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

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23 **Abstract** Five contrasting deciduous forest stands were studied to characterise the spatial structural
24 variability in human-influenced forests. These stands are representative of cultural forest types
25 widely represented in western Europe: one plantation, two coppices, one wood-pasture, and one
26 high forest stand. All stems with DBH > 5 cm were measured and mapped, and stem DBH
27 distributions, spatial structure of DBH, spatial point patterns and spatial associations were
28 analysed. Spatial autocorrelation for DBH was calculated with Moran's *I* correlograms and
29 semivariograms. Complete spatial randomness hypothesis for spatial point patterns, and both
30 independence and random labelling hypotheses for spatial associations, were analysed using
31 Ripley's *K* function. The results showed that tree sizes were conditioned by particular former
32 management systems, which determined unimodal symmetric, positively skewed, or compound
33 DBH distributions. Spatial structure was more complex when human influence became reduced.
34 Coppice stands showed clumped spatial patterns and independence among size classes, as a
35 consequence of sexual and vegetative establishment of new stems in open areas. The largest
36 clumping intensity was observed in the wood-pasture with an intermediate disturbance frequency
37 and low inter-tree competition. The high forest stand displayed spatial traits consistent with the
38 gap-dynamics paradigm, such as clumping of smaller trees, random arrangement of larger trees,
39 negative association between juveniles and adults, and high structural heterogeneity. It can be
40 expected that after cessation of human interference, coppices and wood-pastures would evolve to a
41 more heterogeneous structure, perhaps with a higher habitat and species diversity.

42

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

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47 **Introduction**

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

57 Statistical analysis of tree stands need suitable methods of spatial statistics, among
58 which geostatistical modelling and the analysis of spatial point processes are mostly used
59 (Liebhold and Gurevitch 2002). Complementary methods used to quantify and model the
60 spatial structure of forest trees include the correlograms of statistics to measure spatial
61 autocorrelation, the variograms to model spatial dependence, and estimating values at
62 unsampled locations by kriging (Legendre and Fortin 1989; Kuuluvainen et al. 1998).
63 Although these methods are generally used as single techniques to quantify spatial
64 autocorrelation, their combined use has been recommended to mitigate the inherent
65 limitations of individual tests (Perry et al. 2002).

66 Null models for spatial point processes can be used as benchmarks to differentiate
67 among types of spatial patterns. The simplest null model is the homogeneous Poisson,
68 which corresponds to the hypothesis of complete spatial randomness (CSR) that allows
69 differentiating among the clumped, random or regular spatial patterns. The relationship
70 between two spatial point processes can be assessed with different null models. The

71 independence model asks questions about the interaction between the two processes, and
72 the random labelling model asks questions about the process that assigns labels to points
73 (Dixon 2002; Goreaud and Pélissier 2003). Random labelling has not been frequently used
74 in forestry research, but it has been implicitly used to assess “random mortality”,
75 considering labels as the live and dead categories (Kenkel 1988).

76 The structural characterization of formerly managed stands would be more useful to
77 anticipate the future forest changes than other approaches based on long-term processes of
78 autogenic succession (McLachlan et al. 2000). The study of both natural and managed
79 stands with spatial analytical methods is essential to generate theories about stand
80 developmental processes in human-influenced forests (Penttinen et al. 1992). Recent
81 research comparing the spatial variability among natural and managed stands of boreal,
82 tropical and southern hemisphere deciduous forests (Kuuluvainen et al. 1996; Batista and
83 Maguire 1998; Fajardo and Alaback 2005) suggest that natural forests are likely to host the
84 highest amount of structural and biological diversity. The history of the forest stands has
85 an important influence on the spatial structure of west-European deciduous forests (Wolf
86 2005). Formerly managed stands revealed a great variety of spatial patterns, from regular
87 distributions derived from active forestry practices, to clumped patterns when management
88 ceased (Koukoulas and Blackburn 2005; Wolf 2005; Rozas 2006). Spatial stand structure
89 has an important role in determining habitat and species diversity and can be quantified to
90 assess habitat quality for conservation purposes (Pommerening 2002; Skov and Svenning
91 2003).

92 In this paper we analyse the spatial structure of tree sizes in five deciduous forest
93 stands with different human influence. These stands are representative of widespread
94 traditional systems formerly used in western Europe: plantations, coppices, wood-pastures
95 and high forests (terminology as by Peterken 1996). The studied stands probably have a

96 long history of management, but during the 20th century this had ceased due to socio-
97 economic changes. The study aims to: (i) describe the spatial structure of tree sizes in man-
98 made and semi-natural deciduous forest stands, (ii) identify and characterize the patterns of
99 stem distribution and the spatial interactions among size classes, and (iii) interpret them in
100 terms of previous management and forest dynamics.

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103 **Materials and methods**

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105 Study areas

106

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

120 Tragamón (Asturias) is a wood-pasture located near Gijón city on deep brown soils on

121 alluvial depositions of gravel, sand and clay. It is composed mainly of *Q. robur* and *C.*
122 *sativa*, and other tree species include *Q. pubescens*, *Acer pseudoplatanus*, *Fraxinus*
123 *excelsior*, *Laurus nobilis*, *Taxus baccata*, *Prunus laurocerasus* and *Ilex aquifolium*.
124 Tragamón has been used as a recreation park since the 1960s. Prior to that time, it was
125 used as a cattle pasture and for the pollarding of mature oak and chestnut trees. A
126 reconstruction of the management history revealed that pollarding of oak trees was intense
127 from 1730 to 1905, but since that year pollarding frequency and intensity has been in
128 decline (Rozas 2004).

129 Caviedes forest (Cantabria) is located on a gentle slope with deep sandy soils, with a
130 bedrock of sandstone and clay. *Fagus sylvatica* and *Q. robur* are the dominant tree species
131 in the forest canopy, and other relevant woody species are *I. aquifolium*, *F. alnus*, *Salix*
132 *atrocinerea*, *Pyrus cordata* and *Corylus avellana*. Characteristics of old-growth, such as
133 standing and fallen dead trees and logs, woody debris, uprooted and snapped trees, soil
134 mound-and-pith topography, large hollow trees and canopy gaps, were observed
135 throughout the forest. The stand in Caviedes had a high forest structure that has been
136 formerly managed by selective logging and pasture by cattle; since the beginning of the
137 20th century this use has rapidly declined (Rozas 2006).

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139 Field sampling

140

141 A complete spatial mapping of tree locations and measurement of stem DBHs (diameter
142 measured at 1.3 m above ground) was carried out for each stand. All living stems over
143 5 cm in DBH were labelled, measured and mapped. In Bora, Pantón, Mondariz and
144 Tragamón, tree mapping was done with a laser total station by accurately measuring
145 horizontal and vertical angles and distances to the center of each labelled stem. In

146 Caviedes, the rectangular stand was divided into 100 m² quadrats, on which the x and y
147 coordinates to the center of labelled stems were measured to the nearest 0.1 m.

148

149 DBH distribution analysis

150

151 DBH data in each stand was tested for normality with the robust and powerful D'Agostino
152 third ($\sqrt{b_1}$) and fourth (b_2) moment tests, which test for deviations from normality
153 associated with skewness and kurtosis, respectively (D'Agostino et al. 1990). The null
154 hypotheses are a skewness of 0 and a kurtosis of 3. These tests were calculated using a
155 SAS macro provided by D'Agostino et al. (1990). The cumulative DBH distributions in 5-
156 cm classes were quantified with the two-parameter Weibull cumulative distribution $F(x) =$
157 $1 - \exp[-(x/b)^c]$, where $F(x)$ is the cumulative frequency of trees in DBH class x , b is the
158 scale parameter, and c is the shape parameter (Cao 2004). The Weibull distribution can
159 assume a wide variety of shapes and degrees of skewness, regulated by the scale parameter
160 b and the shape parameter c . At values of $c < 1$ the distribution is descending monotonic
161 whereas at $c > 1$ the distribution is unimodal (Lorimer and Krug 1983). Forest stands with
162 several age classes, tree species or vertical strata usually have compound diameter
163 distributions with irregular shapes, which can be characterized as a mixture of partially
164 overlapping distributions. Compound distributions can be analysed by fitting the frequency
165 distribution of each component (age class, species, stratum) separately and obtaining the
166 prediction for the whole stand as the sum of component models (Liu et al. 2002). We used
167 this approach by dividing compound DBH distributions at Tragamón and Caviedes in their
168 components on the basis of previously identified tree age-classes (Rozas 2004, 2006).

169

170 Spatial autocorrelation analysis

171

172 The spatial structure of tree diameters was studied with both the Moran's I coefficient and
173 the semivariance of tree diameters. I coefficient is a measure of the autocorrelation of a
174 quantitative variable for all pairs of points separated by a given spatial lag, which can
175 reveal scales of heterogeneity of the forest structure related to the size and distribution of
176 even-sized tree patches (Duncan and Stewart 1991). The hypothesis of spatial
177 independence of stem DBH was tested on correlograms of the standard normal deviates of
178 I coefficients calculated by 5-m distance classes, against the critical values for a standard
179 normal distribution. Since several I coefficients were calculated in each correlogram, a
180 correlogram was considered statistically significant only if at least one coefficient was
181 above or below a Bonferroni-corrected significance level (Legendre and Fortin 1989).
182 Moran's autocorrelation analyses were performed with the software written by R.P.
183 Duncan (Duncan and Stewart 1991).

184 Semivariance is a measure of the degree of spatial dependence between sampled
185 locations and is computed as the sum of squared differences between all pairs of
186 observations that belong to a given distance class (Biondi et al. 1994). Calculating the
187 semivariance for different distance classes produces the experimental semivariogram,
188 which is computed after sorting all possible pairs of locations into classes by distance.
189 Experimental semivariograms were constructed using the VARIOGRAM procedure in
190 SAS, and the exponential and spherical models were fitted to the experimental
191 semivariograms using the NLIN procedure in SAS (SAS Institute 1999). The intercept of
192 the model semivariogram is known as the nugget (C_o), which quantifies spatial variability
193 at near-zero distances. The nugget represents both the variance due to sampling error and
194 the spatial dependence at scales not explicitly sampled. When spatial dependence is
195 present, semivariance typically increases to some asymptote that is called the sill (C_o+C_n).

196 The distance at which the semivariogram model reaches a constant value is called the
197 range (A_o), which marks the limit of spatial dependence. In spherical models, the range
198 indicates the mean size of even-sized tree patches, whereas in exponential models the
199 effective range is estimated as $A_o' = 3A_o$, distance at which the semivariance is
200 approximately $0.95 \cdot (C_o + C_n)$ (Webster and Oliver 1990). If semivariance does not show a
201 trend as a function of scale, it can be concluded that spatial dependence is not present. A
202 relative value of the spatial dependence can be calculated as the ratio $C_n / (C_o + C_n)$. Since the
203 nugget reduces the smoothness of the process, a common measure for the degree of spatial
204 structure is the *relative structured variability*, $RSV = C_n / (C_o + C_n) \times 100\%$, a useful index to
205 make comparisons among semivariograms (Schabenberger and Gotway 2005).

206

207 Spatial point pattern analysis

208

209 To analyse spatial patterns, we used the univariate Ripley's K function (Ripley 1977),
210 which reflects the type and intensity of a pattern at different inter-tree distances d . Details
211 on the calculation of $K(d)$ are available in Dixon (2002). The modified function $L(d) =$
212 $(K(d)/\pi)^{0.5}$ has a more stable variance than $K(d)$, and $L(d) - d$ has an expected value of zero
213 under the assumption of CSR. $K(d)$ was calculated every 0.5 m, and confidence intervals
214 for testing CSR at the 5% significance level were generated from 10,000 Monte Carlo
215 iterations of random processes (Manly 1997). Significant negative values of $L(d) - d$
216 indicate inhibition, i.e. the pattern tends to be regular, while positive values of $L(d) - d$
217 indicate aggregation, i.e. the pattern tends to be clustered. Spatial analyses were performed
218 with the ADS module in the ADE-4 statistical software (Thioulouse et al. 1997). This
219 software integrates edge effect corrections for rectangular as well as irregularly shaped
220 sampling plots (Goreaud and Pélissier 1999). Univariate spatial patterns were analysed for

221 different tree size-classes in each locality (Table 1). Tree size-classes were defined based
222 on a balanced number of individuals among the classes (Bora, Mondariz and Pantón), or
223 previously identified tree age-classes (Tragamón and Caviedes) (Rozas 2004, 2006).

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

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

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

249

250

251 **Results**

252

253 Characteristics of DBH distributions

254

255 Frequency DBH histograms showed that Bora, Mondariz and Pantón stands have unimodal
256 size structure, with a shape parameter >1 when fitted to a two-parameter Weibull
257 distribution. By contrast, Tragamón and Caviedes stands have compound DBH
258 distributions (Fig. 1). DBH distribution in Bora was almost symmetric and normal, while
259 in Mondariz and Pantón tree populations were skewed towards larger diameters (Table 2).
260 DBH distribution in Tragamón was a mixture of three partially overlapped unimodal
261 distributions that extended to almost 170 cm. These three components had shape
262 parameters >1 , and only the component with the smallest mean DBH significantly differed
263 from normality (Table 2). In Caviedes, a compound DBH distribution was observed (Fig.
264 1). The first component of this DBH distribution had shape parameter <1 , indicating a
265 descending monotonic curve, while the second component showed a normal distribution
266 with shape parameter >1 (Table 2).

267

268 Spatial structure

269

270 Stem maps interpolated by kriging revealed that DBH patchiness and patch sizes varied
271 greatly among the stands (Fig. 2). All correlograms were globally significant ($P < 0.05$ in
272 Bora, $P < 0.001$ in all other stands) and the maximum likelihood models fitted to the
273 experimental semivariograms were also statistically significant, except in Bora (Table 3).
274 Correlograms displayed positive autocorrelation at small inter-tree distances (less than
275 10 m in Mondariz, 20 m in Bora, 30 m in Pantón, and 75 m in Tragamón) that
276 corresponded to distances between trees of similar DBH within a patch (Fig. 3). Negative
277 autocorrelations were also discovered at larger scales (45–65 m in Bora, 50–65 m in
278 Mondariz, 50–80 m in Pantón, and 120–165 m in Tragamón). Correlogram for Caviedes
279 displayed alternation of significant positive and negative autocorrelation (Fig. 3).
280 Significant positive autocorrelation at distances of less than 10 m indicated that similarly
281 sized trees occurred together within a patch. Significant positive values at 45–50, 60–65,
282 and 85–90 m indicated the average distances between patches of similar DBH, while
283 significant negative values at 20–35 and 70–75 m represented the average distances
284 between patches of dissimilar DBH.

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

292

293 Spatial point patterns

294

295 Trees in Bora were regularly distributed, as expected, with two main peaks in the regular
296 patterns at 3 and 6.5 m (Fig. 4), which approximately match the initial spacing of the
297 plantation. All size classes in Mondariz and Pantón were clumped, with a wide range of
298 tree clumping in size class 1, up to distances of 22 and 25 m for Mondariz and Pantón,
299 respectively. In size class 2, the pattern was one of alternating patches with clumping and
300 complete spatial randomness. In size class 3, a peak of intense clumping at small scale was
301 evident for both stands, up to inter-tree distances of 1.5 and 2.5 m in Mondariz and Pantón,
302 respectively. Maximum intensity of clumping was observed at 0.5 and 1–1.5 m in
303 Mondariz and Pantón, respectively. In Mondariz, size class 3 displayed also a secondary
304 clumped pattern at 12.5–19.5 m. In Tragamón and Caviedes, size classes 1 and 2 were
305 clumped, while size class 3 did not significantly differ from expectations under the CSR
306 null model, except in Tragamón at distances of 4.5–5.5 m with significant regularity (Fig.
307 4). In Tragamón, distances with significant clumping for size classes 1 and 2 were 2–50
308 and 7.5–50 m, respectively. In Caviedes, distances with clumping for size classes 1 and 2
309 were 0.5–25 and 0.5–16.5 m, respectively.

310

311 Spatial associations

312

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

320 The interaction between size classes 1 and 2 in Tragamón fitted the expectations of
321 spatial independence but displayed a significant negative correlation between both size
322 classes at distances of 2–50 m, with respect to the random labelling model (Fig. 5). Size
323 classes 1+2 and 3 in Tragamón showed a significant negative association at inter-tree
324 distances of 4.5–9 m, according to the spatial independence model. By contrast, the size
325 classes 1 and 2 in Caviedes showed a significant positive association at distances of 0.5–
326 16.5 m, as indicated by the spatial independence model, but were not spatially correlated
327 according to the random labelling model. Size classes 1+2 and 3 were also negatively
328 associated in Caviedes, with significant between-trees repulsion at distances of 4.5–20.5 m
329 (Fig. 5).

330

331

332 **Discussion**

333

334 The results show great variation among stands in size distributions, spatial structure of
335 DBHs, spatial patterns and associations. The *C. sativa* plantation in Bora has a normal,
336 symmetric DBH distribution typical of even-aged populations prior to the onset of self-
337 thinning (Kenkel et al. 1997). In Bora, the exponential and spherical models did not fit to
338 the experimental semivariogram, indicating a weak structure in the spatial distribution of
339 tree sizes. Positive autocorrelation in young plantations may be due to site heterogeneity,
340 and negative autocorrelation to inter-tree competition when trees age (Magnussen 1994). In
341 even-aged plant populations, competition leads to the development of size hierarchies, and
342 asymmetric competition usually predominates once individuals are large enough to shade
343 one another (Kenkel et al. 1997). Moderate tree size and the regular and wide spacing may
344 account for a weak inter-tree competition in Bora.

345 In Mondariz and Pantón, DBH distributions are positively skewed. This is mainly a
346 consequence of the existence of some old, large individuals scattered in a matrix of young
347 stems, and also to tree mortality within the smallest size classes due to self-thinning. High
348 mortality of the smallest individuals usually results in positive skewness in the size
349 distribution of survivors (Kenkel et al. 1997). The existence of dense clumps of small
350 stems in Mondariz and Pantón gives rise to a differential mortality in higher density
351 phases, resulting in the development of a canopy consisting of both dominant and
352 suppressed stems (Kenkel 1988). The prevailing sprouting nature of new stems may
353 explain the significant clumped distribution of the different size classes in clear-cut stands
354 (Fajardo and Alaback 2005), as evidenced in Mondariz and Pantón. The peak of clumping
355 intensity at small spatial scale (up to 1.5 m in Mondariz and 2.5 m in Pantón) for large
356 trees could be the result of stump sprouting after tree logging. Even though no data on tree
357 ages and past management are available for Mondariz and Pantón stands, the establishment
358 of new stems by sexual and vegetative reproduction probably occurred in open areas and
359 also where old trees previously existed, as suggested by the independence between the size
360 classes 1+2 and 3.

361 DBH distribution in Tragamón is in agreement with an age structure composed by
362 three main cohorts. Component A of the DBH distribution correspond to trees aged
363 between 22–110 years, while components B and C correspond to two generations of
364 mature oak and chestnut trees aged between 138–206 and 231–471 years, respectively
365 (Rozas 2004). Stem diameters of component A are positively skewed, suggesting that a
366 process of self-thinning is causing mortality of the smallest trees within dense clumps.
367 Components B and C have large diameters and symmetric DBH distributions,
368 characteristic of mature populations with a low mortality (Kenkel et al. 1997). As revealed
369 by the correlogram and the semivariogram, Tragamón stand is composed of large clumps

370 of even-sized trees of up to 75 m, separated by a mean distance of over 150 m. However,
371 mature trees in Tragamón are randomly or regularly spaced at distances of over 5 m.
372 Several studies suggested that mature trees tend to be randomly distributed as a
373 consequence of inter-tree competition or diseases (Szwagrzyk and Czewczak 1993;
374 Gavrikov and Stoyan 1995). Mature trees in Tragamón are lapsed pollards that were
375 actively managed during the 18th and 19th centuries; since 1905 they have not been
376 pollarded (Rozas 2004). This woodland has also been used for cattle pasture, and during
377 the last century the establishment of a new generation of trees occurred in open areas and
378 within a few canopy gaps. This accounted for a gradient structure of DBHs, revealed by
379 correlogram, and for an intensely clumped distribution of young trees. The spatial
380 independence between size classes 1 and 2 indicates that size class 2 does not interfere
381 with the establishment of individuals of size class 1. Size classes 1 and 2 are negatively
382 correlated, according to expectations from the random labelling null model, because they
383 correspond to two different cohorts established in two different episodes. However, the
384 establishment of at least a part of both these cohorts has been conditioned by the existence
385 of a canopy of mature trees, as suggested by the negative association of size classes 1+2
386 and 3, at a range of distances of 4.5–9 m.

387 The Caviedes stand derives from a high forest formerly affected by cattle grazing, but
388 largely unmanaged during the last 80–100 years. The compound diameter distribution in
389 this stand is comparable to distributions previously described for other mature and old-
390 growth deciduous stands, in which several tree cohorts have been identified
391 (Chokkalingam and White 2001; Fajardo and Alaback 2005; Piovesan et al. 2005).
392 Component A corresponds to a young generation of trees whose ages range between 11–
393 104 years (Rozas 2006). Their descending monotonic shape indicates that establishment of
394 new individuals is occurring. By contrast, component B includes mature *Q. robur* and *F.*

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

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

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

429

430

431 **Conclusions**

432

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

441 Due to the prevalence of vegetative reproduction, coppice stands can be characterised
442 by high clumping intensities at small spatial scales, and spatial independence of large and
443 small stems. As a consequence of an open canopy and new trees established in large open
444 areas, a wood-pasture is characterised by non-clumped patterns at small spatial scale and

445 certain repulsion between large and small trees. A mature stand is characterised by a
446 clumped pattern of small trees and repulsion between small and large trees, as a
447 consequence of new recruitment in canopy gaps. Also the random labelling model proved
448 to be useful to recognise stands in which tree size differentiation occurred at random
449 (forest plantation and mature forest) or following a clustered pattern (coppices and wood-
450 pasture). The results of this descriptive approach suggest that reports on spatial structure of
451 deciduous forests in western Europe should consider the influence of past human activities.
452 Analysis of spatial stand structure and their relationships with habitat quality and species
453 diversity in a temporal context can effectively improve our comprehension of the dynamics
454 of west-European deciduous forests formerly subjected to human management.

455

456

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458

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564

565 **Figure captions**

566

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

570

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

574

575 Fig. 3. Correlograms of the standard normal deviates of Moran's I spatial autocorrelation
576 coefficients (left), and the corresponding experimental semivariograms (right), for the
577 spatial structure of DBH in five forest stands. Values in the correlograms above 1.96 and
578 below -1.96 indicate significant positive and negative autocorrelation, respectively ($P <$
579 0.05). Note that the scale of graphs is different.

580

581 Fig. 4. Spatial point patterns for different size classes in the studied stands, showing the
582 empirical $L(d)-d$ values (solid line) against confidence intervals for the CSR null model
583 (dashed lines) obtained from 10,000 iterations of random processes. Empirical values
584 above and below the confidence intervals indicate significant clustering and regularity,
585 respectively ($P < 0.05$). Note that the scale of graphs is different.

586

587 Fig. 5. Spatial associations between different size classes in the studied stands, showing the
588 empirical $L_{12}(d)-d$ values (solid line) and the confidence intervals for the spatial

589 independence (short dashed lines) and random labelling (long dashed lines) null models.
590 Empirical values above and below the confidence intervals indicate significant positive and
591 negative association, respectively ($P < 0.05$). Note that the scale of graphs is different.
592

593

594

595 Table 1

596 Characteristics of the studied forest stands and differentiation of point patterns on the basis
 597 of diameter classes. Densities refer to stems with $DBH \geq 5$ cm

598

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	2435	333	<i>C. sativa</i>	Bora 1	5 – 24.9	41
							Bora 2	≥ 25	40
Mondariz	42° 14'	8° 27'	90	7579	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	5489	942	<i>Q. pyrenaica</i> , <i>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	37900	83	<i>Q. robur</i> , <i>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	5500	498	<i>F. sylvatica</i> , <i>Q. robur</i>	Caviedes 1	5 – 9.9	148
							Caviedes 2	10 – 24.9	60
							Caviedes 3	≥ 25	66

599

600 *N*: number of points in the pattern.

601

602

603 Table 2

604 Parameters of DBH distributions, test results for skewness and kurtosis (D'Agostino et al. 1990), and adjusted Weibull models. Capital letters in
 605 Tragamón and Caviedes correspond to the components of DBH distributions displayed in Fig. 1. All Weibull models were significant at $P <$
 606 0.001

607

Stand	<i>N</i>	DBH (cm)				Third sample moment test		Fourth sample moment test		Weibull model	
		Mean	SD	Min	Max	$\sqrt{b_1}$	<i>P</i>	b_2	<i>P</i>	<i>n</i>	<i>c</i>
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

608

609 *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.

610

611

612

613 Table 3

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

616

Stand	Model	S (m)	N	r^2	F	P	A_o (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

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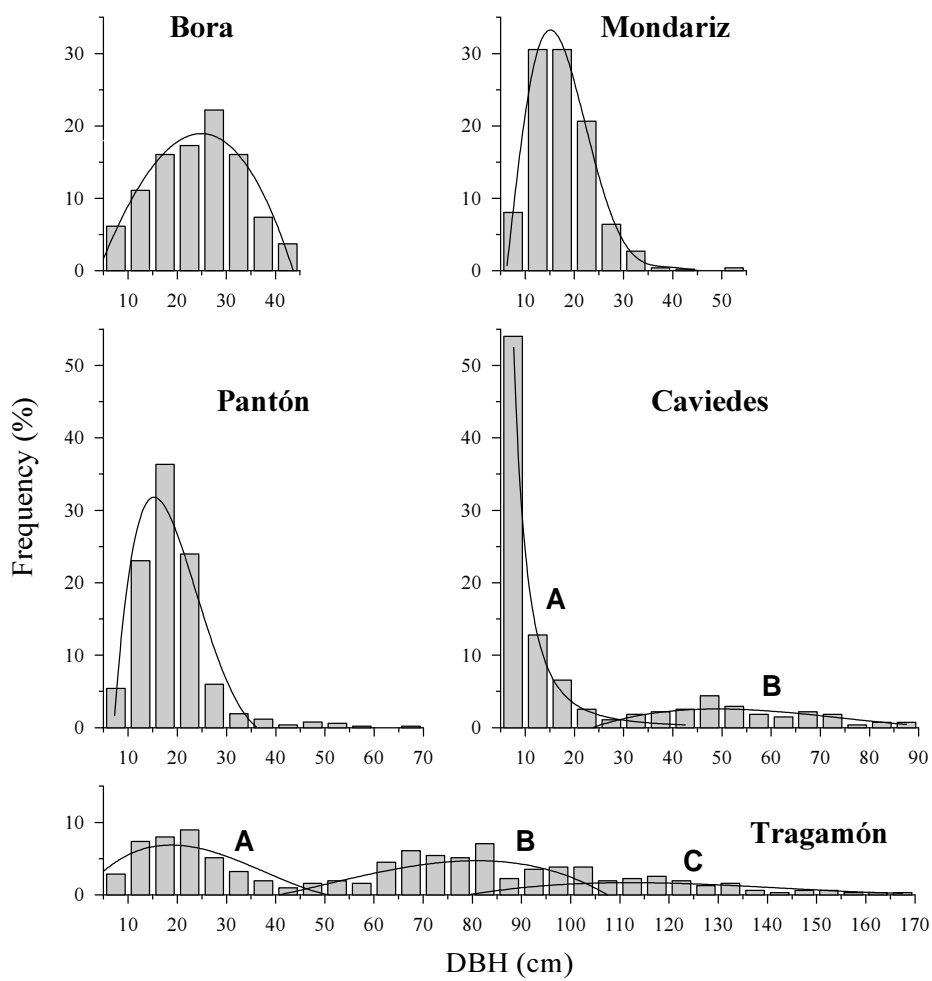
618 S: step size. N : number of distance classes. A_o : range (note that the effective range in
 619 exponential models is estimated as $A_o' = 3A_o$). RSV: relative structured variability, or
 620 $C_n/(C_o+C_n) \times 100$.

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Figure 1
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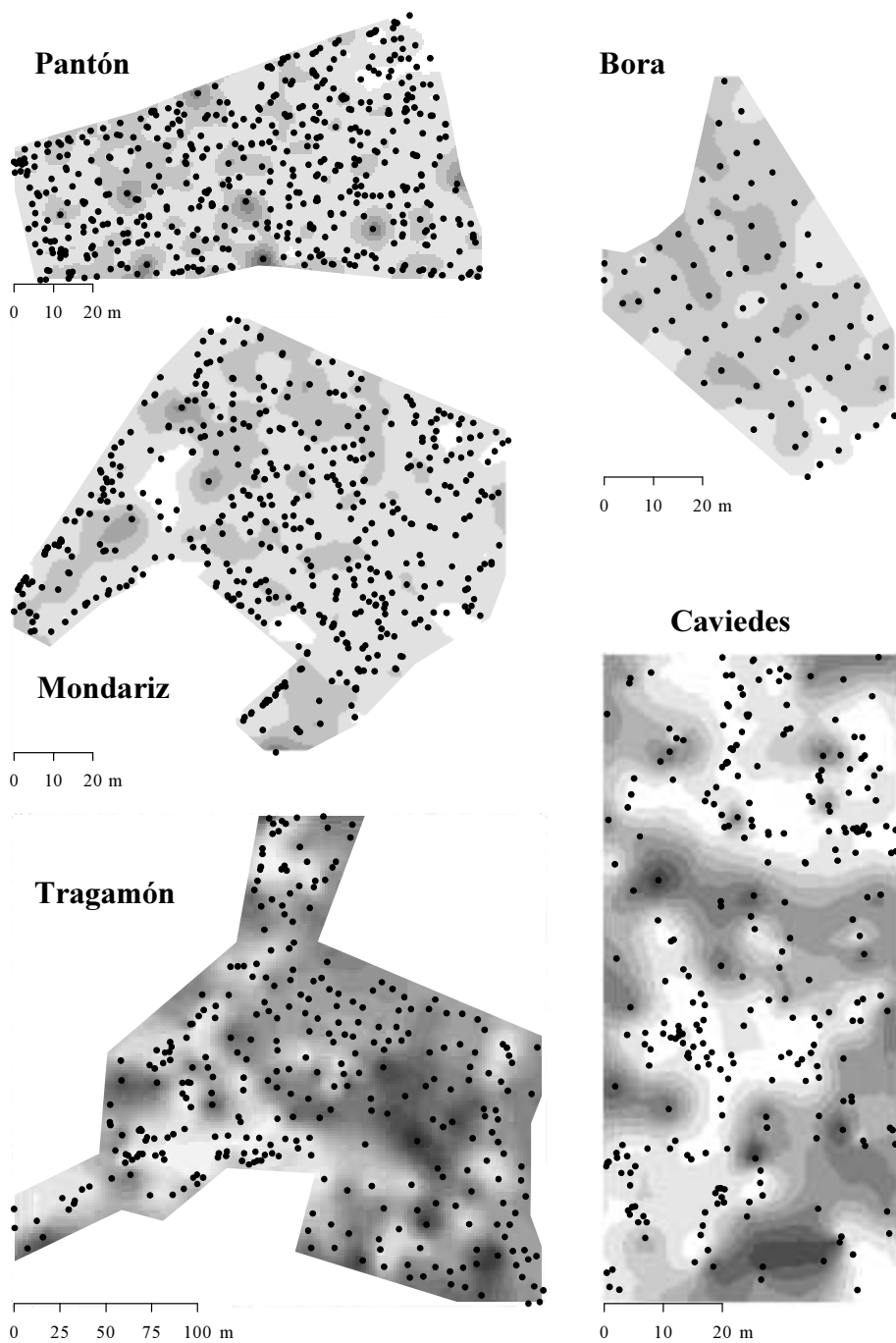
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Figure 2

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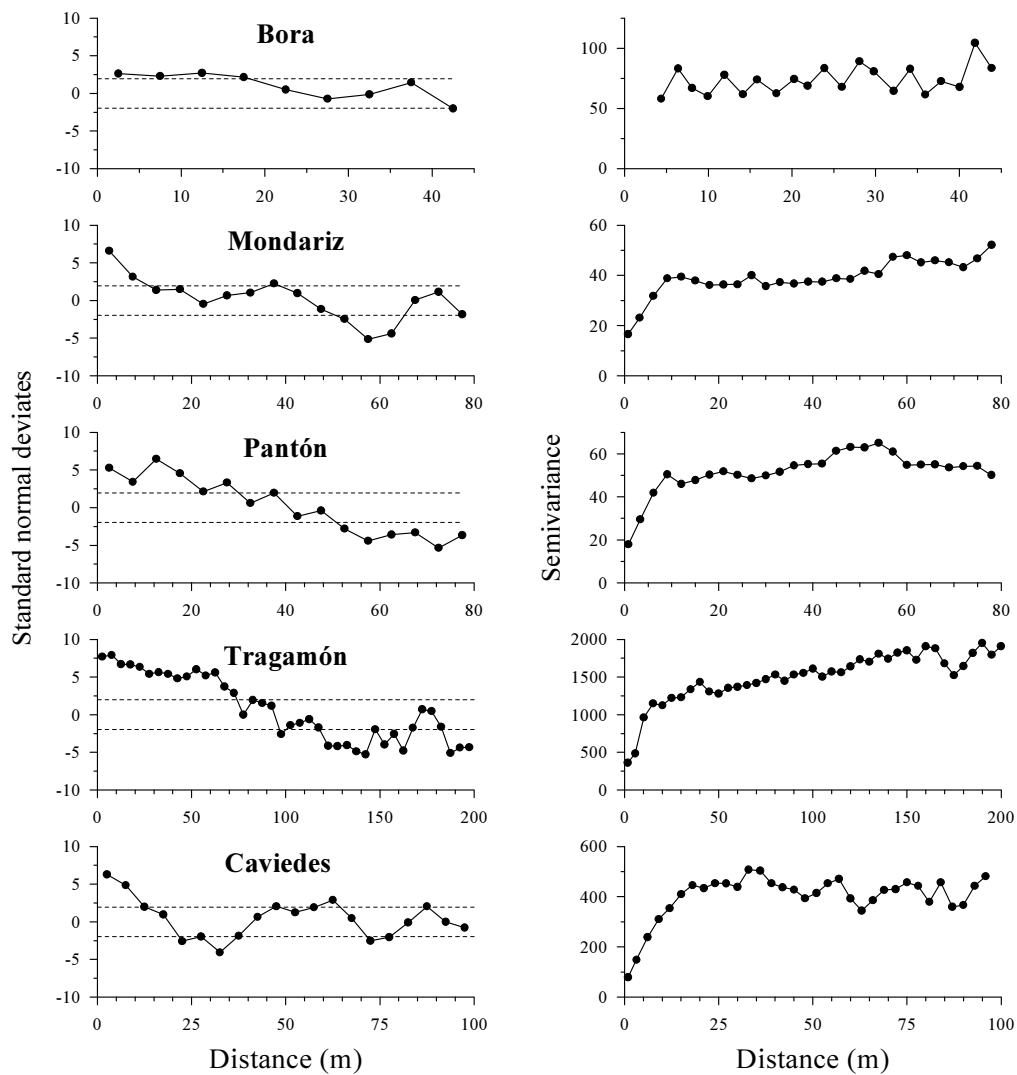
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Figure 3

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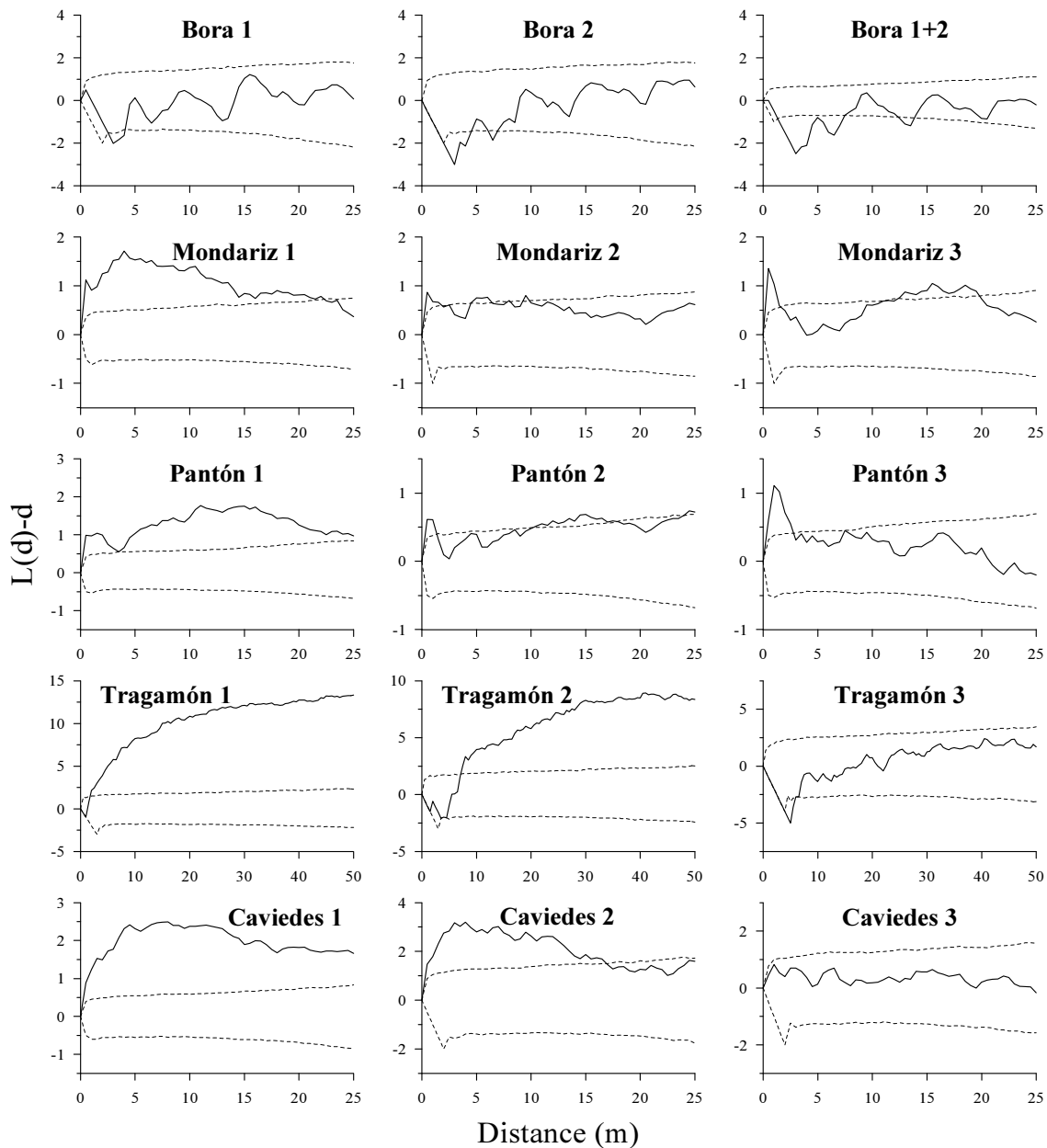


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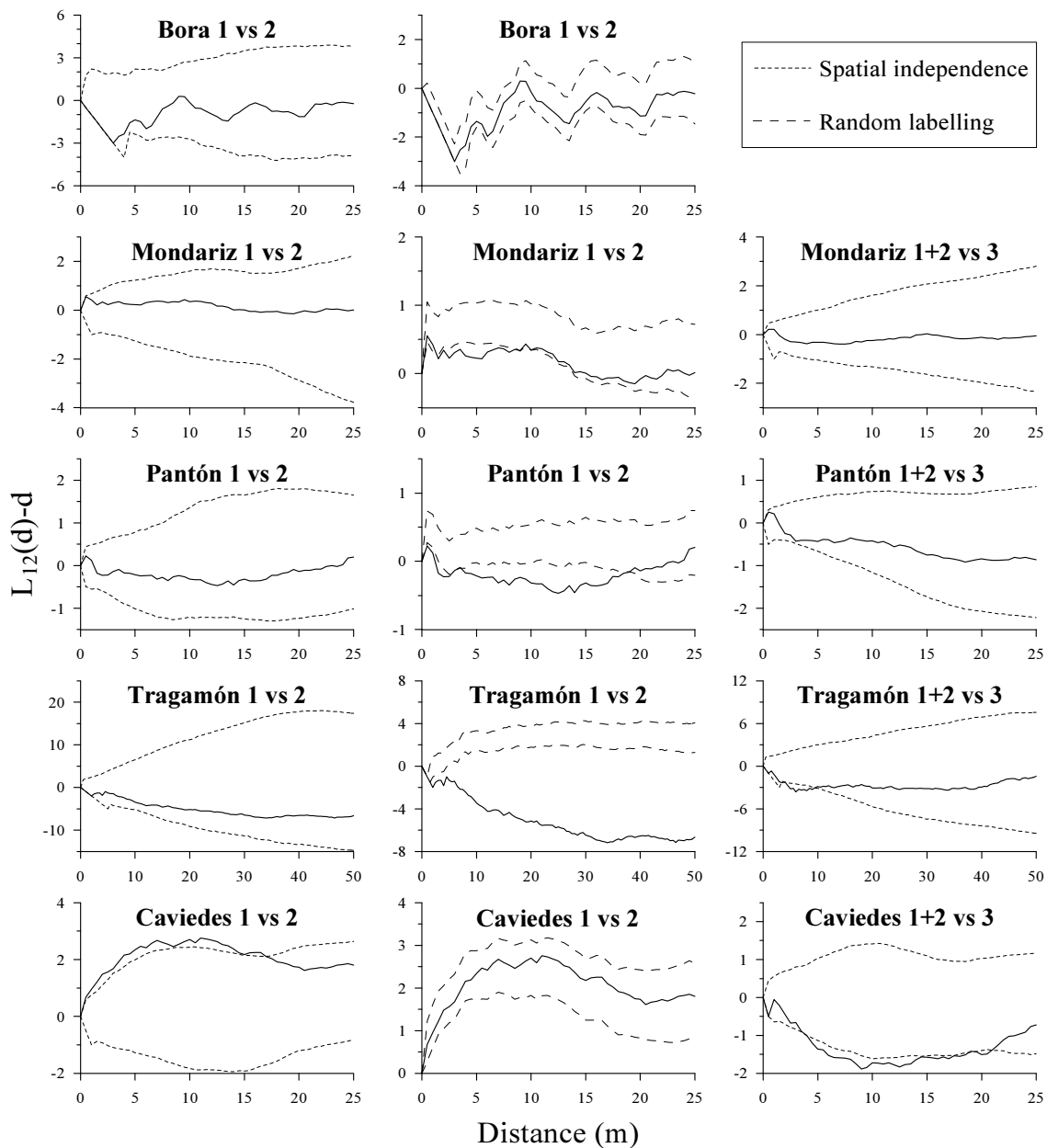
Figure 4
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Figure 5
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