



Fine-scale intraspecific interactions and environmental heterogeneity drive the spatial structure in old-growth stands of a dioecious plant

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ABSTRACT

Spatial aggregation of individual plant species is their common response to biotic and abiotic conditions within heterogeneous environments. While conspecifics are clustered in favorable parts of the environment, they compete for scarce resources in these aggregations. Competitive interactions among conspecifics may negatively influence on their growth rate and other ecological processes. Therefore, the spatial distribution patterns of old-growth wild pistachio (*Pistacia atlantica*) stands were investigated to explore the effects of intraspecific interactions of this dioecious species on the stand spatial structure in the south of Zagros woodlands (Iran). The study was conducted within a 35-ha study plot in a wild pistachio nature reserve and all trees with dbh ≥ 2.5 cm were stem-mapped and measured. Uni- and bivariate pair- and mark correlation functions were applied to describe the interactions of male and female individuals at two life stages (i.e., sapling with dbh < 10 cm and adult with dbh ≥ 10 cm). Our results showed that the study area was dominated by adult trees accounting for 68.9% of all trees (480 adults and 216 saplings) and the proportion of male and female individuals were 37.7% and 62.3%, respectively. Trees were aggregated at small spatial scales. Bivariate tests showed positive spatial correlation of male and female trees at short distances, indicating no spatial segregation of the sexes (SSS). Wild pistachio offsprings were not spatially associated with adults, while strong clustering of offsprings was observed around female individuals up to 16 m distance. However, mark correlation function revealed significant effects of fine-scale competition on wild pistachio growth; therefore, we cannot fully reject SSS hypothesis. If heterogeneity of environmental conditions dominates the intraspecific competitive interactions of wild pistachios, as our findings indicate, then it can significantly influence on the stand spatial structure and coexistence of this dioecious species.

1. Introduction

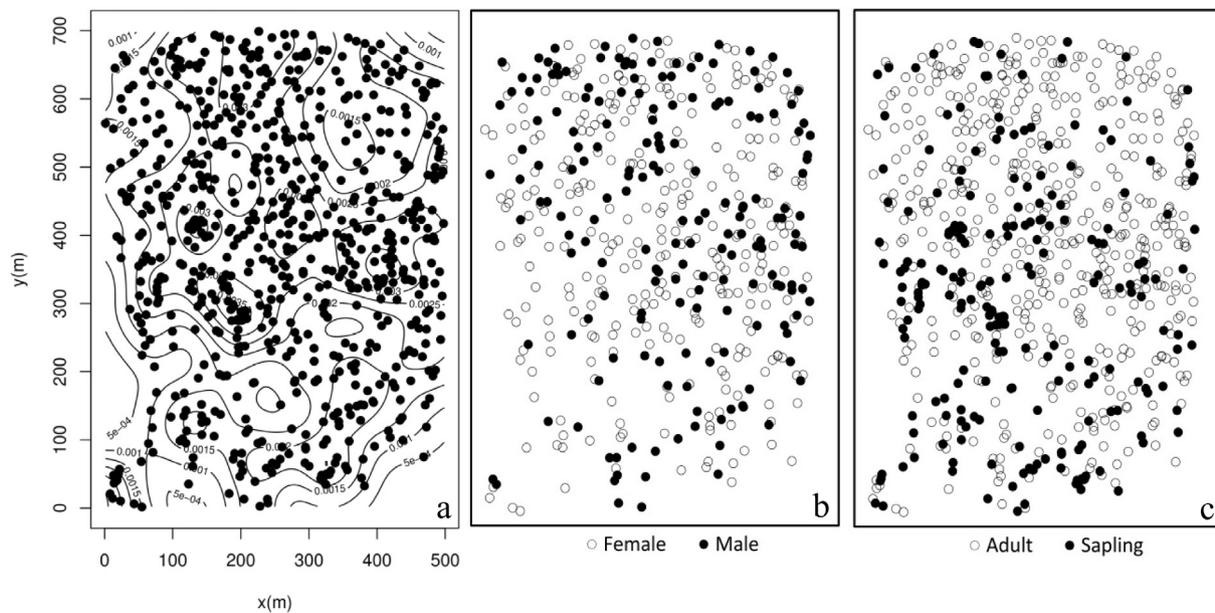
Pure and mixed wild pistachio (*Pistacia* spp.) stands with three species (i.e. *P. atlantica*, *P. vera*, and *P. khinjuk*) are the second most widespread vegetation type after oak stands in Zagros semi-arid woodlands in Western Iran, but coppice management and intensive exploitation of non-woody products (e.g., fruits and resin) over the past decades have influenced stand structure and species composition (Sagheb-Talebi et al., 2014). Wild pistachio stands which have never been subject to wood and good harvesting are rare and confined to few areas mainly in protected areas (Erfanifard et al., 2016). These remnants are important and appropriate reference systems for woodland management and unique reference areas for understanding the underlying processes and natural dynamics in these poorly investigated

ecosystems.

Similar to other dioecious species (six percent of the world flora), female wild pistachio trees bear fruits which are in clusters, but there must be a male individual in the vicinity to pollinate them (Givnish, 1980; Sagheb-Talebi et al., 2014). The positive interactions of sexes can probably account for the aggregation of wild pistachio trees that have been observed in natural semi-arid woodlands in Zagros (Safari et al., 2010; Erfanifard et al., 2016). Due to previous studies in different parts of Zagros woodlands, wild pistachio populations do not exhibit spatial segregation of the sexes (SSS), which has been observed in many dioecious plant species (Bierzychudek and Eckard, 1988; Nuñez et al., 2008). SSS is hypothesized to result from competition between males and females for resources. As such, the sexes occupy different niches due to the differences in reproductive efforts (Freeman et al., 1976).

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lithosol and terrain is characterized by gentle slopes between 7 and 10% and elevations ranging from 1890 to 1940 m a.s.l.

2.2. Data collection

The 35-ha (500 m × 700 m) plot was systematically divided into a grid of 100 m × 100 m. Within each grid cell, all standing wild pistachio trees with dbh ≥ 2.5 cm were stem-mapped using a Leica Viva GS10 differential global positioning system (DGPS). In addition to coordinates and dbh; tree height (by Suunto clinometer), widest crown diameter (d_1), the perpendicular crown diameter (d_2) (by measuring poles of 1 mm precision) of all trees and sex for trees with dbh ≥ 10 cm were also recorded (Fig. 1b). We chose dbh ≥ 10 cm as the cutoff because sex differentiation and regular fruit production begins at a relatively age of 20 years (Owji and Hamzepour, 2012; SaghebTalebi et al., 2014). Crown diameters (d_1 and d_2) were used to quantify crown area (CA) of each individual tree assuming an elliptical crown shape (Eq. (1)).

$$CA = (\pi \times d_1 \times d_2) / 4 \quad (1)$$

All trees were classified into two life stage classes; i.e., saplings with dbh < 10 cm and adults with dbh ≥ 10 cm (Fig. 1c).

2.3. Data analysis

Data on males and females (means of dbh, basal area, tree height, crown area) were compared using Mann-Whitney *U* test ($\alpha = 0.05$) due to the fact that the distributions of the biophysical properties were not normal and this test is more reliable comparing to, for instance, Student's *t*-test. In addition, data of adults were used to model the dbh-crown area and the dbh-tree height curves as well as dbh distributions by sex and the sex ratio which was assessed by G-test of goodness-of-fit (McDonald, 2014).

Point pattern analysis was used to investigate spatial distributions of individuals of all classes. We computed functions related to the Ripley's *K*-function, i.e. univariate and bivariate pair-correlation functions $g(r)$ (Wiegand and Moloney, 2004; Illian et al., 2008), that have been widely applied in recent ecological studies (Shackleton, 2002; Getzin et al., 2006; Law et al., 2009; Wiegand et al., 2016; Wang et al., 2017). The $g(r)$ is distance-dependent correlation function based on plant-to-plant distances. While the univariate form describes aggregation [$g_{11}(r) > 1$] and segregation [$g_{11}(r) < 1$] of the individuals, the bivariate form explains attraction [$g_{12}(r) > 1$] and repulsion [$g_{12}(r) < 1$] between the individuals (i.e., male and female or sapling and adult in this study) at a given distance r . The functions are defined as the expected density of trees with a specific characteristic (i.e., male wild pistachio, called pattern (1) within a ring with a width of Δr at radius r from trees with the same characteristic (univariate functions) or a different characteristic (i.e., female wild pistachio, called pattern (2), respectively (bivariate functions), divided by effective density of trees within the predefined ring at a given distance r from male (respectively female) individuals (Illian et al., 2008; Law et al., 2009). We used bandwidth of $R = 50$ m with Epanechnikov kernel and WM edge correction method for estimation of $g(r)$. Replacing circles applied in $L(r)$ as a cumulative function with rings, the $g(r)$ is changed to a non-cumulative function that can reveal type of interactions at specific spatial scales of interest (Illian et al., 2008; Wiegand and Moloney, 2014; Baddeley et al., 2016).

Table 1

Characteristics of the wild pistachios within the study plot of 35 ha, differentiated by sexes (male and female) and life stages (adult and sapling) (mean ± SD).

	Density (N ha ⁻¹)	dbh (cm)	Basal area (m ²)	Tree height (m)	Crown area (m ²)
Adult	13.7	52.3 ± 26.4	0.27 ± 0.1	5.9 ± 1.9	35.9 ± 24.7
Sapling	6.2	6.5 ± 2.0	–	2.7 ± 0.6	1.68 ± 1.4
Male	5.2	56.9 ± 26.2	0.31 ± 0.1	6.2 ± 1.8	40.5 ± 25.2
Female	8.5	49.4 ± 26.1	0.24 ± 0.1	5.7 ± 1.9	38.1 ± 24.1
All	19.9	38.1 ± 30.5	0.19 ± 0.1	4.9 ± 3.1	25.3 ± 15.9

The observed spatial distribution of wild pistachios was compared to homogeneous Poisson process using the Kolmogorov-Smirnov test to evaluate the hypothesis of complete spatial randomness (CSR) of the distribution. If the trees were not homogeneously distributed on the study plot, inhomogeneous summary statistics would be implemented to analyse their spatial pattern in the study area (Illian et al., 2008).

The impact of scale-dependent interactions of wild pistachios on their biophysical properties was assessed by mark correlation function $k_{mm}(r)$. The $k_{mm}(r)$ is applicable to point patterns that each typical point comprises additional quantitative or qualitative information (or marks) and characterizes the correlation of marks related to pairs of points as a function of spatial scale r (Illian et al., 2008; Fedriani et al., 2015). This function explores the similarity between the quantitative marks (the biophysical properties of wild pistachio trees in this study) of two individuals that are located at a certain distance from one another by the test function $f_1(m_i, m_j) = m_i \times m_j$, where m_i and m_j are biophysical properties of two neighboring trees. For $k_{mm}(r)$, the test function $f_1(m_i, m_j)$ computes the mark product of pair of points located at distance r from one another. The corresponding mean value based on f_1 , i.e. $k_{f1}(r)$, is normalized by dividing by the squared mean mark (biophysical properties in here) and denoted as $k_{mm}(r)$ (Illian et al., 2008). If $k_{mm}(r) = 1$, it describes that the marks are not spatially correlated, while they are positively (mutual stimulation) or negatively (inhibition) correlated, if $k_{mm}(r) > 1$ and $k_{mm}(r) < 1$, respectively. In this context, positive correlation means that wild pistachio individuals benefit from being close together and thus exhibit a tendency of having larger values of the marks than the average of study plot. In this study, we implemented $k_{mm}(r)$ to analyze the marked point patterns of adult wild pistachios in which the quantitative marks were their biophysical properties (i.e., dbh, tree height, and crown area). We followed the instructions suggested by Illian et al. (2008) for further details. If the test function $f_2(m_i, m_j) = 1/2 (m_i \times m_j)^2$, then $k_{f2}(r)$ is the mean value in the case of f_2 which is called mark variogram $\gamma(r)$. The function explores the squared differences of the marks belonged to pairs of trees at distance r (Goncalves and Pommerening, 2012; Ni et al., 2014; Fedriani et al., 2015). It is common in point pattern analysis that significant deviation of summary statistics from CSR is tested by the envelopes constructed by limited number of Monte Carlo simulations. Previous studies have shown that these envelopes may lead to high type I error probabilities (Grabarnik et al., 2011; Myllymäki et al., 2017). We, therefore, applied the analytical global envelope (AGE) goodness-of-fit test which allows computing the corresponding *p*-value. The AGE test is described in detail in Wiegand et al. (2016). All summary statistics and goodness-of-fit tests were computed by Programita grid-based software (Wiegand and Moloney, 2014) and spatstat package (Baddeley and Turner, 2005) in R software, version 3.2.5 (R Development Core Team, 2012), respectively.

3. Results

3.1. Biophysical properties

The total number of wild pistachio individuals with dbh ≥ 2.5 cm was 696, 480 adults and 216 saplings (Table 1). The study plot was dominated by the adults, 68.9% of the stem number, 94.7% of the dbh, and 97.9% of the crown area, while the females formed 62.3% of the

Table 2
Number of individuals and sex ratios of wild pistachios by dbh class, G-value is the result of G-test.

dbh classes	Male	Female	Male/Female	G-value	p-value
10–20	19	52	0.37	15.94	< 0.05
20.1–30	14	37	0.38	10.76	< 0.05
30.1–40	11	21	0.52	3.19	0.07 ^{ns}
40.1–50	24	41	0.59	4.49	< 0.05
50.1–60	36	43	0.84	0.62	0.43 ^{ns}
60.1–70	27	36	0.75	1.29	0.26 ^{ns}
70.1–80	13	28	0.46	5.62	< 0.05
80.1–90	20	22	0.91	0.09	0.76 ^{ns}
90.1–100	9	8	1.13	0.06	0.81 ^{ns}
100.1–110	2	8	0.25	3.85	0.05 ^{ns}
110.1–120	2	3	0.67	0.21	0.65 ^{ns}
All	181	299	0.61	29.31	< 0.05

Note that two dbh classes of 120.1–130 cm (2 males) and 130.1–140 cm (2 males) had no female members, so they were not included in this table. ns = non-significant at 0.05 level.

stem number, 58.9% of the dbh, and 57.4% of the crown area. However, the males showed significantly higher dbh, basal area, tree height, and crown area than females (p -value < 0.05).

The sex ratio of wild pistachio trees on the study plot was significantly female biased. While the pattern was consistent across dbh classes of 10–20 cm, 20–30 cm, 40–50 cm, 70–80 cm, and 100–110 cm; the individuals with dbh \geq 50 cm tended to have sex proportions not significantly different from 1:1 (Table 2).

The dbh distributions of males and females approximately converged to rotated sigmoid shapes with a point of inflection at 30.1–40 cm class in both sexes (Fig. 2). We found a significantly higher number of females than males in dbh classes \leq 80 cm, but no females in the large diameter classes (dbh \geq 120 cm) (Fig. 2).

The males with dbh > 20 cm had larger crown areas than the females (Fig. 3a). The males and females were similar in height while the males were slightly taller than the females in dbh > 40 cm (Fig. 3b). Sex differences in height and crown area increased with diameter (e.g., the tree height and the crown area of a male with 95 cm dbh were 10.5 m and 91.2 m², respectively, compared to 8.4 m and 70.6 m² of a female with similar dbh) (Fig. 3).

3.2. Spatial associations

The Kolmogorov-Smirnov test revealed that the observed spatial pattern of trees did not follow a homogeneous Poisson process (p -value < 0.01). This result provided evidence of heterogeneity on the study plot. Inhomogeneous $g(r)$ function showed that the spatial patterns of all wild pistachios (dbh \geq 2.5 cm) were significantly aggregated up to distances of 16.5 m, although their aggregation was observed at larger spatial scales of 28.5 m (Fig. 4a). No significant

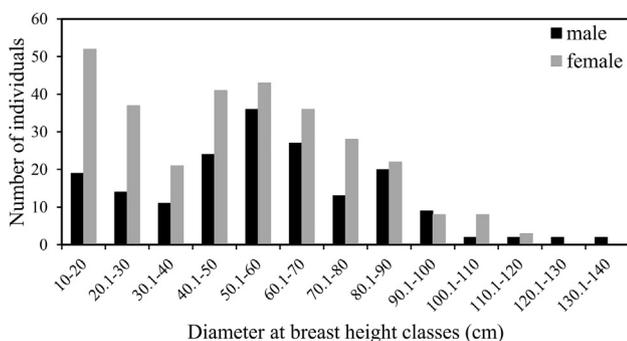


Fig. 2. Diameter at breast height (dbh) frequency distribution of male ($N_{\text{male}} = 181$) and female ($N_{\text{female}} = 299$) wild pistachios on the study plot (35 ha).

spatial interaction was found between the males using univariate pair-correlation function, although they showed aggregation at distances up to 18.5 m (Fig. 4b). In contrast, the spatial distribution of the females was significantly aggregated at short spatial scales (i.e., 0.5–13.5 m), while this strong aggregation was disappeared at larger scales (> 18.5 m) (Fig. 4c). In quantifying the spatial interaction of males and females, we could not reject the null model of randomness in all cases. A short interval of strong attraction occurred at 0.5 to 8.5 m, which was disappeared for distances > 22.5 m (Fig. 4d). Bivariate tests found the density of females around males (vs. the density of males around males) to be significantly higher at short spatial scales (0.5–22.5 m).

Strong aggregation of adult wild pistachios at spatial scales up to 10.5 m was detected by univariate $g(r)$ (Fig. 5a). For saplings, the spatial aggregation was not strong at distances below 16.5 m (Fig. 5b) compared to the adults that their aggregation observed at distances of 12.5–24.5 m was not strong. Generally, the bivariate analysis of wild pistachios at different life stages did not show significant evidence of adult – sapling positive interactions, although they were aggregated at spatial scales of 0.5–16.5 m (Fig. 5c). However, the positive interactions between female wild pistachios and saplings were characterized by bivariate summary statistics. The females were positively associated with saplings up to 24.5 m distance, whereas it was significant at spatial scales below 16.5 m (Fig. 5d). This strong attraction indicated that saplings were more frequently distributed within neighborhood of the females than expected by their random distribution pattern.

The mark variogram exhibited similar trends for all marks, showing a positive correlation of the marks at short to medium spatial scales. Results showed the biophysical properties similarity of pairs of wild pistachios up to 10.5 m distance. Additionally, mark correlation functions revealed inhibition between the marks at short spatial scales. Strong inhibition of dbh up to 6.5 m distance was followed by weak inhibition at medium spatial scales; i.e. between 6.5 m and 12.5 m. In the case of the correlation between tree locations and other marks (tree height and crown area), both marks showed negative correlations at short distances (below 8.5 m and 14.5 m, respectively), although it was not significant at these spatial scales (Fig. 6). Comparing to tree height and crown area, the inhibition was stronger for tree dbh and the spatial scale of this inhibition was greater, extending to 6.5 m (Fig. 6b).

4. Discussion

4.1. Biophysical properties

Based on dbh distribution of the adults, the results suggested an uneven-aged and old-growth structure of wild pistachio dioecious trees within the study plot. The dbh distribution of females closely approximated a rotated sigmoid shape, which is a commonly observed model of stem diameter distribution in old-growth forests (Pach and Podlaski, 2015). Furthermore, a reduction was observed in the presence of male and female trees with dbh of 30–40 cm that was likely due to low recruitment rates or high mortality among saplings. The similarity of stem diameter distribution in males and females indicated a convergence between them with respect to intraspecific interactions that determined the presence of either sex. Moreover, it suggests an approximately balanced demographic structure by sex within the study plot. Additionally, the correlation between dbh, crown area, and height revealed that crown size increased with increasing dbh and the trees reacted to gap dynamics, although height did not follow the same trend when the trees reached height of approximately 8 m (Fig. 3). Low density of wild pistachios within the study plot (approximately 20 trees ha⁻¹, Table 1) and single layer canopy cover with a simple vertical structure prevented the competition for light among the individuals and the formation of high trees as they grew in dbh and crown size.

While the density of females dominated the adult wild pistachio population and the sex ratio was significantly female biased (1.65

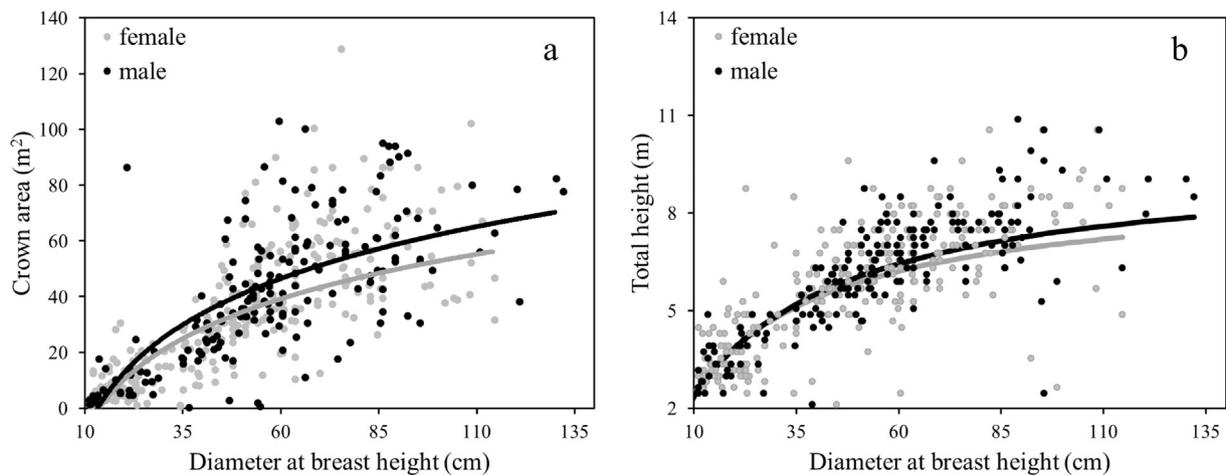


Fig. 3. (a) Diameter at breast height-crown area relationship of male and female wild pistachios, fitted with a Michaelis-Menten equation ($R^2_{\text{male}} = 0.81$, $R^2_{\text{female}} = 0.94$). (b) Diameter at breast height-tree height relationship of male and female individuals, fitted with a Michaelis-Menten equation ($R^2_{\text{male}} = 0.85$, $R^2_{\text{female}} = 0.88$) ($N_{\text{male}} = 181$, $N_{\text{female}} = 299$). Black and grey non-linear regression lines show the positive relationship of male and female biophysical attributes, respectively.

female:1 male), the averages of all biophysical properties were significantly higher in the males. This finding is in accordance with the conclusions of Yu and Lu (2011), who studied sex ratio in 30 pistachio (*Pistacia chinensis*) populations on separate islands in the Thousand-Island Lake reservoir (China). Similar to the findings in this study, Zhang et al. (2010) reported that the dbh of male *Fraxinus mandshurica* were significantly higher than those of females in an old-growth forest. Our results also showed that the sex ratio of older adults (larger dbh) was maintained at approximately 1:1 within the study plot. This is in line with the results of Osunkoya (1999) who showed that sex ratio was not departed from 1:1 as the stem size increased in some populations of a dioecious shrub (*Gardenia actinocarpa*).

The males exhibited larger tree height and crown area compared to similar-aged females (similar dbh), while the females had lower dbh, tree height, crown area and, consequently, higher mortality rates.

Investigating differences in size between males and females, Yu and Lu (2011) found that male pistachio trees (*Pistacia chinensis*) are more competitive in habitats with unfavorable conditions. Our results concur with Yu and Lu (2011) and support the hypothesis that heterogeneous environmental conditions significantly influence the size of female wild pistachios. This phenomenon is probably connected with flower production and period of sexual maturation. Females make a significantly higher reproductive effort, as they should produce not only flowers but also fruits (Osunkoya, 1999; Wang et al., 2015). However future investigations are needed to explore the effect of environmental conditions (e.g., soil nutrient and moisture content) on growth rates of male and female wild pistachios that would be an evidence of their size differentiation in arid and semi-arid woodlands.

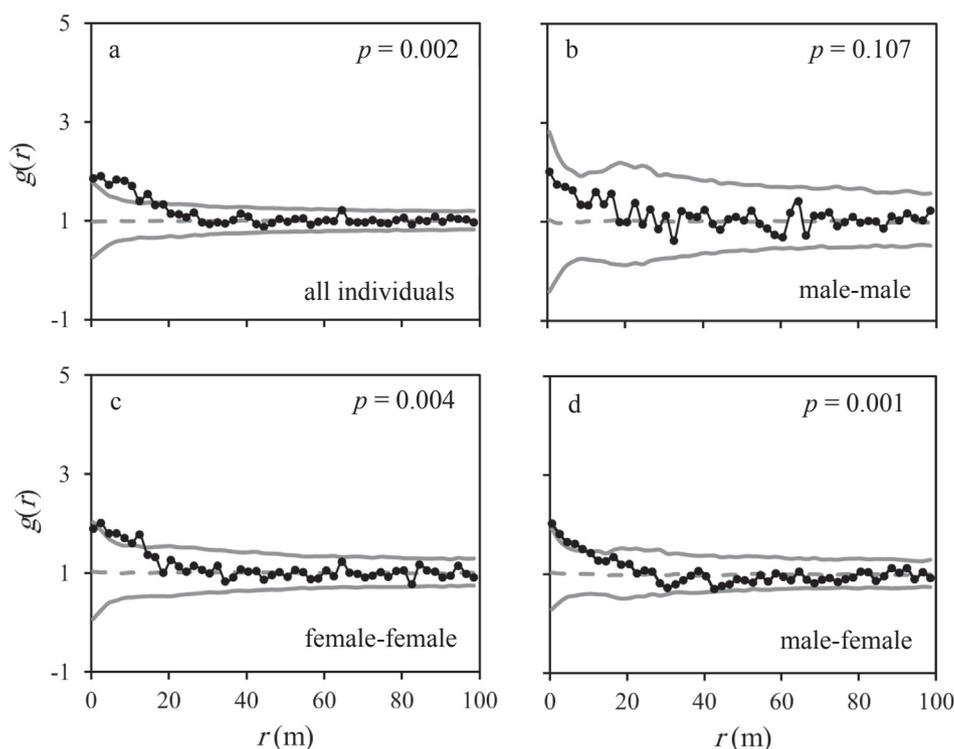


Fig. 4. The spatial pattern of all wild pistachios with dbh ≥ 2.5 cm ($N = 696$), contrasted to analytical global envelopes (AGE), using inhomogeneous pair-correlation function $g(r)$ (a). Spatial relationships within and between male (pattern 1, $N = 181$) and female (pattern 2, $N = 299$) wild pistachios using univariate inhomogeneous pair-correlation function $g(r)$ (b and c), and bivariate inhomogeneous $g(r)$ (d), respectively. Black circles display the empirical summary statistics, grey solid lines are the envelopes taken over the 0.5–98.5 m range with a distance bin of 1 m (the values at bin = 2 m were presented), and grey dashed lines are the expectation values under complete spatial randomness.

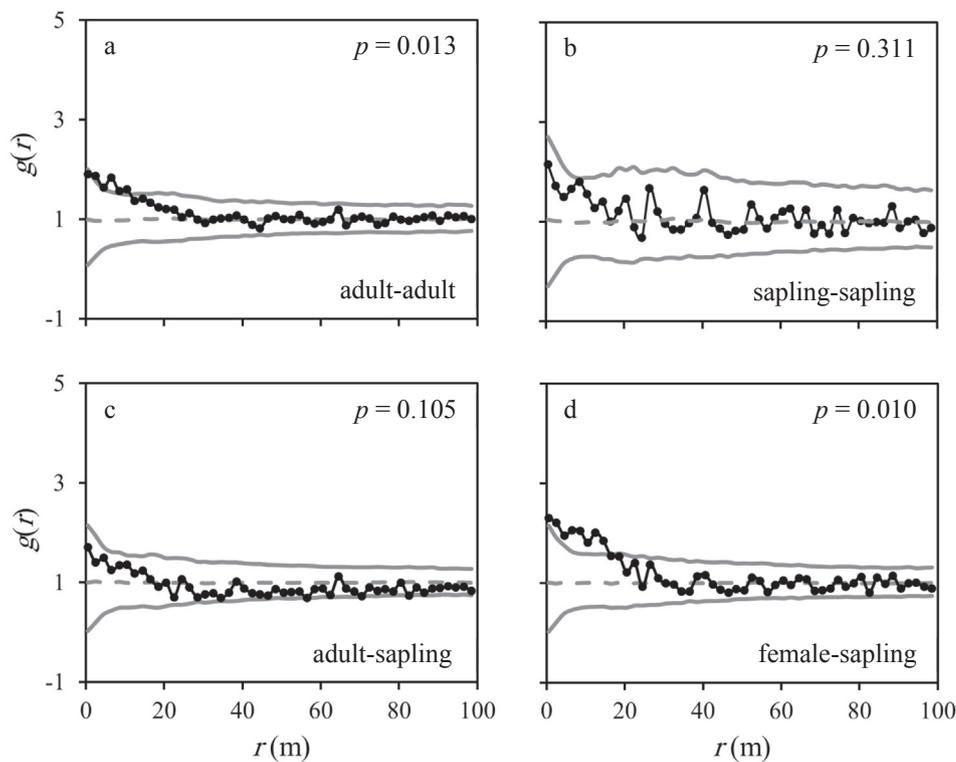


Fig. 5. Spatial interactions of adult wild pistachios with dbh ≥ 10 cm (pattern 1, $N = 480$) and saplings with dbh < 10 cm (pattern 2) ($N = 216$), analysed by univariate inhomogeneous pair-correlation function $g(r)$ (a and b). The bivariate inhomogeneous $g(r)$ was applied to investigate the interactions between adults and females with saplings. The details are as described in Fig. 4.

4.2. Spatial associations

The results obtained by second-order summary statistics clearly point toward a strong aggregated pattern of adult wild pistachios as suggested in our first hypothesis. Heterogeneity of the spatial distribution of wild pistachios and clustering of the individuals suggest that wild pistachios are likely aggregated at higher quality locations (e.g. higher soil moisture and nutrients). Significant aggregation of males and females revealed by bivariate summary statistics at short distances (0.5–8.5 m; Fig. 4) is congruent with the aggregated distribution of adult trees discovered by univariate summary statistics at the same spatial scales (Fig. 5), and suggests that the males and the females have strong positive spatial correlations in clusters. This positive association of males and females was also explored by Schmidt (2008) who analyzed the spatial patterns of different sexes of a dioecious shrub in Georgia and South Carolina (USA).

We hypothesized that wild pistachios would exhibit strongly positive intraspecific correlations due to their dioecy. The spatial aggregation of the individuals explored in our study supports this hypothesis, and concurs with the achievements, for example, of Queenborough et al. (2007) who observed spatial aggregation among dioecious trees of Amazonian tropical forests in Ecuador. In contrast, previous studies have documented spatial dispersion of sexes in more than 25 plant species (Bierzchudek and Eckard, 1988; Nuñez et al., 2008). SSS may be explained by niche partitioning, in which males and females compete for resources and form spatial segregation (Iszkuło et al., 2011). As previously argued by Garbarino et al. (2015) and also found in our study, SSS alone would not necessarily influence the spatial distribution of wild pistachio dioecious species in such harsh environments with limited resources. Considering the role of environmental heterogeneity on spatial patterns of plants, Law et al. (2009) showed that large-scale heterogeneity had clear effects on the spatial structure of stands in two temperate forests. Future studies should address the effect of changes along environmental gradients on the spatial distribution of sexes of dioecious plants in low quality sites (e.g., arid regions) that may prevail over intraspecific competition.

We hypothesized that wild pistachio offsprings would exhibit strong

spatial associations with adults, and that is likely to be one of the reasons behind spatial clustering of wild pistachios within our study plot. However, in contrast to Zhang et al. (2009) and Miao et al. (2014) who investigated monoecious species, the results of bivariate summary statistics that explained the spatial interactions of adults and saplings did not confirm this hypothesis. Interestingly, we found that saplings were significantly associated with the females, but not the adults generally. Seeds produced by wild pistachio females, which are gravity-dispersed, are usually fallen close (within 0.5–16.5 m) to their mother trees. Thus, primary seed dispersal mode plays a significant role in the spatial pattern of wild pistachios in semi-arid woodlands, similar to the results of Seidler and Potkin (2006) in tropical forests and Montes et al. (2007) in temperate forests. Also, significant aggregation of saplings only around the females observed on the study plot indicates lack of successful natural regeneration in other parts of the study plot and agrees with the results of Schurr et al. (2004), in which it was noted that heterogeneity of environmental conditions, such as soil nutrients, in semi-arid regions significantly influence seed germination and seedling survival.

Mark correlation function was used to explore whether the clustered spatial distributions observed in second-ordered summary statistics (i.e., uni- and bivariate pair-correlation functions) are the result of positive intraspecific interactions and positively influences tree size. We tested whether aggregation of wild pistachios facilitates their growth and whether biophysical properties of trees are positively correlated to one another (mutual stimulation). Instead, the results showed the inhibition of biophysical properties within clusters reflecting significant spatial negative correlation of the individuals (Fig. 6). Thus, we concluded that aggregation of wild pistachios negatively affects their size despite their clustered patterns on the study plot. In contrast to Gonçalves and Pommerening (2012) who reported inhibition of cone production (mark) for *Pinus pinea* trees spatially segregated in pure even-aged stands in Portugal, we observed inhibition of biophysical properties of wild pistachios spatially aggregated on the study plot. Similarly to Gray and He (2009), who found aggregation of dominant species (trembling aspen, white spruce and balsam poplar) in a boreal forest chronosequence in Alberta, the mark correlation function of dbh

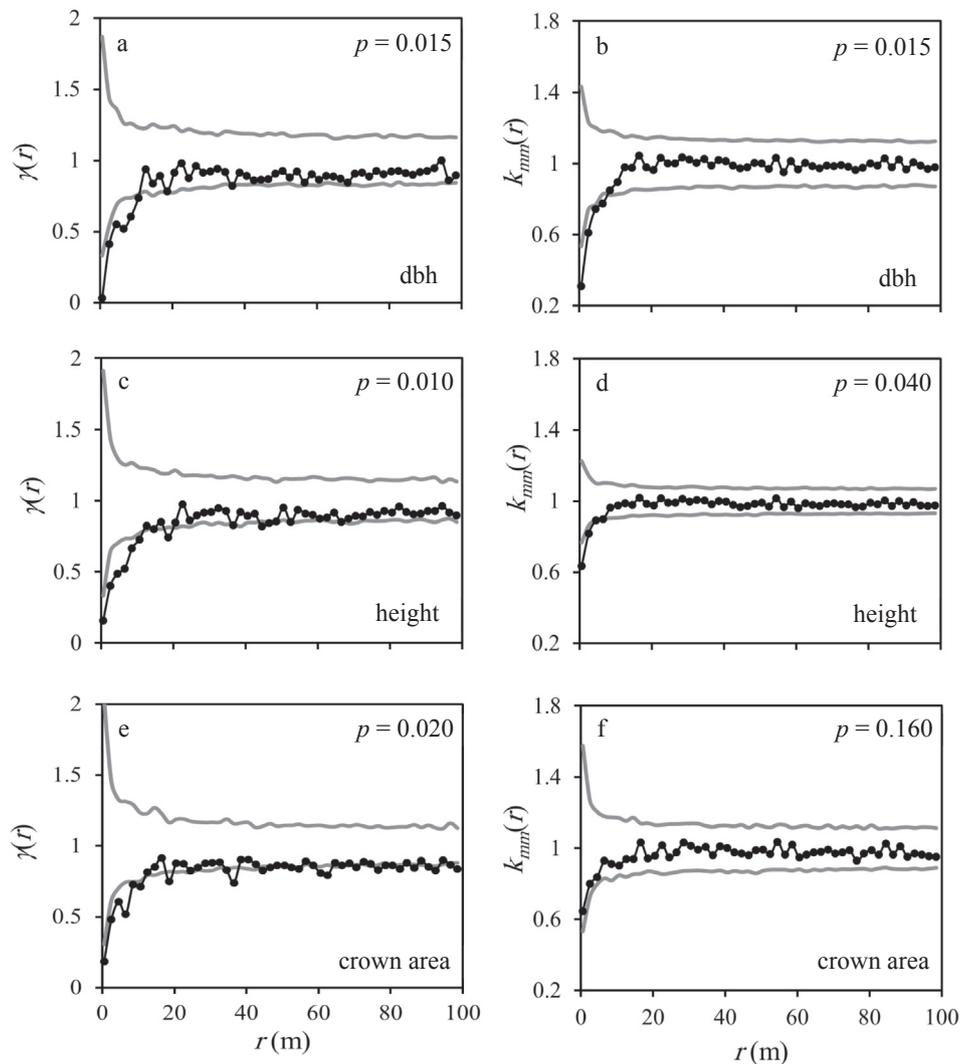


Fig. 6. Mark variogram $\gamma(r)$ and correlation functions $k_{mm}(r)$, using diameter at breast height (dbh) (a, b), tree height (c, d) and crown area (e, f) of adult wild pistachios ($N = 480$). The details are as described in Fig. 4.

indicated strong negative correlation (inhibition). The significant negative correlation among the biophysical properties as marks shown by the $k_{mm}(r)$ for wild pistachios on the study plot indicates that the individuals with similar size repel one another probably as a result of competition for limited resources. In addition, we cannot fully reject SSS hypothesis due to the results of mark correlation function; although, we observed significant spatial aggregation of the sexes. We believe that male and female wild pistachios were spatially aggregated within the study plot because of the heterogeneity of environmental conditions, despite their fine-scale competition revealed by $k_{mm}(r)$ and demonstrated by SSS hypothesis. Aggregations of wild pistachio individuals are probably established in environmentally rich parts of the study area, although they compete for scarce resources and these competitive interactions have negative effects on their biophysical properties.

Restoration and conservation of the remnant stands by native species, such as Persian oak and wild pistachio, are the main strategies in sustainable management of open woodlands in Zagros. Furthermore, wild pistachio is a dioecious species and plants with this type of mating system are significantly considered more vulnerable to extinction compared to monoecious plant species. The findings of our spatial analyses suggest that wild pistachio trees are aggregated in clusters, although the analysis of the mark correlation function revealed that fine-scale intraspecific competition likely have negative effects on tree

size in the study plot. Our achievements suggest that wild pistachio individuals should not be spatially located close to each other due to their significant competitive interactions at spatial scales up to 6.5 m and man-made thinning is recommended in dense clusters to enhance growth and productivity of the species.

5. Conclusions

The findings of this study on the intraspecific interactions of wild pistachios in the southern part of Zagros semi-arid woodlands provided hypotheses on the underlying mechanisms that influence the spatial distribution of this dioecious species. Contradicting our hypothesis, wild pistachios experience fine-scale intraspecific competition that significantly affects on their biophysical properties. Additionally, their aggregation is most probably not due to positive interactions of males and females. The clustering of saplings around female trees observed in this study may be explained by limited dispersal of heavy seed clusters beneath female crowns caused by gravity. We suggest that heterogeneity of environmental conditions may be the most determining factor for the spatial aggregation of wild pistachios, although their competitive interactions cause significant inhibition of the biophysical properties. However, further studies and precise analyses of environmental conditions are needed to support this outcome and to get more profound insights into the spatial stand structure of this species.

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