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

Yousef Erfanifard[a,*], Hong Hai Nguyen[b], John Paul Schmidt[c], Andrew Rayburn[d]

[a] Dept. of Natural Resources and Environment, College of Agriculture, Shiraz University, 71441 Shiraz, Iran
[b] Dept. of Forest Inventory and Planning, Faculty of Silviculture, Vietnam Forestry University, Hanoi, Viet Nam
[c] Odum School of Ecology, University of Georgia, Athens, GA, USA
[d] Jefferson County Open Space, CO, USA

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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 (SaghebTalebi 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; SaghebTalebi 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 (Bierzchudek 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).

* Corresponding author.
E-mail addresses: erfanifard@shirazu.ac.ir (Y. Erfanifard), hainh@vfu.edu.vn (H.H. Nguyen).

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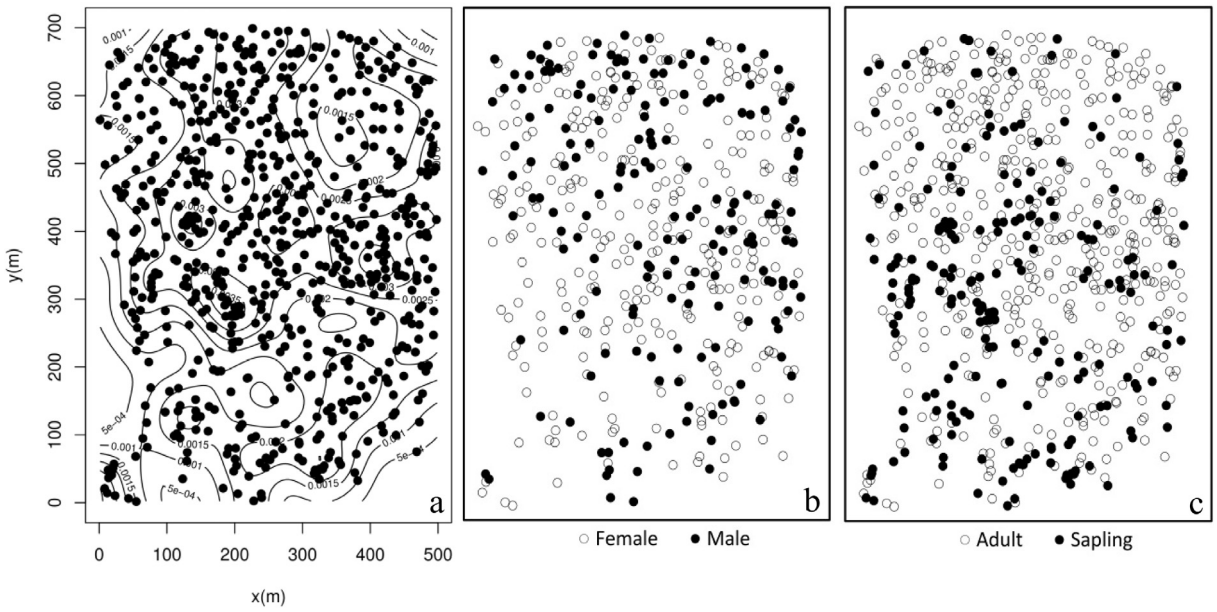

Fig. 1. (a) Map of all wild pistachios (N = 696) on the 35-ha study plot in Zagros, Iran, with the density function of the distribution of trees. (b) The spatial distribution of adult males (●) (N = 181) and females (○) (N = 299). (c) The spatial distribution of adults (○) (N = 480) and saplings (●) (N = 216), having a dbh ≥ 10 cm and < 10 cm, respectively.

Bierzchudek and Eckard (1988), therefore, defined SSS as a biased sex ratio of a dioecious species across different habitats. Most studies on sex ratio in stressful environments have noted that sex ratio bias is due to the higher rate of mortality of females. Compared with males, female individuals often invest more efforts on reproduction than growth and annual increment. Thus, intraspecific interactions of dioecious species are influenced by environmental heterogeneity, and growth at different life stages (Schmidt, 2008; Garbarino et al., 2015).

Wild pistachio establishes clusters of trees in pure and mixed stands. Offsprings are clustered near parent trees that serve as nurse plants providing hospitable microenvironments and make it easier for the offsprings to grow in semi-arid woodlands, especially at low soil moisture and nutrient contents (Owji and Hamzepour, 2012). Clustered distributions may be necessary to species coexistence in mixed and pure stands (Safari et al., 2010; Erfanifard et al., 2016), but it is not clear, whether their spatial aggregations are resulted from facilitation of offsprings by mature trees and positive effects of clustering between male and female trees or environmental heterogeneity. Whereas spatial patterns in wild pistachio stands in the vegetation of Zagros region of western Iran have been studied (Safari et al., 2010), intraspecific interactions of males and females of this dioecious species have not been investigated.

Seed dispersal and plant recruitment, conspecific and heterospecific competitive or facilitative interactions, pollination by wind and neighborhood of (e.g. differently sized) plants may leave significant imprints on vertical and horizontal structures of vegetation (Wiegand et al., 2009). Facilitative interactions among plants encourage their aggregated spatial patterns that may be intensified by availability of resources in specific locations of a heterogeneous site as proposed by stress gradient hypothesis (Maestre et al., 2009), whereas competitive interactions of plants for scarce resources in arid regions (e.g. water and soil nutrients) may promote more dispersed spatial patterns and consequently, their spatial separation at some scales (Pommerening et al., 2011; Erfanifard and Sheikholeslami, 2017). Correlations between biological processes and spatial distributions can reveal underlying mechanisms that shape spatial patterns (Pretzsch, 2009). The intensity of different processes can create different spatial patterns, and complex processes acting simultaneously or separately may generate similar patterns. Therefore, understanding fine-scale spatial patterns in dioecious plants can provide insights into the mechanisms of their coexistence and other significant ecological processes that construct their spatial structure.

We, therefore, hypothesized that clusters of wild pistachio trees distributed in Zagros woodlands are caused by a combination of effects resulting from positive interactions of sexes (dioecy) and environmental heterogeneity. We primarily quantify the spatial distributions of pistachio trees (contrasting by sex and life stage), using univariate and bivariate forms of pair-correlation function $g(r)$. We also hypothesized a strong positive correlation between the biophysical properties (i.e., diameter at breast height [dbh], tree height, and crown area) of wild pistachios. We tested the hypothesis to find out if the spatial aggregation of wild pistachio trees has positive effects on the growth of individuals within clusters. Therefore, we analyzed relationships between tree dimension measures and sex ratio of males and females. Moreover, we investigated the influence of their scale-dependent interactions on tree size using mark correlation function $k_{mm}(r)$. Results may provide a deep understanding of how intraspecific interactions of wild pistachios and environmental heterogeneity determine their spatial structure in mixed and pure stands distributed in Zagros semi-arid woodlands.

2. Materials and methods

2.1. Study area

The present study was carried out on a 35 ha plot dominantly covered by wild pistachios (more than 80% of canopy cover) accompanied by wild almonds (*Amygdalus* spp.) as suppressed shrub species within a wild pistachio nature reserve (Fig. 1a). In some parts of the study area, thorny shrubs of wild almond protect natural regeneration of wild pistachios from grazing by animals. The nature reserve was established in 1996 and is located in the semi-arid woodlands scattered on foothills of Zagros Mountains, Western Iran (Owji and Hamzepour, 2012). To the best of our knowledge, the study area has not received any management and human interventions for cutting trees. The climate is semi-arid with an annual mean temperature of 22.8 °C. Annual mean precipitation is 383 mm, more than 76% of which occurs between November and March (from data of 1980–2010 provided by Iran Meteorological Organization). Bedrock is limestone and the most common soil type is a