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**Sex-related spatial segregation along environmental gradients in the dioecious
conifer, *Taxus baccata***

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1 **Abstract**

2 Sex-related differences in dioecious woody plants commonly result in spatial segregation of the
3 sexes and a male-biased sex ratio, leading to strongly structured populations. We report results
4 from more than 1000 precisely georeferenced individuals of a threatened European dioecious tree
5 species, *Taxus baccata* in central Italy. We hypothesized differences between males and females
6 in both spatial distribution and growth pattern. We used point pattern analysis (PPA) to evaluate
7 the spatial distribution of trees as influenced by dioecy and tree size, and dendrochronological
8 methods to study growth pattern differences between males and females. We found a dominance
9 of female trees giving a SR of 0.79, which increased along a gradient of elevation and slope. At
10 the microsite level, female *Taxus* trees were clumped to a scale of 30 m while male trees were
11 randomly distributed. We observed a significant effect of both sex and decade in the growth
12 pattern of *Taxus* trees, where annual radial growth of females was 8.3% greater than that of
13 males. Female trees are more commonly found in wetter sites and males are widely but sparsely
14 distributed, causing the absence of a clear spatial segregation of the sexes. Observed differences
15 in spatial and growth patterns of males and females have the potential to influence the climate
16 change response of *T. baccata* and other dioecious tree species, given that range expansion
17 depends upon the availability of seed-bearing, female trees that tend to be clumped in climatically
18 favorable sites.

19

20 **Keywords**

21 Dioecy; Tree-ring; Point pattern analysis; Spatial Segregation of the Sexes; Multi-scale approach

22

23

24 **Introduction**

25 Ecological differences between males and females in populations of dioecious plants have been
26 demonstrated by several studies (e.g. Bierzychudek and Eckhart 1988). Sex ratio (SR), defined as
27 the proportion of male to female trees, strongly influences the reproductive success and
28 conservation status of dioecious species (Grant and Mitton 1979). Particularly important for
29 reproductive success is the spatial distribution of the sexes that is often influenced by
30 environmental heterogeneity (Hultine et al. 2007). In harsh environments with limited resources,
31 microhabitat differences are responsible for the spatial segregation of the sexes (SSS -
32 Bierzychudek and Eckhart 1988). The underlying hypothesis of SSS is that females require more
33 resources for reproduction than males, leading to the prediction that females are more common in
34 high-resource microsites and males in low-resource microsites (Hultine et al. 2007). The
35 reproductive biology that causes SSS can thus contribute to the vulnerability of dioecious trees to
36 global change because females, requiring a greater reproductive effort, typically show slower
37 growth (de Jong and van der Meijden 2004; Iszkulo et al. 2009). On the poorer sites where males
38 dominate, lower seed availability can contribute to increased potential for regeneration failure in
39 the more resource limited portions of the species range, possibly accelerating species decline on
40 the trailing edgell in a climate change context (Hampe and Petit 2005). However, if SSS due to
41 niche partitioning is adaptive, then climatic changes could diversify resource availability and a
42 subsequent concentration of females on wetter sites.

43 The occurrence of male and female plants on different sites, and thus their spatial pattern,
44 can be used as an index of gender-environmental covariance and environmental heterogeneity
45 (Iglesias and Bell 1989). The influences of dioecy on the spatial pattern of tree populations have
46 rarely been studied (Gibson and Menges 1994; Nanami et al. 1999; Hultine et al. 2007), because

47 the majority of studies on dioecious species have been conducted without considering male and
48 female trees separately (e.g. Garcia et al. 2005; Martínez et al. 2010).
49 Spatial point pattern analysis (PPA - Moloney 1993; Wiegand et al. 2007) can be used to analyze
50 spatial association patterns in plant communities (Ripley 1981; Stoyan and Stoyan 1994). These
51 techniques quantify how neighborhood density changes with distance, thus providing a scaling
52 approach that is valuable for describing spatial heterogeneity in community ecology (Levin
53 1992). The contribution of dioecy to the spatial structure of tree communities can be measured by
54 performing a bivariate analysis that shows at different scales if there is significant attraction or
55 repulsion between males and females of the same species.

56 *T. baccata* is a dioecious tree species that plays an important role for the biodiversity of
57 European forests (Linares 2013). *T. baccata* is a relict species that is declining due to poor
58 regeneration (e.g. Sanz et al. 2009), habitat fragmentation (Dubreuil et al. 2010), and reduced
59 genetic variation (e.g. González-Martínez et al. 2010). Other studies have assessed the population
60 structure (Piovesan et al. 2009), structural diversity (Ruprecht et al. 2010), dendrochronological
61 potential (Moir 1999), radial growth (Cedro and Iszkulo 2011), sexual dimorphism (Iszkulo et al.
62 2009) and regeneration pattern (Devaney et al. 2014; Vessella et al. 2015) of *T. baccata*, but
63 sexual variation in distribution pattern and spatial associations among males and females remain
64 unknown. We tested the hypothesis that sex-related trait differences cause spatial segregation of
65 the sexes at three different scales:

- 66 1. SR varies consistently with water availability as expressed by elevation and precipitation
67 gradients across the species range throughout Europe.
- 68 2. SR is influenced by water availability as expressed by topographic gradients (elevation
69 slope, continentality) within our 162-ha study area in central Italy.

70 3. Sex-specific ecological differences cause spatial segregation of the sexes (SSS) at
71 microsite scales: female trees are clustered in more productive sites, whereas males are
72 located on more stressful sites.

73 Additionally, we hypothesized that resource limitation associated with dioecy influences growth
74 patterns following sexual maturity: male trees grow more than female ones.

75

76 **Materials and methods**

77 *Study area*

78 Macchia delle Tassinete (MdT) has been a floristic protected area since 1974 and is now a Site of
79 Community Importance (SCI) included in the Natura 2000 network (SCI IT5330013). MdT is
80 located in the vicinity of Cingoli village (43°21'N; 13°12'E) in the Marche region, central Italy.
81 The research area occupies 162 ha on predominantly north-facing slopes with elevation ranging
82 from 450 to 770 m a.s.l. The bedrock is limestone or marlstone and cambisols of the 'Calcic
83 Siltic Chernozem' are the dominant soil type. Annual precipitation (1921 - 1990) averages 912
84 mm and mean annual temperature (1950 - 1990) averages 13°C (Cingoli, 631 m a.s.l.). MdT is
85 classified as a 'mesoxeric Orno-Ostryetum' forest type (IPLA 2001), but tree species dominance
86 changes locally. Most frequent species are *Ostrya carpinifolia* Scop., *Fraxinus ornus* L., *Quercus*
87 *cerris* L., *Fagus sylvatica* L. and *Taxus baccata* L. Other locally abundant species are *Corylus*
88 *avellana* L., *Acer opalus* Mill. subsp. *obtusatum* (Waldst. & Kit. ex Willd.) Gams, *Laburnum*
89 *anagyroides* Medik., *Sorbus torminalis* (L.) Crantz, *Sorbus domestica* L., *Acer platanoides* L.,
90 *Quercus pubescens* Willd., and *Acer campestre* L. The current forest structure is the result of
91 previous coppicing on hardwood species and release of *Taxus* standards. The historical presence
92 of *Taxus* at MdT is documented by several historical monuments and documents in the Cingoli

93 village (Avicenna 1644). *Taxus* trees have been protected since 1500, in order to sustainably use
94 their valuable wood and to attract birds for hunting (Appignanesi 1982). However, the entire
95 MdT forest experienced clear-cut harvesting ca. 1870, for land consolidation after the Italian
96 unification process.

97

98 *Field and laboratory methods*

99 In 2011, all *Taxus* trees having a DBH > 15 cm were tagged and mapped with a Trimble GeoXT
100 GPS receiver and a differential correction through Pathfinder Office 4.2 software was performed
101 (0.5-1 m estimated accuracy). For each of 1030 mapped *Taxus* trees, we recorded sex, DBH, total
102 height, canopy height, and four canopy radii. Sex could be determined for 951 (92.3%) of *Taxus*
103 trees.

104 From a subsample of 10% of *Taxus* trees, selected according their diameter frequency
105 distribution, we collected two orthogonal wooden cores per tree (189 cores, 110 trees) at 1.3 m
106 height to perform a standard dendrochronological analysis. In the laboratory, all cores were glued
107 to grooved wooden mounts and sanded to a high polish until optimal surface resolution allowed
108 annual rings to be detected under magnification.

109

110 *Data analyses*

111 We assessed the spatial heterogeneity of tree sex distribution adopting a multi-scale approach.
112 At the species range scale (Europe), we compared the SR of our study site with SR of other *T.*
113 *baccata* forests by using literature data (Dhar et al. 2008; Iszkulo et al. 2009; Vessella et al.
114 2015), and used simple linear regression analysis to quantify relationships between SR and
115 elevation, and SR and annual precipitation. At the landscape scale, we explored SR behavior

116 within our study site through regression analysis along tree structural (DBH and height) and
117 environmental (elevation, slope and distance from the Adriatic Sea) gradients.

118 At the microsite scale, univariate and bivariate Point Pattern Analyses (PPA) were applied
119 to a data set of mapped *Taxus* locations (Moeur 1993) to assess tree spatial patterns within the
120 study area and the spatial associations between the two sexes or two DBH classes across spatial
121 scales from 0 – 50 m. The spatially explicit dataset that was used in the analyses comprised 419
122 males and 532 females, 784 small (DBH < 30 cm) and 56 large (DBH > 40 cm) trees. We used
123 pair-correlation functions $g(r)$ (Stoyan and Stoyan 1994) to avoid possible misinterpretation of
124 results due to the cumulative effect typically found in other methods such as K -function analysis
125 (Ripley 1977; Perry et al. 2006). The univariate pattern of *Taxus* trees as a whole was contrasted
126 against the heterogeneous Poisson null model to account for first-order effects. This null model
127 differs from complete spatial randomness (CSR) in that a function $\lambda(x, y)$ varies with location (x ,
128 y) but maintains the independence of the occurrence of any point with respect to any other
129 (Wiegand and Moloney 2004). For the bivariate analyses between males vs. females and small
130 vs. large trees, we applied the random labeling null model that simply randomizes tree category
131 without changing geographic position (Wiegand and Moloney 2004). The latter is a conservative
132 method to test the significance of spatial association between two categories (e.g. males vs
133 females). The 95% confidence intervals for both univariate and bivariate analyses were computed
134 from 999 Monte Carlo simulations (Stoyan and Stoyan 1994; Wiegand and Moloney 2004) and
135 the goodness-of-fit (GoF) test for null hypothesis was performed (Diggle 2003). All analyses
136 were done only for classes with more than 15 trees (Camarero et al. 2000), applying a 1 m lag
137 distance and a maximum distance of 100 m with the grid-based software Programita (Wiegand
138 and Moloney 2004) adopting a grid size of 1 m² and a ring width of 5 m.

139 Tree-ring widths were measured using a LINTAB semi-automatic optical system (Rinntech
140 2003) at a precision of 0.001 mm. All tree-ring series were first visually and then statistically
141 checked for cross-dating and measurement errors using the CDI (Cross Dating Index) run by
142 TSAP-Win software (Rinntech 2003). Mean tree-ring chronologies for male and female *Taxus*
143 trees were compiled from selected crossdated series using the ARSTAN program (Cook and
144 Holmes 1997). To remove interannual frequency variations each tree-ring series was standardized
145 with a spline function using a 50% frequency response. Statistical indices were calculated on a
146 common interval of 100 years (1909-2009) in order to compare male and female chronologies.
147 Tree-ring statistics included: the mean sensitivity (MS) which is the mean percent change from
148 each measured yearly ring value to the next to assess the high-frequency variation of the series
149 (Fritts 1976); the first-order autocorrelation on raw (AC) and standardized data (AC1); the
150 average correlation between series (RBAR) that was calculated for all series using the running
151 means method on overlay periods of 50 and 25 years; the Expressed Population Signal (EPS), a
152 measure of how the mean chronology derived from the sample trees represents a hypothetical
153 infinite replicated chronology (Wigley et al. 1984). Additionally, cumulative ring width and basal
154 area increment (BAI) curves were obtained from the mean chronologies of male and female trees.

155 A general linear mixed-effects model (GLMM) was used to detect radial growth differences
156 between males ($n = 32$) and females ($n = 38$) over the 1920 – 2010 time period. Radial growth
157 (decadal mean) was log transformed prior to analysis, to normalize distributions and stabilize
158 variance of residual errors. Log transformed radial growth (RG-ln) was used as the response
159 variable and sex and decade were used as independent factors. Individual tree identity was
160 specified as a random intercept term to allow the overall growth rate to vary by tree (accounting
161 for differences in genetics, microsite variability, etc.). GLMM was fitted by using the Linear and

162 Nonlinear Mixed Effects Models package (nlme 3.1-105 ver.) within the R statistical software
 163 (2.15.2 ver.).

164

165 **Results**

166 *Sex ratio at broad scales*

167 We found 419 males and 532 females, giving an overall SR of 0.79 (Table 1). Males were
 168 slightly larger (25.6 cm VS 25.14 cm DBH) and shorter (6.52 m VS 6.65 m height) than females,
 169 but these differences were not significant ($t = 0.729$; $p = 0.47$ for DBH and $t = -1.02$; $p = 0.309$
 170 for height).

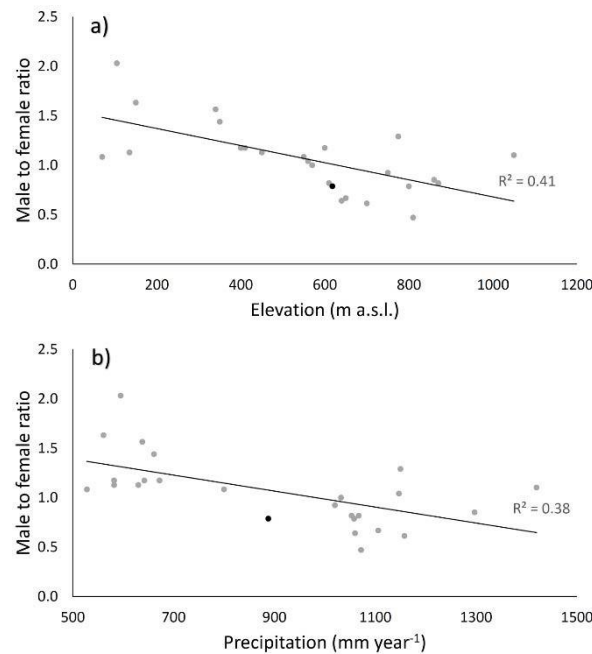
171

172 **Table 1.** Summary statistics (mean, median and standard error) of structural attributes and environmental variables
 173 of *Taxus* trees at MdT study site. DBH = diameter at breast height (cm); H = height (m), V = Volume (m³).

SEX (n)	Statistics	DBH (cm)	H (m)	Crown H (m)	Crown V (m ³)	Elevation (m a.s.l.)	Slope (°)	Sea Dist. (Km)
Males (419)	Mean	25.61	6.52	1.89	77.35	700.76	24.23	39.73
	Median	24.00	6.50	1.90	58.11	700.00	25.20	39.79
	SE	0.47	0.09	0.03	3.42	1.11	0.33	0.02
Females (532)	Mean	25.14	6.65	1.98	80.31	699.05	22.72	39.78
	Median	23.00	6.50	2.00	56.37	699.22	23.62	39.85
	SE	0.41	0.08	0.02	3.91	0.87	0.31	0.01
Undetermined (79)	Mean	25.01	6.95	1.80	99.92	640.66	21.63	39.33
	Median	22.00	6.60	1.80	62.30	681.12	24.69	39.33
	SE	1.08	0.24	0.07	10.47	8.68	1.21	0.07

174 At the species range scale, the MdT study site occupies an intermediate position in a topo-
175 climatic gradient of 24 European research studies reporting the SR of *Taxus* (Fig. 1). The MdT
176 site fits within an annual precipitation range (750 – 950 mm) that was rarely considered in
177 previous studies, and has a lower SR than expected for its precipitation level. Across the range of
178 *T. baccata*, the SR decreased with increasing elevation and precipitation.

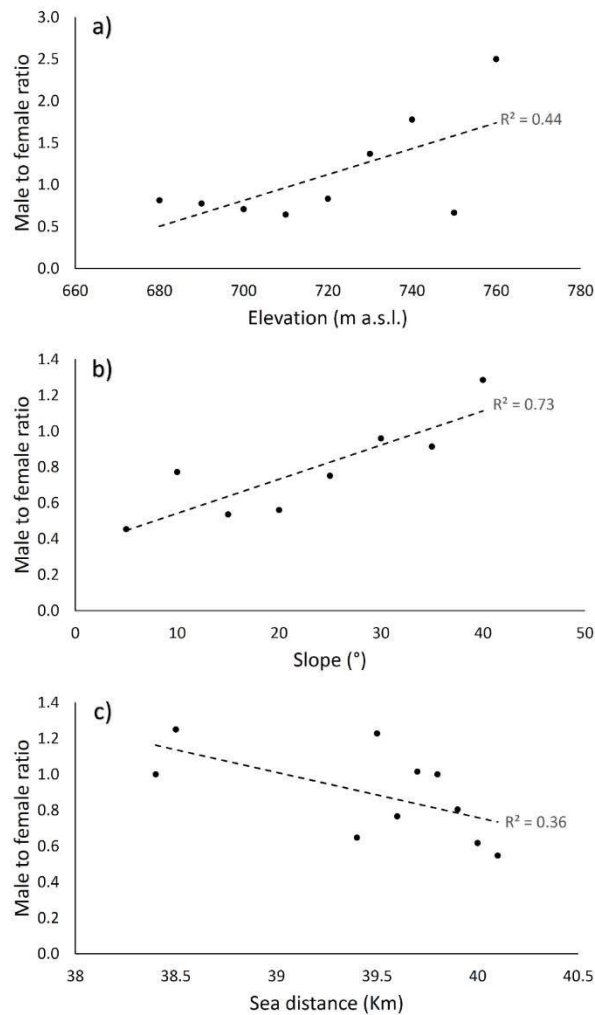
179
180 **Figure 1.** Male to female ratio (SR) observed at MdT (black dot) related to elevation (a) and precipitation (b)
181 compared to other 25 European forests (grey dots) with *T. baccata* (Dhar et al. 2008; Iszkulo et al. 2009; Vessella et
182 al. 2015).



183
184
185 At the landscape scale, SR increased with elevation and slope steepness and decreased with
186 distance to the Adriatic Sea (Fig. 2). SR approximated unity in those sites located at lower
187 elevations and closer to the sea.

188

189 **Figure 2.** Male to female ratio (SR) observed at MdT against environmental gradients of elevation (a), slope (b) and
190 distance from the Adriatic Sea (c).

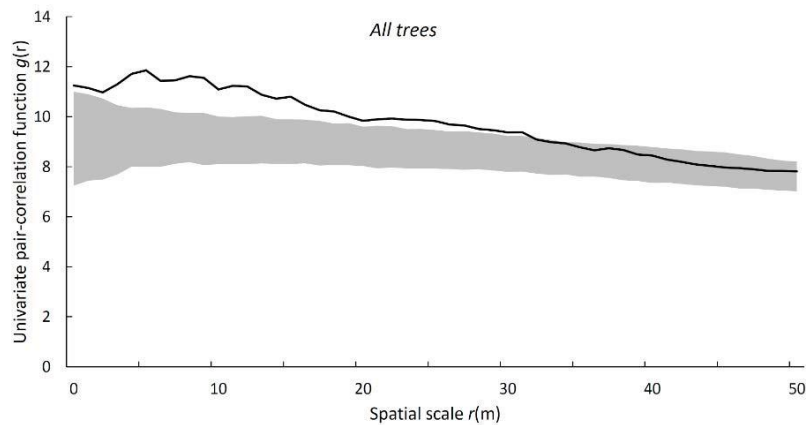


191
192
193 *Fine scale spatial pattern*
194 *Taxus* trees, pooled among both sexes and all DBH classes, showed significant aggregation ($p \leq$
195 0.01) to a distance of 30 m (Fig. 3). When considered separately in univariate analyses (Fig. 4),
196 males were randomly distributed, while females were weakly grouped ($p \leq 0.01$) at 15 and 35-40
197 m. The univariate $g(r)$ function showed a clear tendency towards aggregation ($p \leq 0.01$) for small
198 trees, whereas large trees were randomly distributed. By assessing the univariate pattern of a

199 combination between DBH and sex, we observed a similar pattern in males and females. Small
200 trees were weakly aggregated ($p \leq 0.01$) while large trees were randomly distributed.

201

202 **Figure 3.** Univariate analysis of the spatial pattern of 1030 *Taxus* trees at MdT. The bold line indicates the pair-
203 correlation function $g(r)$, and shaded areas encompass the non-significant, i.e. random, distribution and represent
204 points within the 2.5th and 97.5th percentile $g(r)$ values of the 999 simulations of the null model assuming a
205 heterogeneous Poisson distribution.



206

207

208 The bivariate spatial association between sexes showed a random pattern (Fig. 5).

209 However, significant spatial segregation ($p \leq 0.01$) was observed between small and large
210 diameter trees, with stronger segregation for males than for females.

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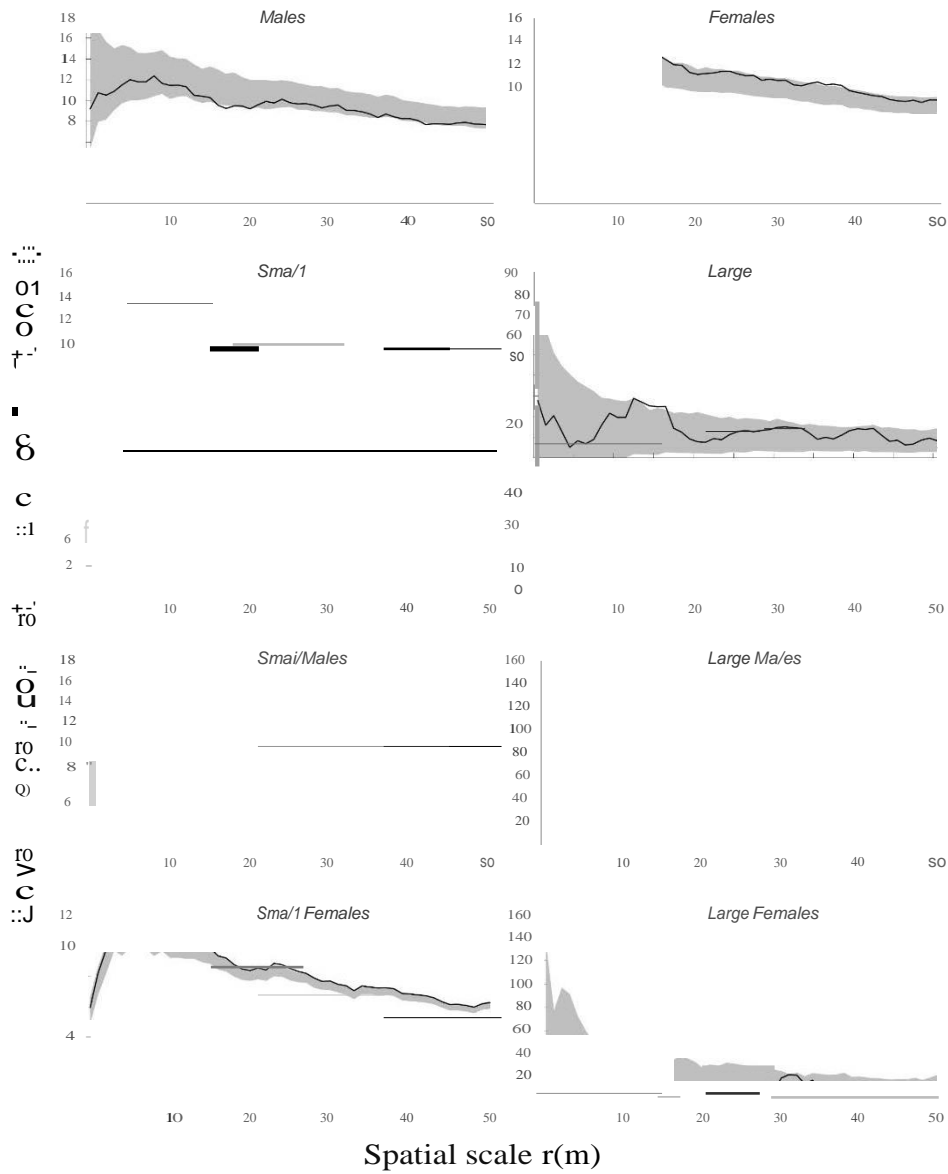
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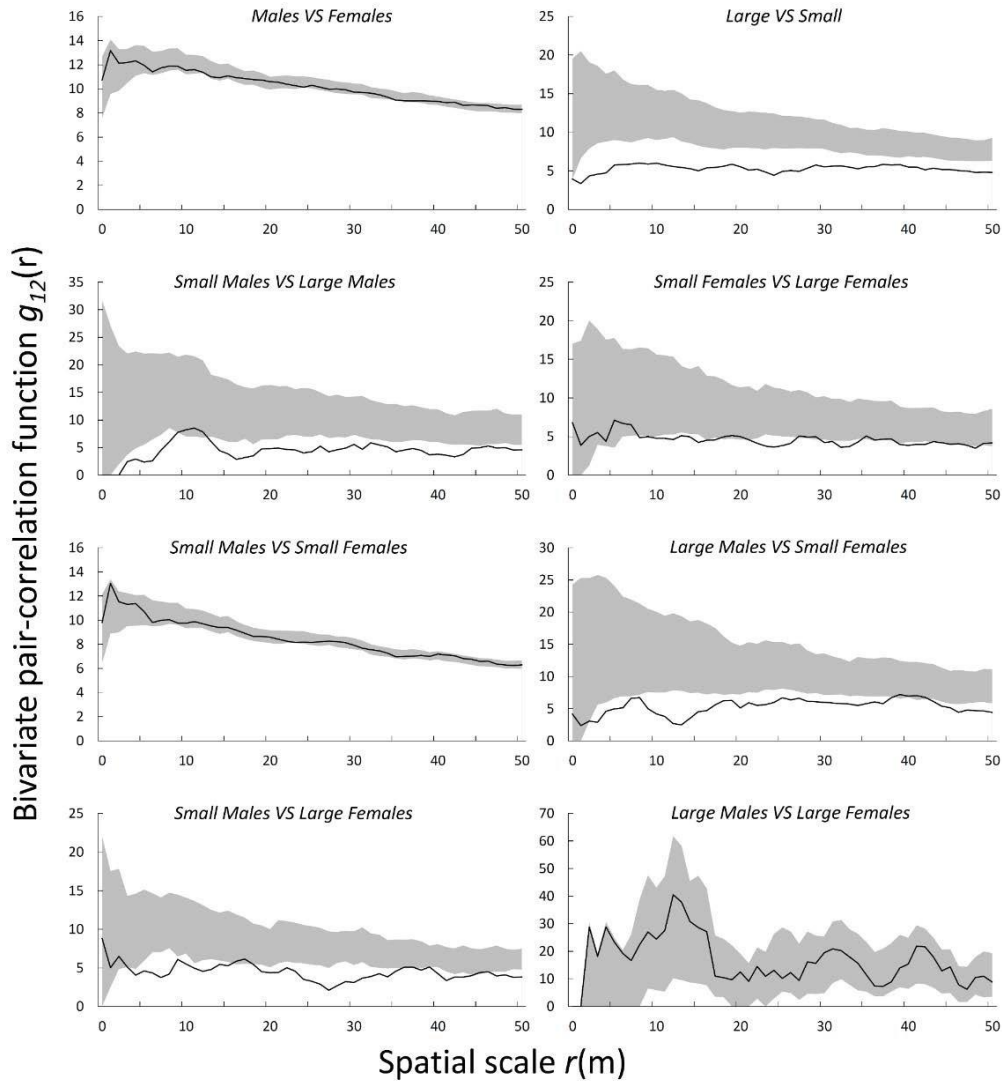
218

219 Figure 4. Univariate analysis of the spatial pattern of *Taxus* trees, considering sex (males and females), DBH (small
 220 and large), and their combinations (e.g. small males and large females), using the pair-correlation function $g(r)$.
 221 Black lines indicate the pair-correlation functions $g(r)$, and shaded areas encompass random distribution and
 222 represent points within the 2.5th and 97.5th percentile $g(r)$ values of the 999 simulations of the null model (Random
 223 Labeling).



224
 225
 226
 227

228 **Figure 5.** Bivariate analysis of the spatial pattern of *Taxus* trees, considering sex (males and females) and DBH
 229 (small and large), and their combinations (e.g. small males VS large females), using the pair-correlation function
 230 $g_{12}(r)$. Black lines indicate the pair-correlation functions $g_{12}(r)$, and shaded areas encompass random distribution
 231 and represent points within the 2.5th and 97.5th percentile $g_{12}(r)$ values of the 999 simulations of the null model
 232 (Random Labeling).



233
 234 *Growth pattern*
 235 Male and female tree-ring chronologies were well crossdated and showed similar values in most
 236 dendrochronological descriptors (Table 2): time spans were 1879-2010 for males and 1881-2010

237 for females. Males and females showed similar mean ring width (0.99 mm and 1.06 mm), mean
 238 sensitivity (high-frequency variability), first-order autocorrelation (low-frequency variability),
 239 correlation between tree-ring series (Rbar), and adequacy of the chronologies (EPS). The two
 240 BAI curves (Fig. 6a) show similar trends particularly in recent years, with a growth oscillation of
 241 approximately 30 yrs caused by a coppice rotation cut on hardwood species in 1984 and the
 242 resulting canopy regrowth. The periods of greatest differences between male and female growth
 243 were 1907-1915, 1943-1959, and 1963-1975. Finally the cumulative ring width curves showed a
 244 coincident growth pattern of male and female *Taxus* trees up to the 1950's and a slightly
 245 increasing divergence thereafter (Fig. 6b).

246 The GLMM showed a significant effect of sex on radial growth of *Taxus* trees ($p =$
 247 0.028). Annual radial growth of female trees was 8.3% greater than that of male trees (95% CI:
 248 0.9% to 15.1%), after accounting for decade of growth and the random effects of growth
 249 variability among individuals growing in different microsites.

250

251 **Table 2.** Comparison of males and females chronologies by common statistical dendrochronology indices (MRW:
 252 mean ring width; MI = mean index value; Rbar = average correlation between series; EPS = expressed population
 253 signal; MS = mean sensitivity of the average chronology; AC1 = first-order autocorrelation on raw data; AC =
 254 autocorrelation on standardized data).

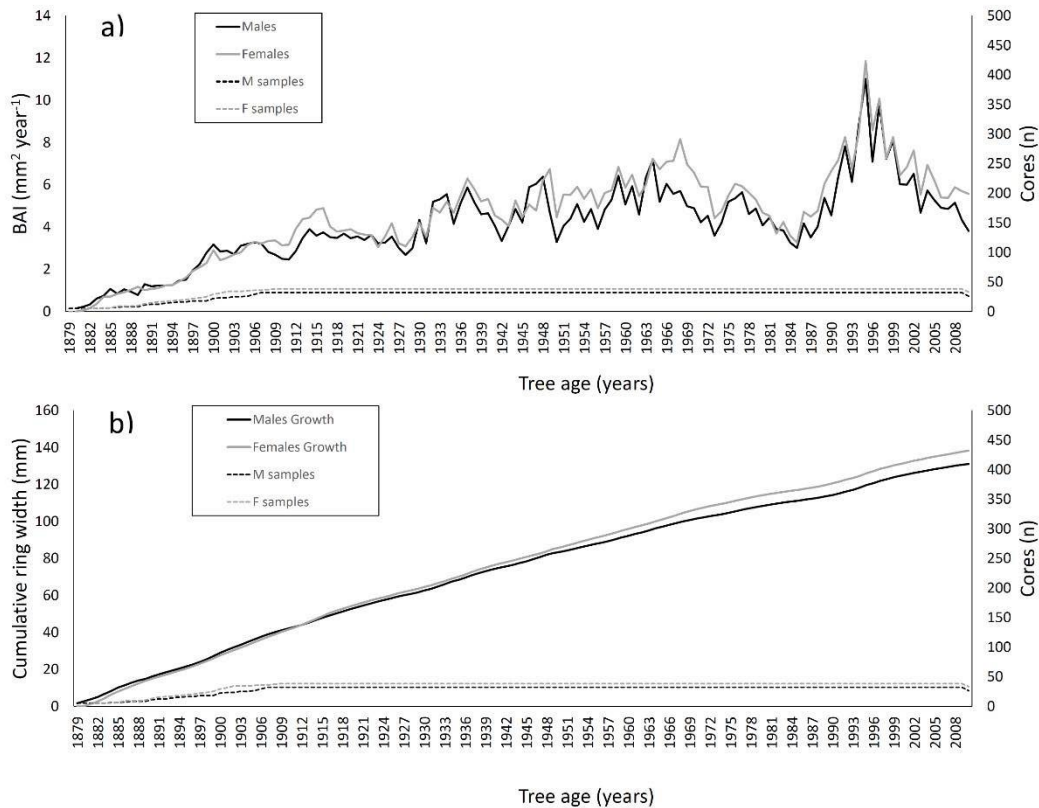
Series (n)	Time Interval (yrs)	Common Interval (yrs)	MRW (mm)	MI	Rbar	EPS	MS	AC1	AC
Males (32)	1879-2010	1909-2009	0.99	0.97	0.16	0.86	0.16	0.7	-0.1
Females (38)	1881-2010	1909-2009	1.06	0.98	0.14	0.86	0.12	0.8	-0.2

255

256

257

258 **Figure 6.** Basal Area Increment (a) and cumulative ring width for males (n = 32) and females (n = 38) at MdT study
 259 site. Continuous lines indicate BAI and cumulative ring width and dotted lines indicate the number of sampled cores.



260
 261
 262 **Discussion**
 263 *Sex ratio at species range and landscape scales*
 264 At the regional scale, our study site occupies an intermediate position along a European
 265 environmental gradient where the SR decreased with increasing elevation and precipitation (Fig.
 266 2). We observed SRs that were female-biased, and lower than would be expected given regional
 267 levels of precipitation and elevation. Female-biased populations have also been found on wetter
 268 sites in the Alps (Hilfiker et al. 2004) and in the Andes (Nuñez et al. 2008), adding support to the
 269 hypothesis that the proportion of females increases with water availability.

270 At the landscape-scale in our MdT study area, we observed a high SR on steeper, higher
271 elevation sites, the opposite relationship as observed for the regional-scale comparisons. This
272 apparent discrepancy likely arises because the sites closer to the ridge are more water-limited
273 because of shallow, rocky soils, and thus are least favorable for female *Taxus* trees. On the
274 contrary, at a regional scale higher elevation sites coincided with increased water availability
275 (Iszkulo et al. 2009).

276 Males were less abundant than females at MdT and the difference between them in tree
277 size (DBH and height) was not significant. These findings are partly discordant with other studies
278 on *T. baccata* of central Europe that found larger and more abundant males on drier sites (Iszkulo
279 et al. 2009).

280 SR increased with increasing diameter, but decreased with increasing height consistently
281 with other European studies on SR of *Taxus* trees (e.g. Iszkulo et al. 2009). Taken together, these
282 data suggest that males put more carbon into diameter growth, and females into height growth,
283 when they are in the older growth stages. However, this could also be a matter of where they
284 grow: possibly the females, growing on the wetter sites, have more side-pressure from competing
285 trees and so allocate more carbon to height growth.

286

287 *Influence of dioecy on spatial patterns at microsite scales*

288 Adult *Taxus* trees (DBH > 15 cm) were strongly grouped at fine spatial scales (< 30 m) at MdT,
289 probably representing a pattern of repeated clustering. On the contrary, other authors have found
290 random distribution in adult *Taxus* trees (Martinez et al. 2010). Considering the two sexes
291 separately, we observed a weak but clustered pattern in females and a random pattern in males.
292 The observed patterns were consistent with the hypothesis of males being the more stress tolerant

293 that can occupy a broader spectrum of suitable microsites (Hultine et al. 2007; Iszkulo et al.
294 2009).

295 We did not find spatial segregation of the sexes (SSS) at MdT, meaning that there was not
296 significant aggregation nor repulsion between males and females. This was probably because
297 female trees were clustered and more common in wetter portions of the elevation gradient,
298 whereas males were widely distributed. Homogeneity of habitats at fine scales can be another
299 possible cause of absence of spatial segregation of the sexes (Ueno et al. 2007; Schmidt 2008;
300 Iszkulo et al. 2011). However, female *Taxus* trees at MdT exhibited a clear tendency towards
301 clustering in wetter sites. Another possible explanation for the absence of SSS at MdT could be
302 that seed dispersal in *T. baccata* is primarily by birds causing a wide distribution of seeds
303 (Hubbell 1979; Murray 1988) that can in turn weaken the effect of dioecy on the spatial
304 heterogeneity of trees (Nanami et al. 1999). Birds can spread seeds across long distances, but
305 often distribute seeds in a clustered manner (e.g. burial sites for seed-caching species; below
306 favorite roosting sites).

307 Nevertheless, we found spatial segregation between smaller and larger trees, a pattern
308 already described for adult *Taxus* trees and regeneration in other European sites (Dovčiak 2002;
309 Piovesan et al. 2009; Devaney et al. 2014). As expected, small trees were aggregated for both
310 males and females, whereas large trees were randomly distributed. The spatial segregation
311 between smaller and larger trees is probably due to a negative intraspecific neighborhood effect
312 that has been previously reported for *T. baccata* (Dovčiak 2002; Piovesan et al. 2009; Devaney et
313 al. 2014) and for other species (He and Duncan 2000). Moreover, the traditional coppice system
314 with dense *Taxus* standards may have favored the establishment of *Taxus* regeneration into forest
315 canopy gaps close to adult *Taxus* trees.

316

317 *Influence of dioecy on growth patterns*

318 The mean chronologies of male and female *Taxus* trees emerged as being very similar showing
319 that the overall growth patterns were analogous. However, despite wide variability among
320 individual trees, female *Taxus* trees in our study area showed a significantly higher growth rate.
321 Nonetheless, other authors have reported a radial growth reduction of female trees associated
322 with the achievement of sexual maturity in the studied population (e.g. Obeso 2002; Bañuelos
323 and Obeso 2004; Cedro and Iszkulo 2011). Female individuals may require more resources than
324 males because of higher reproduction effort (Iszkulo et al. 2009). A possible explanation of the
325 counter-intuitive pattern observed at MdT is that female growth can be favored by the more
326 productive sites that they occupy, as opposed to males that occur across a wide variety of
327 microsite conditions. Where female trees of dioecious species occupy more favorable sites than
328 males, greater resource availability may compensate for greater reproductive requirements. Other
329 authors found no significant differences between sexes in *Araucaria angustifolia* mean radial
330 growth in South America, but they observed a higher growth rate of females in the last two
331 decades (Cattaneo et al. 2013).

332 Our results highlight that in order to relate observed spatial patterns in dioecious species
333 to habitat conditions, we need to consider abiotic and biotic constraints of tree establishment.
334 Future research should investigate the spatial pattern of male and female trees along wide
335 environmental gradients, in order to better understand the role of climate and topography in the
336 SSS process. Site conditions, habitat variability, and water availability in particular are expected
337 to strongly influence the strength of segregation between sexes in dioecious species (Dawson and
338 Bliss 1989; Dudley 2006). Spatial distribution modeling of dioecious species requires accounting
339 for the different resource requirements and distribution patterns of male and female trees,

340 particularly in the climate change context where range expansion to favorable sites depends upon
341 the availability of seed-bearing, female trees (Tognetti et al. 2012; Hultine et al. 2013).

342

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350

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