the distribution function of nearest-neighbour (NN) distances (Diggle 2003) quantify the small-scale spatial correlation structure of a pattern which contains information on the positive or negative type of interaction among plants. In addition, point pattern analysis is ideally suited to control for environmental heterogeneity and to focus on neighbourhood processes. For example, inhomogeneous variants of the *K*- or pair-correlation functions consider first-order effects such as environmental heterogeneity and quantify second-order effects caused by, for example direct plant–plant interaction. Thus, controlling for site-specific heterogeneities, it is possible to directly compare second-order effects of sites that differ in environmental heterogeneity.

Differences in second-order effects between sites indicate feedbacks between heterogeneity and demographic processes.

To undertake a heuristic example study on how environmental heterogeneity influences the spatial patterns and the demographics of plant communities, we performed comparative analyses of two old-growth stands both dominated by shade-intolerant pioneer Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco), and the shade-tolerant species, western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don). The stands were located in north and south environmental conditions in the Greater Victoria Watershed, on southern Vancouver Island. At large-scales, the old-growth north (OG-N; Fig. 1) plot showed homogeneous environmental conditions and mature adult trees were randomly distributed. Consequently, possible regeneration sites for our main study species, western hemlock, were scattered over the entire plot. In contrast, the old-growth south (OG-S; Fig. 2) plot showed large-scale habitat heterogeneity and some edaphic gaps (e.g. rock outcrops or wet drainage sites) prevented tree growth. In this plot, canopy cover of mature adult trees was clumped and possible regeneration sites for western hemlock were spatially more aggregated.

In this study, we used point pattern analyses to examine how the different site characteristics affect the successional dynamics of western hemlock, its spatial pattern formation, and its demographic change from seedlings to small and large saplings, and to adult trees at the two plots. We divided the spatial analyses into four parts. In a first analysis we tested our basic hypothesis that the environmental conditions of the OG-N and OG-S plots were indeed homogeneous and heterogeneous, respectively. In a second analysis we corrected for heterogeneity and compared the strength of clustering among size classes and between corresponding size classes of the two plots. Comparison of clustering among size classes explores whether and at which life stage self-thinning occurs (Moeur 1997), whereas comparison between sites investigates whether heterogeneity has only proportional effects on population dynamics or if feedback effects between heterogeneity and demographic processes may be present. Third, to obtain (indirect) evidence for small-scale limitation in seedling establishment and/or dispersal characteristics between the two sites, we quantified the distribution of NN distances for adult trees and seedlings to the nearest adult. Finally, we used a random-labelling null model (Diggle & Chetwynd 1991) to quantify changes in the spatial structure of subsequent age classes and to compare them between the two sites. This allowed us to explore possible mutual effects of density-dependent thinning and of patchy regeneration sites on the pattern of different size classes. The four analyses and respective hypotheses are summarized in Table 1.

Methods

SPECIES

The native range of western hemlock is the Pacific coast between northern California and southern Alaska, but it also prevails in the

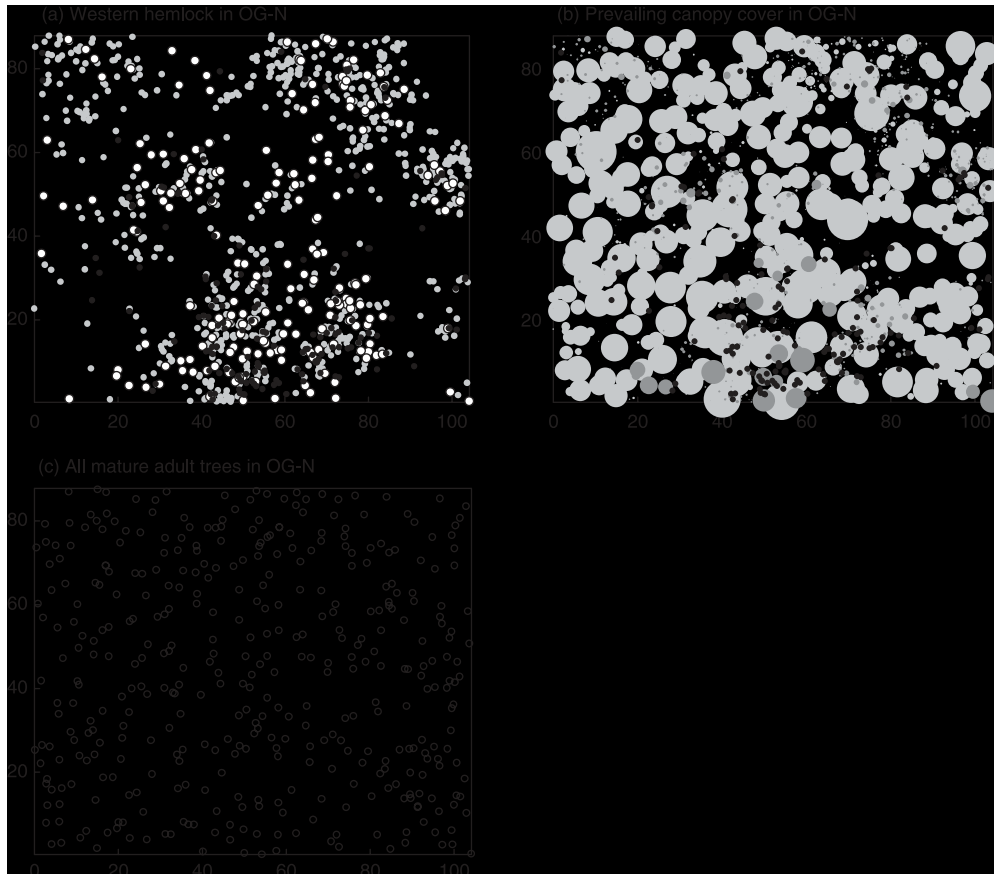


Fig. 1. Western hemlock in old-growth north (OG-N). (a) Spatial distributions of seedlings (black dots), small and large saplings (grey dots), and adult trees (open circles). (b) Prevailing canopy cover of all other trees, being mainly Douglas-fir (light grey circles) and western hemlock (dark grey circles), represented by circles with a radius proportionally to the d.b.h. of the trees, shown together with western hemlock seedlings (black dots). (c) Spatial distribution of stems of all mature adult trees in the plot with a d.b.h. ≥ 15 cm. The unit of (x,y) -axes is meters.

northern Rocky Mountains. As a shade-tolerant late-successional species, western hemlock is the primary successor in Douglas-fir forest and it colonizes the post-fire habitats after mortality of pioneer Douglas-fir opens up canopy gaps (Huff 1995). Although western hemlock has clustered regeneration within these gaps (He & Duncan 2000; Getzin *et al.* 2006) seedlings can also grow in relatively large numbers under partial or full canopy (LePage *et al.* 2000; Coates 2002). Western hemlock usually produces more seeds than most associated tree species (up to 19.8 million seeds per ha have been recorded; Burns & Honkala 1990). Two-year-old seedlings are usually < 20 cm tall, but once established, seedlings in full light may have an annual growth rate of 60 cm (Burns & Honkala 1990).

STUDY AREA AND DATA COLLECTION

We studied western hemlock in two old-growth stands of Douglas-fir on south-eastern Vancouver Island. Both stands originated from catastrophic wildfires. The OG-N stand (48°38' N, 123°43' W) had an age of 325 years and average Douglas-fir d.b.h. (diameter at breast height) of 43.0 cm. This plot on a 40% WSW slope had large-scale homogeneous habitat conditions with Douglas-fir being apparently evenly spaced over the entire study region (Fig. 1). The plot was at 465 m elevation and had a straight surface profile. The soil was an Orthic Humo-Ferric Podzol with fine-silty and loamy family particle size classes (Trofymow *et al.* 1997; He & Duncan 2000).

The OG-S stand (48°33' N, 123°38' W) had an age of 254 years and average Douglas-fir d.b.h. of 52.2 cm. This plot on a 40% NNE slope was influenced by large-scale habitat heterogeneity such as edaphic gaps (e.g. rock outcrops or wet drainage sites) with Douglas-fir growing in spatially restricted aggregations (Fig. 2). The plot was at 390 m elevation and had a straight surface profile. The soil was a well-drained Orthic Dystric Brunisol overlain by a mull-like moder humus form (Trofymow *et al.* 1997; Getzin *et al.* 2006).

Data were collected on plots 0.9 ha (OG-N) and 0.7 ha (OG-S) in size. Data from British Columbia on the dispersal kernels of western hemlock indicate mean dispersal distances of less than 20 m in old-growth (LePage *et al.* 2000). The plot sizes are therefore appropriate to capture processes related with recruitment kernels. All dead and live trees, and seedlings were stem-mapped. D.b.h. was measured at 1.4 m above-ground. Including live and dead trees, we classified western hemlock into four basic size classes: (1) 'seedlings' below a height of 1.4 m, hence having no measured d.b.h., (2) 'small saplings' with d.b.h. < 5 cm, (3) 'large saplings' with d.b.h. ranging from 5 to < 10 cm, and (4) 'adult trees' with d.b.h. ≥ 10 cm. We have chosen d.b.h. ≥ 10 cm for adult hemlock because regular cone production begins at a relatively young adult age of 25–30 years (Burns & Honkala 1990) and because this cut-off provided enough spatial data for adequate statistical comparisons between the largest and smaller size classes. However, for the purpose of describing large-scale variation in habitat quality (see next section for details) we defined an extra size class of 'all mature adult trees', consisting

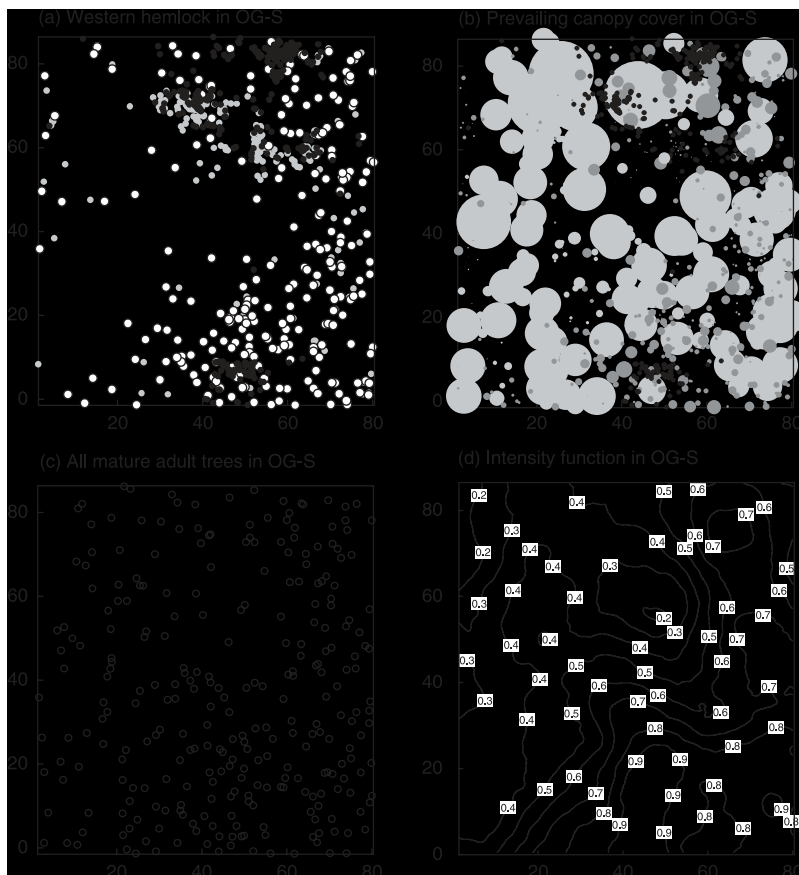


Fig. 2. Western hemlock in old-growth south (OG-S). (a), (b), (c) as in Fig. 1. (d) The intensity function of the distribution of all mature adult trees, normalized between 0 and 1, and estimated using an Epanechnikov kernel with bandwidth 15 m. The unit of (x, y) -axes is meters.

of individuals of all species with d.b.h. ≥ 15 cm (LePage *et al.* 2000). Mature adult trees were dominated by the following species: 78.1% Douglas-fir, 9.5% western hemlock, 12.3% western redcedar in OG-N but 33.8% Douglas-fir, 47.0% western hemlock, and 16.0% western redcedar in OG-S.

SPATIAL PATTERN ANALYSIS

Homogeneous and inhomogeneous second-order statistics

We used the pair-correlation function and a transformation of Ripley's K -function to analyse the spatial pattern of tree distributions (Ripley 1976; Stoyan & Stoyan 1994; Illian *et al.* 2008). For approximately homogeneous patterns, the bivariate K -function $K_{12}(r)$ is defined as the expected number of type 2 points within distance r of an arbitrary type 1 point, divided by the intensity λ_2 of pattern 2. The bivariate pair-correlation function $g_{12}(r)$ is related to the derivative of the K -function, i.e. $g_{12}(r) = K'_{12}(r)/(2\pi r)$ (Illian *et al.* 2008). Due to its non-cumulative properties, $g(r)$ is recommended for exploratory data analysis to identify specific scales of deviation from a null model (Wiegand & Moloney 2004; Perry *et al.* 2006; Illian *et al.* 2008). For ease of visual interpretation, we used the square root transformed K -function $L(r) = (K(r)/\pi)^{0.5} - r$, known as L -function (Besag 1977).

To construct inhomogeneous second-order statistics to account for spatial heterogeneity at the OG-S plot, the 'thinning approach' of Baddeley *et al.* (2000) was used. For the construction of inhomogeneous K - and g -functions, the assumption is made that the observed point pattern resulted from a two-step process, where an initially homogeneous pattern was independently thinned by an inhomogeneous

thinning surface (Baddeley *et al.* 2000). The thinning surface $\lambda(x)$ which describes the environmental heterogeneity is proportional to the intensity of the two-step process and depends on location x . This approach is appropriate because at this plot, heterogeneity appears to mainly reduce establishment success and to increase mortality in areas of lower habitat suitability (Fig. 2). In the OG-S study plot, spatial variations in habitat quality were related to rock outcrops or wet drainage sites.

If one point of the final heterogeneous pattern was located at location x , we may expect on average $1/\lambda(x)$ points for the initial, pre-thinning homogeneous pattern at this location. Thus, the inhomogeneous K - and g -functions may be estimated analogously to homogeneous K - and g -functions, but by weighting each data point by $1/\lambda(x)$. Details on the estimators of the inhomogeneous functions are given in the Appendix S1 in the Supplementary Material.

Although theoretically appealing, the problem with inhomogeneous K - and g -functions is that the thinning surface is in general not known and using an estimate of the intensity of the pattern itself as the thinning surface is problematic because in this case, both first- and second-order properties have to be determined from the same pattern simultaneously (Baddeley *et al.* 2000; Diggle 2003). This problem can be solved by using additional information (Diggle *et al.* 2007; cf. *Analysis 1* below for our solution).

BIOLOGICAL HYPOTHESES AND NULL MODELS

Analysis 1: Environmental heterogeneity

The basic hypothesis of *Analysis 1* is that environmental conditions are homogeneous at the OG-N plot and heterogeneous at the OG-S

Table 1. Main hypotheses, applied point pattern analyses, and related figures of this study

Hypotheses	Point pattern analyses/null models	Related figures
(1) The spatial distribution of trees in old-growth south (OG-S) is affected by large-scale environmental heterogeneity but not in old-growth north (OG-N).	Pair-correlation function, <i>L</i> -function, and null-model 'complete spatial randomness' applied to 'all mature adult trees' in a plot.	Fig. 4
(2) The strength of clustering of all four size classes from seedlings to hemlock adults is different in OG-N and OG-S, even after having statistically corrected for the pure effects from heterogeneity.	Homogeneous <i>g</i> -function applied to each size class in OG-N. Inhomogeneous <i>g</i> -function applied in OG-S, based on the thinning surface of 'all mature adult trees'. No null model.	Fig. 5
(3) The relative concentration of seedlings near adults is greater than that of adults at small neighbourhood distances due to clustered establishment of seedlings.	Bivariate distribution function of nearest-neighbour distances of adults around seedlings compared to the univariate function of adults around adults. No null model.	Fig. 6
(4) a) Under homogeneous and heterogeneous environmental conditions, adult hemlock and smaller size classes similarly exploit the spatially available habitat. b) Smaller size classes show an additional clustering. The additional clustering declines with increasing size class, indicating density-dependent thinning. The strength in density-dependent thinning is different in OG-N and OG-S.	Bivariate random labelling within a case-control design as null model: 1 = control = adults, 2 = cases = seedlings, small, or large saplings. a) If $g_{12}(r) - g_{11}(r) \approx 0$, cases and controls follow the same overall pattern, relative to the 'first-order' environmental conditions. b) If $g_{21}(r) - g_{22}(r) \ll 0$, an additional clustering mechanism of cases occurs, independent of the control pattern.	Figs 7 and 8

Table 2. Composition of different size classes of western hemlock in homogeneous (OG-N) and heterogeneous (OG-S) study areas. NN = nearest neighbour

Plot	Number of individuals		Mean d.b.h. (cm)		Median NN distance (m)	
	OG-N	OG-S	OG-N	OG-S	OG-N	OG-S
Seedlings	155	382	–	–	1.37	0.31
Small saplings, d.b.h. < 5 cm	443	193	2.8	1.9	1.20	0.89
Large saplings, d.b.h. 5 to < 10 cm	251	120	7.0	7.1	1.92	2.42
Adults, d.b.h. ≥ 10 cm	101	234	18.4	18.1	3.34	2.09

plot. To describe the environmental heterogeneity and to determine an appropriate thinning surface for *Analysis 2*, we used biological arguments and additional information provided by the spatial pattern of 'all mature adult trees' in the plots with d.b.h. ≥ 15 cm (Figs 1c, 2c). Our assumption was that the large-scale intensity (i.e. above the scale of direct tree–tree interactions) of all mature adult trees of all species should be a good indicator of environmentally driven habitat quality, e.g. caused by rock outcrops or wet drainage sites because mature trees have undergone excessive thinning and are expected to have exploited all available sites. By using the mature adult trees of all species, we captured strong environmental habitat factors common to all species.

Before constructing a thinning surface it should be confirmed that the pattern is heterogeneous. Clustering and heterogeneity cannot be distinguished statistically without additional biological information (Diggle 2003). In plant communities, large-scale aggregation is usually attributed to environmental heterogeneity, whereas small-scale clustering is attributed to plant–plant interactions (Wiegand *et al.* 2007a). Large-scale heterogeneity causes locally elevated tree densities leading to a weak increase of the pair-correlation function and strong increase of the *L*-function at larger scales (Wiegand & Moloney 2004). Although homogeneity and CSR are different concepts, significant deviation of a pattern from a homogeneous

Poisson process (CSR) at scales $r > 10$ m beyond direct tree–tree interaction (Stoyan & Penttinen 2000) is usually interpreted as environmental heterogeneity.

In this study, significant departure from CSR was evaluated using the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations to generate approximately 99% simulation envelopes. In case that CSR was rejected at scales > 10 m, we used a nonparametric method to estimate the intensity $\lambda(x)$ of the spatial distribution of the mature adult trees which combines a moving window estimator with an Epanechnikov kernel (for details see e.g. Stoyan & Stoyan 1994; Wiegand *et al.* 2007a, and Appendix S1).

Analysis 2: Strength of clustering of different size classes

Western hemlock is typically clustered (He & Duncan 2000; Getzin *et al.* 2006) and the clustering is expected to decline with increasing size class due to self-thinning (Moeur 1997). Therefore, we described the spatial patterns for four different life-history stages (seedlings to adults, cf. Table 2) using pair-correlation functions. The aim was to compare the species-specific spatial correlation structure of individuals of a given size class (i.e. strength of clustering) between homogeneous and heterogeneous site conditions without the confounding effect of environmental heterogeneity. To this end we used homogeneous

g -functions for homogeneous site conditions and inhomogeneous g -functions based on the thinning surface of the locations of all mature adult trees for heterogeneous conditions.

The inhomogeneous pair-correlation function assumes proportional effects of habitat suitability on tree density. Thus, if the homogeneous pair-correlation functions of the homogeneous site are similar to its inhomogeneous counterpart at the heterogeneous site no feedback between heterogeneity and neighbourhood processes occurs. However, strong differences provide evidence for feedback effects between heterogeneity and demographic processes.

Analysis 3: Seedling to adult relationship

We used the bivariate distribution function $G_{12}(y)$ of NN distances y to describe the relationship between seedlings (pattern 1) and adult trees (pattern 2), and the univariate distribution function $G_{22}(y)$ to describe the relationship among adults (pattern 2). While pair-correlation functions are based on all tree–tree distances, the $G(y)$ -functions are ‘short-sighted’ and consider only the distances to the nearest neighbour (Illian *et al.* 2008). This property, however, is important when exploring dispersal characteristics because here the distances between seedlings and their nearest adult (i.e. the potential parent tree) are of interest.

The bivariate $G_{12}(y)$ was compared to the univariate distribution $G_{22}(y)$ to assess the relative concentration of seedlings and adults in OG-N and OG-S. Similar distributions $G_{12}(y)$ and $G_{22}(y)$ mean that adults are not more frequent around seedlings than adults around adults. This analysis is particularly sensitive to small-scale differences between the two plots because it is based on a straightforward interpretation of immediate neighbourhood relations. For example, infrequent small-scale distances of adults around seedlings (both western hemlock) under the dense canopy of dominant pioneer Douglas-fir would indicate overall establishment limitation due to abiotic or biotic constraints. In contrast, frequent small-scale seedling–adult distances may indicate overall more suitable light conditions for establishment in the neighbourhood of adults.

Analysis 4: Density-dependent thinning

As trees within clusters increase in size, density-dependent competition and also pathogen effects result in mortality which thins the clusters and increases the distances between neighbouring trees. This process is observed from the smallest seedlings to the largest overstorey trees (Moeur 1997).

We applied the random-labelling null model within a case-control design to estimate the mutual effects of density-dependent thinning and of the availability of regeneration sites within suitable habitat on the pattern of different size classes. Case-control is a commonly used epidemiological design to study the spread of disease cases (Diggle & Chetwynd 1991; Gattrell *et al.* 1996) where the control pattern is necessary to account for possible environmental heterogeneity in the population at risk. If the cases do not show any additional pattern to that of the controls, the random-labelling null model applies, that is the cases are a random subset of the joined pattern of cases and controls.

We used the adult class of western hemlock with d.b.h. ≥ 10 cm (Burns & Honkala 1990) as ‘control’ because our working hypothesis is that the large-scale pattern of older trees reflects the underlying heterogeneity (cf. *Analysis 1*, Results *Analysis 2*, Fig. 5b). We then compared the ‘cases’ of smaller size classes relative to the ‘control’ pattern of adult trees. A decline in clustering with increasing size class reflects self-thinning and the strength of this decline relative to

the ‘control’ pattern reflects the strength of density-dependent thinning.

The g -functions are invariant under random thinning, hence under random labelling we would expect $g_{12}(r) = g_{21}(r) = g_{11}(r) = g_{22}(r)$. Departure from bivariate random labelling is assessed by using the differences $g_{12}(r) - g_{11}(r)$ and $g_{21}(r) - g_{22}(r)$ as test statistics (Getzin *et al.* 2006). With control = pattern 1 = adults and case = pattern 2, a value of $g_{12}(r) - g_{11}(r) \approx 0$ means that, for example seedling cases surround adult trees at scale r in the same way as adults surround adults. Hence, both life-history stages exploit the spatially available habitat at these scales in a similar way. However, if there would be additional clustering within the cases that is independent from the control pattern of adults (e.g. larger gaps with suitable conditions for seedling establishment and survival), this would not be noticed by the test statistic $g_{12}(r) - g_{11}(r)$, but we would expect $g_{21}(r) - g_{22}(r) \ll 0$. Thus, $g_{12}(r) - g_{11}(r)$ reveals if cases and adults follow the same overall pattern and $g_{21}(r) - g_{22}(r)$ reveals if there is an additional pattern within the cases that is independent from the location of the adult pattern, irrespective of whether heterogeneity is present or not (Getzin *et al.* 2006; Watson *et al.* 2007).

The analysis was done by computing the test statistics from the observed data then randomly re-sampling sets of n_2 cases from the joined pattern of n_2 case and n_1 control trees to generate the simulation envelopes. Significant departure from random labelling was evaluated using the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations to generate approximately 99% simulation envelopes.

To complement the random-labelling analysis, we also applied the mark-connection function $p_{12}(r)$ as test statistic (Gavrikov & Stoyan 1995; Illian *et al.* 2008). The mark-connection function $p_{12}(r)$ was estimated as

$$p_{12} = \frac{\lambda_1 \lambda_2}{(\lambda_1 + \lambda_2)^2} \frac{g_{12}(r)}{g(r)},$$

using the identity $g(r) = [\lambda_1 \lambda_1 g_{11}(r) + \lambda_1 \lambda_2 g_{12}(r) + \lambda_2 \lambda_1 g_{21}(r) + \lambda_2 \lambda_2 g_{22}(r)] / [\lambda_1 + \lambda_2]^2$. The function $p_{12}(r)$ can be interpreted as the conditional probability that of two arbitrarily chosen points of the joined case and control pattern, the first is a control (adult, pattern 1) and the second a case (pattern 2), given that both trees are separated by distance r . Note that the estimator of $p_{12}(r)$ involves division by $g(r)$ and that $g(r)$ is the expectation of the test statistics $g_{12}(r)$ under random labelling. Therefore, possible large-scale heterogeneity in the joined pattern of cases and controls is factored out and $p_{12}(r)$ compares the ‘pure’ effects of tree–tree interactions to random labelling. The $p_{12}(r)$ is not invariant under random thinning and thus contains information about the absolute clustering of cases around controls (adults). This function can be seen as a modern counterpart of Pielou’s segregation index (Pielou 1961).

All point pattern analyses were done using the grid-based software *Programita* (Wiegand & Moloney 2004). A summary of the applied spatial statistics of *Analyses 1–4* is given in Table 1.

Results

COMPOSITION OF LIFE-HISTORY STAGES, MORTALITY AND D.B.H. DISTRIBUTION

In the homogeneous OG-N plot, hemlock seedlings were less numerous and less dense than seedlings in the heterogeneous OG-S plot (Table 2). The median NN distance between trees in a size class increased overall 2.4-fold

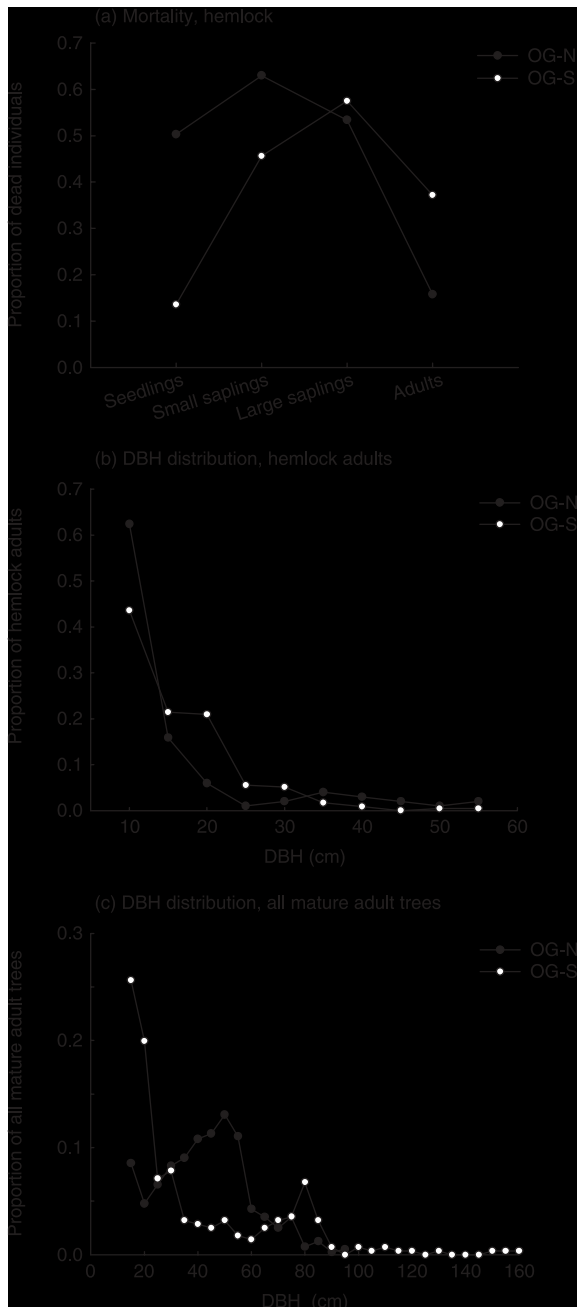


Fig. 3. (a) Mortality of western hemlock within separate life-history stages in old-growth north (OG-N) and south (OG-S). (b) d.b.h. distribution within hemlock adult trees (d.b.h. ≥ 10 cm) and (c) within all mature adult trees (d.b.h. ≥ 15 cm) at the two plots.

from seedlings to adults in OG-N but 6.7-fold in OG-S, indicating overall stronger thinning effects under heterogeneous conditions (Table 2). With 234 individuals, adult trees were more numerous and denser in OG-S than the 101 adults in OG-N.

In both plots, mortality of western hemlock was highest in the sapling stages (Fig. 3a). Probably due to limited light under small gaps, seedling mortality was high in OG-N (50.3%). In contrast we found low seedling mortality in OG-S (13.6%), despite higher local seedling density. In OG-N,

mortality increased slightly for small saplings and declined already for large saplings. However, in OG-S, mortality strongly increased for small saplings, probably due to high local densities and increasing competition experienced by small saplings. Mortality further increased for large saplings in OG-S. Adult mortality was 15.8% in OG-N and 37.2% in OG-S (Fig. 3a).

The average d.b.h. of hemlock adult trees was 18.4 cm in OG-N and 18.1 cm in OG-S (Table 2). Also, the d.b.h. distributions of western hemlock adults were nearly equal in both stands, although the OG-S plot was about 70 years younger (Fig. 3b).

The d.b.h. distributions of all mature adult trees differed substantially between both plots (Fig. 3c). At the OG-N plot, the d.b.h. distribution had a strong peak at 50 cm d.b.h. and a weaker peak at small diameters of 15 cm. In contrast, at the OG-S plot, the bimodal distribution had an absolute peak at 15 cm d.b.h. and a much weaker peak at an intermediate size of 80 cm. Probably due to the differences in site quality, trees grew bigger in OG-S (up to d.b.h. = 160 cm) than in the homogeneous OG-N plot.

ANALYSIS 1: ENVIRONMENTAL HETEROGENEITY

We compared the pattern of all mature adult trees in the plots with d.b.h. ≥ 15 cm to the CSR null model to find out if the two plots showed large-scale heterogeneity or not (Fig. 4). The L -function showed no large-scale departure from CSR at the OG-N plot (Fig. 4a), but a clear departure at scales $r > 10$ m at the OG-S plot (Fig. 4b). Also the g -function was > 1 for large-scales at the OG-S plot. These findings provide evidence that the OG-N plot shows large-scale homogeneity while the OG-S plot exhibits large-scale heterogeneity. Due to these contrasting results, we used the homogeneous and inhomogeneous g -functions for the spatial pattern analysis at the OG-N plot and OG-S plot, respectively.

The observed tendency to regularity at small scales was expected and indicates inter-tree competition. At the OG-N plot, significant regularity occurred up to scales of 1.5 m (Fig. 4a), but otherwise the pair-correlation function well-approximated the value $g(r) = 1$, a trend being expected for a homogeneous pattern. At the OG-S plot, the tendency to regularity was not significant (Fig. 4b).

ANALYSIS 2: STRENGTH OF CLUSTERING OF DIFFERENT SIZE CLASSES

In both plots the strength of clustering declined systematically from seedlings to adult hemlock (Fig. 5) as expected from the self-thinning hypothesis. However, between the two plots, there were marked differences in the strength and the range of clustering (cf. Fig. 5a,b) which suggests joint effects of heterogeneity and neighbourhood processes. The range of clustering of seedlings and small saplings extended only up to roughly 3 m in OG-N but up to 10 m in OG-S. The small-scale clustering (e.g. at $r = 0.5$ m) of seedlings and small saplings was over four times stronger in the OG-S plot (Fig. 5b)

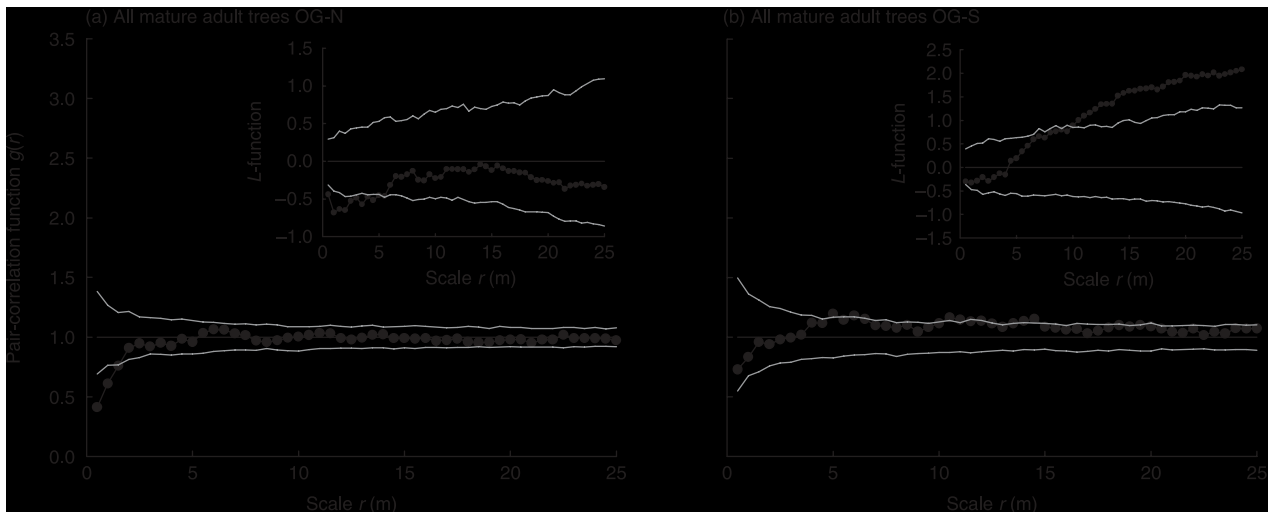


Fig. 4. The pattern of all mature adult trees in a plot with a d.b.h. ≥ 15 cm, contrasted to the null model of complete spatial randomness (CSR), using the homogeneous L -function (inset figure) and the homogeneous pair-correlation function. Approximately 99% simulation envelopes (grey solid lines) were constructed using the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations of the CSR null model. Environmental heterogeneity is indicated by large-scale departure of the L -function from CSR (b).

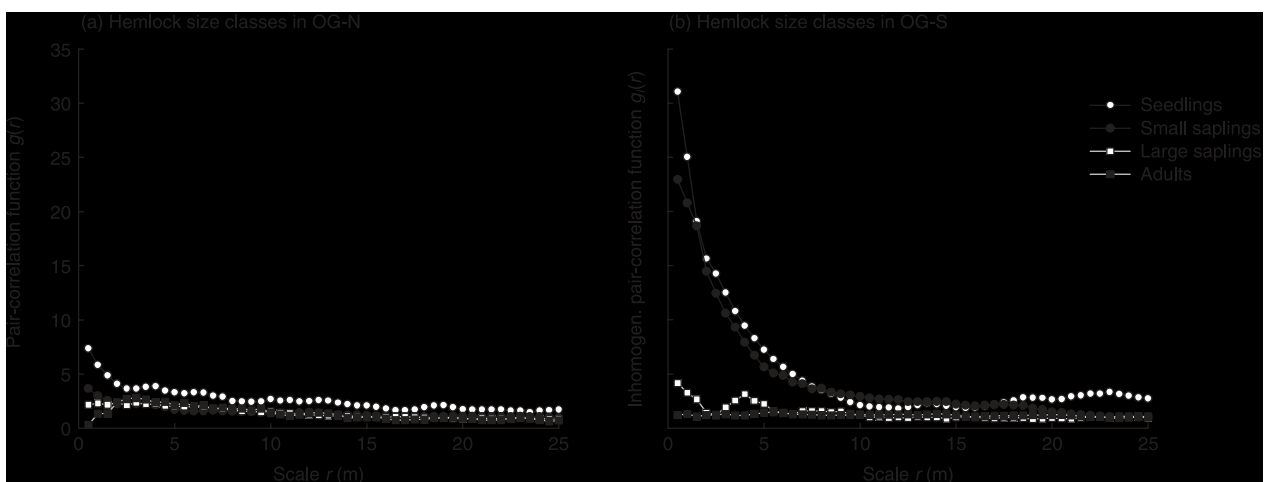


Fig. 5. Comparison of the strength of clustering of different size classes of western hemlock using the homogeneous g -functions for OG-N (a) and the inhomogeneous g -functions for OG-S (b). The inhomogeneous g -functions were constructed using the intensity of the positions of all mature adult trees with d.b.h. ≥ 15 cm as thinning surface. Strong deviation from the proportional thinning effect of habitat suitability on tree density indicates feedback effects between spatial habitat structure and demographic processes (i.e. seedlings and small saplings in OG-S).

relative to the OG-N plot. While seedlings and small saplings were strongly clustered at the heterogeneous OG-S plot, large saplings (and adults) lost most of this clustering, thus substantiating the finding of peak mortality in the large sapling class at this heterogeneous plot (Fig. 3c).

Our results show striking differences between both plots in the spatial distribution of hemlock during the first establishment phases due to synergetic effects between spatial habitat structure and neighbourhood processes. This is because the inhomogeneous pair-correlation function removed the ‘pure’ effects of habitat heterogeneity (i.e. proportional reduction in establishment probability and mortality with lower habitat suitability) on clustering. Our approach uses the spatial pattern of all mature adult trees from all tree species in the plot as a reference point for proportional effects of habitat

heterogeneity. If no additional ‘niche effects’ of hemlock occur, the inhomogeneous pair-correlation function of adult hemlock trees should approach $g(r) = 1$ for all scales. Indeed, this expectation was met (Fig. 5b). Thus, our assumption that the locations of older trees could be used as surrogate for the large-scale heterogeneity at the OG-S plot was valid.

ANALYSIS 3: SEEDLING TO ADULT RELATIONSHIP

At a small scale of 2 m radius in OG-N, the proportion of adults having an adult as nearest neighbour was slightly greater than that of seedlings having an adult as nearest neighbour (Fig. 6a). In OG-N, the slightly less frequent 2 m distance between seedlings and adults is most probably not due to competition between seedlings and hemlock adults

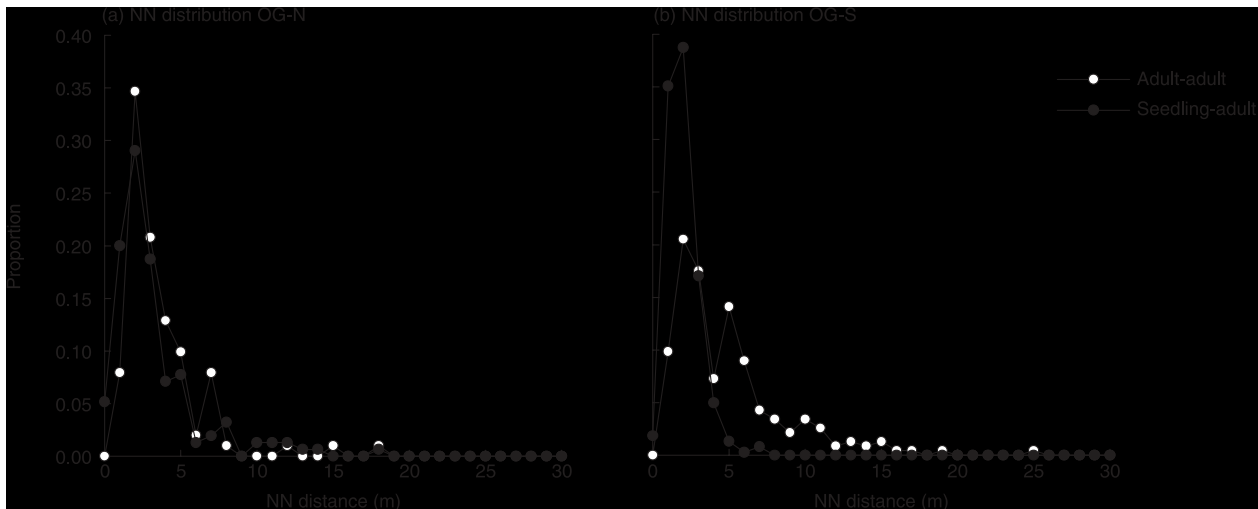


Fig. 6. Distribution of nearest-neighbour (NN) distances of seedlings to the nearest adult (potential parent) tree (filled circles) and of adults to the nearest adult (open circles). Note that relative seedling concentrations were higher than adult concentrations at small distances of 2 m in OG-S but the opposite occurred under the low light resources in OG-N.

because seedling facilitation near parent trees is usually expected due to the benefit from increased stem flow and species-specific micro-site requirements (Hille Ris Lambers & Clark 2003). The low seedling concentration relative to adults in OG-N is probably caused by the out-shading canopy cover of dominant Douglas-fir. Mature adults of Douglas-fir made up nearly 80% of all mature adult trees in the plot and thereby reduced seedling concentrations near the few adult hemlock in the plot (cf. Fig. 1b).

In contrast, at distances of 2 m in OG-S the proportion of seedlings having an adult nearest neighbour was almost double that of adults having an adult nearest neighbour (Fig. 6b). However, the high small-scale seedling concentration at the OG-S plot was probably caused by a patchy distribution of regeneration sites due to larger canopy openings where many seedlings were close to a few adult trees (Fig. 2b). At large radii of 4–17 m, this patchy distribution of regeneration sites caused a large proportion of adults to have no seedling in their neighbourhood as can be seen by the constantly larger proportion of adults around adults (Fig. 6b).

ANALYSIS 4: DENSITY-DEPENDENT THINNING

At the OG-N plot, the case-control analysis showed that the distribution of seedlings around adult trees followed the same overall pattern as adults relative to adult trees (Fig. 7a, inset figure). The test statistic $g_{12}(r) - g_{11}(r)$ did not differ significantly from zero, indicating a spatially homogeneous mingling in the distribution of seedlings and adults. Interestingly, also the small and large saplings followed the same overall pattern of the adult trees (Fig. 7b,c, inset figures). This demographic pattern suggests a spatially homogeneous succession of western hemlock throughout all life-history stages.

However, for seedlings at OG-N, the test statistic $g_{21}(r) - g_{22}(r)$ differed significantly, albeit slightly, from the random-

labelling null model at almost all scales (Fig. 7a, main figure), indicating a weak additional clustering of the seedlings independent of the adult pattern (probably some smaller gaps in the canopy). This weak additional clustering disappeared for small saplings (Fig. 7b) and the large sapling stage also shows virtually no additional clustering (Fig. 7c). This indicates an early culmination in density-dependent mortality, agreeing with the early decline in mortality already for the large saplings in OG-N (cf. Fig. 3a).

Departures from random labelling were more obvious at the heterogeneous OG-S plot. The test statistic $g_{12}(r) - g_{11}(r)$ again did not differ significantly from random labelling at smaller scales (Fig. 7d, inset figure), which indicates that the distribution of seedlings around adult trees followed the overall adult pattern in the plot. This finding also applies to the small and large saplings (Fig. 7e,f, inset figures), but small saplings showed at larger scales a weak additional clustering independent of the pattern of adults.

However, for seedlings at OG-S, the test statistic $g_{21}(r) - g_{22}(r)$ revealed strong departures from random labelling pointing to an aggregation mechanism of seedlings independent of the adult pattern. Due to the availability of large, and thus favourable, gaps for establishment in OG-S (cf. Fig. 2b), there was a very strong seedling–seedling clustering, independent from the seedling–adult relation (Fig. 7d). In contrast to the OG-N plot, this strong clustering persisted into the small sapling stage (Fig. 7e), but disappeared in the large sapling stage (Fig. 7f). This later culmination in density-dependent thinning agrees with the late peak in mortality for large saplings in OG-S (cf. Fig. 3a). The overall stronger decline in additional clustering following density-dependent thinning also agrees with the greater difference in mortality in OG-S, that is an increase of about 32% from seedlings towards small saplings (cf. Fig. 3a) and with the greater increase in NN distances with increasing size class (cf. Table 2).

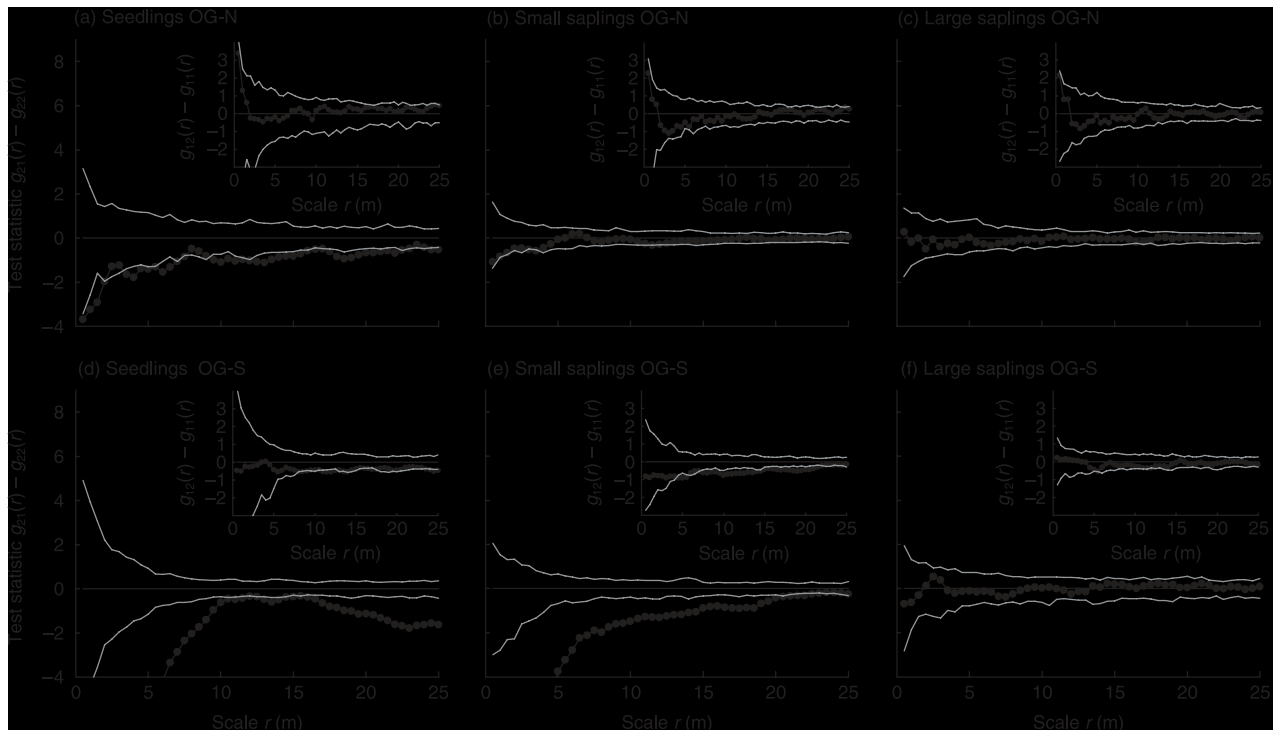


Fig. 7. Case-control study of western hemlock where the larger-scale pattern of hemlock adult trees (pattern 1) serves as control pattern, which corrects for possible heterogeneity in habitat quality. The test statistic $g_{12}(r) - g_{11}(r)$ evaluates if cases of a size class (seedlings, small, large saplings; pattern 2) follow the adult pattern, both relative to the control (inset figure). If this is true, $g_{12}(r) - g_{11}(r) \approx 0$. The test statistic $g_{21}(r) - g_{22}(r)$ evaluates if there is an additional clustering within a size class that is independent from the hemlock adult pattern. If this is true, $g_{21}(r) - g_{22}(r) \ll 0$. The stronger the decline in additional clustering is the stronger is the density-dependent thinning. Approximately 99% simulation envelopes (grey solid lines) were constructed using the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations of the null model.

The complementary analyses using the mark-connection function as test statistic supported this trend of *Analysis 4*. For hemlock in OG-N, overall departures from random labelling were not significant but adults and saplings showed a tendency to attraction at small distances (Fig. 8a–c). However, in OG-S strongly significant segregation was observed for seedlings and small saplings. This is because seedlings and small saplings were strongly aggregated and because many adults had no seedling or small sapling in their neighbourhood (Fig. 2a). Therefore, when randomly picking two trees with a given distance r there was a high probability that both were seedlings (or saplings) or that both were adults. However, large saplings showed increased spatial mingling with the distribution of adults (Fig. 8d–f).

Discussion

The overall goal of our study was to find out if and how environmental heterogeneity may influence the spatial patterns and the demographics of tree species. In the simplest case, heterogeneity would only modulate the density of trees by introducing a proportional thinning to the spatial patterns due to lower establishment success and higher mortality at low quality sites. However, our study demonstrates that habitat heterogeneity does influence the emerging spatial patterns and demographics in a complex way, giving rise to

qualitatively different population dynamics under homogeneous and heterogeneous site conditions.

Our analyses provided a clear picture of the spatial structure of our study species under contrasting environmental conditions. By comparing a homogeneous (OG-N) and an inhomogeneous (OG-S) old-growth plot, we found that large-scale environmental heterogeneity had clear effects on the population dynamics of western hemlock. A striking finding is that successional dynamics under habitat heterogeneity were faster as seen by the equal d.b.h. distribution and the equal mean d.b.h. of hemlock adult trees in both plots, in combination with the considerable difference in stand age (325 years at OG-N vs. 254 years at OG-S). Our detailed pattern analyses shed some light on the basis of these demographic differences.

We used inhomogeneous pair-correlation functions to factor out the ‘pure’ effect of heterogeneity (*Analysis 2*). The analyses pointed to clear differences in the spatial clustering of seedlings and saplings between the two sites which were well-beyond the pure, proportional effect of heterogeneity. At the heterogeneous OG-S plot, the strong clustering persisted into the small sapling stage and its large range of about 10 m radius indicates availability of larger gaps for establishment (cf. Figs 2a, 5b). This spatial disposition and its consequences for establishment, recruitment, and long-term survival had cascading effects on the population structure in the heterogeneous OG-S plot.

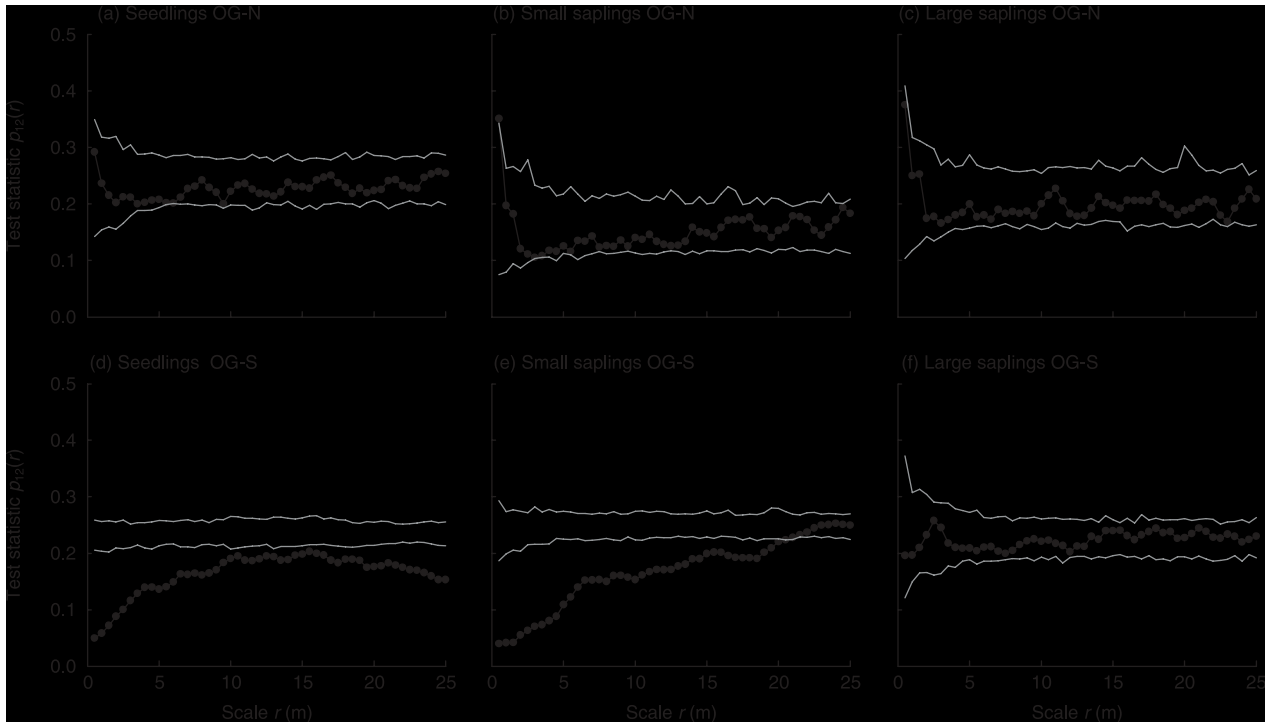


Fig. 8. The mark-connection function $p_{12}(r)$ describes the conditional probability that of two randomly selected points (belonging to the joined pattern of adult hemlock and the pattern of a smaller size class) the first is an adult and the second a non-adult, given that they are separated by distance r . Approximately 99% simulation envelopes (grey solid lines) were constructed using the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations of the null model.

Under the large canopy gaps in OG-S, seedling abundance and survival were very high. These findings agree with other studies and suggest that establishment in distinct tree-fall gaps enhances initial survival of hemlock whereas the opposite occurs under more shady cover (Huff 1995; Moeur 1997; LePage *et al.* 2000). The relatively small canopy openings at the homogeneous OG-N plot provided only weak light conditions under the even spacing of pioneer Douglas-fir (He & Duncan 2000). Thus, seedling survival was strongly limited. This explains the high mortality and low density of seedlings in OG-N and also the unexpected result that there were less nearest neighbouring adults around seedlings than adults around adults at the small-scale radius of 2 m (*Analysis 3*). Under the homogeneous canopy, seedling recruitment into the next higher size class was affected relatively little by competitive exclusion because density-dependent thinning was weak and it culminated already in the small sapling stage (*Analysis 4*). This explains the slight increase in mortality towards small saplings and the decline in mortality already in the large sapling stage (Fig. 3a). In short, the ‘seed-flooding strategy’ of western hemlock (Getzin *et al.* 2006) assured sufficient seedling numbers even under homogeneous canopy cover (LePage *et al.* 2000; Coates 2002), but seedling survival and subsequent recruitment was rather abiotically determined as a function of ‘lucky’ random arrival. Overall, succession in OG-N was slow because, due to the low-light condition under dense canopy of Douglas-fir, hemlock mainly relied on the shade-tolerant strategy (He & Duncan 2000).

In contrast, strongly biotic feedback mechanisms operated at the heterogeneous site. An increase in aggregation with heterogeneity may elevate competition between individuals, but this is outweighed by the initial benefit of favourable habitat association (North & Ovaskainen 2007). This explains the high survival rate of seedlings in the large gaps of the OG-S plot. However, once the number of individuals in a given space is high, increased density-dependent mortality and processes such as intraspecific competition, pathogen transmission, or host-specific predation will change the population structure of the cohort (Rees *et al.* 1996; Hille Ris Lambers & Clark 2003). This change can simply cause an overall quantitative decline in local density with increasing size (Moeur 1997). We observed such quantitative changes consistently in *Analyses 2* and *4*, showing decreased clustering from seedlings to adults and strong density-dependent mortality up to the large sapling stage.

However, a qualitative change in population structure with significant consequences for the speed and intensity of successional dynamics is also possible. We hypothesize that the spatial distribution of resources itself explains the overall faster tree growth in OG-S as compared to OG-N. At the homogeneous OG-N plot, spatial light availability was more symmetrically intercepted by all mature adult trees, limiting maximal sizes of individuals to < 100 cm d.b.h. In contrast, at the 70 years younger heterogeneous plot, edaphic gaps caused asymmetric light availability. This did not allow for equilibrated competition but led to both more small and more

large trees, allowing sizes up to 160 cm d.b.h. (Fig. 3c). For this asymmetric competition, it is the amount and spatial distribution of resource-acquiring organs, relative to the directionality of light resources, that confers a competitive advantage (Schenk 2006). Particularly in dense forests where most of the competition is for light, asymmetric access to the light resource is disproportionately absorbed by taller plants (Blair 2001).

According to Colasanti & Hunt (1997), symmetric 'scramble' competition will occur if the resource is dispersed homogeneously and if individuals have equal access to the resource. If the resource is spatially heterogeneous, 'contest' competition can occur when the competitive interactions are mediated indirectly through resources by physical occupation of space. The individual that has most access to the resource is disproportionately favoured in terms of growth. While in the homogeneous plot 'scramble' competition led to a decline in local density and regularly spaced pioneer Douglas-fir (He & Duncan 2000), 'contest' competition in the heterogeneous plot led to aggregated patterns of Douglas-fir (Getzin *et al.* 2006) and more clustered recruitment opportunities for hemlock. For maturation over time, heterogeneous site conditions and dense seedling clusters appear to be more rewarding for the succession of hemlock since heavy seed crops are produced at short intervals of 3–4 years while Douglas-fir seed crops occur at irregular intervals of about 7 years (Burns & Honkala 1990). This could have given hemlock a temporal advantage in the spatial occupation of newly formed tree-fall gaps in OG-S. Our *Analyses 3* and *4* support this hypothesis because seedlings and also small saplings showed an independent large-scale distribution that did not follow the pattern of adults. However, ultimately large saplings and adult hemlock similarly exploited the spatially heterogeneous habitat over all scales, which is evidence for an overall successful colonization strategy (Fig. 7c, inset).

An alternative, though not mutually exclusive, explanation for the overall faster tree growth in OG-S is that local selection pressures within heterogeneous environments may cause a diversification in genetic response (Petit & Thompson 1998) and the much stronger density-dependent mortality within seedling clusters may select for 'survival of the fittest' (Paul 1988). For example, Donohue *et al.* (2000) have shown that genetic variation to enable plastic response to changing plant densities may be great in high resource patches where responses are strongly mediated by light. For the excessive small-scale clustering in OG-S, it is plausible that only the fittest seedlings equipped with the 'best set of genes', for example for resource acquirement, meristem allocation, or pathogen resistance, will survive into the next larger size class. This is because neighbouring seedlings are so tightly packed that small-scale abiotic growth conditions are likely to be very similar in the centres of the clusters where usually most seedlings occur. The genetic diversity and the amount of low frequency alleles are most often greater in hemlock seedlings than in their parent trees and this may allow for sufficient variation in the genetic disposition of competing seedlings

(El-Kassaby *et al.* 2003). The higher heterozygosity in early life stages is often linked to traits favourable to seedling establishment or pathogen resistance. However, traits advantageous to initial seed and seedling survival may have a cost in terms of growth for mature trees. Hence, after successful establishment in dense seedling clusters, there is probably a strong selection process to also grow faster to survive into the next higher size classes.

This mechanism could be an alternative explanation for the accelerated succession with faster growing adult trees in the heterogeneous plot. In contrast, in the homogeneous OG-N plot, the more abiotically determined survivors rather represent a random subset of a gene pool and not necessarily the fittest individuals. In this case, even the less fit individuals may survive as long as they were 'lucky' to reach a suitable gap of sufficient size (den Boer 1999). However, examination of such hypotheses by linking spatial pattern analysis with genetic analysis is required to reveal more directly the underlying processes of spatio-temporal selection (e.g. Stratton & Bennington 1996; Jacquemyn *et al.* 2007).

Put into a greater context, our empirical findings from comparisons between homogeneous and heterogeneous environments in field conditions agree with model predictions by Bolker & Pacala (1999). Although the cause of endogenous spatial structure was more due to biotic than to abiotic factors in their model, our results support their hypothesis that population dynamics may be faster in heterogeneous communities.

Conclusions

Most modern ecological research up to the 1990s has been conducted under relatively homogeneous conditions to eliminate environmental or ecological variability in space so that ecological processes and relationships can be examined without bias (Wiens 1999). We took advantage of a unique situation of having data of the same tree community under both homogeneous and inhomogeneous conditions and used advanced techniques of point pattern analysis to investigate the influence of heterogeneity on spatial patterns and demographics in forest stands. Our approach is an elegant way to use biological information from the locations of mature trees as surrogate for environmental heterogeneity. This approach is less labour-expensive than collecting abiotic co-variables for large study regions and it can be followed in forest research to investigate the effects of large-scale heterogeneity on spatial plant dynamics. We could demonstrate that spatial habitat structures have not only a proportional effect (i.e. introducing simply a thinning to the spatial patterns), but can show cascading feedback effects where plant demographics interact with spatial structure. This suggests that more emphasis should be placed on investigating the role of spatial heterogeneity in plant demographics and pattern formation. Our results are encouraging and the approach taken here could be widely applied to more deeply elucidate the role of environmental heterogeneity in spatio-temporal plant community dynamics.

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References

- Amarasekare, P. (2003) Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters*, **6**, 1109–1122.
- Baddeley, A., Møller, J. & Waagepetersen, R. (2000) Non- and semi-parametric estimation of interaction in inhomogeneous point patterns. *Statistica Neerlandica*, **54**, 329–350.
- Besag, J. (1977) Contribution to the discussion of Dr. Ripley's paper. *Journal of the Royal Statistical Society B*, **39**, 193–195.
- Blair, B. (2001) Effect of soil nutrient heterogeneity on the symmetry of belowground competition. *Plant Ecology*, **156**, 199–203.
- den Boer, P.J. (1999) Natural selection or the non-survival of the non-fit. *Acta Biotheoretica*, **47**, 83–97.
- Bolker, B.M. & Pacala, S.W. (1999) Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *American Naturalist*, **153**, 575–602.
- Burns, R.M. & Honkala, B.H. (1990) *Silvics of North America: 1. Conifers*. Agriculture Handbook 654, U.S. Department of Agriculture, Forest Service, Washington, DC.
- Clark, D.B., Clark, D.A. & Read, J.M. (1998) Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *Journal of Ecology*, **86**, 101–112.
- Coates, K.D. (2002) Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. *Forest Ecology and Management*, **155**, 387–398.
- Colasanti, R.L. & Hunt, R. (1997) Resource dynamics and plant growth: a self-assembling model for individuals, populations and communities. *Functional Ecology*, **11**, 133–145.
- Condit, R., Ashton, P.S., Baker, P., Bunyavejehwin, S., Gunatilleke, S., Gunatilleke, N., et al. (2000) Spatial patterns in the distribution of tropical tree species. *Science*, **288**, 1414–1418.
- Coomes, D.A., Rees, M. & Turnbull, L. (1999) Identifying aggregation and association in fully mapped spatial data. *Ecology*, **80**, 554–565.
- Dieckmann, U., O'Hara, B. & Weisser, W. (1999) The evolutionary ecology of dispersal. *Trends in Ecology and Evolution*, **14**, 88–90.
- Diggle, P.J. (2003) *Statistical Analysis of Point Processes*. Academic Press, London.
- Diggle, P.J. & Chetwynd, A.G. (1991) Second-order analysis of spatial clustering for inhomogeneous populations. *Biometrics*, **47**, 1155–1163.
- Diggle, P.J., Gómez-Rubio, V., Brown, P.E., Chetwynd, A.G. & Gooding, S. (2007) Second-order analysis of inhomogeneous spatial point processes using case-control data. *Biometrics*, **63**, 550–557.
- Donohue, K., Pyle, E.H., Messigou, D., Heschel, M.S. & Schmitt, J. (2000) Density dependence and population differentiation of genetic architecture in *Impatiens capensis* in natural environments. *Evolution*, **54**, 1969–1981.
- El-Kassaby, Y.A., Dunsworth, B.G. & Krakowski, J. (2003) Genetic evaluation of alternative silvicultural systems in coastal montane forests: western hemlock and amabilis fir. *Theoretical and Applied Genetics*, **107**, 598–610.
- Gatrell, A.C., Bailey, T.C., Diggle, P.J. & Rowlingson, B.S. (1996) Spatial point pattern analysis and its application in geographical epidemiology. *Transactions of the Institute of British Geographers*, **21**, 256–274.
- Gavrikov, V. & Stoyan, D. (1995) The use of marked point processes in ecological and environmental forest studies. *Environmental and Ecological Statistics*, **2**, 331–344.
- Getzin, S. & Wiegand, K. (2007) Asymmetric tree growth at the stand level: random crown patterns and the response to slope. *Forest Ecology and Management*, **242**, 165–174.
- Getzin, S., Dean, C., He, F., Trofymow, J.A., Wiegand, K. & Wiegand, T. (2006) Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography*, **29**, 671–682.
- Gratzler, G., Canham, C., Dieckmann, U., Fischer, A., Iwasa, Y., Law, R., Lexer, M.J., Sandmann, H., Spies, T.A., Splechtina, B.E. & Szwagrzyk, J. (2004) Spatio-temporal development of forests – current trends in field methods and models. *Oikos*, **107**, 3–5.
- Hartgerink, A.P. & Bazzaz, F.A. (1984) Seedling-scale environmental heterogeneity influences individual fitness and population structure. *Ecology*, **65**, 198–206.
- He, F. & Duncan, R.P. (2000) Density-dependent effects on tree survival in an old-growth Douglas fir forest. *Journal of Ecology*, **88**, 676–688.
- He, F., Legendre, P. & LaFrankie, J.V. (1997) Distribution patterns of tree species in a Malaysian tropical rain forest. *Journal of Vegetation Science*, **8**, 105–114.
- Hewitt, J.E., Thrush, S.F., Dayton, P.K. & Bonsdorff, E. (2007) The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. *American Naturalist*, **169**, 398–408.
- Hille Ris Lambers, J. & Clark, J.S. (2003) Effects of dispersal, shrubs, and density dependent mortality on seed and seedling distributions in temperate forests. *Canadian Journal of Forest Research*, **33**, 783–795.
- Hovestadt, T., Poethke, H.J. & Messner, S. (2000) Variability in dispersal distances generates typical successional patterns: a simple simulation model. *Oikos*, **90**, 612–619.
- Huff, M.H. (1995) Forest age structure and development following wildfires in the Western Olympic Mountains, Washington. *Ecological Applications*, **5**, 471–483.
- Illian, J., Penttinen, A., Stoyan, H. & Stoyan, D. (2008) *Statistical Analysis and Modelling of Spatial Point Patterns*. John Wiley & Sons, Chichester.
- Jacquemyn, H., Brys, R., Vandepitte, K., Honnay, O., Roldán-Ruiz, I. & Wiegand, T. (2007) A spatially-explicit analysis of seedling recruitment in the terrestrial orchid *Orchis purpurea*. *New Phytologist*, **176**, 448–459.
- Lancaster, J. (2006) Using neutral landscapes to identify patterns of aggregation across resource points. *Ecography*, **29**, 385–395.
- LePage, P.T., Canham, C.D., Coates, K.D. & Bartemucci, P. (2000) Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. *Canadian Journal of Forest Research*, **30**, 415–427.
- Moeur, M. (1997) Spatial models of competition and gap dynamics in old-growth *Tsuga heterophylla* / *Thuja plicata* forests. *Forest Ecology and Management*, **94**, 175–186.
- Neatrou, M.A., Jones, R.H. & Golladay, S.W. (2007) Response of three floodplain tree species to spatial heterogeneity in soil oxygen and nutrients. *Journal of Ecology*, **95**, 1274–1283.
- North, A. & Ovaskainen, O. (2007) Interactions between dispersal, competition, and landscape heterogeneity. *Oikos*, **116**, 1106–1119.
- Paul, D.B. (1988) The selection of the 'survival of the fittest'. *Journal of the History of Biology*, **21**, 411–424.
- Perry, G.L.W., Miller, B.P. & Enright, N.J. (2006) A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. *Plant Ecology*, **187**, 59–82.
- Petit, C. & Thompson, J.D. (1998) Phenotypic selection and population differentiation in relation to habitat heterogeneity in *Arrhenatherum elatius* (Poaceae). *The Journal of Ecology*, **86**, 829–840.
- Pielou, E.C. (1961) Segregation and symmetry in two-species populations as studies by nearest-neighbour relationships. *Journal of Ecology*, **49**, 255–269.
- Plotkin, J.B., Chave, J. & Ashton, P.S. (2002) Cluster analysis of spatial patterns in Malaysian tree species. *American Naturalist*, **160**, 629–644.
- Rees, M., Grubb, P.J. & Kelly, D. (1996) Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *American Naturalist*, **147**, 1–32.
- Ribbens, E., Silander, J.A. Jr. & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**, 1794–1806.
- Ripley, B.D. (1976) The second-order analysis of stationary point processes. *Journal of Applied Probability*, **13**, 255–266.
- Ripley, B.D. (1981) *Spatial Statistics*. Wiley, New York.
- Ronce, O., Brachet, S., Olivieri, I., Gouyon, P.H. & Clobert, J. (2005) Plastic changes in seed dispersal along ecological succession: theoretical predictions from an evolutionary model. *Journal of Ecology*, **93**, 431–440.
- Schenk, H.J. (2006) Root competition: beyond resource depletion. *Journal of Ecology*, **94**, 725–739.
- Spieth, P.T. (1979) Environmental heterogeneity: a problem of contradictory selection pressures, gene flow, and local polymorphism. *American Naturalist*, **113**, 247–260.
- Stoyan, D. & Penttinen, A. (2000) Recent applications of point process methods in forestry statistics. *Statistical Science*, **15**, 61–78.
- Stoyan, D. & Stoyan, H. (1994) *Fractals, Random Shapes and Point Fields. Methods of Geometrical Statistics*. Wiley, Chichester.
- Stratton, D.A. & Bennington, C.C. (1996) Measuring spatial variation in natural selection using randomly-sown seeds of *Arabidopsis thaliana*. *Journal of Evolutionary Biology*, **9**, 215–228.

- Trofymow, J.A., Porter, G.L., Blackwell, B.A., Arksey, R., Marshall, V. & Pollard, D. (1997) Chronosequences for research into the effects of converting coastal British Columbia old-growth forests to managed forests: an establishment report. *Canadian Forest Service*, BC-X-374.
- Watson, D.M., Roshier, D.A. & Wiegand, T. (2007) Spatial ecology of a parasitic shrub: patterns and predictions. *Austral Ecology*, **32**, 359–369.
- Wiegand, T. & Moloney, K.A. (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos*, **104**, 209–229.
- Wiegand, T., Gunatilleke, C.V.S. & Gunatilleke, I.A.U.N. (2007a) Species associations in a heterogeneous Sri Lankan dipterocarp forest. *American Naturalist*, **170**, 77–95.
- Wiegand, T., Gunatilleke, C.V.S., Gunatilleke, I.A.U.N. & Okuda, T. (2007b) Analyzing the spatial structure of a Sri Lankan tree species with multiple scales of clustering. *Ecology*, **88**, 3088–3102.
- Wiens, J.A. (1999) Landscape ecology: scaling from mechanisms to management. *Perspectives in Ecology* (ed. A. Farina), pp. 13–24. Backhuys Publishers, Leiden.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Estimation of the thinning surface.

This material is available as part of the online article from:
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