



Recruitment facilitation in expanding forests of Mediterranean juniper is sex-biased

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ARTICLE INFO

Keywords:

Dioecious species
Forest expansion gradient
Juniperus thurifera
Regrowth
Sapling recruitment
Tree sex

ABSTRACT

Despite noticeable concern about the deforestation rate worldwide, the forest surface in Europe has considerably expanded over the past centuries as a consequence of the rural exodus and abandonment of agrarian practices. Tree recruitment associated with forest regrowth is a multi-stage process influenced by several biotic and abiotic factors. Yet, it is uncertain whether their influence on recruitment patterns and dynamics varies along a gradient of forest expansion. Similarly, for dioecious species, the influence of tree sex in recruitment is not entirely understood. Here, we aim to elucidate what drives Spanish juniper recruitment in expanding forests. Specifically, we hypothesized that facilitation by conspecifics and heterospecific woody species would occur at the expanding front, where environmental conditions are harsher and that recruitment would be preferably associated to female trees because of the likelihood of mature cones produced by them germinating in the nearby area. The study was conducted in Mediterranean forests of *Juniperus thurifera* in central Spain. A total of 17 plots were delimited along a gradient of forest expansion including three stages: i) old forests, ii) an intermediate zone and iii) novel forests at the expanding front. Within each plot all *J. thurifera* individuals (saplings and adults) were mapped. We also recorded bio-volumetric characteristics and tree sex for all adult trees and estimated the percentage of cover of heterospecific woody species within the area of influence of each adult individual. We analysed the spatial pattern of *J. thurifera* individuals for each stand (plot). Using a novel spatial approach, we evaluated how conspecific (female and male tree sizes) and heterospecific (woody cover) vegetation influenced sapling density along a forest expansion gradient. We also studied the effects of the stage of the forest expansion gradient and the sex of adult trees on the spatial association between adults and saplings. Our results showed that sapling recruitment was negatively influenced by conspecific adult size along the whole gradient, while the effect of heterospecific woody vegetation was always positive. Conspecific facilitation of recruitment in *J. thurifera* forests occurred at their expanding front where saplings were associated to male adult trees. Despite having been overlooked in conservation policies, recently colonised areas in extreme environments are key targets to implement management measures aimed at achieving forest restoration, which aligns with the Aichi targets and the biodiversity policies of the European Union.

1. Introduction

In our path to a decarbonised economy, forest regrowth is known to play a central role in climate change mitigation through carbon sequestration (Cook-Patton et al., 2020; Martín-Forés et al., 2020). Thus, conservation efforts in Europe highlight the importance of managing

forests sustainably (CBD 2010; Storch and Winkel, 2013), especially those included in the Natura 2000 network (European Commission, 2013; de Koning et al. 2014). The European Green Deal recognised forests as crucial carbon sinks as far as they capture up to 12% of CO₂ anthropogenic emissions (Janssens et al., 2003). Yet, this regulation service that forest ecosystems provide hardly depends on forest

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<https://doi.org/10.1016/j.foreco.2021.119937>

Received 16 September 2021; Received in revised form 1 December 2021; Accepted 3 December 2021

Available online 12 December 2021

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management practices (Bastin et al., 2019), being actually related to conservational and assisting natural regeneration and recruitment (FAO 2010; d'Annunzio et al., 2015; Cook-Patton et al., 2020).

Land use change has been pointed out as one of the major drivers of global change (Vitousek, 1994; Valladares et al., 2019). In Southern Europe a process of rural exodus towards urban areas has taken place over the past decades (Lepart & Debussche, 1992), resulting in an abandonment of former agrarian fields and the subsequent expansion of the adjacent forest and shrubs over them (Schröter et al., 2005; Roussenvell et al., 2006; Chauchard et al., 2007; Rey Benayas et al., 2007; Hampe et al. 2020; Garbarino et al. 2020). This forest expansion has led to an increase of natural carbon sinks (Martín-Forés et al., 2020).

Within this scenario, some conservation and management practices have been oriented to passively assist natural regeneration through a gradual forest regrowth (including both expansion and densification; Holl & Aide, 2011; Martín-Forés et al., 2020). Forest regrowth is intricately linked to successful recruitment of seedlings (Murphy & Lovett-Doust, 2004), and has beneficial effects beyond carbon sequestration, such as habitat provision for biodiversity and the control of erosion rates (Sandom et al., 2013; Pereira and Navarro, 2015).

Seedling recruitment is a complex and multi-stage process, including successful seed germination, seedling survivorship, and seedling growth (Eriksson et al., 2008) and it is driven by a combination of abiotic and biotic factors (Pulido et al., 2010). In Mediterranean-climate regions, abiotic factors such as temperature, summer drought events, irradiance and soil moisture, strongly determine the suitable environmental conditions for successful seed germination and seedling survival and growth (Sánchez-Gómez et al., 2006). This process is also affected by of biotic interactions with the nearby vegetation, which can either facilitate or hinder seedling establishment (Gworek et al., 2007).

Competition or facilitation processes affecting seedling survival in expanding forests can be driven by both resource availability and density-dependency mechanisms (e.g. being affected by the presence and amount of conspecific adult trees; Miriti, 2006). In fact, the effective density experienced by an individual depends on the location and size of its immediate neighbours (Kenkel, 1988). In this sense, tree architecture of dominant conspecific trees has been seen to play an important role in density-dependency mechanisms (Chen et al. 2018). In the case of dioecious tree species, different reproductive effort between sexes can be translated in unbalanced sex ratio (Ortiz et al. 2002), differential growth (Iszkulo et al. 2011), contrasting neighbouring effects (Nanami et al. 2005) and spatial segregation (Hultine et al. 2007; Garbarino et al. 2015) under harsh environmental conditions. Sex-dependent effects might be therefore determinant for recruitment patterns, as saplings can establish differentially in the proximity of male or female adult trees (Montesinos et al., 2007).

In environments with high resource supply, reduced survival rates of seeds and seedlings have been seen associated with closeness to conspecific adults as a result of negative density-dependence (NDD; Chesson, 2000; Bai et al. 2012) or the Janzen-Connell model (Janzen, 1970; Connell, 1971; Terborgh, 2020). In contrast, in stressful environments, such as semi-arid Mediterranean forests, it is common that facilitation mechanisms predominate (Pugnaire & Luque, 2001; Maestre et al., 2003). Facilitation can occur through the formation of 'resource islands' under tree canopies, by ameliorating harsh microclimate conditions typical from semi-arid Mediterranean ecosystems, including improving soil moisture, increasing soil nutrients and microbial activity, and reducing high temperatures and irradiance levels (Moro et al., 1997; Caldeira et al., 2014). For example, it has been reported that female trees of *Juniperus sabina* have a nurse effect for seedlings of *Juniperus communis* (Verdú & García-Fayos, 2003).

In fact, the spatial pattern of seedlings, saplings and adult trees are usually employed to assess the ecological processes responsible of forest dynamics (McIntire & Fajardo 2009). Regular spatial patterns normally reflect strong competition, whereas processes underlying aggregated or clumped distributions are more complex to unravel (Kenkel, 1988), and

can be due to facilitation mechanisms or perch-effect (Pausas et al. 2006). Spatial patterns can also vary associated with the forest regrowth process; for example, in boreal forests, clustered or aggregated patterns occurred at early phases of the forest ontogeny, and more regular patterns due to self-thinning towards light competition are displayed later on (Kenkel, 1988). However, for semi-arid Mediterranean forests, it is uncertain whether the abiotic and biotic factors influencing tree recruitment and therefore spatial patterns remain constant along the process of forest regrowth (e.g., along a gradient of forest expansion). This information would be useful to improve sustainable management of these abandoned rural areas allowing a faster recovery of the forest dynamic and functionality.

Spanish juniper (*Juniperus thurifera* L.) forests are recognized within the 2000 Natura Network as a priority habitat for conservation, so they inherently constitute an important historical-cultural legacy in the centre of Spain (Olano et al., 2008; Escribano-Avila et al., 2012; Pías et al., 2014). Most of these forests are located in areas where accentuated land abandonment has occurred since the 1960s (Milanova, 2005) have triggered their regrowth (Gimeno et al., 2012). Therefore, they constitute the ideal candidate to study sapling recruitment in regrowing forests.

Our main goals were to elucidate how biotic factors and conspecific tree sex affected the recruitment process of Spanish juniper (*Juniperus thurifera* L.) forests along a gradient of forest expansion. We used sapling density as a proxy for successful seedling recruitment *sensu* Eriksson et al. (2008). Specifically, we expected that a higher density of saplings would be associated with greater cover of heterospecific woody vegetation, due to interspecific facilitation on new individuals' recruitment via providing protection for the extreme temperatures and wind conditions of the area of study. We also hypothesized that the spatial pattern of *J. thurifera* saplings would be associated with adult trees at the expanding front (where the conditions have been reported to be harsher than in old stands; Close et al., 2003; Acuña-Míguez et al., 2020) due to intraspecific facilitation processes causing resource islands for recruitment. We expected this sapling-adult association to be stronger for female adult trees than for male trees due to the fact that females produce mature cones and therefore seeds will be more likely dispersed around female tree canopies.

We tested these hypotheses using new methods for the analysis of replicated point patterns (Baddeley et al., 2015; Ramón et al. 2016), which allow testing hypotheses about the factors influencing spatial patterns under a replicated, design-based sampling scheme. This is the first time that such convenient approach is used for studying recruitment patterns.

Our results inform processes occurring in novel regrowing forests of *J. thurifera*, which could help better designing and leveraging conservation strategies towards passive restoration of these forests included in the Nature 2000 network. This in turn will help achieving forest surface increase and climate change mitigation.

2. Methods

2.1. Study species and area

Juniperus thurifera (Cupressaceae) is a tree species endemic to the Western Mediterranean Basin, with a relict Tertiary distribution, confined mainly to high altitude Mediterranean-climate areas of the Iberian Peninsula and Morocco (Terrab et al., 2008).

Juniperus thurifera is usually the dominant species in low-density open forests with a climate ranging from semi-arid to sub-humid Mediterranean-types (Gauquelin et al., 1999). It is adapted to grow on harsh environmental conditions, including high levels of incident radiation, severe drought and rocky, shallow and poor-nutrient soils (Montesinos et al., 2010). Juniper trees normally reach 5–10 m tall and have a pyramidal crown shape with scaly leaves. *Juniperus thurifera* is a dioecious species, both males and females flower during late winter and wind-

pollinated female cones mature for over a year until they ripen. Mastig episodes are common for this species; thus, fruit production results highly variable over time (Montesinos et al., 2012; Mezquida & Olano 2013; Mezquida et al., 2016). Mature female cones are dispersed by endozoochory, mainly by birds such as thrushes (*Turdus* sp.) and some mammals, including red foxes (*Vulpes vulpes*), rabbits (*Oryctolagus cuniculus*) and domestic goats and sheep (Santos et al., 1999; Escribano-Avila et al., 2012).

Our study was conducted in three sites in the Alto Tajo Natural Park and the surrounding areas (Guadalajara, central Spain; Fig. 1; supplemental table S1). The climate in the area is continental Mediterranean, characterised by hot and dry summers and cold winters. Altitude of the sites ranges from 1000 to 1300 m above sea level; the mean total annual rainfall ranges between 565 and 640 mm, the mean annual temperature ranges between 10 and 12 °C (Ninyerola et al., 2005). In all the study area, the population of *J. thurifera* were traditionally decimated by timber extraction and forest clearance for agriculture and extensive livestock grazing (Gimeno et al., 2012). Over the last half century, these practices have ceased or at least considerably decreased allowing the recolonization of previously deforested areas and therefore reversing land-use changes.

2.2. Study design

We selected 17 plots along a forest expansion gradient. We considered three different stages along the forest expansion gradient: (i) the core-forest of juniper, consisting of old forests characterised by a denser matrix of adult trees with age distribution spanning different generations; (ii) an intermediate zone between the edge of the core-forest and the area of recent colonisation; and finally (iii) expanding fronts, i.e., more open novel forests on former old-fields that have been recently colonised. The three forest expansion stages (hereafter referred as forest stages) could readily be distinguished in the *J. thurifera* forests thanks to

the large spatial dimension of its expansion, which has originated discernible ‘recolonization waves’ spanning up to a few kilometers. In addition, the assignment of individual study plots to the different forest stages was confirmed based on a series of aerial photographs dating back to 1950 s (see Vilellas et al., 2020 for further information), thus stands considered old forests already existed prior to 1950 s. This experimental design was replicated in three different locations in the study area encompassing a total of 7 plots in Maranchón, 5 plots in Huertahernando and 5 plots in Ribarredonda (Fig. 1; supplemental table S1). All forest expansion stages were represented in each of the sites, resulting in a total of 5 plots for the old forests, 6 plots for intermediate zone and 6 plots for expanding fronts. Selected plots differed in their surface, ranging from 0.35 to 1.85 ha; plots located at the expanding front were generally larger due to their lower density in order to achieve a minimum number of 35 adult trees. Note that although large sample sizes, e. g., from 50 (Wiegand & Moloney 2014) to 100 points (Pommerening & Stoyan 2006) are recommended for spatial point pattern analysis, this recommendation applies for the analysis of individual patterns. Analysing replicated point patterns allows borrowing strength and avoids the lack of power associated to small sample sizes (Baddeley et al. 2015).

2.3. Data collection

In each plot, we mapped all *J. thurifera* adult trees and saplings, recording their coordinates with a DGPS (Trimble GeoXT GeoExplorer 2008) with a spatial accuracy of at least 80 cm. We considered adult trees all individuals higher than 1.40 m, and which trunk diameter at breast height (1.3 m; hereafter dbh) was equal or >3 cm, because this was the minimum size for which we found them to be reproductive. Note, however, that not all the individuals ≥ 3 cm were already reproductive; thus, those adults not displaying male flowers or female cones were recorded as non-reproductive. Accordingly, those individuals taller than 5 cm and lower than 1.40 m or with a dbh lower than 3 cm were



Fig. 1. Map of the study area.

considered saplings. Recently emerged seedlings, which were not yet filtered by the summer mortality event characteristic of Mediterranean-climate regions (Gómez-Aparicio et al., 2008) were discarded.

To study how conspecific and heterospecific interactions affected sampling density, for each juniper adult tree, we measured several size traits: dbh or quadratic diameter (Curtis & Marshall, 2000) for mono and multi-stemmed trees, respectively (hereafter both named as dbh for simplicity); maximum tree height (using a hypsometer-Haglof Vertex IV) and the crown diameter (the average of the largest crown diameter and the diameter perpendicular to it, both measured with a DME-distance measurer Haglöf Sweden). We also calculated the area of influence of each adult tree as the circular surface around each individual which radius equal to twice the average crown diameter (see Acuña-Míguez et al., 2020 for details). In the area of influence of each adult tree, we visually estimated the percentage of cover occupied by heterospecific woody species.

To study the differential spatial distribution with regards to tree sex, we recorded whether adult trees were male, female or non-reproductive. In case differences were found between sexes, we also measured some architecture-related traits to check for differences between male and female trees. Architecture-related traits included the number of stems, the percentage of tree height at which the first branch was located, and two qualitative indices: one of tree straightness (estimated with a scale ranging from 1 to 5, being 1 very twisted and 5 very straight) and other of branching angle (estimated with a scale ranging from 1 to 5, using 1 for very acute angle and 5 for branches hanging down), and we assigned a phytosanitary status (estimated with a semi quantitative scale from 0 to 4; see supplemental table S2 and Acuña-Míguez et al. 2020 for details).

For each plot, we built also three rasters (1×1 m pixel size) to describe the spatial variation of female and male tree sizes, and vegetation cover. These rasters were Gaussian kernel smoothed estimates (bandwidth = 10 m) computed with the *Smooth.ppp* function of the *spatstat* package (Baddeley et al., 2015).

2.4. Data analyses

2.4.1. Differences among stages of the gradient of forest expansion

We used Kruskal-Wallis tests to explore differences in tree density, conspecific individual tree size and heterospecific woody vegetation among the three forest stages. Thus, we explored differences in tree densities, sex (male vs. female) and life-stage (adult vs. sapling) ratios, and we tested for differences in tree size (i.e. the log-transformed dbh, tree height, average crown diameter, and tree age) as well as in surrounding vegetation cover (i.e. cover of heterospecific woody species). When there were significant differences among forest stages, we conducted Dunn's non-parametric all-pairs comparison to test for differences between pairs of forest stages. We adjusted p-values with Bonferroni correction. These analyses were performed with the functions *kruskalTest* and *kwAllPairsDunnTest* from the *PMCMRplus* package (Pohlert, 2020).

2.4.2. Factors determining the density of saplings

We analysed which biotic and abiotic factors influenced sapling density at plot level. For that, we fitted an inhomogeneous Poisson model (Baddeley et al. 2015; Batista & Maguire, 1998) to the intensity (i.e., density of saplings). For each of n replicated point patterns $y^{(i)}$, $i = 1, \dots, n$, we assume that the pattern is a Poisson process with intensity function

$$\lambda^{(i)}(u; \beta) = \exp\{\alpha + \beta^T \mathbf{x}^{(i)}(u)\},$$

where $\lambda(u)$ is the intensity at location u , β is a vector of coefficients and $\mathbf{x}^{(i)}(u) = (x_1^{(i)}(u), \dots, x_p^{(i)}(u))$ are explanatory spatial variables. The loglikelihood for the entire model is the sum of the loglikelihoods of the individual Poisson processes (Baddeley et al. 2015). We included as

explanatory variables the forest stage, the rasters describing the influence of the size of neighbour male and female *J. thurifera* trees, and the heterospecific woody vegetation cover, and also the interactions of woody vegetation cover with forest stage. We compared a set of possible models differing in the structure of fixed effects, and we selected the best-fit model (i.e., the one with the lowest Akaike Information Criterion, AIC). The Poisson models were fitted with the *mppm* function of the *spatstat* package, which allows fitting spatial point process models to replicated spatial point patterns.

2.4.3. Association between adults and saplings.

For each plot, we estimated the spatial association between saplings and adult trees using the multitype K_{ij} function (Lotwick & Silverman, 1982). In a multitype point pattern, where λ_j is the intensity of points of type j , $\lambda_j K_{ij}(r)$, measures the expected number of type j points within a circle of radius r around an arbitrary point of type i . We calculated two types of K_{ij} functions. First, to study the association between adults (a) and saplings (s) (regardless the sex of the adult trees) we computed $K_{as}(r)$. Then to evaluate whether the association between adults and saplings depended on the sex of the adult trees, we computed $K_{ms}(r)$ and $K_{fs}(r)$ (for male and female trees, respectively). In all cases, $K_{ij}(r)$ was estimated from $r = 0.1$ up to $r = 15.0$ m, with 0.1 m steps, using the isotropic correction to account for edge effects (Baddeley et al., 2015).

To assess whether the association between saplings and trees (K_{as}) depended on the stage along the gradient of forest expansion, we conducted a one-way ANOVA-like analysis (Diggle et al. 1991). This analysis compares the variability of the observed K functions among the levels of a treatment factor (in this case, the stage along the forest expansion gradient). After finding significant differences among stages we performed a post-hoc analysis to test for differences in the association between pairs of stages of the gradient of forest expansion. We adjusted the p-values using the false discovery rate (Benjamini & Hochberg 1991) to account for multiple testing.

To assess whether the association between saplings and trees depended on tree sex (i.e., K_{ms} and K_{fs}) and whether this dependence varied across forest expansion stages, we performed a two-way ANOVA-like analysis (Ramón et al., 2016). This is similar to the one-way ANOVA but allows testing the significance of the interaction between the two factors considered (tree sex and forest stage).

For these analyses, we used the function *K2w* from the *replicatedpp2w* package (Ramón et al., 2016) which tests the effects of the interaction of two factors (i.e. forest stage and sex of the adult tree) on the spatial structure of replicated point patterns.

When sex had an effect on seedling recruitment, we conducted Wilcoxon rank sum tests in order to unveil differences in tree architecture-related traits between male and female adult trees at a certain forest stage. We conducted all the analyses in R v 4.0.3 (R Core Team 2020).

3. Results

A total of 1530 individuals (816 adults and 714 saplings) were mapped in the 17 plots (supplemental table S3). Total tree density, as well as adults' and saplings' densities decreased along the gradient of forest expansion. Higher densities were found in old forests, while the proportion of saplings (calculated as the quotient between the number of saplings and the number of total juniper individuals) increased towards expanding fronts (Table 1; Supplemental figure S2). In every forest stage, there were more male than female trees (Table 1), suggesting that Spanish juniper forests are male-biased (Alfaro-Sánchez et al. 2021). In comparison with the other forest stages, adult trees had greater sizes (i.e. greater dbh, height and average crown diameter) and worse phytosanitary status at old forest plots (Table 2). Finally, heterospecific woody cover has larger coverage at the expanding front than in old stands ($\chi^2 = 6.5$, p-value > 0.05).

Table 1

Mean values and standard errors of the number and density of *Juniperus thurifera* individuals for each stage of the forest expansion gradient.

	Old forests	Intermediate zone	Expanding front
Total density (individuals/ha)	205.0 ± 20.1	153.7 ± 13.5	64.9 ± 4.5
Adults density (adults/ha)	113.9 ± 3.8	78.3 ± 6.3	33.2 ± 2.4
Saplings density (saplings/ha)	91.1 ± 16.6	75.4 ± 9.1	31.7 ± 2.8
Percentage of saplings (%)	36.1 ± 4.4	45.1 ± 2.8	47.5 ± 1.8
Percentage of males (%)	62.1 ± 0.9	62.9 ± 1.8	67.1 ± 1.3

Table 2

H statistic and significance for the Kruskal-Wallis test, and mean values and standard errors of the variables measured at tree level for each stage of the forest expansion gradient. Different letters indicate significant differences among stages from Kruskal-Wallis tests based on Dunn's non-parametric all-pairs comparison test and adjusted p-values with Bonferroni correction. Significance levels (* < 0.05; ** < 0.01; *** < 0.001).

	H (significance)	Old forests	Intermediate zone	Expanding front
Dbh (cm)	81.8 ***	20.4 ± 0.7 ^a	14.9 ± 0.5 ^b	11.6 ± 0.5 ^c
Height (m)	130.9 ***	5.4 ± 0.1 ^a	4.3 ± 0.1 ^b	3.8 ± 0.1 ^c
Average crown diameter (m)	63.8***	5.0 ± 0.1 ^a	4.4 ± 0.1 ^b	3.7 ± 0.1 ^c
Phytosanitary status (0–4)	65.9 ***	2.3 ± 0.1 ^b	2.7 ± 0.1 ^a	2.9 ± 0.1 ^a
%Woody vegetation	6.5 *	40.8 ± 1.1 ^b	42.5 ± 1.0 ^{ab}	43.6 ± 1.1 ^a

3.1. Factors determining the intensity of saplings

The model which best described the variation in the intensity of saplings included male and female size, and the interaction between forest stage and heterospecific woody vegetation cover as predictors (supplemental table S4). Sapling recruitment differed among stages (Table 3), being larger at the old forests (Table 1). Sapling density was negatively influenced by greater size of both male and female conspecific adult trees, while heterospecific woody vegetation had a positive effect although differentially associated with the forest stages (Table 3).

3.2. Association between adults and saplings

When performing the one-way ANOVA-like analysis considering adult trees regardless their sex, we found a significant effect of the stage of the gradient of forest expansion ($p = 0.012$), with saplings being associated with adult trees only at the expanding front. This association occurred at a certain distance from the adult tree (approximately from four meters onwards; Fig. 2a). We observed significant differences between the expanding front and the intermediate zone ($p = 0.039$) and marginally significant between the expanding front and the old forest stands ($p = 0.059$), whereas no significant differences were found between the intermediate zone and the old stands ($p = 0.484$) (Supplemental figure S3).

In the two-way ANOVA-like analysis, we found a significant effect of the interaction between forest stage and tree sex ($p = 0.031$). In comparison with other forest stages, at the expanding front, saplings recruited more frequently at a certain distance ($r > 5$ m) around male adult trees (Fig. 2b). This association of saplings to males at the expanding front was not related to differences in size, architectural traits and phytosanitary status between male and female adult trees at the expanding front (supplemental table S5).

Table 3

Factors affecting the density of *Juniperus thurifera* saplings as resulted from the inhomogeneous Poisson models. Factors included were: stage along the forest expansion gradient (Stage), the average crown diameter of male and female adult trees (Male size and Female size, respectively), the percentage of cover of heterospecific woody species (Woody vegetation), as well as the interaction between stage and woody vegetation. Degrees of freedom (Df). Levels of significance whether the effect is positive or negative calculated with type II ANOVAs for each factor included in the model. Significance levels (* < 0.05; ** < 0.01; *** < 0.001; ns: non-significant). NA: not applicable.

	Df	Wald- χ^2 (significance)	Effect	Estimate	t (significance)
Male size	1	51.05 (***)	(-)	-0.266	-4.72 (***)
Female size	1	13.11 (***)	(-)	-0.134	-2.39(*)
Stage	2	19.91 (***)			
Stage:	0.811	1.63 (ns)			
Intermediate zone					
Stage: Mature forest	-0.932	-1.46 (ns)			
Woody vegetation	1	14.58 (***)	(+)	0.019	2.52 (*)
Woody vegetation *	2	41.23 (***)			
Stage					
Woody vegetation *	0.005	0.52 (ns)			
Intermediate zone					
Woody vegetation *	0.043	3.92 (***)			
Mature forest					

4. Discussion

Our results showed that in *J. thurifera* forests, conspecifics facilitate sapling recruitment at their expanding front, being juniper saplings associated to male adult trees. Sapling density appeared positively influenced by the cover of heterospecific woody vegetation and negatively influenced by conspecific adult size, influences which were probably driven, respectively, by interspecific facilitation and intra-specific competition.

The environmental conditions of the Mediterranean juniper forest become harsher along the forest expansion gradient partially due to intrinsic characteristics of the forest physiognomy (smaller tree crown and lower juniper density at the expanding front; Acuña-Míguez et al. 2020). Due to the increased canopy openness in the expanding front, the enhanced irradiance may induce photoinhibition (Close et al., 2003) and wind, frost and snow could affect saplings more strongly than in old stands due to reduced protection by existing vegetation (Acuña-Míguez et al. 2020). Consequently, ecological processes and biotic and abiotic factors driving recruitment vary differentially along this gradient. As we expected, facilitation predominates in more stressful environments with less availability of suitable microhabitats –typical of recently colonised old fields– (as has also been seen for other woody species; Flores & Jurado, 2003; Wu et al., 2013; Flinn & Marks, 2007).

Regarding the factors influencing sapling density, the negative effect of both male and female tree sizes that we observed is in line with previous showing strong negative interactions between conspecific neighbours with increased size (Wright, 2002; Chen et al., 2018). Increased size of adult trees can trigger competition by limiting light and water resources, and therefore hindering seedling recruitment under their crowns (Comita & Hubbell, 2009). Following our expectations, interspecific facilitation favoured sapling recruitment along the gradient; this may be related to the favourable microenvironmental conditions heterospecific woody vegetation provide, therefore protecting saplings from the harsh environmental conditions of the area (e. g. summer drought, wind and frost) and from being predated, and

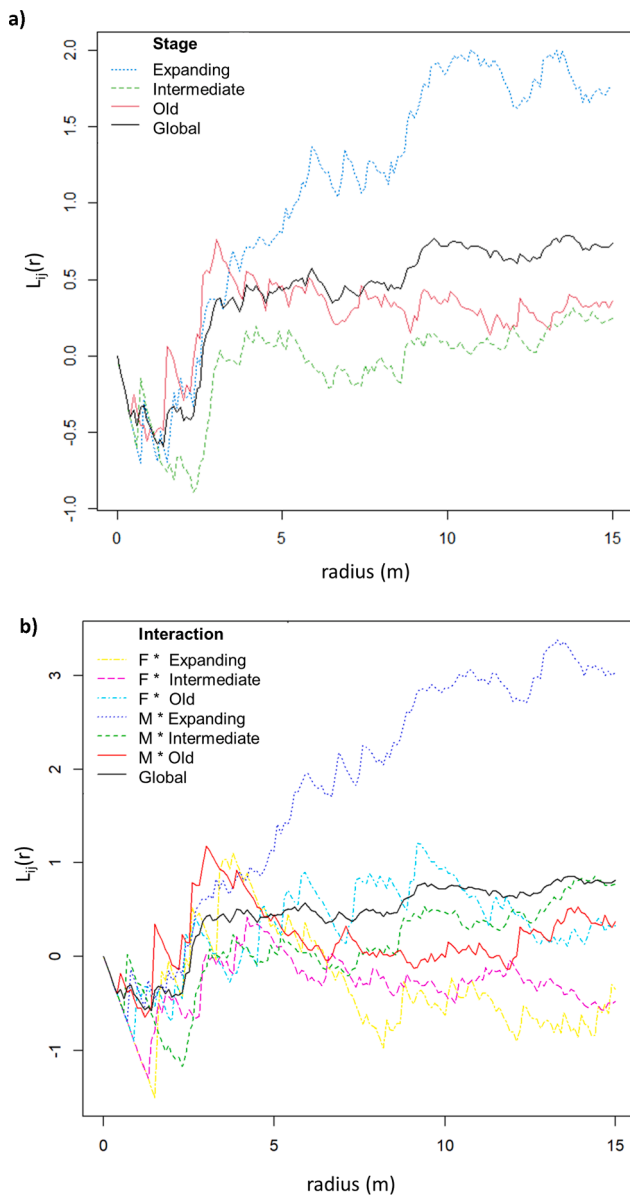


Fig. 2. Results of the two-way ANOVA-like analysis. Instead of $K_{ij}(r)$ functions, we represent the linearized version $L_{ij}(r) = [K_{ij}(r)/\pi]^{0.5} \cdot r$ (Dixon 2006). Coloured curves represent the weighted averages of the functions for each stage (a) or for the combination of sex and stage (b). Global: weighted average of the functions of all sex and stages. They measure the association between *J. thurifera* saplings (*i*) and adult (a) or either and male (M) and female (F) *J. thurifera* adults (*j*) in each forest stage (b). Positive $L_{ij}(r)$ values indicate positive spatial association while negative ones indicate spatial segregation.

subsequently favouring their initial survival (Benavides et al., 2016). This trend has also been shown in the recruitment process of other tree species such as *Quercus ilex* that successfully recruited new individuals in shrub encroached areas (Pulido et al., 2010). Specifically, in our study plots we normally found vegetation patches of *Genista scorpius* (L.) DC. and *J. thurifera* individuals located together. This thorny species may have a positive effect on recruitment due to nitrogen fixation ability of leguminous shrubs, previously observed in other semiarid ecosystems in the south of Spain (Pugnaire et al., 1993). Moreover, other accompanying species such as *Prunus spinosa* L. and *Rosa canina* L. have also strong thorns, which may provide protection for herbivores in the early stages of sapling development (Gómez-Aparicio et al., 2004).

Regarding the association between adults and saplings, our results aligned with our expectations, suggesting intraspecific facilitation of

saplings recruitment at the expanding front, where environmental conditions are harsher. However, contrary to our expectations, such facilitation was mediated mainly by male adult trees only. This pattern of higher recruitment of individuals at a certain distance from a supposed nurse plant (i.e. from 5 m onwards from male trees in our study) has been denominated ‘facilitation in the halo’ in an intra-specific context (Pescador et al. 2014). Note that the average crown diameter, at the expanding front is around 4 m (Table 2). This distance between recruited saplings and adult trees would permit a balance between the facilitation provided by the adult canopies –against the severe abiotic conditions at the expanding front– and the negative density-dependence among seedlings and direct competition with adults at closer locations. In fact, we found a consistent pattern along the whole gradient in which juniper saplings density decreased with the proximity to larger conspecific adult trees (both male and female), which points out to increased competitiveness when adult neighbours are bigger (Chen et al. 2018), diluting the process of ‘facilitation in the halo’. From a dynamic perspective, this recruiting pattern guarantees the colonization of empty spaces between adult trees (instead of clustering under the adult tree), and probably contributes to a faster forest regrowth.

The sex-biased pattern of sapling attraction found around male adult trees at the expanding front is surprising as previous studies showed a female-biased spatial association in *J. thurifera* recruitment patterns (Montesinos et al., 2007) as well as in other dioecious species such as *Ceratiola ericoides* (Gibson & Menges, 1994). In our study, this male-biased spatial association was not due to differences in size, morphology or phytosanitary differences between tree sexes (supplemental table S5). As it occurs in other dioecious species, this sex-biased pattern of sapling attraction might be related to increased competition of female trees in comparison to males, including higher concentrations of secondary compounds and allelopathic defences (Cornelissen & Stiling, 2005) and enhanced root growth and resources allocation (Freeman et al., 1976; Dong et al., 2017). In the related *Juniperus sabina*, it is known that some physiological attributes vary between sexes with female individuals showing lower shoot water potential than male ones when associated to other individuals, thus reflecting greater competitive ability of female individuals (Verdú et al., 2004). This, together with the fact that seed predation increased under female *J. thurifera* (Hulme, 1994; Pías et al. 2014) points out to lower competitive ability of male juniper trees and the associated pattern between saplings and male adults at the expanding front. Due to the differences among sexes in favouring seedling recruitment in regrowing forests, it is important to consider tree sex ratio in gradients of forest expansion displaying differential environmental conditions (Tognetti, 2012).

Space-for-time substitution studies are an alternative to long-term studies, constituting an important asset in ecology to studying temporal dynamics. There are inherent limitations associated with the employment of a chronosequence method, because its assumption that abiotic and biotic factors affecting sapling density have remained constant over the time span of the successional change under study (Johnson & Miyanishi, 2008). However, the employment of chronosequence is recommended in studies such as this one, which was designed based on evidence that sites of different ages had been following the same trajectory in the past centuries (Walker et al. 2010).

Our results shed light on the importance of focusing on the expanding front of juniper forests to fully comprehend recruitment patterns and their potential effect on forestry dynamics. Although these areas, with the presence of only some isolated adult individuals, have historically lacked ecological and conservational attention, centring conservation strategies in them could be key to increase both forest extension and climate change mitigation. It is in these former old fields, that have recently been colonised, where tree recruitment is mainly driven by biotic interactions (Cramer et al., 2008), existing a compromise between environmental harshness and key ecosystem processes such as facilitation by conspecifics. As a result, forest regrowth through increased and successful recruitment that appears hindered in old forests

seems to be recovered at the expanding front. This buffer area where rural exodus and abandonment of low productive old fields permits forest regrowth (Rousenvell et al., 2006) needs to get noticed and be valued by the scientific community and the political sphere. Understanding the recruitment processes in these recently colonised areas and their role in the recovery of ecosystem functionality is crucial to better leverage conservation strategies and design appropriate restoration policies, which should be oriented to recover biotic functionality rather than to amend abiotic constraints.

The fact that *J. thurifera* forests facilitate the recruitment of their individuals associated to male adult trees at their expanding front involves that these areas of recent colonisation that have been overlooked in conservation policies are potential targets to implement management measures. These measures can include those aimed at reversing habitat degradation, achieving the reduction of deforestation, as stated in the Aichi Targets, and in line with the biodiversity policies of the European Union. Likewise, modelling future scenarios of expanding forests and land-use changes in Europe will allow designing strategies to mitigate global change over forestry systems by recovering ecosystem functionality.

Authors' contributions

I.M.F. and F.V. conceived the ideas and designed the sampling methodology; M.C. designed the spatial analyses; I.M.F. and B.A.M. collected the data; I.M.F., C.C.B. and M.C. analysed the data; I.M.F. led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

Data statement

The dataset will be published in a public repository upon the acceptance of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was made possible by the International Laboratory on Global Change LINGGlobal (www.lincg.uc-csic.es) and funding from the grants SPONFOREST (BiodivERsA3-2015-58, PCIN-2016-055, financed by the Spanish Research Agency (AEI) and the Spanish Ministry of Economy, Industry and Competitiveness (MINECO)), COMEDIAS (MINECO, CGL2017-83170-R) and REMEDINAL TE (Ref. TE-CM. S2018/EMT-4338, 2019-2023-Comunidad de Madrid). Coauthor CCB was supported by a postdoctoral fellowship from the Ramon Areces Foundation. We are especially grateful for the support provided by David López Quiroga, José Miguel Olano, Adrián Escudero, Pablo Álvarez García, Esteban Manrique, Eduardo Serna, Miguel Díaz Carro, Alicia Forner and Ludmila Aglai. We are also thankful to José Antonio Lozano, director of the Alto Tajo Natural Park, for making possible the permissions to sample in the area. Likewise, we would like to thank the local population of the sampled villages for their kindness. Two anonymous reviewers provided insightful comments that have improved this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119937>.

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