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

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Abstract

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

Keywords

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

Introduction

Ecological differences between males and females in populations of dioecious plants have been demonstrated by several studies (e.g. Bierzychudek and Eckhart, 1988; Geber et al., 1999). Sex ratio (SR), defined as the proportion of male to female trees, strongly influences the reproductive success and conservation status of dioecious species (Grant and Mitton, 1979). Particularly important for reproductive success is the spatial distribution of the sexes that is often influenced by environmental heterogeneity (Hultine et al., 2007). In harsh environments with limited resources, microhabitat differences are responsible for the spatial segregation of the sexes (SSS - Bierzychudek and Eckhart, 1988). The underlying hypothesis of SSS is that females require more resources for reproduction than males, leading to the prediction that females are more common in high-resource microsites and males in low-resource microsites (Hultine et al., 2007). The reproductive biology that causes SSS can thus contribute to the vulnerability of dioecious trees to global change because females, requiring a greater reproductive effort, typically show slower growth (de Jong and van der Meijden, 2004; Iszkulo et al., 2009). On the poorer sites where males dominate, lower seed availability can contribute to increased potential for regeneration failure in the more resource limited portions of the species range, possibly accelerating species decline on the “trailing edge” in a climate change context (Hampe and Petit, 2005). However, if SSS due to niche partitioning is adaptive, then climatic changes could diversify resource availability and a subsequent concentration of females on climatically favorable sites.

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

because the majority of studies on dioecious species have been conducted on the whole community structure (e.g. Garcia et al., 2005; Martínez et al., 2010). Spatial point pattern analysis (PPA – Moloney, 1993; Wiegand et al., 2007) can be used to analyze spatial association patterns in plant communities (Ripley, 1981; Stoyan and Stoyan, 1994). These techniques quantify how neighborhood density changes with distance, thus providing a scaling approach that is valuable for describing spatial heterogeneity in community ecology (Levin, 1992). The contribution of dioecy to the spatial structure of tree communities can be measured by performing a bivariate analysis that shows at different scales if there is significant attraction or repulsion between males and females of the same species.

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

1. SR is influenced by water availability as expressed by topographic gradients (elevation slope, continentality) within our 162-ha study area in central Italy.

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

We also compared the SR of our study area along elevation and precipitation gradients across the species range throughout Europe. Additionally, we hypothesized that resource limitation associated with dioecy influences growth patterns following sexual maturity: male trees grow more than female ones.

Materials and methods

Study area

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

previous coppicing on hardwood species and release of *Taxus* standards. The historical presence of *Taxus* at MdT is documented by several historical monuments and documents in the Cingoli village (Avicenna, 1644). *Taxus* trees have been protected since 1500, in order to sustainably use their valuable wood and to attract birds for hunting (Appignanesi, 1982). However, the entire MdT forest experienced clear-cut harvesting ca. 1870, for land consolidation after the Italian unification process.

Field and laboratory methods

In 2011, all *Taxus* trees having a DBH > 15 cm were tagged and mapped with a Trimble GeoXT GPS receiver and a differential correction through Pathfinder Office 4.2 software was performed (0.5-1 m estimated accuracy). For each of 1030 mapped *Taxus* trees, we recorded sex, DBH, total height, canopy height, and four canopy radii. We used a conservative DBH threshold to collect only those trees that reached sexual maturity. However, sex could be determined for 951 (92.3%) of *Taxus* trees. Topographic variables such as elevation and slope were derived from a regional digital elevation model with a geometric resolution of 10 m.

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

Data analyses

We assessed the spatial heterogeneity of tree sex distribution adopting a multi-scale approach.

At the species range scale (Europe), we compared the SR of our study site with SR of other *T. baccata* forests by using literature data (Dhar et al., 2008; Iszkulo et al., 2009; Vessella et al., 2015), and used simple linear regression analysis to quantify relationships between SR and elevation, and SR and annual precipitation. At the landscape scale, we explored SR behavior within our study site through regression analysis along tree structural (DBH and height) and environmental (elevation, slope and distance from the Adriatic Sea) gradients.

At the microsite scale, univariate and bivariate Point Pattern Analyses (PPA) were applied to a data set of mapped *Taxus* locations (Moeur, 1993) to assess tree spatial patterns within the study area and the spatial associations between the two sexes or two DBH classes across spatial scales from 0 – 50 m. The spatially explicit dataset that was used in the analyses comprised 419 males and 532 females, 336 small (DBH \leq 20 cm) and 694 large (DBH $>$ 20 cm) trees. We used pair-correlation functions $g(r)$ (Stoyan and Stoyan, 1994) to avoid possible misinterpretation of results due to the cumulative effect typically found in other methods such as *K*-function analysis (Ripley, 1977; Perry et al., 2006). The univariate pattern of *Taxus* trees as a whole was contrasted against the heterogeneous Poisson null model to account for first-order effects. This null model differs from complete spatial randomness (CSR) in that a function $\lambda(x, y)$ varies with location (x, y) but maintains the independence of the occurrence of any point with respect to any other (Wiegand and Moloney, 2004). Heterogeneous Poisson null model is particularly suited for study areas featuring environmental heterogeneity or strong gradients (Getzing et al., 2008). For the bivariate analyses between males vs. females and small vs. large trees, we applied the random labeling null model that simply randomizes tree category without changing geographic position (Wiegand and Moloney, 2004). The latter is a conservative method to test the significance of spatial association between two categories (e.g. males vs females). The 95% confidence intervals for both univariate and bivariate analyses were computed from 999 Monte Carlo simulations

(Stoyan and Stoyan, 1994; Wiegand and Moloney, 2004) and the goodness-of-fit (GoF) test for null hypothesis was performed (Diggle, 2003). All analyses were done only for classes including more than 100 trees (Pommerening et al., 2013), applying a 1 m lag distance and a maximum distance of 50 m with the grid-based software Programita (Wiegand and Moloney, 2004) adopting a grid size of 1 m² and a ring width of 5 m.

Tree-ring widths were measured using a LINTAB semi-automatic optical system (Rinntech, 2003) at a precision of 0.001 mm. All tree-ring series were first visually and then statistically checked for cross-dating and measurement errors using the CDI (Cross Dating Index) run by TSAP-Win software (Rinntech, 2003). Mean tree-ring chronologies for male and female *Taxus* trees were compiled from crossdated series with at least 100 tree-rings (n. 70) using the ARSTAN program (Cook and Holmes, 1997). To remove interannual frequency variations each tree-ring series was standardized with a spline function using a 50% frequency response. Statistical indices were calculated on a common interval of 100 years (1909-2009) in order to compare male and female chronologies. Tree-ring statistics included: the mean sensitivity (MS) which is the mean percent change from each measured yearly ring value to the next to assess the high-frequency variation of the series (Fritts, 1976); the first-order autocorrelation on raw (AC) and standardized data (AC1); the average correlation between series (RBAR) that was calculated for all series using the running means method on overlay periods of 50 and 25 years; the Expressed Population Signal (EPS), a measure of how the mean chronology derived from the sample trees represents a hypothetical infinite replicated chronology (Wigley et al., 1984). Some tree-ring statistics were calculated on raw data (i.e. Mean width, MS and AC1), other on indexed series (EPS, RBAR, AC1). Additionally, cumulative ring width curve was obtained from the mean chronologies of male and female trees adding the annual tree-ring growth.

Basal area increment (BAI) was derived from ring width and radius length. BAI at year t , was computed from the difference in area between two consecutive circles (at $t-1$ and t).

A general linear mixed-effects model (GLMM) was used to detect radial growth differences between males ($n = 32$) and females ($n = 38$) over the 1920 – 2010 time period. Radial growth (decadal mean) was log transformed prior to analysis, to normalize distributions and stabilize variance of residual errors. Log transformed radial growth (RG-ln) was used as the response variable and sex and decade were used as independent factors. Individual tree identity was specified as a random intercept term to allow the overall growth rate to vary by tree (accounting for differences in genetics, microsite variability, etc.). GLMM was fitted by using the Linear and Nonlinear Mixed Effects Models package (nlme 3.1-105 ver.) within the R statistical software (2.15.2 ver.).

Results

Sex ratio at broad scales

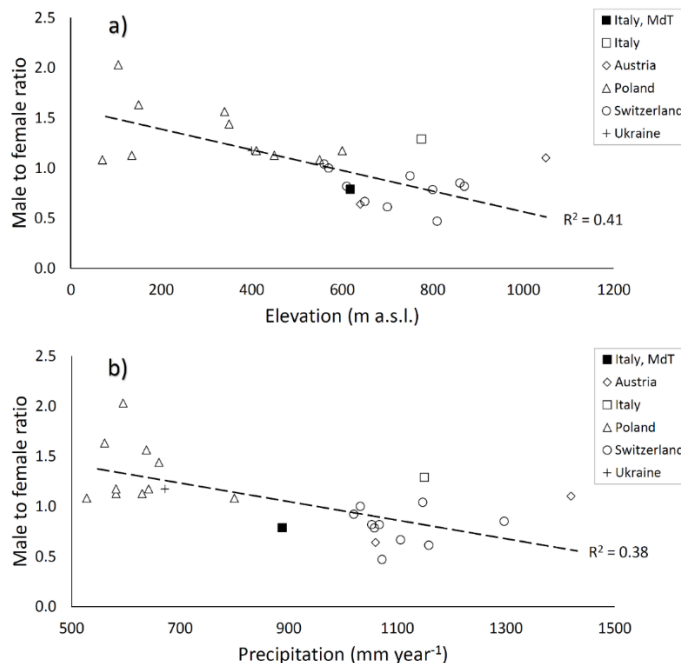
We found 419 male and 532 female trees, giving an overall SR of 0.79 (Table 1). Males were slightly larger (25.6 cm VS 25.14 cm DBH) and shorter (6.52 m VS 6.65 m height) than females, but these differences were not significant ($t = 0.729$; $p = 0.47$ for DBH and $t = -1.02$; $p = 0.309$ for height).

Table 1. Summary statistics (mean, median and standard error) of structural attributes and environmental variables of *Taxus* trees at MdT study site. DBH = diameter at breast height (cm); H = height (m), V = Volume (m^3).

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

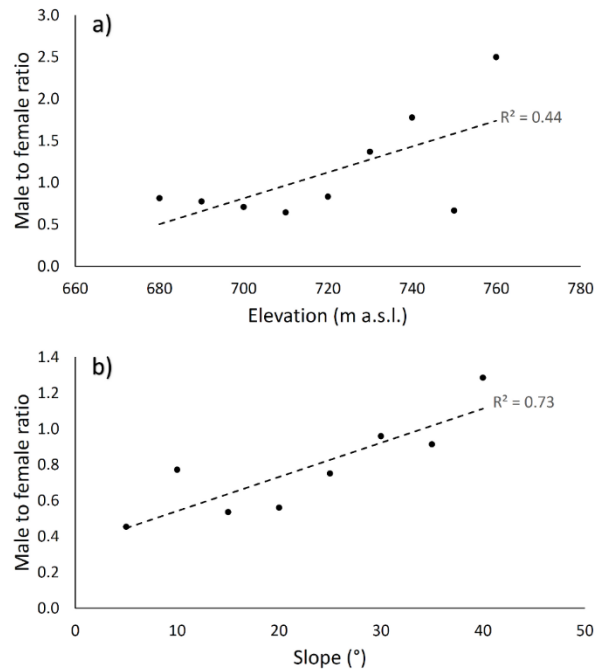
At the species range scale, the MdT study site occupies an intermediate position in a topo-climatic gradient of 24 European research studies reporting the SR of *Taxus* (Fig. 1). The MdT site fits within an annual precipitation range (750 – 950 mm) that was rarely considered in previous studies, and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

Figure 1. Male to female ratio (SR) observed at MdT (filled square) related to elevation (a) and precipitation (b) compared to other 25 European forests (open dots) with *T. baccata* (Dhar et al. 2008; Iszkulo et al. 2009; Vessella et al. 2015). Both linear models were statistically significant ($p < 0.001$ and $p = 0.0012$ respectively).



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

Figure 2. Male to female ratio (SR) observed at MdT against environmental gradients of elevation (a) and slope (b). Both linear models were statistically significant ($p = 0.043$ and $p = 0.0063$ respectively).

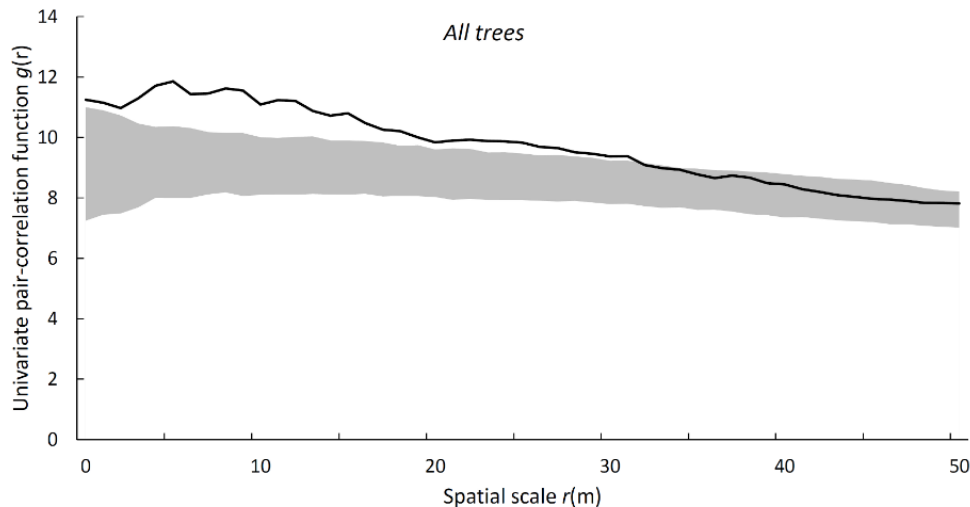


Fine scale spatial pattern

Taxus trees, pooled among both sexes and all DBH classes, showed significant aggregation ($p \leq 0.01$) to a distance of 30 m (Fig. 3). When considered separately in univariate analyses (Fig. 4), males were randomly distributed, while females were weakly grouped ($p \leq 0.01$) at 15 and 35-40 m. The univariate $g(r)$ function showed a clear tendency towards aggregation ($p \leq 0.01$) to a distance of 30 m for small trees, whereas large trees were randomly distributed at short distances (0 – 25 m). By assessing the univariate pattern of a combination between DBH and sex, we observed a similar pattern in males and females. Small trees were weakly aggregated ($p \leq 0.01$) while large trees were randomly distributed.

Figure 3. Univariate analysis of the spatial pattern of 1030 *Taxus* trees at MdT. The bold line indicates the pair-correlation function $g(r)$, and shaded areas encompass the non-significant, i.e. random, distribution and represent

points within the 2.5th and 97.5th percentile $g(r)$ values of the 999 simulations of the null model assuming a heterogeneous Poisson distribution.



The bivariate spatial association between sexes showed a random pattern (Fig. 5). However, significant spatial segregation ($p \leq 0.01$) was observed between small and large diameter trees, with stronger segregation for females than for males. A significant spatial segregation ($p \leq 0.01$) was observed also between small males and large females.

Figure 4. Univariate analysis of the spatial pattern of *Taxus* trees, considering sex (males and females), DBH (small and large), and their combinations (e.g. small males and large females), using the pair-correlation function $g(r)$. Black lines indicate the pair-correlation functions $g(r)$, and shaded areas encompass random distribution and

represent points within the 2.5th and 97.5th percentile $g(r)$ values of the 999 simulations of the null model (Random Labeling).

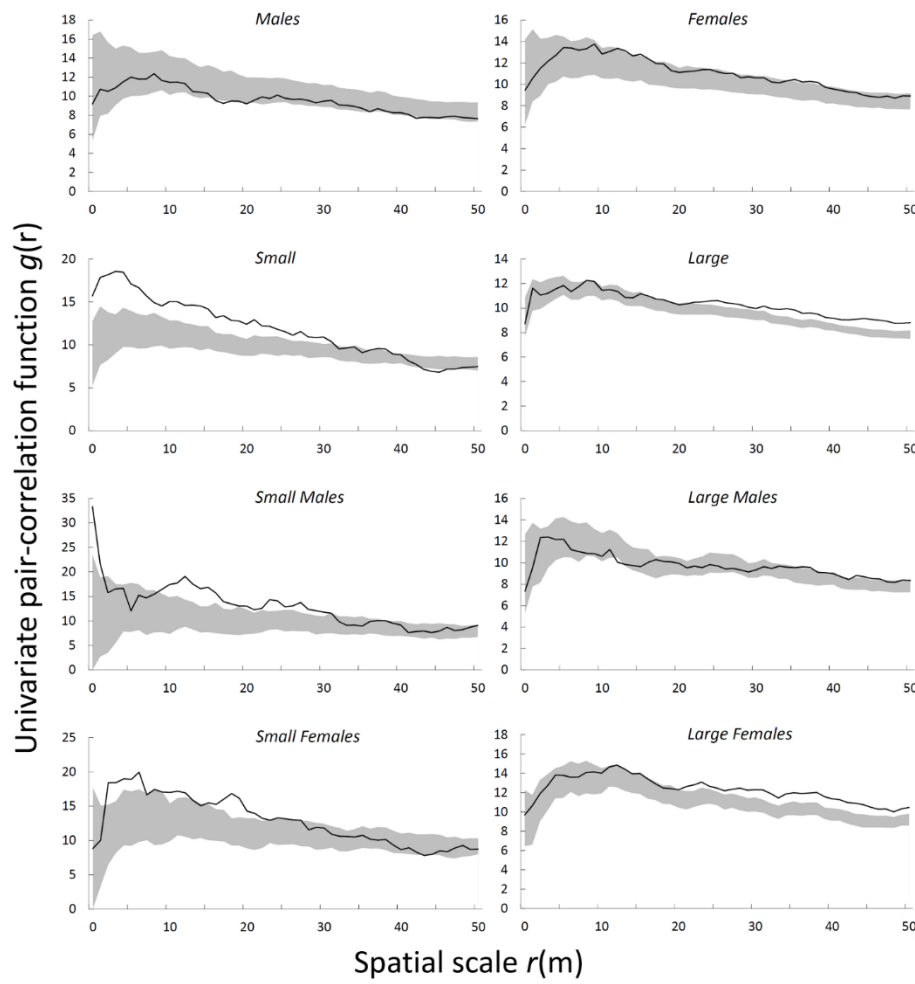
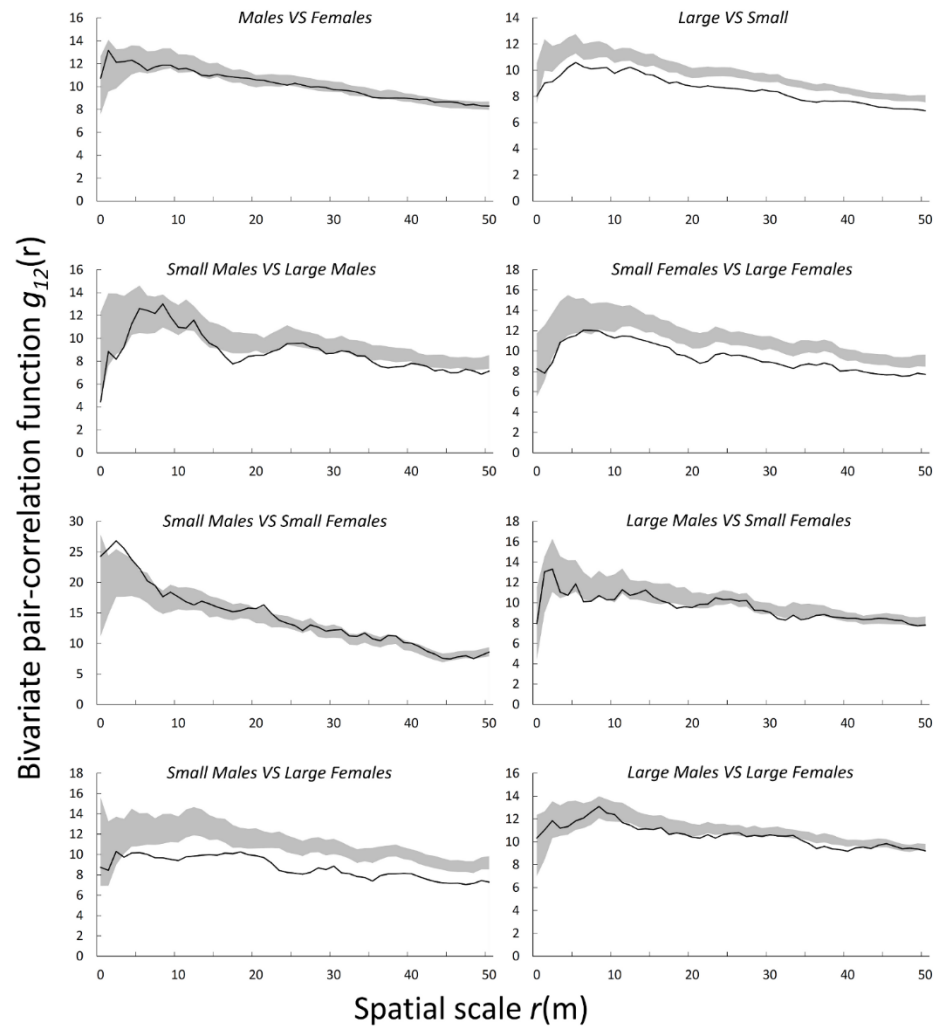


Figure 5. Bivariate analysis of the spatial pattern of *Taxus* trees, considering sex (males and females) and DBH (small and large), and their combinations (e.g. small males VS large females), using the pair-correlation function $g_{12}(r)$. Black lines indicate the pair-correlation functions $g_{12}(r)$, and shaded areas encompass random distribution

and represent points within the 2.5th and 97.5th percentile $g_{12}(r)$ values of the 999 simulations of the null model (Random Labeling).



Growth pattern

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

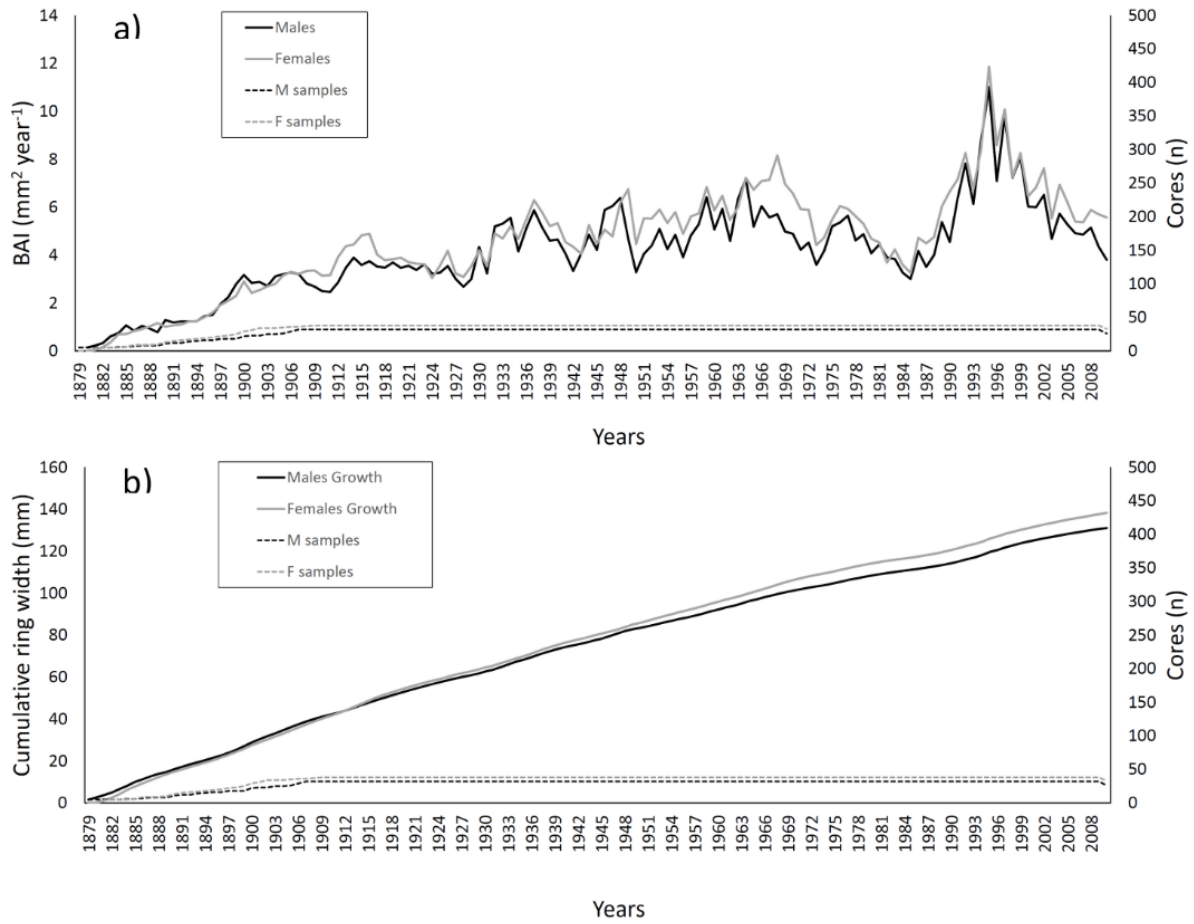
for females. Males and females showed similar mean ring width (0.99 mm and 1.06 mm), mean sensitivity (high-frequency variability), first-order autocorrelation (low-frequency variability), correlation between tree-ring series (\bar{R}), and adequacy of the chronologies (EPS). The two BAI curves (Fig.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

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

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

Series (n)	Time Interval (yrs)	Common Interval (yrs)	MRW (mm)	MI	\bar{R}	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

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



Discussion

Sex ratio at species range and landscape scales

Our study site occupies an intermediate position along a European environmental gradient where the SR decreased with increasing elevation and precipitation (Fig. 2). We observed SRs that were female-biased, and lower than would be expected given regional levels of precipitation and elevation. Female-biased populations have also been found on wetter sites in the Alps (Hilfiker et al., 2004) and in the Andes (Nuñez et al., 2008), adding support to the hypothesis that the proportion of females increases with water availability.

In our MdT study area, we observed a high SR on steeper, higher elevation sites, the opposite relationship as observed for the species range comparisons. This apparent discrepancy likely arises because the sites closer to the ridge are more water-limited because of shallow, rocky soils, and thus are less favorable for female *Taxus* trees. On the contrary, at the species range (Europe) higher elevation sites coincided with increased water availability (Iszkulo et al., 2009).

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

SR increased with increasing diameter, but decreased with increasing height consistently with other European studies on SR of *Taxus* trees (e.g. Iszkulo et al., 2009). Taken together, these data suggest that males put more carbon into diameter growth, and females into height growth, when they are in the older growth stages.

Influence of dioecy on spatial patterns at microsite scales

Adult *Taxus* trees (DBH > 15 cm) were strongly grouped at fine spatial scales (< 30 m) at MdT, probably representing a pattern of repeated clustering (Iszkulo et al., 2012). On the contrary, other authors have found random distribution in adult *Taxus* trees (Martínez et al., 2010). Considering the two sexes separately, we observed a weak but clustered pattern in females and a random pattern in males. The observed patterns were consistent with the hypothesis of males being the more stress tolerant that can occupy a broader spectrum of suitable microsites (Hultine et al., 2007; Iszkulo et al., 2009).

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

Nevertheless, we found spatial segregation between smaller and larger trees, a pattern already described for adult *Taxus* trees and regeneration in other European sites (Dovčiak, 2002; Piovesan et al., 2009; Devaney et al., 2014). As expected, small trees were aggregated for both males and females, whereas large trees were randomly distributed. The spatial segregation between smaller and larger trees is probably due to a negative intraspecific neighborhood effect

that has been previously reported for *T. baccata* (Dovčiak, 2002; Piovesan et al., 2009; Devaney et al., 2014) and for other species (He and Duncan, 2000). Moreover, the traditional coppice system with dense *Taxus* standards may have favored the establishment of *Taxus* regeneration into forest canopy gaps close to adult *Taxus* trees.

Influence of dioecy on growth patterns

The mean chronologies of male and female *Taxus* trees emerged as being very similar showing that the overall growth patterns were analogous. However, despite wide variability among individual trees, female *Taxus* trees in our study area showed a significantly higher growth rate. Nonetheless, other authors have reported a radial growth reduction of female trees associated with the achievement of sexual maturity in the studied population (e.g. Obeso, 2002; Bañuelos and Obeso, 2004; Cedro and Iszkulo, 2011). Female individuals may require more resources than males because of higher reproduction effort (Iszkulo et al., 2009). A possible explanation of the counter-intuitive pattern observed at MdT is that female growth can be favored by the more productive sites that they occupy, as opposed to males that occur across a wide variety of microsite conditions. Where female trees of dioecious species occupy more favorable sites than males, greater resource availability may compensate for greater reproductive requirements.

Our results highlight that in order to relate observed spatial patterns in dioecious species to habitat conditions, we need to consider abiotic and biotic constraints of tree establishment. Future research should investigate the spatial pattern of male and female trees along wide environmental gradients, in order to better understand the role of climate and topography in the SSS process. Site conditions, habitat variability, and water availability in particular are expected to strongly influence the strength of segregation

between sexes in dioecious species (Dawson and Bliss, 1989; Dudley, 2006). Spatial distribution modeling of dioecious species requires accounting for the different resource requirements and distribution patterns of male and female trees, particularly in the climate change context where range expansion to favorable sites depends upon the availability of seed-bearing, female trees (Tognetti et al., 2012; Hultine et al., 2013).

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