

Spatial structure of deciduous forest stands with contrasting human influence in northwest Spain

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Abstract Five contrasting deciduous forest stands were studied to characterize the spatial structural variability in human-influenced forests. These stands are representative of cultural forest types widely represented in western Europe: one plantation, two coppices, one wood-pasture forest and one high forest stand. All stems with DBH > 5 cm were measured and mapped, and stem DBH distributions, spatial structure of DBH, spatial point patterns and spatial associations were analysed. Spatial autocorrelation for DBH was calculated with Moran's *I* correlograms and semivariograms. Complete spatial randomness hypothesis for spatial point patterns, and both independence and random labelling hypotheses for spatial associations were analysed using Ripley's *K* function. The results showed that tree sizes were conditioned by particular former management systems, which determined unimodal symmetric, positively skewed or compound DBH distributions. Spatial structure was more complex when human influence became reduced. Coppice stands showed clumped spatial patterns and independence among size classes, as a consequence of sexual and vegeta-

tive establishment of new stems in open areas. The largest clumping intensity was observed in the wood-pasture with an intermediate disturbance frequency and low inter-tree competition. The high forest stand displayed spatial traits consistent with the gap-dynamics paradigm, such as clumping of smaller trees, random arrangement of larger trees, negative association between juveniles and adults, and high structural heterogeneity. It can be expected that after cessation of human interference, coppices and wood-pastures would evolve to a more heterogeneous structure, probably with a higher habitat and species diversity.

Keywords Geostatistics · Spatial autocorrelation · Moran's *I* coefficient · Spatial pattern · Null models · Random labelling · Ripley's *K* function · Stand structure

Introduction

The study of tree spatial patterns in forest stands has become a relevant tool in the analysis of the structure and dynamics of forest communities, and provides a measure of habitat quality (Pommerening 2002). Trees live too long to allow opportunity for experimental research, but their positions are stationary and therefore the ecological and historical processes that influence tree spatial patterns can be statistically analysed (Gavrikov and Stoyan 1995). Although ecological and historical processes cannot be deduced directly from observed patterns, they themselves and their changes can provide a basis for generating hypothesis about underlying processes (Wiegand and Moloney 2004).

Statistical analysis of tree stands need suitable methods of spatial statistics, among which geostatistical modelling and the analysis of spatial point processes are mostly used

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(Liebhold and Gurevitch 2002). Complementary methods used to quantify and model the spatial structure of forest trees include the correlograms of statistics to measure spatial autocorrelation, the variograms to model spatial dependence, and estimating values at unsampled locations by kriging (Legendre and Fortin 1989; Kuuluvainen et al. 1998). Although these methods are generally used as single techniques to quantify spatial autocorrelation, their combined use has been recommended to mitigate the inherent limitations of individual tests (Perry et al. 2002).

Null models for spatial point processes can be used as benchmarks to differentiate among types of spatial patterns. The simplest null model is the homogeneous Poisson, which corresponds to the hypothesis of complete spatial randomness (CSR) that allows differentiating among the clumped, random or regular spatial patterns. The relationship between two spatial point processes can be assessed with different null models. The independence model asks questions about the interaction between the two processes, and the random labelling model asks questions about the process that assigns labels to points (Dixon 2002; Goreaud and Pélissier 2003). Random labelling has not been frequently used in forestry research, but it has been implicitly used to assess “random mortality”, considering labels as the live and dead categories (Kenkel 1988).

The structural characterization of formerly managed stands would be more useful to anticipate the future forest changes than other approaches based on long-term processes of autogenic succession (McLachlan et al. 2000). The study of both natural and managed stands with spatial analytical methods is essential to generate theories about stand developmental processes in human-influenced forests (Penttinen et al. 1992). Recent research comparing the spatial variability among natural and managed stands of boreal, tropical and southern hemisphere deciduous forests (Kuuluvainen et al. 1996; Batista and Maguire 1998; Fajardo and Alaback 2005) suggest that natural forests are likely to host the highest amount of structural and biological diversity. The history of the forest stands has an important influence on the spatial structure of west-European deciduous forests (Wolf 2005). Formerly managed stands revealed a great variety of spatial patterns, from regular distributions derived from active forestry practices, to clumped patterns when management ceased (Koukoulas and Blackburn 2005; Wolf 2005; Rozas 2006). Spatial stand structure has an important role in determining habitat and species diversity and can be quantified to assess habitat quality for conservation purposes (Pommerening 2002; Skov and Svenning 2003).

In this paper we analyse the spatial structure of tree sizes in five deciduous forest stands with different human influence. These stands are representative of widespread traditional systems formerly used in western Europe: plan-

tations, coppices, wood-pastures and high forests (terminology as by Peterken 1996). The studied stands probably have a long history of management, but during the 20th century this had ceased due to socio-economic changes. The study aims to: (1) describe the spatial structure of tree sizes in man-made and semi-natural deciduous forest stands, (2) identify and characterize the patterns of stem distribution and the spatial interactions among size classes and (3) interpret them in terms of previous management and forest dynamics.

Materials and methods

Study areas

Five stands characteristic of the study areas, but with specific and contrasting conditions were selected (Table 1). The selected stands are representative of different management systems with a descending human influence: one artificial tree plantation, two coppice stands with different species composition, one multi-aged wood-pasture mainly composed of lapsed pollards and one uneven-aged high forest stand. Bora (Pontevedra province) is a plantation of *Castanea sativa* established about 25 years ago near Pontevedra city on a sandy acidic soil. Weeds were periodically controlled during the initial 10 years after plantation, and no other tree species are present in this stand. Mondariz (Pontevedra) and Pantón (Lugo) are typical oak coppice stands of Galicia on acidic soils over granite bedrock, traditionally used for brushwood production in short rotations. Pantón is composed by *Quercus robur* and *Q. pyrenaica* in an intimate mixture while in Mondariz the dominant species is *Q. robur*. Sporadic *Castanea sativa*, *Betula alba* and *Frangula alnus* individuals are also present in both stands.

Tragamón (Asturias) is a wood-pasture located near Gijón city on deep brown soils on alluvial depositions of gravel, sand and clay. It is composed mainly of *Q. robur* and *Castanea sativa*, and other tree species include *Q. pubescens*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Laurus nobilis*, *Taxus baccata*, *Prunus laurocerasus* and *Ilex aquifolium*. Tragamón has been used as a recreation park since the 1960s. Prior to that time, it was used as a cattle pasture and for the pollarding of mature oak and chestnut trees. A reconstruction of the management history revealed that pollarding of oak trees was intense from 1730 to 1905, but since that year pollarding frequency and intensity has been in decline (Rozas 2004).

Caviedes forest (Cantabria) is located on a gentle slope with deep sandy soils, with a bedrock of sandstone and clay. *Fagus sylvatica* and *Q. robur* are the dominant tree species in the forest canopy, and other relevant woody species are *I. aquifolium*, *Frangula alnus*, *Salix atrocinerea*,

Table 1 Characteristics of the studied forest stands and differentiation of point patterns on the basis of diameter classes

Stand	North latitude	West longitude	Altitude (m)	Area (m ²)	Stem density (ha ⁻¹)	Dominant species	Point pattern	DBH range (cm)	<i>N</i>
Bora	42° 26'	8° 35'	150	2,435	333	<i>C. sativa</i>	Bora 1	5–24.9	41
							Bora 2	≥25	40
Mondariz	42° 14'	8° 27'	90	7,579	637	<i>Q. robur</i>	Mondariz 1	5–14.9	186
							Mondariz 2	15–19.9	148
							Mondariz 3	≥20	149
Pantón	42° 30'	7° 36'	450	5,489	942	<i>Q. pyrenaica, Q. robur</i>	Pantón 1	5–14.9	147
							Pantón 2	15–19.9	188
							Pantón 3	≥20	182
Tragamón	43° 31'	5° 38'	40	37,900	83	<i>Q. robur, C. sativa</i>	Tragamón 1	5–44.9	120
							Tragamón 2	45–89.9	111
							Tragamón 3	≥90	83
Caviedes	43° 20'	4° 18'	150	5,500	498	<i>F. sylvatica, Q. robur</i>	Caviedes 1	5–9.9	148
							Caviedes 2	10–24.9	60
							Caviedes 3	≥25	66

Densities refer to stems with DBH ≥ 5 cm

N number of points in the pattern

Pyrus cordata and *Corylus avellana*. Characteristics of old-growth, such as standing and fallen dead trees and logs, woody debris, uprooted and snapped trees, soil mound-and-pith topography, large hollow trees and canopy gaps, were observed throughout the forest. The stand in Caviedes had a high forest structure that has been formerly managed by selective logging and pasture by cattle; since the beginning of the 20th century this use has rapidly declined (Rozas 2006).

Field sampling

A complete spatial mapping of tree locations and measurement of stem DBHs (diameter measured at 1.3 m above ground) was carried out for each stand. All living stems over 5 cm in DBH were labelled, measured and mapped. In Bora, Pantón, Mondariz and Tragamón, tree mapping was done with a laser total station by accurately measuring horizontal and vertical angles and distances to the centre of each labelled stem. In Caviedes, the rectangular stand was divided into 100 m² quadrats, on which the *x* and *y* coordinates to the centre of labelled stems were measured to the nearest 0.1 m.

DBH distribution analysis

DBH data in each stand was tested for normality with the robust and powerful D'Agostino third ($\sqrt{b_1}$) and fourth (b_2) moment tests, which test for deviations from normality associated with skewness and kurtosis, respectively (D'Agostino et al. 1990). The null hypotheses are a skewness

of 0 and a kurtosis of 3. These tests were calculated using a SAS macro provided by D'Agostino et al. (1990). The cumulative DBH distributions in 5-cm classes were quantified with the two-parameter Weibull cumulative distribution $F(x) = 1 - \exp[-(x/b)^c]$, where $F(x)$ is the cumulative frequency of trees in DBH class x , b is the scale parameter, and c is the shape parameter (Cao 2004). The Weibull distribution can assume a wide variety of shapes and degrees of skewness, regulated by the scale parameter b and the shape parameter c . At values of $c < 1$ the distribution is descending monotonic whereas at $c > 1$ the distribution is unimodal (Lorimer and Krug 1983). Forest stands with several age classes, tree species or vertical strata usually have compound diameter distributions with irregular shapes, which can be characterized as a mixture of partially overlapping distributions. Compound distributions can be analysed by fitting the frequency distribution of each component (age class, species, stratum) separately and obtaining the prediction for the whole stand as the sum of component models (Liu et al. 2002). We used this approach by dividing compound DBH distributions at Tragamón and Caviedes in their components on the basis of previously identified tree age-classes (Rozas 2004, 2006).

Spatial autocorrelation analysis

The spatial structure of tree diameters was studied with both the Moran's *I* coefficient and the semivariance of tree diameters. *I* coefficient is a measure of the autocorrelation of a quantitative variable for all pairs of points separated by a given spatial lag, which can reveal scales of heterogeneity

of the forest structure related to the size and distribution of even-sized tree patches (Duncan and Stewart 1991). The hypothesis of spatial independence of stem DBH was tested on correlograms of the standard normal deviates of I coefficients calculated by 5-m distance classes, against the critical values for a standard normal distribution. Since several I coefficients were calculated in each correlogram, a correlogram was considered statistically significant only if at least one coefficient was above or below a Bonferroni-corrected significance level (Legendre and Fortin 1989). Moran's autocorrelation analyses were performed with the software written by R.P. Duncan (Duncan and Stewart 1991).

Semivariance is a measure of the degree of spatial dependence between sampled locations and is computed as the sum of squared differences between all pairs of observations that belong to a given distance class (Biondi et al. 1994). Calculating the semivariance for different distance classes produces the experimental semivariogram, which is computed after sorting all possible pairs of locations into classes by distance. Experimental semivariograms were constructed using the VARIOGRAM procedure in SAS, and the exponential and spherical models were fitted to the experimental semivariograms using the NLIN procedure in SAS (SAS Institute 1999). The intercept of the model semivariogram is known as the nugget (C_o), which quantifies spatial variability at near-zero distances. The nugget represents both the variance due to sampling error and the spatial dependence at scales not explicitly sampled. When spatial dependence is present, semivariance typically increases to some asymptote that is called the sill ($C_o + C_n$). The distance at which the semivariogram model reaches a constant value is called the range (A_o), which marks the limit of spatial dependence. In spherical models, the range indicates the mean size of even-sized tree patches, whereas in exponential models the effective range is estimated as $A_o' = 3A_o$, distance at which the semivariance is approximately $0.95 \cdot (C_o + C_n)$ (Webster and Oliver 1990). If semivariance does not show a trend as a function of scale, it can be concluded that spatial dependence is not present. A relative value of the spatial dependence can be calculated as the ratio $C_n/(C_o + C_n)$. Since the nugget reduces the smoothness of the process, a common measure for the degree of spatial structure is the relative structured variability (RSV) = $C_n/(C_o + C_n) \times 100\%$, a useful index to make comparisons among semivariograms (Schabenberger and Gotway 2005).

Spatial point pattern analysis

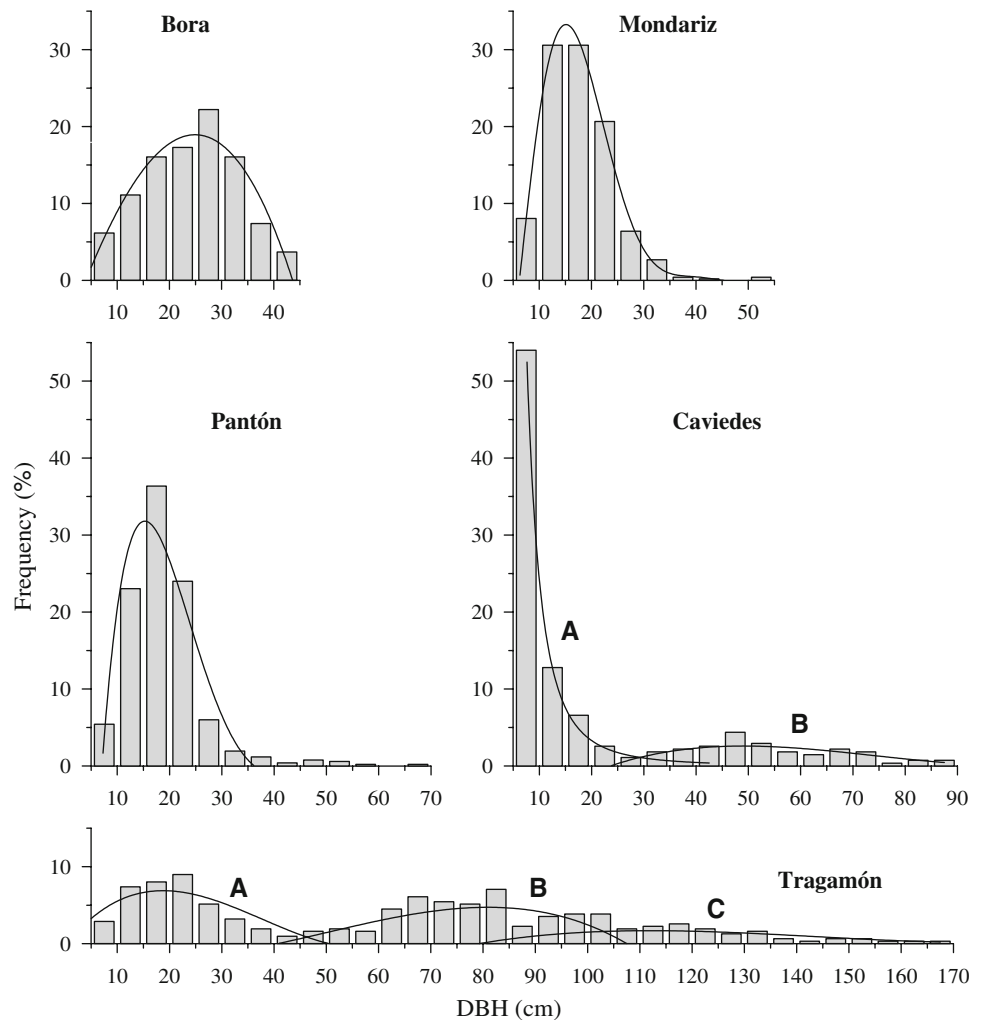
To analyse spatial patterns, we used the univariate Ripley's K function (Ripley 1977), which reflects the type and intensity of a pattern at different inter-tree distances d . Details on

the calculation of $K(d)$ are available in Dixon (2002). The modified function $L(d) = (K(d)/\pi)^{0.5}$ has a more stable variance than $K(d)$, and $L(d) - d$ has an expected value of 0 under the assumption of CSR. $K(d)$ was calculated every 0.5 m, and confidence intervals for testing CSR at the 5% significance level were generated from 10,000 Monte Carlo iterations of random processes (Manly 1997). Significant negative values of $L(d) - d$ indicate inhibition, i.e. the pattern tends to be regular, while positive values of $L(d) - d$ indicate aggregation, i.e. the pattern tends to be clustered. Spatial analyses were performed with the ADS module in the ADE-4 statistical software (Thioulouse et al. 1997). This software integrates edge effect corrections for rectangular as well as irregularly shaped sampling plots (Goreaud and Péliissier 1999). Univariate spatial patterns were analysed for different tree size classes in each locality (Table 1). Tree size classes were defined based on a balanced number of individuals among the classes (Bora, Mondariz and Pantón), or previously identified tree age-classes (Tragamón and Caviedes) (Roza 2004, 2006).

The bivariate extension of Ripley's K function (Lotwick and Silverman 1982) was used to analyse spatial associations between two tree size classes. As with the univariate function, the transformation $L_{12}(d) = (K_{12}(d)/\pi)^{0.5}$ linearizes the function and stabilizes its variance. Both the independence model and the random labelling model were tested. Independence assumes that two different self-regulating processes generated the two patterns. The separate second-order structures of the patterns need to be preserved in their observed form in any simulation of the null model, but breaking any dependence between the two patterns (Wiegand and Moloney 2004). Confidence intervals for testing independence at the 5% significance level were generated from 10,000 random toroidal shifts of one set of trees with respect to the other (Dixon 2002). $L_{12}(d) - d$ has an expected value of 0 under the assumption of spatial independence. Significant positive and negative $L_{12}(d) - d$ values indicate positive and negative association between two sets of trees, i.e. spatial attraction and repulsion, respectively.

The random labelling model assumes that the same process generated both patterns, and each of the two groups (e.g. two different size classes within a single cohort) represents a random attribution of labels to points (Wiegand and Moloney 2004). In this work, the lack of correlation among the diameters of neighbour trees was interpreted as random labelling, i.e. the probability of a tree to be classified as large (or small) is the same for all trees and does not depend on neighbours (Goreaud and Péliissier 2003). To test for random labelling, 95% confidence intervals were generated from 10,000 random assignments of case labels of n_1 out of the $n_1 + n_2$ locations of the type 1 and type 2 points (Wiegand and Moloney 2004). $L_{12}(d) - d$ values above the

Fig. 1 DBH frequency distributions in classes of 5 cm for five deciduous forest stands in northwest Spain, and Weibull models fitted to the complete distributions, or their components (*capital letters*) in the case of compound distributions



confidence intervals indicate positive correlation among the sizes of neighbour trees (similarly sized trees tend to occur together), while values below the confidence intervals indicate negative correlation among the sizes of neighbour trees (similarly sized trees tend to occur separately).

Results

Characteristics of DBH distributions

Frequency DBH histograms showed that Bora, Mondariz and Pantón stands have unimodal size structure, with a shape parameter >1 when fitted to a two-parameter Weibull distribution. By contrast, Tragamón and Caviedes stands have compound DBH distributions (Fig. 1). DBH distribution in Bora was almost symmetric and normal, while in Mondariz and Pantón tree populations were skewed towards larger diameters (Table 2). DBH distribution in Tragamón was a mixture of three partially overlapped unimodal distributions that extended to almost 170 cm. These

three components had shape parameters >1 , and only the component with the smallest mean DBH significantly differed from normality (Table 2). In Caviedes, a compound DBH distribution was observed (Fig. 1). The first component of this DBH distribution had shape parameter <1 , indicating a descending monotonic curve, while the second component showed a normal distribution with shape parameter >1 (Table 2).

Spatial structure

Stem maps interpolated by kriging revealed that DBH patchiness and patch sizes varied greatly among the stands (Fig. 2). All correlograms were globally significant ($P < 0.05$ in Bora, $P < 0.001$ in all other stands) and the maximum likelihood models fitted to the experimental semivariograms were also statistically significant, except in Bora (Table 3). Correlograms displayed positive autocorrelation at small inter-tree distances (less than 10 m in Mondariz, 20 m in Bora, 30 m in Pantón and 75 m in Tragamón) that corresponded to distances between trees of

Table 2 Parameters of DBH distributions, test results for skewness and kurtosis (D'Agostino et al. 1990) and adjusted Weibull models

Stand	N	DBH (cm)				Third sample moment test		Fourth sample moment test		Weibull model	
		Mean	SD	Min	Max	$\sqrt{b_1}$	P	b_2	P	n	c
Bora	81	23.4	8.9	6.0	43.5	-0.20	0.430	2.59	0.515	8	2.33
Mondariz	484	17.0	6.4	5.0	52.0	1.18	0.000	6.49	0.000	10	2.39
Pantón	517	18.3	7.3	5.0	68.0	2.13	0.000	11.79	0.000	13	3.17
Tragamón											
A	129	24.0	12.5	7.3	55.1	1.24	0.000	4.42	0.011	10	1.90
B	131	78.6	14.0	39.3	106.5	0.00	0.986	2.57	0.306	15	4.01
C	54	123.4	20.1	79.1	169.6	0.36	0.238	3.04	0.630	20	3.31
Caviedes											
A	209	9.2	4.5	5.0	36.4	1.66	0.000	5.47	0.000	8	0.97
B	65	53.0	15.5	22.9	87.9	0.49	0.092	2.99	0.715	14	2.96

Capital letters in Tragamón and Caviedes correspond to the components of DBH distributions displayed in Fig. 1. All Weibull models were significant at $P < 0.001$

N number of trees, $\sqrt{b_1}$ sample skewness, b_2 sample kurtosis, n number of 5-cm diameter classes, c shape parameter in Weibull models

similar DBH within a patch (Fig. 3). Negative autocorrelations were also discovered at larger scales (45–65 m in Bora, 50–65 m in Mondariz, 50–80 m in Pantón and 120–165 m in Tragamón). Correlogram for Caviedes displayed alternation of significant positive and negative autocorrelation (Fig. 3). Significant positive autocorrelation at distances of <10 m indicated that similarly sized trees occurred together within a patch. Significant positive values at 45–50, 60–65 and 85–90 m indicated the average distances between patches of similar DBH, while significant negative values at 20–35 and 70–75 m represented the average distances between patches of dissimilar DBH.

The range of spherical semivariograms revealed distances with spatial dependency of DBHs of 13–14 m in Mondariz and Pantón, and almost 19 m in Caviedes (Table 3). A range of 51 m was obtained in the exponential model for Tragamón, which indicated a patch size of over 150 m. The RSV values derived from model semivariograms indicated that Bora stand had a weak spatial dependence, Mondariz, Pantón and Tragamón stands displayed intermediate values of RSV, and in Caviedes spatial heterogeneity was very strong, with a RSV value of 87.27% (Table 3).

Spatial point patterns

Trees in Bora were regularly distributed, as expected, with two main peaks in the regular patterns at 3 and 6.5 m (Fig. 4), which approximately match the initial spacing of the plantation. All size classes in Mondariz and Pantón were clumped, with a wide range of tree clumping in size class 1, up to distances of 22 and 25 m for Mondariz and Pantón, respectively. In size class 2, the pattern was one of alternating patches with clumping and CSR. In size class 3,

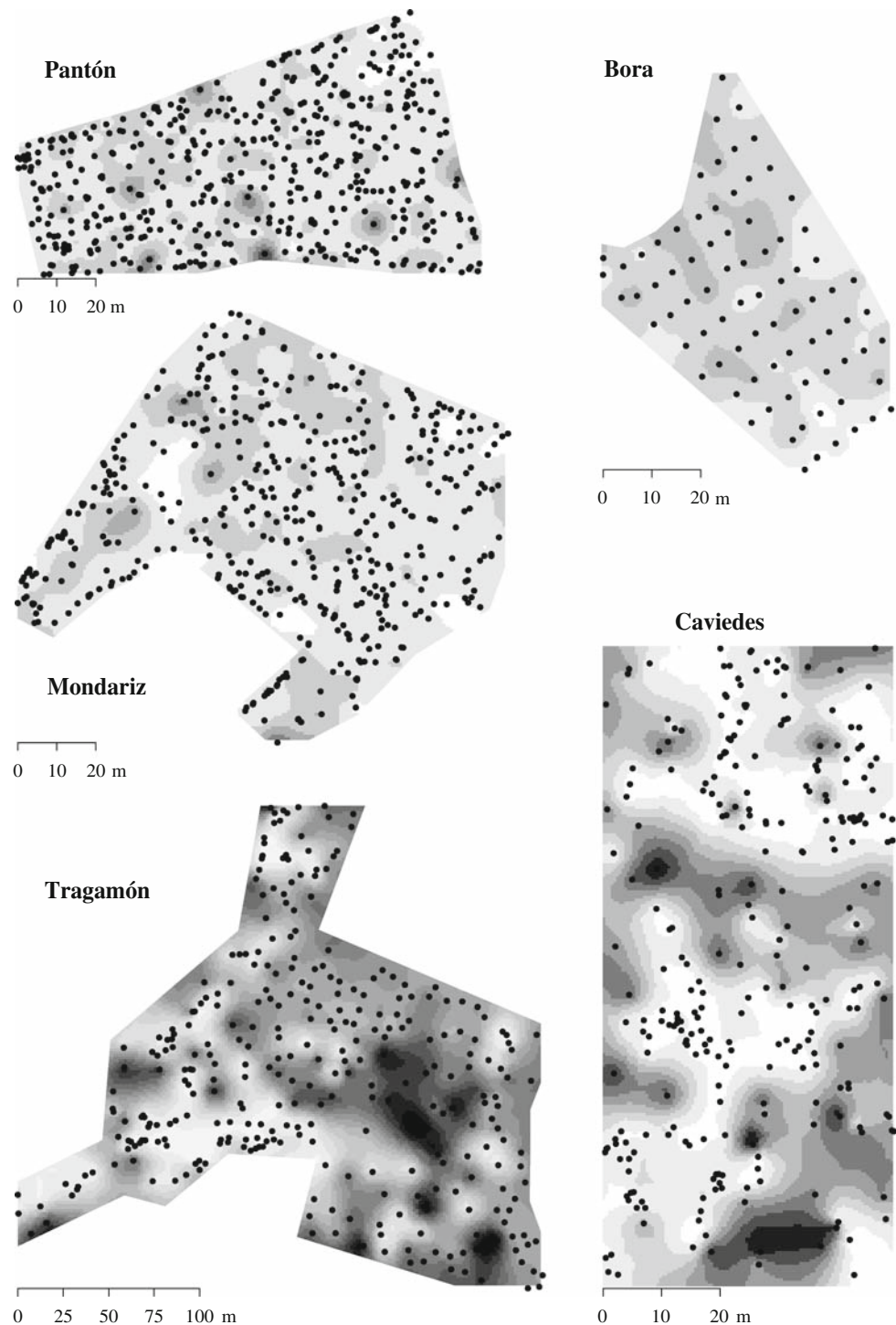
a peak of intense clumping at small scale was evident for both stands, up to inter-tree distances of 1.5 and 2.5 m in Mondariz and Pantón, respectively. Maximum intensity of clumping was observed at 0.5 and 1–1.5 m in Mondariz and Pantón, respectively. In Mondariz, size class 3 displayed also a secondary clumped pattern at 12.5–19.5 m. In Tragamón and Caviedes, size classes 1 and 2 were clumped, while size class 3 did not significantly differ from expectations under the CSR null model, except in Tragamón at distances of 4.5–5.5 m with significant regularity (Fig. 4). In Tragamón, distances with significant clumping for size classes 1 and 2 were 2–50 and 7.5–50 m, respectively. In Caviedes, distances with clumping for size classes 1 and 2 were 0.5–25 and 0.5–16.5 m, respectively.

Spatial associations

The spatial interaction between size classes 1 and 2 in Bora did not significantly differ from expectations under both spatial independence and random labelling (Fig. 5). In Mondariz and Pantón, the interactions between size classes 1 and 2, and between size classes 1 + 2 and 3, were properly described by the model of spatial independence. However, a significant negative correlation between size classes 1 and 2, with respect to the random labelling model, was evidenced at distances of 1.5–8.5 and 0.5–19 m in Mondariz and Pantón, respectively.

The interaction between size classes 1 and 2 in Tragamón fitted the expectations of spatial independence but displayed a significant negative correlation between both size classes at distances of 2–50 m, with respect to the random labelling model (Fig. 5). Size classes 1 + 2 and 3 in Tragamón showed a significant negative association at inter-tree distances of 4.5–9 m, according to the spatial

Fig. 2 Maps of the studied forest stands showing stems with $DBH \geq 5$ cm, along with 10-cm-DBH nested isolines interpolated by kriging. High shade intensity indicates large DBH values



independence model. By contrast, the size classes 1 and 2 in Caviedes showed a significant positive association at distances of 0.5–16.5 m, as indicated by the spatial independence model, but were not spatially correlated according to the random labelling model. Size classes 1 + 2 and 3 were also negatively associated in Caviedes, with significant between-trees repulsion at distances of 4.5–20.5 m (Fig. 5).

Discussion

The results show great variation among stands in size distributions, spatial structure of DBHs, spatial patterns and associations. The *Castanea sativa* plantation in Bora has a normal, symmetric DBH distribution typical of even-aged populations prior to the onset of self-thinning (Kenkel et al. 1997). In Bora, the exponential and spherical models did

Fig. 3 Correlograms of the standard normal deviates of Moran’s *I* spatial autocorrelation coefficients (*left*), and the corresponding experimental semivariograms (*right*), for the spatial structure of DBH in five forest stands. Values in the correlograms above 1.96 and below -1.96 indicate significant positive and negative autocorrelation, respectively ($P < 0.05$). Note that the scale of graphs is different

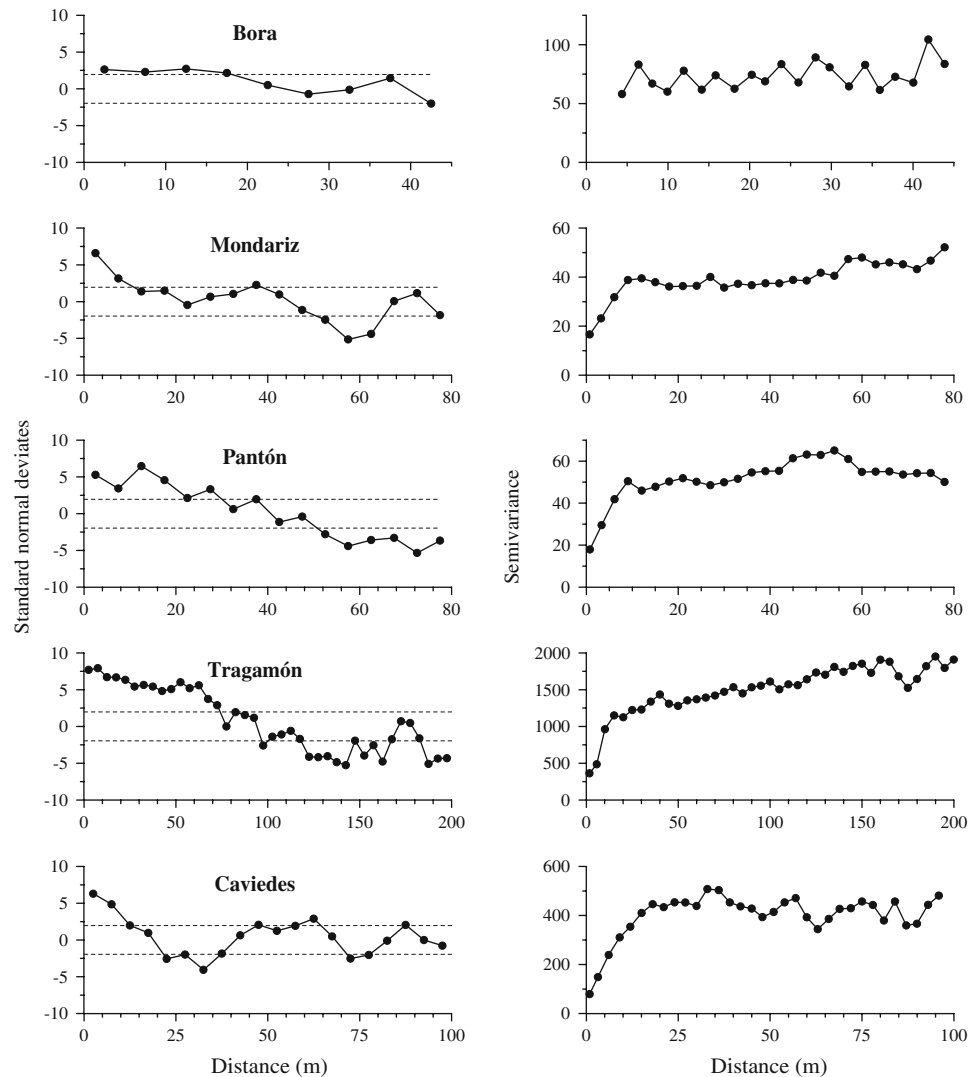


Table 3 Parameters of the maximum likelihood adjustments obtained for the exponential (EXP) or spherical (SPH) models fitted to the experimental semivariograms in Fig. 3

Stand	Model	S (m)	N	r^2	F	P	A_0 (m)	RSV (%)
Bora	EXP	2	22	0.17	3.92	0.062	4.07	19.76
Mondariz	SPH	3	28	0.66	23.67	<0.001	13.06	66.38
Pantón	SPH	3	28	0.76	42.20	<0.001	14.19	70.59
Tragamón	EXP	5	43	0.87	139.56	<0.001	51.04	66.80
Caviedes	SPH	3	32	0.84	77.80	<0.001	18.82	87.27

S step size, N number of distance classes, A_0 range (note that the effective range in exponential models is estimated as $A_0' = 3A_0$), RSV relative structured variability, or $C_s/(C_o + C_s) \times 100$

not fit to the experimental semivariogram, indicating a weak structure in the spatial distribution of tree sizes. Positive autocorrelation in young plantations may be due to site heterogeneity, and negative autocorrelation to inter-tree competition when trees age (Magnussen 1994). In even-aged plant populations, competition leads to the development of size hierarchies, and asymmetric competition

usually predominates once individuals are large enough to shade one another (Kenkel et al. 1997). Moderate tree size and the regular and wide spacing may account for a weak inter-tree competition in Bora.

In Mondariz and Pantón, DBH distributions are positively skewed. This is mainly a consequence of the existence of some old, large individuals scattered in a

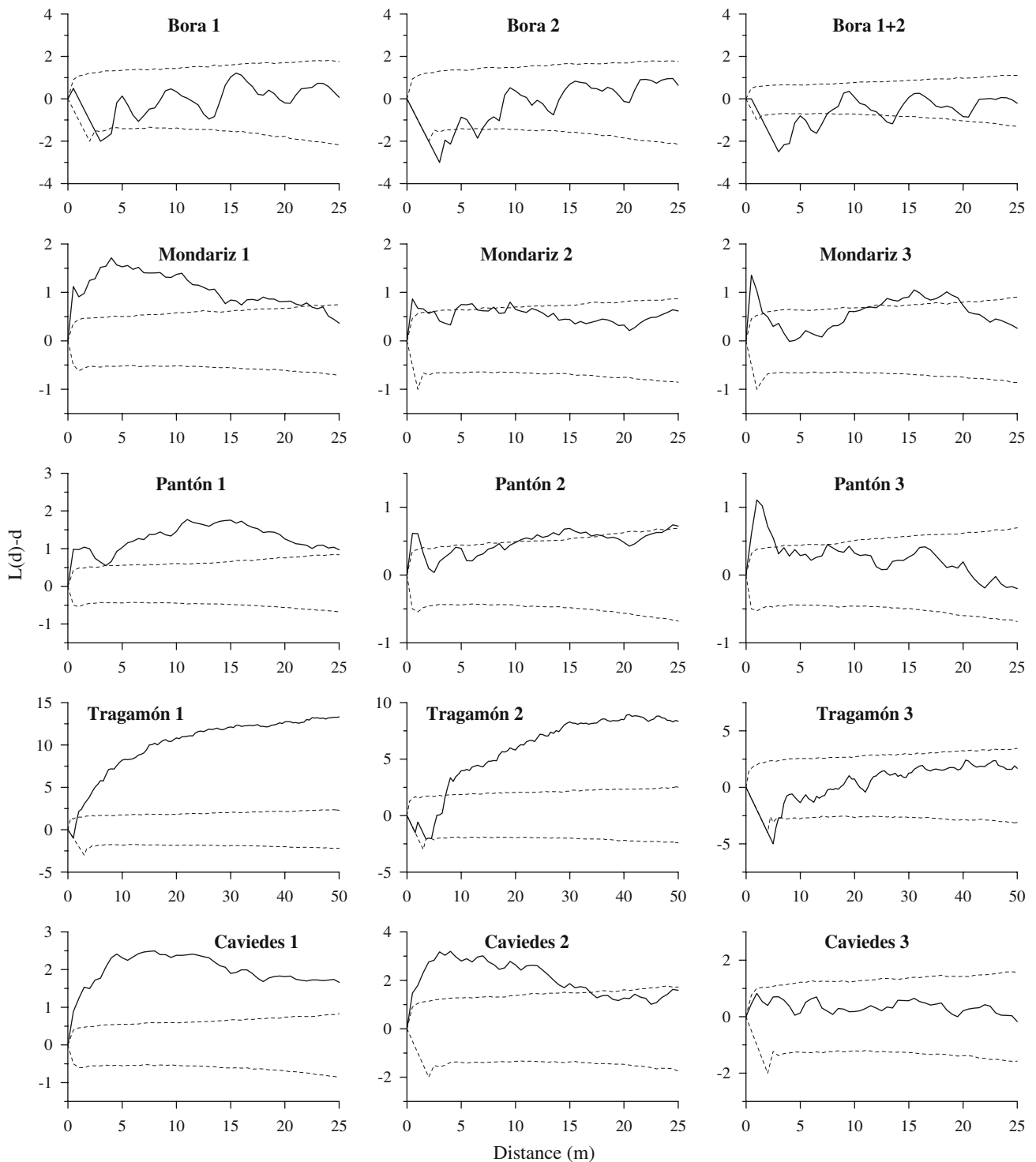


Fig. 4 Spatial point patterns for different size classes in the studied stands, showing the empirical $L(d) - d$ values (solid line) against confidence intervals for the CSR null model (dashed lines) obtained from

10,000 iterations of random processes. Empirical values above and below the confidence intervals indicate significant clustering and regularity, respectively ($P < 0.05$). Note that the scale of graphs is different

matrix of young stems, and also to tree mortality within the smallest size classes due to self-thinning. High mortality of the smallest individuals usually results in positive skewness in the size distribution of survivors (Kenkel et al. 1997).

The existence of dense clumps of small stems in Mondariz and Pantón gives rise to a differential mortality in higher density phases, resulting in the development of a canopy consisting of both dominant and suppressed stems (Kenkel

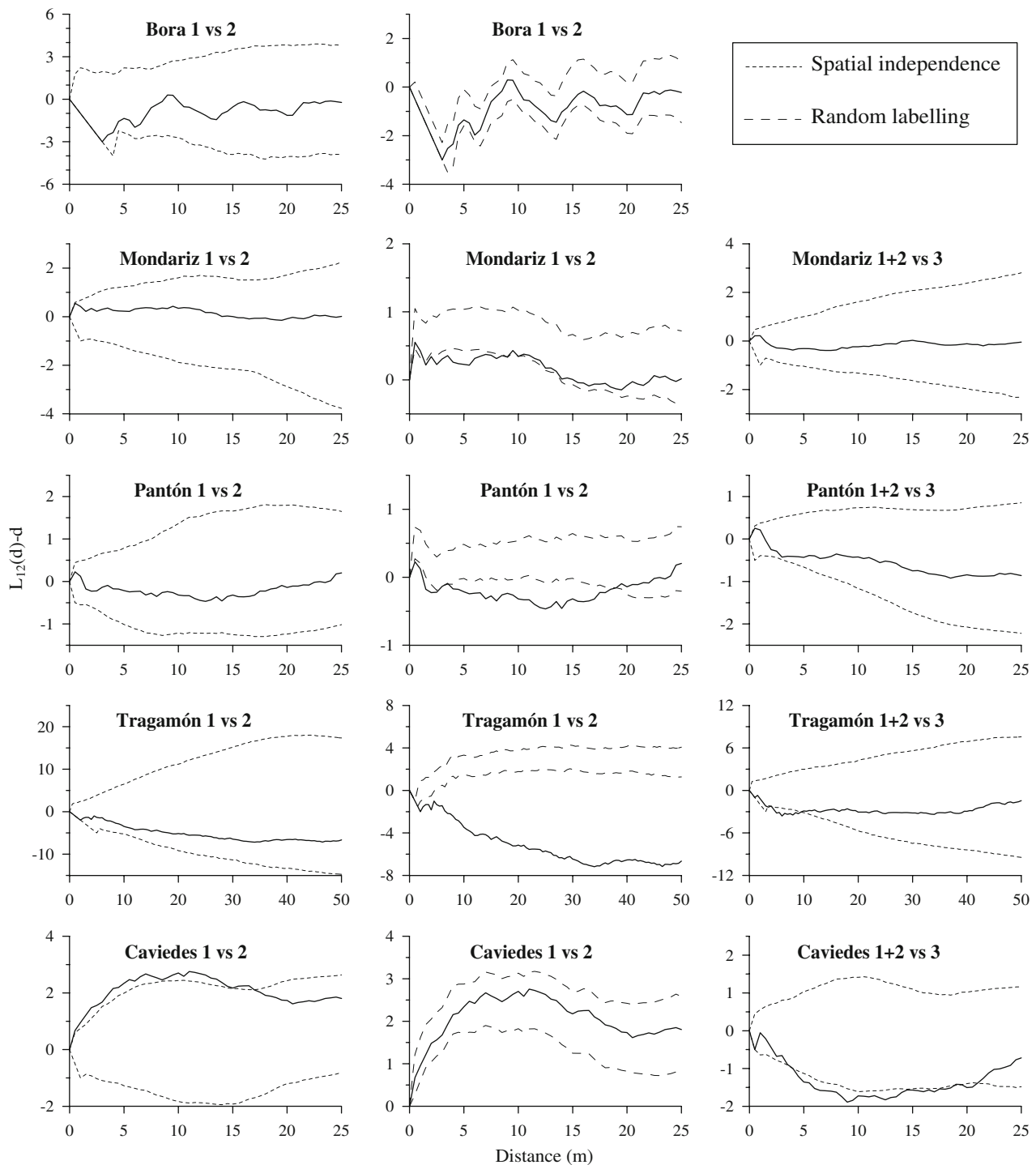


Fig. 5 Spatial associations between different size classes in the studied stands, showing the empirical $L_{12}(d) - d$ values (solid line) and the confidence intervals for the spatial independence (short dashed lines) and random labelling (long dashed lines) null models. Empirical

values above and below the confidence intervals indicate significant positive and negative association, respectively ($P < 0.05$). Note that the scale of graphs is different

1988). The prevailing sprouting nature of new stems may explain the significant clumped distribution of the different size classes in clear-cut stands (Fajardo and Alaback 2005), as evidenced in Mondariz and Pantón. The peak of clumping intensity at small spatial scale (up to 1.5 m in Mondariz

and 2.5 m in Pantón) for large trees could be the result of stump sprouting after tree logging. Even though no data on tree ages and past management are available for Mondariz and Pantón stands, the establishment of new stems by sexual and vegetative reproduction probably occurred in open

areas and also where old trees previously existed, as suggested by the independence between the size classes 1 + 2 and 3.

DBH distribution in Tragamón is in agreement with an age structure composed by three main cohorts. Component A of the DBH distribution correspond to trees aged between 22 and 110 years, while components B and C correspond to two generations of mature oak and chestnut trees aged between 138 and 206 and between 231 and 471 years, respectively (Rozas 2004). Stem diameters of component A are positively skewed, suggesting that a process of self-thinning is causing mortality of the smallest trees within dense clumps. Components B and C have large diameters and symmetric DBH distributions, characteristic of mature populations with a low mortality (Kenkel et al. 1997). As revealed by the correlogram and the semivariogram, Tragamón stand is composed of large clumps of even-sized trees of up to 75 m, separated by a mean distance of over 150 m. However, mature trees in Tragamón are randomly or regularly spaced at distances of over 5 m. Several studies suggested that mature trees tend to be randomly distributed as a consequence of inter-tree competition or diseases (Szwagrzyk and Czewczak 1993; Gavrikov and Stoyan 1995). Mature trees in Tragamón are lapsed pollards that were actively managed during the 18th and 19th centuries; since 1905 they have not been pollarded (Rozas 2004). This woodland has also been used for cattle pasture, and during the last century the establishment of a new generation of trees occurred in open areas and within a few canopy gaps. This accounted for a gradient structure of DBHs, revealed by correlogram, and for an intensely clumped distribution of young trees. The spatial independence between size classes 1 and 2 indicates that size class 2 does not interfere with the establishment of individuals of size class 1. Size classes 1 and 2 are negatively correlated, according to expectations from the random labelling null model, because they correspond to two different cohorts established in two different episodes. However, the establishment of at least a part of both these cohorts has been conditioned by the existence of a canopy of mature trees, as suggested by the negative association of size classes 1 + 2 and 3, at a range of distances of 4.5–9 m.

The Caviedes stand derives from a high forest formerly affected by cattle grazing, but largely unmanaged during the last 80–100 years. The compound diameter distribution in this stand is comparable to distributions previously described for other mature and old-growth deciduous stands, in which several tree cohorts have been identified (Chokkalingam and White 2001; Fajardo and Alaback 2005; Piovesan et al. 2005). Component A corresponds to a young generation of trees whose ages range between 11 and 104 years (Rozas 2006). Their descending monotonic shape indicates that establishment of new individuals is occurring.

By contrast, component B includes mature *Q. robur* and *Fagus sylvatica* trees aged between 150 and 255 years, with unimodal symmetric DBH distribution. The spatial structure of DBHs and the spatial associations among size classes probably have been greatly conditioned by gap-phase dynamics. The spatial dependence obtained from the experimental semivariogram in Caviedes ($RSV = 87.27\%$) is comparable to values previously calculated for an old-growth forest, which ranged from 78 to 92% (Biondi et al. 1994). However, one should be careful to use this index for comparative purposes unless one has a perfect semivariogram, especially because non-stationary processes and trends in site factors can be quite common. Size classes 1 and 2 are clumped and positively associated, but are not correlated according to the random labelling null model. This is because both size classes belong to the same generation of young trees, and size differentiation within this cohort occurs at random. The negative association of size classes 1 + 2 and 3 in Caviedes is coherent with a patch-dynamics perspective, in which trees mainly establish in canopy gaps (Rozas 2006). The clumped distribution of recruits seems to be the more natural state after cessation of human intervention in formerly managed forests (Aldrich et al. 2003; Wolf 2005).

It is generally considered that tree clumping can result from a balance between disturbance frequency and competition intensity. Intermediate levels of disturbance and competition are expected to maximize the intensity of aggregation (Davis et al. 2005). The wood-pasture in Tragamón illustrates the long-term effects of a management practice consisting in the pollarding of trees combined with grazing of the understorey. The elementary functional patches in this stand are large in comparison to patches reported in the other stands, and clumping is intense due to the absence of frequent disturbances and to the low intensity of inter-tree competition. From a dynamic perspective, it can be expected that after cessation of human interference and without significant disturbances, coppices and wood-pastures would evolve to a more heterogeneous structure.

Given that multiple tests of null hypothesis were undertaken, and many of these tests involved non-independent parameters, an experiment-wide error rate should have been considered. It should also be acknowledged that the observed stands are random realizations of a super-population through a complex stochastic process. Therefore, inference was occasionally coined as the observed stand(s) were the focus of attention. Since only one replication of this complex process was considered, the ability to infer about the process is limited and model bias would be a reality. The foundation of the variogram is a model with a random spatial process, and any inference about this spatial process requires the notion of a super-population.

Conclusions

If it is assumed that the main characteristics of the stand spatial patterns can be used as indicators of past dynamics (Moravie and Robert 2003), the obtained results are useful to describe the spatial structure in deciduous forest stands subjected to contrasting management systems. Spatial structure was more complex when human influence became reduced. Since spatial stand structure has an important role in determining habitat and species diversity, heterogeneous stand structures are desirable for conservation purposes. This conclusion may sound obvious, yet many foresters continue to establish regular plantations in forest restoration projects.

Due to the prevalence of vegetative reproduction, coppice stands can be characterized by high clumping intensities at small spatial scales, and spatial independence of large and small stems. As a consequence of an open canopy and new trees established in large open areas, a wood-pasture is characterized by non-clumped patterns at small spatial scale and certain repulsion between large and small trees. A mature stand is characterized by a clumped pattern of small trees and repulsion between small and large trees, as a consequence of new recruitment in canopy gaps. Also the random labelling model proved to be useful to recognize stands in which tree size differentiation occurred at random (forest plantation and mature forest) or following a clustered pattern (coppices and wood-pasture). The results of this descriptive approach suggest that reports on spatial structure of deciduous forests in western Europe should consider the influence of past human activities. Analysis of spatial stand structure and their relationships with habitat quality and species diversity in a temporal context can effectively improve our comprehension of the dynamics of west-European deciduous forests formerly subjected to human management.

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References

- Aldrich PR, Parker GR, Ward JS, Michler CH (2003) Spatial dispersion of trees in an old-growth temperate hardwood forest over 60 years of succession. *For Ecol Manage* 180:475–491
- Batista JLF, Maguire DA (1998) Modeling the spatial structure of tropical forests. *For Ecol Manage* 110:293–314
- Biondi F, Myers DE, Avery CC (1994) Geostatistically modeling stem size and increment in an old-growth forest. *Can J For Res* 24:1354–1368
- Cao QV (2004) Predicting parameters of a Weibull function for modeling diameter distribution. *For Sci* 50:682–685
- Chokkalingam U, White A (2001) Structure and spatial patterns of trees in old-growth northern hardwood and mixed forests of northern Maine. *Plant Ecol* 156:139–160. doi:10.1023/A:1012639109366
- D'Agostino RB, Belanger A, D'Agostino AB Jr (1990) A suggestion for using powerful and informative tests of normality. *Am Stat* 44:316–321. doi:10.2307/2684359
- Davis MA, Curran C, Tietmeyer A, Miller A (2005) Dynamic tree aggregation patterns in a species-poor temperate woodland disturbed by fire. *J Veg Sci* 16:167–174. doi:10.1658/1100-9233(2005)016[0167:DTAPIA]2.0.CO;2
- Dixon P (2002) Ripley's K function. In: El-Shaarawi AH, Piergorsch WW (eds) *Encyclopedia of environmetrics*. Wiley, New York, pp 1796–1803
- Duncan RP, Stewart GH (1991) The temporal and spatial analysis of tree age distributions. *Can J For Res* 21:1703–1710. doi:10.1139/x91-236
- Fajardo A, Alaback P (2005) Effects of natural and human disturbances on the dynamics and spatial structure of *Nothofagus glauca* in south-central Chile. *J Biogeogr* 32:1811–1825. doi:10.1111/j.1365-2699.2005.01331.x
- Gavrikov V, Stoyan D (1995) The use of marked point processes in ecological and environmental forest studies. *Environ Ecol Stat* 2:331–344. doi:10.1007/BF00569362
- Goreaud F, Pélissier R (1999) On explicit formulas of edge effect correction for Ripley's K -function. *J Veg Sci* 10:433–438. doi:10.2307/3237072
- Goreaud F, Pélissier R (2003) Avoiding misinterpretation of biotic interactions with the intertype K_{12} -function: population independence vs. random labelling hypotheses. *J Veg Sci* 14:681–692. doi:10.1658/1100-9233(2003)014[0681:AMOBW]2.0.CO;2
- Kenkel NC (1988) Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69:1017–1024. doi:10.2307/1941257
- Kenkel NC, Hendrie ML, Bella LE (1997) A long-term study of *Pinus banksiana* population dynamics. *J Veg Sci* 8:241–254. doi:10.2307/3237353
- Koukoulas S, Blackburn GA (2005) Spatial relationships between tree species and gap characteristics in broad-leaved deciduous woodland. *J Veg Sci* 16:587–596. doi:10.1658/1100-9233(2005)16[587:SRBTSA]2.0.CO;2
- Kuuluvainen T, Penttinen A, Leinonen K, Nygren M (1996) Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests. An example from boreal spruce forest in southern Finland. *Silva Fenn* 30:315–328
- Kuuluvainen T, Järvinen E, Hokkanen TJ, Rouvinen S, Heikkinen K (1998) Structural heterogeneity and spatial autocorrelation in a natural mature *Pinus sylvestris* dominated forest. *Ecography* 21:159–174. doi:10.1111/j.1600-0587.1998.tb00670.x
- Legendre P, Fortin MJ (1989) Spatial pattern and ecological analysis. *Vegetatio* 80:107–138. doi:10.1007/BF00048036
- Liebold AM, Gurevitch J (2002) Integrating the statistical analysis of spatial data in ecology. *Ecography* 25:553–557. doi:10.1034/j.1600-0587.2002.250505.x
- Liu C, Zhang L, Davis CJ, Solomon DS, Gove JH (2002) A finite mixture model for characterizing the diameter distributions of mixed-species forest stands. *For Sci* 48:653–661
- Lorimer CG, Krug AG (1983) Diameter distributions in even-aged stands of shade-tolerant and midtolerant tree species. *Am Midl Nat* 109:331–345. doi:10.2307/2425414

- Lotwick HW, Silverman BW (1982) Methods for analyzing spatial processes of several types of points. *J R Stat Soc B Stat Methodol* 44:406–413
- Magnussen S (1994) A method to adjust simultaneously for spatial microsite and competition effects. *Can J For Res* 24:985–995. doi:10.1139/x94-129
- Manly BFJ (1997) Randomization, bootstrap and Monte Carlo methods in biology, 2nd edn. Chapman & Hall, London
- McLachlan JS, Foster DR, Menalled F (2000) Anthropogenic ties to late-successional structure and composition in four New England hemlock stands. *Ecology* 81:717–733
- Moravie MA, Robert A (2003) A model to assess relationships between forest dynamics and spatial structure. *J Veg Sci* 14:823–834. doi:10.1658/1100-9233(2003)014[0823:AMTARB]2.0.CO;2
- Penttinen A, Stoyan D, Henttonen HM (1992) Marked point processes in forest statistics. *For Sci* 38:806–824
- Perry JN, Liebhold AM, Rosenberg MS, Dungan J, Miriti M, Jakomulska A, Citron-Pousty S (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography* 25:578–600. doi:10.1034/j.1600-0587.2002.250507.x
- Peterken GF (1996) Natural woodland. Ecology and conservation in Northern temperate regions. Cambridge University Press, Cambridge
- Piovesan G, Di Filippo A, Alessandrini A, Biondi F, Schirone B (2005) Structure, dynamics and dendroecology of an old-growth *Fagus* forest in the Apennines. *J Veg Sci* 16:13–28. doi:10.1658/1100-9233(2005)016[0013:SDADOA]2.0.CO;2
- Pommerening A (2002) Approaches to quantifying forest structures. *Forestry* 75:305–324. doi:10.1093/forestry/75.3.305
- Ripley BD (1977) Modelling spatial patterns (with discussion). *J R Stat Soc B Stat Methodol* 39:172–212
- Rozas V (2004) A dendroecological reconstruction of age structure and past management in an old-growth pollarded parkland in northern Spain. *For Ecol Manage* 195:205–219
- Rozas V (2006) Structural heterogeneity and tree spatial patterns in an old-growth deciduous lowland forest in Cantabria, northern Spain. *Plant Ecol* 185:57–72. doi:10.1007/s11258-005-9084-1
- SAS Institute (1999) SAS/STAT user's guide, Version 8. SAS Institute, Inc., Cary
- Schabenberger O, Gotway CA (2005) Statistical methods for spatial data analysis. Chapman & Hall/CRC, Boca Raton, p 140
- Skov F, Svenning JC (2003) Predicting plant species richness in a managed forest. *For Ecol Manage* 180:583–593
- Szwagrzyk J, Czewczak M (1993) Spatial patterns of trees in natural forests of East-Central Europe. *J Veg Sci* 4:469–476. doi:10.2307/3236074
- Thioulouse J, Chessel D, Dolédec S, Olivier JM (1997) ADE-4: a multivariate analysis and graphical display software. *Stat Comput* 7:75–83. doi:10.1023/A:1018513530268
- Webster R, Oliver MA (1990) Statistical methods in soil and land resource survey. Oxford University Press, Oxford
- Wiegand T, Moloney KA (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104:209–229. doi:10.1111/j.0030-1299.2004.12497.x
- Wolf A (2005) Fifty year record of change in tree spatial patterns within a mixed deciduous forest. *For Ecol Manage* 215:212–223