

Spatial patterns in an old-growth *Nothofagus obliqua* forest in south-central Chile

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Abstract

Data from a 1 ha permanent sample plot in an old-growth *Nothofagus obliqua* dominated forest were used to study spatial patterns of dead and live trees using the Ripley's $K(t)$ function. Univariate and bivariate analyses were conducted. We computed confidence envelopes for a random (Poisson) spatial distribution using Monte Carlo simulations. An edge effect correction was applied. The spatial pattern of *Aextoxicon punctatum* (the dominant species) changed from a random distribution at short spatial intervals of analysis to a clustered distribution at broader spatial scales. *N. obliqua* appeared to be more regularly distributed, but was not statistically significantly different from a random distribution at 95% confidence. There was a negative interaction (i.e. repulsion) between shorter (generally younger than 100 years) and taller (generally older than 250 years) trees. On the other hand, there was a positive interaction (i.e. attraction) between shorter, younger trees and standing dead trees.

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1. Introduction

Lowland *Nothofagus obliqua*, *Laurelia sempervirens*, and *Persea lingue* dominated old-growth forests are scarce and ecologically important in south-central Chile. These forests once covered the central depression (low-elevation, below 400 m) of south-central Chile (between 38° and 41°S latitude) (Schmithüsen, 1956; Donoso, 1995). They were largely cleared for agriculture (Veblen et al., 1996) and only some remnants of these forests now exist (Donoso, 1995). They now occur either as private estates, such as with the forest studied by Veblen et al. (1979), or as areas retained by research institutions, such as the forest studied by Ramírez et al. (1989a,b) and Frank (1998). The area of these forests is estimated as less than 2% (C. Donoso, personal communication) of the *N. obliqua*–*N. alpina*–*N. dombeyi* forest type described by Donoso (1995). However, some stands are more ecologically limited, occurring as small isolated islands or as stands greatly altered through human

disturbance, leaving about 4000 ha of this forest type. *N. obliqua* dominated old-growth forests are uneven-aged, have multiple height strata, and, in successional terms, they are close to a steady-state condition (Veblen et al., 1979; Donoso, 1995). This forest ecosystem is characterized as being unique in the world, with both large timber volumes (Donoso, 1995) and high biodiversity (Frank, 1998; Salas, 2001). However, they are not represented in Chile's national system of protected areas (SNASPE).

Even though these forests have been considered important for Chilean conservational initiatives (Muñoz et al., 1996), little research exists for these lowland *Nothofagus* dominated old-growth forests. Some research has been conducted on floral composition (Ramírez et al., 1989a,b; Frank, 1998), tree regeneration (Veblen et al., 1979), and structure and dynamics (Veblen et al., 1980; Donoso, 1995; Frank and Finckh, 1998). Spatial distributions and spatial patterns (both vertical and horizontal) of trees in forests are important elements for understanding forest ecosystem dynamics (Veblen et al., 1979), and the potential for ecological understanding has not been fully recognized (Franklin et al., 2002). Nevertheless, few studies on the spatial distributions of trees have been conducted in these forests (Veblen et al., 1979, 1980, 1981). The focus of these studies has been on analysing spatial patterns of

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regeneration, commonly the focus of studies on spatial patterns in forests (Tomppo, 1986). However, knowledge of the spatial distributions of trees would be useful in: (1) understanding inter- and intra-species relationships; (2) designing silvicultural regimes that mimic natural processes; (3) forest inventory planning and design (Tomppo, 1986); (4) improving stand dynamics models by including inter-tree (and inter-species) measures of competition.

A spatial point pattern is a set of locations, irregularly distributed within a region of interest, which have been generated by some unknown spatial process (Diggle, 1983). Many methods and indexes have been developed to interpret and assess spatial distributions (Greig-Smith, 1952; Clark and Evans, 1954; Morisita, 1957; Pielou, 1959; Ripley, 1977, 1979, 1981). These methods can be classified into three main groups, depending upon the type of data required (Ripley, 1981):

- (1) Quadrat (plot) counts, where fixed-area sample plots are established and the number of points (e.g., trees or seedlings) is counted within each plot (e.g., Greig-Smith, 1952). Based on quadrat count data, Fisher et al. (1922) proposed the sample variance-to-mean ratio as an index of dispersion, and Morisita (1957) developed an index of randomness.
- (2) Nearest distance methods, where the distance between the subject (e.g., tree) and its nearest neighbour (nearest neighbour distances) (Clark and Evans, 1954) or the distance from a point to its nearest neighbour (point to nearest distances) (Pielou, 1959) is determined. Neighbours other than the nearest neighbour may be also be used.
- (3) Mapped data, where the location of each object (e.g., tree) is recorded, and used to indicate spatial pattern. Ripley's $K(t)$ function (Ripley, 1977, 1979, 1981) can be used to examine patterns using mapped point data. Although a number of different methods have been applied, this approach has been most commonly applied in ecological spatial pattern analyses in recent years (Liebhold and Gurevitch, 2002).

Variograms and correlograms can also be useful for spatial pattern analyses (Duncan and Stewart, 1991; García, 1992), although these methods are more commonly used for continuous rather than point processes.

As pointed out by Moeur (1993), researchers have used both quadrat and distance methods for assessing forest spatial patterns. Both quadrat and distance methods are largely affected by sampling procedures. Payandeh (1970) tested the quadrat, nearest neighbour, and point-to-plant methods, and stated that the point-to-plant distance performed best, even though all behaved well. However, Condes and Martinez (1998) showed that the aggregation index commonly used with the quadrat method is not efficient. Moreover, quadrat methods are greatly affected by the plot size (Payandeh, 1970; Pielou, 1977; Diggle, 1983; Tomppo, 1986), and by the proportion of plots without points (i.e. zero counts). Nevertheless, the variance-to-mean ratio based on quadrat plots is still widely used (Tomppo, 1986), since data collection and analysis are relatively straightforward. Analysing the distribution of nearest neighbour distances may give insights to competition and other processes (Moeur, 1993). However,

important patterns and processes might exist beyond the nearest neighbour, and would be missed if only the nearest neighbour distances are examined. As pointed out by Haase (1995), both quadrat and distance methods have been frequently modified, resulting in an increasing number of approaches. However, problems remain in using these methods. Ripley's $K(t)$ function (Ripley, 1977, 1979, 1981) overcomes many of the problems cited by Haase (1995). Since Ripley's $K(t)$ function uses distances between all possible pairs of trees, via increasing the radius from the target tree, spatial patterns at many scales can be more easily detected, which is particularly useful for forests with very high spatial variability (Moeur, 1993).

Most of the spatial pattern studies in natural Chilean forests have been conducted using point-to-plant measures, nearest neighbour methods (Barasorda, 1977; Morales, 1981; Alvarez, 1982; Peters, 1985), or Morisita's index (Veblen et al., 1979, 1980). These methods have resulted in difficult interpretations of spatial patterns for old-growth *Nothofagus* trees, largely due to the small numbers of the trees in these stands (Barasorda, 1977; Alvarez, 1982; Peters, 1985) and to the use of relatively small plot sizes (Veblen et al., 1979, 1980). Alternatively, Ripley's $K(t)$ function (Ripley, 1977, 1979, 1981) is particularly useful for forests with very high spatial variability since spatial patterns at many scales can be more easily detected. Ripley's $K(t)$ function has been applied to *N. obliqua*–*N. alpina* second-growth (Martin, 1995), evergreen (Gutiérrez, 2002), and *Gomortega keule* (Villegas et al., 2003) forests, with some success. No study of the spatial distribution of *Nothofagus* old-growth forests using Ripley's $K(t)$ function was found in the literature.

In this study, we use Ripley's $K(t)$ function to examine spatial patterns of trees in mature *N. obliqua* forest remnants in Rucamanque, near the city of Temuco, a forest considered important for Chilean conservation goals (Muñoz et al., 1996). The main reason for examining these spatial patterns is to gain insights into inter-tree competition, and to spatial relationships related to stand structure. This information could be used to inform management practice (e.g., to mimic natural spatial patterns) and to alter models of stand dynamics.

2. Data

2.1. Study area

We studied a stand of 18.3 ha, in Rucamanque (38°39'S, 72°35'W), at 376 m of altitude, County of Temuco, Cautín province, IX Region, Chile. This stand is part of a 230 ha late successional stage forest, dominated by shade-tolerant tree species, with scattered 260–460-year-old *N. obliqua* trees (Salas and García, 2006). This old-growth stand averages 590 trees/ha, 93.7 m²/ha of basal area, and 1096.7 m³/ha total volume, with the most abundant tree species being *Aextoxicon punctatum*. *N. obliqua* constitutes about 20% of the volume and basal area, with approximately 30 trees/ha and diameter at breast height (dbh) values over 70 cm (Fig. 1). Stands of this type are remnants of the original sub-type of the *N. obliqua*–*N. alpina*–*N. dombeyi* forest type according to Donoso (1995).

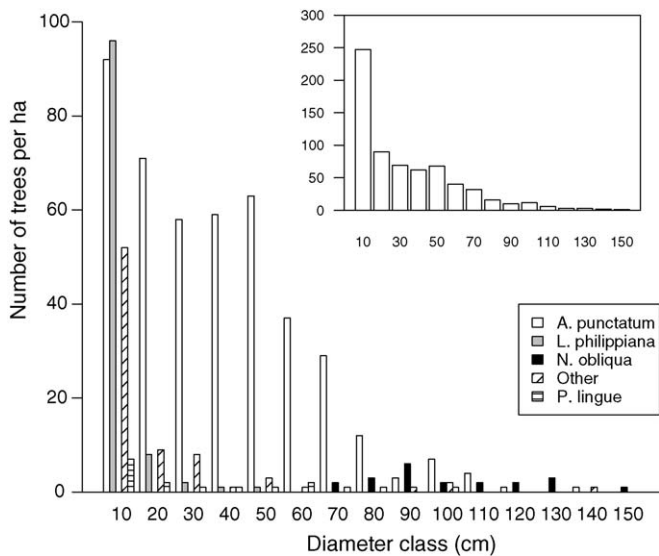


Fig. 1. Diameter distribution for all live trees of each major species and for all species combined (inset).

Botanically, this type of forest is classified as the *Lapagerio–Aextoxiconetum punctatii* association according to Oberdorfer (1960). Further details about ecology of these species can be found in Veblen et al. (1979, 1996), Veblen and Schlegel (1982), and Donoso (1994, 1995).

This forest has had very limited human intervention (Ramírez et al., 1989a,b; Salas, 2001, 2002). The site falls in Growth Region 1 of Donoso et al. (1993), which represents the best growth rates over the natural range of *N. obliqua*. The high productivity of the site is due to very rich soil features and climatic conditions that promote tree growth for this species (Frank, 1998; Salas, 2001).

2.2. Measurements

A 1 ha permanent square sample plot was established in this stand in 2002. The plot was located in an average stand condition based on information from four other 1000 m² permanent sample plots established in the same stand. The coefficients of variation for these four plots were 31.8, 23.3, and 23.6% for the number of trees, basal area, and stand volume, respectively. The established 1 ha permanent sample plot represents a natural (i.e. with minimum human intervention) density condition. On all live and dead standing trees with dbh ≥ 5 cm, species, dbh, and crown class were measured. When trees were multi-stemmed, each stem was considered a separate tree, if the stem-division was 1.3 above ground. Total height (*h*) was measured on 238 trees, selected with probability proportional to basal area in each diameter class. For non-sampled height trees, total height was imputed using species-specific height–diameter equations. Gross volume was estimated with group-species equations fitted by Salas (2002) for Rucamanque. The location of each tree was recorded, via conventional measurements of distance, slope, and azimuth. The position of each tree on a Cartesian plane was later determined using trigonometric relationships.

3. Methods

3.1. Statistical analysis

We used Ripley's $K(t)$ function (Ripley, 1977, 1979, 1981) to examine tree spatial arrangements. Since this method considers the distances between all pairs of point (trees) in the plane (Moeur, 1993; Haase, 1995), more detailed analyses of interactions among points, both within a class of points (i.e. same species, whole stand level) and also between separate point populations (i.e. between species 1 and 2), were possible (Moeur, 1993). The function counts the number of neighbour trees within a circular plot of radius t , centered at each tree in the study area. This process is repeated using increasingly larger values (radii) of t .

For both univariate (i.e. within a class of points) and bivariate (i.e. between two class of points) analyses, only groups with more than 10 trees in the permanent sample plot were used (e.g., single species as a group, or all live trees as a group). All the analyses were conducted using the software package Spatial Point Pattern Analysis (SPPA), Version 2.0.3, created by Dr. Peter Haase.

3.1.1. Univariate analysis

We determined the spatial distribution for live trees by species, specifically: *A. punctatum*, *N. obliqua*, *P. lingue*, and *Laureliopsis philippiana*. For each species, the Ripley's $K(t)$ function (Ripley, 1976, 1981) was calculated as

$$\hat{K}(t) = \frac{A}{n^2} \sum_{i=1}^n \sum_{j=1}^n \frac{1}{w_{ij}} I_t(u_{ij}), \quad (1)$$

where A is the plot size (m²), n the number of trees measured for the plot, u_{ij} the distance (m) between the i th subject tree and the j th tree, I_t a counter, equal to 1 if $u_{ij} \leq t$ (the tree is within the circular plot of radius t) or 0 otherwise, and w_{ij} is an edge correction factor. The edge effect arises from the unobservability of points outside the 1 ha plot.

Ripley's $K(t)$ values were computed both from the i th to the j th tree and vice versa. $K(t)$ values can be interpreted as the expected number of trees within distance t of an arbitrary tree (Tomppo, 1986; Moeur, 1993). Edge effects were corrected using the following expression proposed by Haase (1995):

$$w_{ij} = 1 - \frac{2 \cos^{-1}(e_1/u_{ij}) + 2 \cos^{-1}(e_2/u_{ij})}{2\pi}, \quad (2)$$

where w_{ij} is the correction factor for i th border tree and its j th neighbour tree, e_1 and e_2 the distances to the two closer borders from the i th tree, and \cos^{-1} refers to the inverse cosine function.

We used 0.5 m as the interval for incrementing t , starting with $t = 0.5$, and ending with a maximum value of $t = 50$ m, following the recommendation of Haase (1995), to minimize edge problems and approximation errors in the location measurement of trees (Hanus et al., 1998). Also, beyond 50 m, we expected interactions between trees to be minimal (i.e. Moeur, 1993 used 12.2 m (40 ft)). To facilitate the interpretation of the resulting Ripley's $K(t)$ function, Besag (1977)

proposed an estimator $\hat{L}(t)$ resulting in a linear pattern of L versus t under a Poisson (random) spatial process. This was slightly modified by Ripley (1979, 1981). We used the following estimator (Ripley, 1979):

$$\hat{L}(t) = \sqrt{\frac{\hat{K}(t)}{\pi}} - t. \quad (3)$$

The estimator $\hat{L}(t)$ also stabilizes the variance and gives an expected value equal to 0 for a Poisson (random) spatial distribution (Besag, 1977; Ripley, 1979). Therefore, $\hat{L}(t)$ indicates the difference between the number of trees within a circular plot of radius t and the number of trees expected under a Poisson (random) spatial process (Hanus et al., 1998).

Monte Carlo simulations were conducted to test the null hypothesis of a Poisson process, suitable for unknown distributions and for smaller sample sizes and commonly used with spatial indices (Besag and Diggle, 1977). For each simulation, each tree was randomly relocated over the permanent sample plot, then the $\hat{L}(t)$ was computed for each t . Following Haase (1995), we conducted 19 simulations. Based on the resulting empirical distribution of $\hat{K}(t)$, a 95% confidence envelope over t was computed for $\hat{K}(t)$ under a random spatial process.

Based on the confidence envelope under a random process, three different outcomes are possible. If the values of $\hat{L}(t)$ are inside of the confidence envelope, the observed spatial distribution is likely random. If $\hat{L}(t)$ is larger than the upper values of the confidence envelope, the distribution is aggregated or clustered. Finally, if $\hat{L}(t)$ falls under the lower limit of the confidence envelope, the distribution is likely uniform or regular.

3.1.2. Bivariate analysis

The bivariate version of Ripley's $K(t)$ function was used to investigate potential spatial relationships among two groups of trees, specifically:

- (1) live trees < 15 m tall (group 1, the shortest height class) versus live trees 35 m and taller (group 2, the tallest height class),
- (2) all live trees versus standing dead trees, and
- (3) live trees (group 1) versus standing dead trees.

A number of indices (or methods) can be used to indicate vertical diversity (Staudhammer and LeMay, 2001), but few give both vertical and horizontal diversity (LeMay and Staudhammer, in press). One way to indicate both vertical and horizontal diversity is to divide trees into relevant height strata, and use these to calculate a bivariate spatial index. The 20 m interval between the two vertical strata provided separation into understory versus overstory trees. The bivariate Ripley's $K(t)$ function indicated spatial relationships between these height strata. This bivariate spatial pattern is also reflective of stand dynamics, since trees in the shorter height class were younger (mostly less than 100 years), whereas trees in the taller class were older (more than 250 years). Also, a similar approach was used by Moeur's (1993) study and,

therefore, comparisons were possible. The interactions between live and dead trees were also of interest, in particular, whether shorter live trees might be associated with standing dead trees, indicating regeneration in proximity to standing dead trees.

The bivariate version of Ripley's $K(t)$ function was used to detect the degree of repulsion, attraction, or indifference between the two groups (Andersen, 1992; Haase, 2001; Lotwick and Silverman, 1982). The estimators $\hat{K}_{12}(t)$ and $\hat{K}_{21}(t)$ of the pooled distribution for each of the two groups of interest were calculated (Lotwick and Silverman, 1982). First, $\hat{K}_{12}(t)$, the interaction (or in this case spatial association) between groups 1 and 2, was calculated as

$$\hat{K}_{12}^*(t) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} \frac{1}{w_{ij}} I_t(u_{ij}), \quad (4)$$

where n_1 and n_2 are the numbers of trees in groups 1 and 2, respectively, and u_{ij} is the distance (m) between the i th subject tree of group 1 and the j th tree of group 2.

The interaction between groups 2 and 1 was then calculated using

$$\hat{K}_{21}^*(t) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} \frac{1}{w_{ji}} I_t(u_{ji}), \quad (5)$$

and, finally, the bivariate index was calculated using

$$\hat{K}_{12}(t) = \frac{n_2 \cdot \hat{K}_{12}^*(t) + n_1 \cdot \hat{K}_{21}^*(t)}{n_1 + n_2}. \quad (6)$$

By a similar argument as before, we also calculated

$$\hat{L}_{12}(t) = \sqrt{\frac{\hat{K}_{12}(t)}{\pi}} - t. \quad (7)$$

As for the univariate case, a 95% confidence envelope for a random spatial process was found using Monte Carlo simulations. For this bivariate case, when values of $\hat{L}_{12}(t)$ are inside the confidence envelope, the two groups are considered independent (no interaction). If $\hat{L}_{12}(t)$ is greater than the upper limit of the confidence envelope, the two groups are positively associated, meaning there is an attraction between the two groups. Finally, if $\hat{L}_{12}(t)$ falls under the lower limit of the confidence envelope, the association between the two groups is negative, indicating a repulsion between the two groups of trees.

4. Results

4.1. Stand characterization

Stand variables are summarized in Table 1 (see also Fig. 1). These statistics are similar to those reported for this type of forest in Veblen et al. (1979), and to those given for a similar forest in Veblen et al. (1980) where *N. dombeysi* plays the ecological role of *N. obliqua* in Rucamanque. However, a much larger plot size was used for our study.

Table 1
Stand variables summary by species and over all species

	Number of trees		Basal area (m ² /ha)		Gross volume (m ³ /ha)	
	Live	Standing dead	Live	Standing dead	Live	Standing dead
<i>A. punctatum</i>	437	30	68.5	3.41	706.3	30.2
<i>N. obliqua</i>	21	12	17.2	6.77	248.8	33.4
<i>P. lingue</i>	17	5	2.6	0.23	33.5	1.9
<i>L. philippiana</i>	108	2	1.1	0.01	8.6	0.1
Other	78	6	5.7	1.01	63.1	9.3
Total	661	55	95.1	11.4	1060.3	74.9

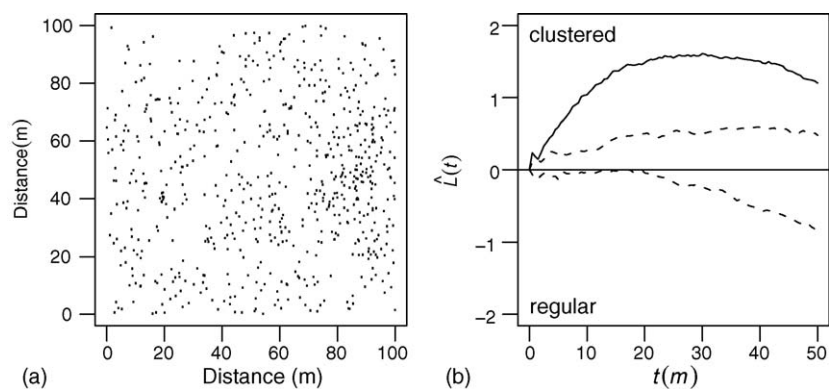


Fig. 2. (a) Locations map of all live trees in a 100 m × 100 m permanent sample plot at Rucamanque Forest, Chile. (b) Ripley's $K(t)$ results. The sample statistic $\hat{L}(t)$ is shown as a solid line, whereas the pointwise 95% confidence envelope for a random spatial process is given as dotted lines.

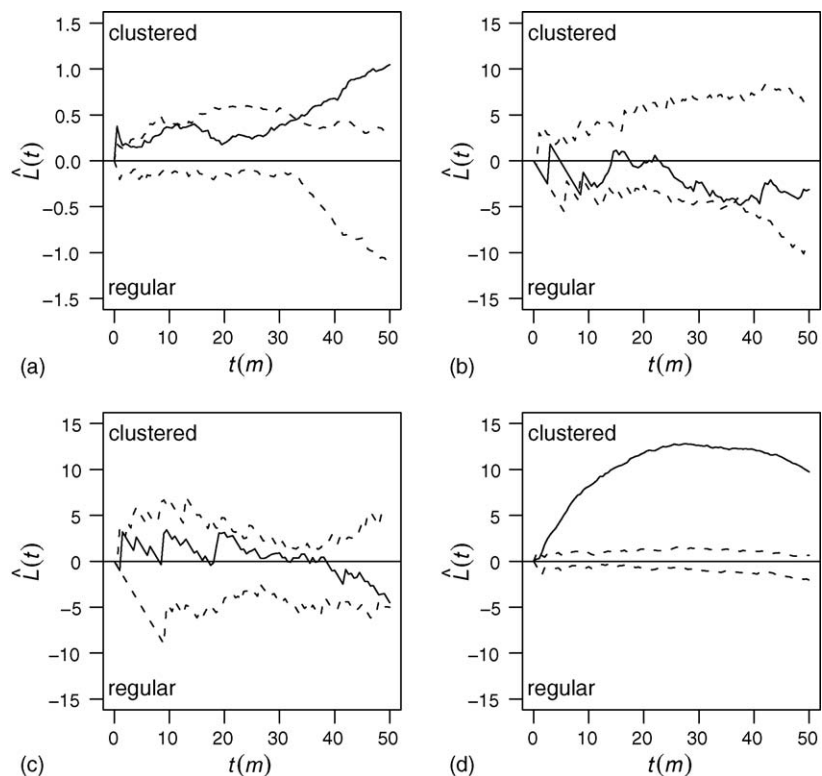


Fig. 3. Ripley's $K(t)$ results for standing live trees for: (a) *Aextoxicon punctatum*, (b) *Nothofagus obliqua*, (c) *Persea lingue*, and (d) *Laureliopsis philippiana*. The sample statistic $\hat{L}(t)$ is shown as a solid line, whereas the pointwise 95% confidence envelope for a random spatial process is given as dotted lines.

The main species, by decreasing basal area, are: *A. punctatum*, *N. obliqua*, *L. philippiana*, *L. sempervirens*, *P. lingue*, and *Eucryphia cordifolia* (Table 1). Species within the class “others” are primarily *E. cordifolia*, *Gevuina avellana*, and *Lomatia dentata*. The stand is an old-growth forest with a reversed J-shaped distribution of tree diameters when pooled for all species (inset in Fig. 1). This is a typical feature for uneven-aged and multi-species stands (Donoso, 1995), with a high concentration of smaller, younger trees, showing that there is abundant regeneration of shade-tolerant species, especially of the very shade-tolerant, *A. punctatum* and *L. philippiana* (Fig. 1). *N. obliqua* occur as emergent trees, as well do *E. cordifolia*. *A. punctatum*, *L. sempervirens*, and *P. lingue* are dominant and codominant canopy tree

species, but *A. punctatum* is present in all height strata. *L. philippiana* is mainly concentrated in the smaller diameter classes and in sub-intermediate and intermediate crown classes.

4.2. Univariate analysis

The map of tree spatial positions for all live trees did not show any obvious clustering (Fig. 2 a). However, the plot of $\hat{L}(t)$ over t for the 1 ha plot indicates that $\hat{L}(t)$ is larger than expected under a random spatial distribution, indicating significant clustering ($P < 0.05$) at all levels of t (Fig. 2b). The maximum level of aggregation occurs at around 30 m.

The four species shown in Fig. 3 have very different spatial patterns. *A. punctatum* showed a random distribution until 33 m and a clustered distribution for this and larger distances (Fig. 3a). *N. obliqua* showed a clear trend toward a regular spatial distribution for over the 22 m of distance (Fig. 3b), but this was not significantly different from a random distribution ($P > 0.05$). *P. lingue* showed a random distribution (Fig. 3c), but there was some evidence of a trend toward a clustered distribution with distances between 3 and 9 m, and other distances, but this was not significant. *L. philippiana* clearly showed a clustered spatial distribution ($P < 0.05$), with highest values at 26.5 m (Fig. 3d).

4.3. Bivariate analysis

There was a negative interaction (repulsion) between short (< 15 m tall) and tall trees (35 m and taller) (Fig. 4 a). Shorter, younger trees were less frequent near tall live trees ($t \geq 9$ m), likely because of shading, and competition for other resources.

There was evidence of a positive interaction (attraction) between live and standing dead trees (Fig. 4b), indicating a tendency for trees to regenerate close to dead standing trees. This is supported by Fig. 4c, which shows that shorter, younger trees are associated with dead standing trees at all but the farthest spatial distances.

5. Discussion

5.1. Stand characterization

Stand features similar to that of this study were reported both by Veblen et al. (1979, 1980) and by Alvarez (1982) for forest remnants in other locations in Chile, and also by Salas (2001) for the average condition of old-growth Rucamanque forests. The current structure is a result of a long-term process of successional dynamics. After disturbance, *N. obliqua* dominates the structure and composition, as it is an early seral (pioneer) and shade-intolerant species (Veblen et al., 1996). After a long period of time, in the case of Rucamanque forest approximately 450 years (Salas and García, 2006), the most shade-tolerant (*A. punctatum* and *L. philippiana*) (Figueroa and Lusk, 2001) and other semi-shade-tolerant species (*P. lingue* and *L. sempervirens*) dominate the stand structure (Donoso, 1995). In this stand, *A. punctatum* was the dominant species

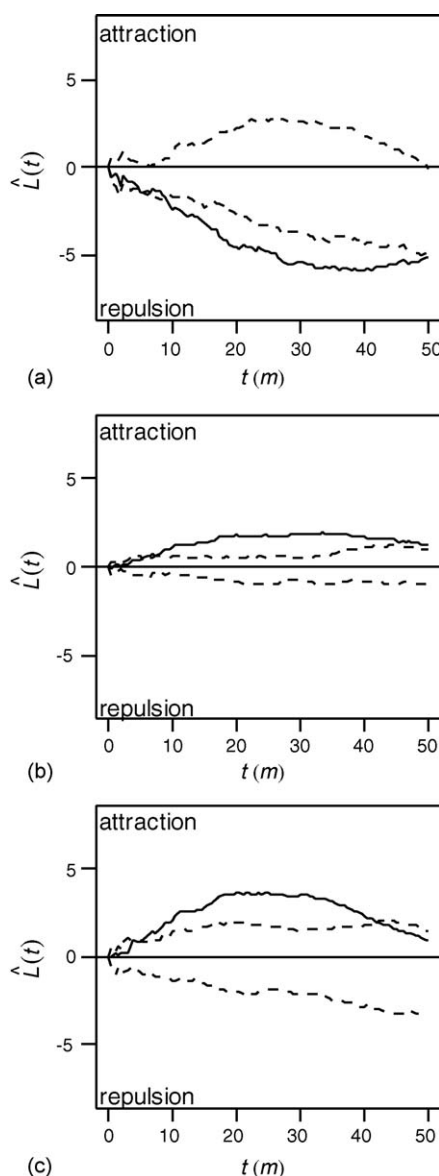


Fig. 4. Ripley's $K(t)$ results for the interaction of: (a) live trees < 15 m tall with live trees 35 m and taller, (b) live trees with standing dead trees, and (c) live trees < 15 m tall with standing dead trees. The sample statistic $\hat{L}(t)$ is shown as a solid line, whereas the pointwise 95% confidence envelope for a random spatial process is given as dotted lines.

with 72% of the stand basal area (Table 1). The gross volume was high, due to the large dimensions of the old-growth trees of *N. obliqua* and the high density of *A. punctatum*, representing 90% of the stand volume. *A. punctatum* trees occur in all diameter classes (Fig. 1), showing continuous regeneration (Veblen et al., 1979, 1980). Conversely, *N. obliqua* was only represented in the very large diameter classes (> 70 cm) and in the emergent tree stratum. *L. philippiana* is the most shade-tolerant species of this forest type, and, therefore was represented by a large number of trees in the smaller diameter classes, with few in the medium and larger size classes. *P. lingue* appears to be still regenerating due to its semi-shade-tolerance, but at a rate far lower than *A. punctatum* and *L. philippiana*, features also reported by Veblen et al. (1979, 1980). Further details about strata composition were reported by Veblen et al. (1979) for a similar forest and by Ramírez et al. (1989a,b) and Frank (1998) for Rucamanque.

5.2. Univariate analysis

Clustered spatial distributions are often typical in naturally regenerated stands (van Laar and Akça, 1997). For very old forests at Wind River on the Pacific Coast of the USA, North et al. (2004) found that trees were clustered at all distances. In *Nothofagus* forests, shade and semi-shade-tolerant species established in small gaps, resulting in small groups of juvenile trees (Veblen et al., 1979). In this study, spatial distribution for all trees seemed very similar to that of *L. philippiana*, suggesting a great influence of this species on the spatial distribution of trees in the stand.

A. punctatum occurred in larger spatial clusters of trees (in some cases 40 trees), resulting in evidence of clustering at larger spatial scales. Clustering also appeared to be present at shorter distances, although this was not detected as being different from a random spatial process. Veblen et al. (1979) also detected a random spatial distribution using Morisita's index for *A. punctatum* with dbh < 10 cm. However, they did not detect clustering at larger scales, possibly due to a smaller sample plot size, and problems in using Morisita's index. In general, the *A. punctatum* spatial distribution was more clustered than for *P. lingue*, indicating that *A. punctatum* regenerated in gaps, even though this species is able to regenerate under a continuous canopy cover (Veblen et al., 1979).

The spatial distribution of *N. obliqua* in this type of forest is likely influenced by their longevity of more than 400 years (Salas and García, 2006). This very old stand may have started with 40,000 *N. obliqua* seedlings/ha (Veblen et al., 1996), but, through self-thinning, it is now composed of just 20 very large-crowned *N. obliqua* trees/ha. There was some evidence of a regular distribution, but this was not detected as being different from a random process, possibly due to the small number of trees. Even though there are few trees, however, 18% of the stand basal area was represented by this species. *N. obliqua* is not able to regenerate under the current conditions of a continuous canopy cover and little exposed bare mineral soil, and is frequently replaced by very-shade-tolerant species such

as *A. punctatum* and *L. philippiana* (Veblen et al., 1980, 1996). Unless large disturbance occurs, the early seral species will not regenerate, and this forest could be considered to be in a steady state. Veblen et al. (1980) postulated that the emergent crown classes of *N. alpina* and *N. dombeyi* for the Valdivian low-land forests were established as a consequence of drastic perturbations, rather than from gaps produced by one or two trees falling. However, Veblen et al. (1979, 1980, 1981) did not report spatial distribution results for their old-growth *Nothofagus*. The sample plot size for these studies (2400 m²) may have been too small to represent the high spatial heterogeneity of these forests.

P. lingue showed a random spatial distribution. There was some evidence of a trend toward clustering, even though not significant, in "waves" of around 10 m (between 3 and 9, 9 and 19, and 19 and 29 m) up to a distance of 30 m. This phenomenon creates small (of around 10 m of radii) even-sized groups of *P. lingue* trees, growing under a continuous cover of an uneven-aged stand. Above 38 m, where distances between the tallest and smallest trees are captured, there was some evidence of a trend toward regularity (not significant). Clustered distributions are common for small trees (dbh's around 10 cm) located in gaps. The progressive change to a random distribution in older stages was likely the result of competition within these clumps, as noted by Veblen et al. (1979) for *P. lingue*.

L. philippiana can regenerate well under a continuous canopy cover, and can reproduce vegetatively, resulting in clumps (average area of 2206 m², based on a radii of 26 m) of similar-sized trees. Most of the *L. philippiana* trees were small in diameter. Similar results were reported by Peters (1985) using distance methods. Clumps are also likely due to abundant regeneration as a result of high seed production and the establishment of trees in small gaps (Veblen et al., 1979, 1980, 1981). Veblen et al. (1980) found a random distribution for this species at a large scale of analysis; however, they noted that their results were confounded by using a small number of trees in computing Morisita's index. The high proportion of both *L. philippiana* and *A. punctatum* in this forest is a clear example of the dynamics of the lowland old-growth *Nothofagus* forests (Donoso, 1995), when old-growth *Nothofagus* are replaced by very shade-tolerant species.

5.3. Bivariate analysis

The repulsion between short and tall trees found in this study was also reported by Moeur (1993) for natural uneven-aged forests in Idaho (USA), as well as by Van Pelt and Franklin (2000) for understory versus canopy trees in old-growth forests along the Pacific Coast of the USA. Taller trees in the upper canopy as a result of a long-term process (around of 450 years in the Rucamanque's case) with increasing competitive capabilities tended to be more randomly distributed. Conversely, lower canopy trees tended to be clustered in gaps and areas around gaps created by the fall of tall, and usually older, large diameter trees. Similar to the results of this study, North et al. (2004) found a repulsion between shade-tolerant and

shade-intolerant trees in old-growth forests of the Pacific Coast of the USA. As noted by Lusk and Ortega (2003) for second-growth *Nothofagus* stands in Chile, emergent trees often do not affect the basal area or abundance of canopy trees, when the overstory canopy is 15–20 m above the lower canopy.

In Chile, few studies on dead trees and their role within the forest ecosystem have been conducted. However, Franklin et al. (1987, 2002) and Spiering and Knight (2005) noted that there is now more emphasis on studying the importance of these dead trees to forest ecosystem function. In this study, there was evidence of attraction between live and standing dead trees, likely the result of regeneration following tree mortality. This was more clearly shown by the strong spatial attraction between short, younger trees and standing dead trees (significant for $t < 42$ m), which was also noted during data collection. This is a property of a forest with minimal or no human intervention, where horizontal diversification is occurring (e.g., when gap development is the dominant process in the forest; Franklin et al., 2002), in this case, over more than 400 years.

6. Concluding remarks

Univariate and bivariate Ripley's $K(t)$ functions were used to identify spatial patterns for trees of different species, and across vertical height strata for an old-growth *N. obliqua* forest in south-central Chile. These functions gave insights on stand history, as noted in other studies of spatial patterns. Information on spatial patterns could also be used to improve the development and use of growth models. Tree-level distance-dependent growth models are most suited to these complex forests. In using these models to project growth, tree spatial positions may not always be available, and instead, an expected spatial pattern must be supplied. Based on this study, different spatial patterns would need to be supplied for each species and vertical stratum in these and other complex forests. Alternatively, this spatial information could be used to supplement a tree-level distance-independent model to increase the precision without the cost of tree spatial measures. The bivariate functions were used to examine relationships across height strata and between live versus dead trees in this study, but other relationships could be examined, including inter-species interactions as an aid to modelling successional processes. Finally, although this study examined spatial patterns for a single point in time, knowledge of spatial patterns over time would give further insights into the competitive processes of these species to better model forest dynamics, and also into natural spatial patterns of largely undisturbed forests to inform management decisions.

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References

- Alvarez, M., 1982. Análisis de la estructura y dinámica de los bosques vírgenes y alterados en el fundo San Martín. Tesis Ingeniero Forestal, Universidad Austral de Chile, Valdivia, Chile, 114 pp.
- Andersen, M., 1992. Spatial analysis of two-species interactions. *Oecologia* 91 (1), 134–140.
- Barasorda, M., 1977. Estudio de distribución horizontal y densidad en bosques de *Nothofagus glauca* (Phil.) Krasser. Tesis Ingeniero Forestal, Universidad de Chile, Santiago, Chile, 37 pp.
- Besag, J., 1977. Contribution to the discussion of Dr. Ripley's paper. *J. R. Stat. Soc. B* 39 (2), 193–195.
- Besag, J., Diggle, P.J., 1977. Simple Monte Carlo test for spatial pattern. *Appl. Stat.* 26 (3), 327–333.
- Clark, P., Evans, E., 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35 (4), 445–453.
- Condes, S., Martínez, J., 1998. Comparación entre los índices de distribución espacial de árboles más usados en el ámbito forestal. *Investigación Agraria: Sistemas y Recursos Forestales* 7 (1–2), 173–187.
- Diggle, P.J., 1983. *Statistical Analysis of Spatial Point Patterns*. Academic Press, London, England, 148 pp.
- Donoso, C., 1994. *Ecología Forestal. El Bosque y su Medio Ambiente*, fourth ed. Editorial Universitaria, Santiago, Chile, 369 pp.
- Donoso, C., 1995. *Bosques Templados de Chile y Argentina. Variación, Estructura y Dinámica*, third ed. Editorial Universitaria, Santiago, Chile, 484 pp.
- Donoso, P., Donoso, C., Sandoval, V., 1993. Proposición de zonas de crecimiento de renovales de roble (*Nothofagus obliqua*) y raulí (*Nothofagus alpina*) en su rango de distribución natural. *Bosque* 14 (2), 37–55.
- Duncan, R.P., Stewart, G.H., 1991. The temporal and spatial analysis of tree age distributions. *Can. J. Forest Res.* 21 (12), 1703–1710.
- Figueroa, J.A., Lusk, C.H., 2001. Germination requirements and seedling shade tolerance are not correlated in a Chilean temperate rain forest. *New Phytol.* 152 (3), 483–489.
- Fisher, R.A., Thornton, H.G., Mackenzie, W.A., 1922. The accuracy of the plating method of estimating the density of bacterial populations, with particular reference to the use of Thornton's agar medium with soil samples. *Ann. Appl. Biol.* 9, 325–359.
- Frank, D., 1998. *Umweltauswirkungen des Landnutzungswandels in der IX. Region Chile: Untersuchung von Waldökosystemen und forstlichen Monokulturen am Beispiel der Umgebung Temucos*. Mensch und Buch Verlag, Berlin, Germany, 222 pp.
- Frank, D., Finckh, M., 1998. Laurophyllisation of deciduous *Nothofagus*-forest in southern Chile. In: Klötzky, F., Walther, F. (Eds.), *Recent Shifts in Vegetation Boundaries of Deciduous Forest*. Birkhäuser Verlag, Basel, Germany, pp. 317–331.
- Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. *BioScience* 37 (8), 550–556.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Raeborg, D., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecol. Manage.* 155 (1–3), 399–423.
- García, O., 1992. What is a diameter distribution? In: Minowa, M., Tsuyuki, S. (Eds.), *Proceedings of the Symposium on Integrated Forest Management Information Systems*. Japan Society of Forest Planning Press, Tsukuba, Japan, pp. 11–29.

- Greig-Smith, P., 1952. The use of random and contiguous quadrats in the study of structure in plant communities. *Ann. Bot.* 16 (2), 293–316.
- Gutiérrez, A., 2002. Aplicación de una metodología dendroecológica en un rodal del tipo forestal siempreverde en la isla grande de Chiloé. Tesis Ingeniero Forestal, Universidad de Chile, Santiago, Chile, 57 pp.
- Haase, P., 1995. Spatial pattern in ecology based on Ripley's *K*-function: introduction and methods of edge correction. *J. Vegetation Sci.* 6 (4), 575–582.
- Haase, P., 2001. Can isotropy vs. anisotropy in the spatial association of plant species resolve physical vs. biotic facilitation? *J. Vegetation Sci.* 12 (1), 127–136.
- Hanus, M.L., Hann, D.W., Marshall, D.D., 1998. Reconstructing the spatial pattern of trees from routine stand examination measurements. *Forest Sci.* 44 (1), 125–133.
- LeMay, V.M., Staudhammer, C. Indices of stand structural diversity: mixing discrete, continuous, and spatial variables, extended abstract. In: *Proceedings of the IUFRO Sustainable Forestry in Theory and Practice: Recent Advances in Inventory & Monitoring, Statistics, Information & Knowledge Management, and Policy Science Conference*. Edinburgh, Scotland, 4 pp., in press.
- Liebold, A.M., Gurevitch, J., 2002. Integrating the statistical analysis of spatial data in ecology. *Ecography* 25 (5), 553–557.
- Lotwick, H.W., Silverman, B.W., 1982. Methods for analysing spatial processes of several types of points. *J. R. Stat. Soc. B* 44 (3), 406–413.
- Lusk, C.H., Ortega, A., 2003. Vertical structure and basal area development in second-growth *Nothofagus* stands in Chile. *J. Appl. Ecol.* 40 (4), 639–645.
- Martin, M., 1995. Análisis de la distribución espacial en rodales de roble (*Nothofagus obliqua* (Mirb) (Oerst)) y raulí (*Nothofagus alpina* (Poepp et Endl)) en la zona de Malleco. Tesis Ingeniero Forestal, Universidad de Chile, Santiago, Chile, 82 pp.
- Moeur, M., 1993. Characterizing spatial patterns of trees using stem-mapped data. *Forest Sci.* 39 (4), 756–775.
- Morales, R., 1981. Estudio de intervenciones en un bosque tipo Coigüe según su estructura y distribución horizontal. Tesis Ingeniero Forestal, Universidad Austral de Chile, Valdivia, Chile, 85 pp.
- Morisita, M., 1957. A new method for the estimation of the spacing method applicable to non-randomly distributed population. *Physiol. Ecol.* 7 (4), 215–235 (in Japanese, available as Forest Service Translation 11116, USDA Forest Service).
- Muñoz, M., Núñez, H., Yáñez, J., 1996. Libro rojo de los sitios prioritarios para la conservación de la biodiversidad biológica en Chile. Corporación Nacional Forestal, Santiago, Chile, 203 pp.
- North, M., Chen, J., Oakley, B., Song, B., Rudnicki, M., Gray, A., Innes, J., 2004. Forest stand structure and pattern of old-growth western hemlock/Douglas-fir and mixed-conifer forests. *Forest Sci.* 50 (3), 299–311.
- Oberdorfer, J., 1960. *Pflanzensoziologische Studien in Chile; Ein Vergleich mit Europa. Flora et Vegetatio Mundi II*. Verlag Von J. Cramer, Weinheim, Germany, 208 pp.
- Payandeh, B., 1970. Comparison of methods for assessing spatial distributions of trees. *Forest Sci.* 16 (3), 312–317.
- Peters, H., 1985. Estudio de distanciamiento para tres bosques nativos del género *Nothofagus*. Tesis Ingeniero Forestal, Universidad Austral de Chile, Valdivia, Chile, 107 pp.
- Pielou, E., 1977. *Mathematical Ecology*. John Wiley & Sons, 386 pp.
- Pielou, E.C., 1959. The use of point to plant distances in the study of the pattern of plant populations. *J. Ecol.* 47 (3), 607–613.
- Ramírez, C., Hauenstein, E., San Martín, J., Contreras, D., 1989a. Study of the flora of Rucamanque, Cautín province, Chile. *Ann. Missouri Bot. Gardens* 76 (2), 444–453.
- Ramírez, C., San Martín, J., Hauenstein, E., Contreras, D., 1989b. Estudio fitosociológico de la vegetación de Rucamanque (Cautín, Chile). *Studia Bot.* 8, 91–115.
- Ripley, B.D., 1976. The second-order analysis of stationary processes. *J. Appl. Prob.* 13 (2), 255–266.
- Ripley, B.D., 1977. Modelling spatial patterns. *J. R. Stat. Soc. B* 39 (2), 172–212 (with discussion).
- Ripley, B.D., 1979. Test of randomness for spatial point patterns. *J. R. Stat. Soc. B* 41 (3), 368–374.
- Ripley, B.D., 1981. *Spatial Statistics*. John Wiley & Sons, 252 pp.
- Salas, C., 2001. Caracterización básica del relicto de biodiversidad Rucamanque. *Bosque Nativo* 29, 3–9.
- Salas, C., 2002. Ajuste y validación de ecuaciones de volumen para un relicto del bosque de roble-laurel-lingue. *Bosque* 23 (2), 81–92.
- Salas, C., García, O., 2006. Modelling height development of mature *Nothofagus obliqua*. *Forest Ecol. Manage.* 229 (1–3), 1–6.
- Schmithüsen, J., 1956. Die räumliche Ordnung der chilenischen Vegetation. *Bonner Geographische Abhandlungen* 17, 1–89.
- Spiering, D.J., Knight, R.L., 2005. Snag density and use by cavity-nesting birds in managed stands of the black hills national forest. *Forest Ecol. Manage.* 214 (1–3), 40–52.
- Staudhammer, C., LeMay, V.M., 2001. Introduction and evaluation of possible indices of stand structural diversity. *Can. J. Forest Res.* 31 (7), 1105–1115.
- Tomppo, E., 1986. Models and methods for analysing spatial patterns of trees. In: *Communications Instituti Forestalis Fenniae*, vol. 138, The Finnish Forest Research Institute, Helsinki, Finland, 65 pp.
- van Laar, A., Akça, A., 1997. *Forest Mensuration*. Cuvillier Verlag, Göttingen, Germany, 418 pp.
- Van Pelt, R., Franklin, J.F., 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. *Can. J. Forest Res.* 30 (8), 1231–1245.
- Veblen, T.T., Ashton, D.H., Schlegel, F.M., 1979. Tree regeneration strategies in a lowland *Nothofagus*-dominated forest in south-central Chile. *J. Biogeogr.* 6 (4), 329–340.
- Veblen, T.T., Donoso, C., Kitzberger, T., Rebertus, A.J., 1996. Ecology of southern Chilean and Argentinean *Nothofagus* forests. In: Veblen, T.T., Hill, R.S., Read, J. (Eds.), *The Ecology and Biogeography of Nothofagus Forests*. Yale University Press, New Haven/London, pp. 293–353.
- Veblen, T.T., Donoso, C., Schlegel, F.M., Escobar, B., 1981. Forest dynamics in south-central Chile. *J. Biogeogr.* 8 (3), 211–247.
- Veblen, T.T., Schlegel, F.M., 1982. *Reseña ecológica de los bosques del sur de Chile*. *Bosque* 4 (2), 73–115.
- Veblen, T.T., Schlegel, F.M., Escobar, B., 1980. Structure and dynamics of old-growth *Nothofagus* forests in the Valdivian Andes, Chile. *J. Ecol.* 68 (1), 1–31.
- Villegas, P., Le Quesne, C., Lusk, C.H., 2003. Estructura y dinámica de una población de *Gomortea keule* (Mol.) Baillon en un rodal antiguo de bosque Valdiviano, Cordillera de Nahuelbuta, Chile. *Gayana Botánica* 60 (2), 107–113.