Legacy effects of seed dispersal mechanisms shape the spatial interaction network of plant species in Mediterranean forests

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Abstract

1. Seed dispersal by frugivores plays a key role in structuring and maintaining tree diversity in forests. However, little is known about how the spatial legacy of seed dispersal and early recruitment shapes spatial patterns and the spatial interaction network of plant species in mature forest communities.

2. We analysed two fully mapped mixed Pine–Oak forest communities using spatial point pattern analysis to determine (a) the detailed structure of the intraspecific spatial patterns of saplings and adults, (b) the intra- and interspecific spatial interaction of saplings, adults and saplings relative to adults, (c) the spatial patterns of species richness at the community level and (d) whether seed dispersal mechanisms affect the plant–plant interaction networks and the ratio of adult to sapling neighbourhood densities used as surrogate for spatial self-thinning.

3. The intraspecific spatial patterns of saplings and adults showed in general complex nested cluster structures that were similar for sapling and adult stages, despite substantial self-thinning in some dry-fruited species. The spatial network of saplings was characterized by positive spatial interactions. Adults of several tree species facilitated saplings in their proximity; however, adults of dry-fruited species, but not those of fleshy-fruited ones, lost almost all positive interactions that occurred at the sapling stage. Besides, interaction strength between adults was positive and often significantly stronger if both species were fleshy-fruited. At the community level, the forests were structured into multispecies clumps across all life stages.

4. Synthesis. Our analyses highlight the importance of the spatial legacy of seed dispersal and early recruitment in the assembly of plant communities. Particularly, animal seed dispersal can lead to multispecies clusters and positive spatial associations across life stages in Mediterranean forests, with surprisingly little...
signatures of negative interactions. Our analysis suggests that changes of the spatial structure across plant life stages are driven by seed dispersal mechanisms and subsequent spatial self-thinning, generating a spatial footprint at the sapling stage that conditions the long-term interactions between adult plants. Combining spatial point pattern analysis with network analysis and species traits is a promising way to disentangle the processes underlying observed patterns of local diversity.

**KEYWORDS**

coexistence mechanisms, community-assembly, forest dynamics, plant-facilitation, point pattern analysis, recruitment networks, spatial self-thinning, species interactions

1 | INTRODUCTION

The assembly of plant communities and their dynamics have fascinated ecologists for long, and many theories and mechanisms have been proposed to explain plant coexistence (Chesson, 2000; Connell, 1971; Hubbell, 2001; Janzen, 1970). Key processes include seed dispersal, species interactions such as competition or facilitation, and mechanisms governing the interactions of species with their environment (Valladares et al., 2015). Many studies seeking to understand plant coexistence focus on plant–plant interactions, trying to disentangle what processes and species traits can explain co-occurrence of competing species (Kraft et al., 2015; Maestre et al., 2005; Perea, Garrido, et al., 2021). However, this is not always straightforward since processes occurring during early life stages, such as seed dispersal, antagonism, (micro) habitat filtering or facilitation may predetermine the interactions occurring among adult plants (Anthelme & Dangles, 2012; Lara-Romero et al., 2016). Thus, to gain a more comprehensive understanding of the dynamics and assembly of plant communities, we need to examine the legacy of processes that occur early in the life cycle, and how and to what extent they influence the spatial structure of plant–plant interactions in mature plant communities (Hanley & Sykes, 2009).

Seed dispersal is a key process that defines the spatial template for subsequent processes of recruitment (Nathan & Muller-Landau, 2000). Thus, dispersal can have profound implications for community dynamics, driving subsequent species interaction and emerging intra- and interspecific spatial patterns (Beckman & Rogers, 2013). This is especially true for communities of endozoochorous plants (i.e. seed dispersal via ingestion by animals such as birds or mammals) where seeds may be preferentially deposited at specific microsites such as nests, roosts, perches or below large fruit bearing individuals (Arnell et al., 2021). For instance, the bird-dispersed shrub *Pistacia lentiscus* is strongly associated to isolated trees in abandoned orchards, since trees provide perches for frugivorous birds and optimal establishment conditions for this species (Verdú & García-Fayos, 1996). While animal seed dispersal contributes to avoid high densities of juveniles around their parents and therefore reduce local dominance of the species, barochory (i.e. dispersal of seeds by gravity) can lead to a locally high seed and seedling density of a species (Spiegel & Nathan, 2010). Subsequently, density-dependent pathogens may remove the aggregated seeds of a species (Bagchi et al., 2010), and microhabitat suitability may determine the structure of the community of recruits (Gómez-Aparicio, 2008). All of these mechanisms that act during the recruitment stage, are dependent on the initial spatial template set by seed dispersal, but their consequences can reach into the mature stage.

While seed dispersal and microsite suitability contribute to the assembly of the recruits (or sapling bank), adult plants may also exert both positive and negative effects on recruits of other species (Alcántara et al., 2019). Interspecific comparisons of spatial adult–adult and adult–recruit interactions can therefore provide valuable information about the pressure that a mature community exerts on regeneration (Callaway & Walker, 1997). For example, a species can initially facilitate recruits of other species, but this may turn into a competition at the adult stage (Valiente-Banuet & Verdú, 2008). In this case, we would expect a shift in the interspecific spatial adult–juvenile versus adult–adult relationship. Chanthorn et al. (2018) provide an example where adults exert positive effects on juveniles. In a tropical forest in Thailand, they observed that multispecies seed dispersal by primates generated high species richness of juveniles around preferred food-tree species, a pattern that may persist into the adult stage.

The spatial patterns of a plant community may therefore conserve imprints of past processes and constitute an ecological archive from which we may retrieve information about the underlying processes (Murrel et al., 2001; Pacala, 1997; Wiegand et al., 2003; Wiegand & Moloney, 2014). By comparing spatial structures of species at early and late life stages, it should be possible to improve our understanding on the processes that drive community assembly and dynamics (Getzin et al., 2008; Moehr, 1997; Plotkin et al., 2002). This comparison will not be valid if the emerging spatial patterns and their underlying mechanisms change fundamentally during the lifetime of the plants, as for example expected after severe disturbances such as fire, invasive species or significant changes in environmental conditions. One approach to analyse spatial patterns in plant communities is to conduct point pattern analysis (Baddeley et al., 2015; Illian et al., 2008; Velázquez et al., 2016; Wiegand & Moloney, 2014),
based on datasets where the spatial location and the species identity of all relevant ecological objects (e.g. adult trees, saplings) is mapped within a sufficiently large area.

Spatial patterns in communities of endozoochorous plants should be especially complex due to the activity of animal seed dispersers and result in highly non-random patterns, both within and between species (Arnell et al., 2021; Martinez et al., 2010). For example, the activity of several animal seed dispersers, where each can have a specific seed deposition behaviour (Muller-Landau & Hardesty, 2005), is likely to generate highly non-random spatial patterns of saplings with a variety of complex structures such as small clusters nested within large clusters (Wiegand et al., 2009). The complex spatial patterns at the sapling stage may persist into the adult stage or, alternatively, the dynamics may follow conceptual models of old-growth forest development (Duncan, 1991; Moeur, 1997) where subsequent self-thinning results in substantially simplified random or regularly spaced patterns of adults. Cluster point process models (Wiegand et al., 2009; Wiegand & Moloney, 2014) can be used to describe the intraspecific patterns of adults and saplings. Fitting these models allows to quantify key properties of the patterns, including the typical radius of the clusters, the number of clusters in the plot, the density of individuals in a cluster, and possible heterogeneities in the distribution of the number of individuals in the clusters.

Shared seed dispersers may give rise to multispecies clusters of saplings under preferred perches, especially below the canopies of adult trees. This behaviour can imprint positive interspecific association among saplings, among adults and saplings, and may even remain until the adult stage (Arnell et al., 2021; Martinez et al., 2010). Whether signatures of the foraging behaviour of seed dispersers remain from the seedlings to the adult stages will depend on the strength of subsequent density-dependent processes. These interspecific associations can be conceptualized as a weighted and directed network, where the species are the nodes of the network and the strength and direction of the pairwise spatial associations between species defines the weights of the edges. Spatial point pattern analysis can be used to quantify the weights of the edges by determining the direction and strength of departures from the null model of spatial independence (Losapio et al., 2018). For example, a positive interaction between species 1 and 2 occurs if individuals of species 2 are more often than expected in the neighbourhood of individuals of species 1. Finally, the weights of the networks can then be related to species traits (Chanthorn et al., 2018) to obtain a more mechanistic understanding of the observed spatial association patterns.

Comparison of the weights for sapling-sapling, adult-adult and sapling-adult associations will allow us, given our assumptions about absence of severe disturbances, to determine the degree of legacy of seed dispersal with respect to intraspecific and interspecific spatial patterns across life stages.

To better understand how legacy effects of seed dispersal influence the assembly and dynamics of plant communities, we quantify in this study the spatial patterns of adult trees and saplings in stem-mapped Mixed Pine–Oak forest communities in south-eastern Spain. More specifically, we use recent techniques of spatial point pattern analysis (see Table 1) to:

**TABLE 1** Scheme of the analyses used in this work. Analysis 1, 2 and 3 were conducted by spatially explicit point pattern analysis, whereas analysis 4 was conducted by generalised linear models. Columns represent: aim of each analysis, null models used, variants for each null model, summary statistic used for each analysis and questions to answer.

| Analyses | Aim | Null models used | Null model variants | Summary statistics | Questions |
|----------|-----|------------------|---------------------|-------------------|-----------|
| Analysis 1 | Determining the spatial structure of each life stage across species and communities | CSR | — | $L(r)$, $g(r)$, $D(r)$ and $H(s)$ | Do the spatial patterns simplify from sapling to adult? Do species show spatial self-thinning? |
| Analysis 2 | Determining significant interspecific interactions and their strength | Toroidal-shift | Multivariate saplings–saplings: Multivariate adults–adults | $K_{12}(r)$ and $D_{12}(r)$ for significance | Which type of interaction is more frequent? Which species interact? What is the strength of these interactions? |
| Analysis 3 | Determining distance decay of species richness for the communities | Toroidal-shift | Multivariate | Cumulative Simpson index $\alpha(r)$ | Does multispecies clustering exist? |
| Analysis 4 | Determining whether seed dispersal mechanisms drive interaction strength across life stages and spatial self-thinning of species | Generalised linear models | Dependent variable | Interaction strength or spatial self-thinning | Can seed dispersal mechanisms drive the strength of spatial associations? And the spatial self-thinning? |
1. quantify the intraspecific spatial patterns of saplings and adults in detail and estimate the ratio of sapling to adult neighbourhood densities as surrogate of self-thinning,
2. quantify the interspecific spatial association networks of saplings, of adults and of saplings relative to adults by using weighted and directed networks where the weights of species pairs are defined as the strength and direction of departures from the null model of independent placement of the species,
3. find out if species tend to form multispecies or single-species clusters, and lastly
4. relate the weights of the interspecific spatial association networks and spatial self-thinning to the seed dispersal mechanism of each species.

Comparison of the spatial patterns of the sapling and adults, as well as the sapling–adult associations, allow us to assess whether the footprints of seed dispersal remain or disappear across life stages. We hypothesized that if seed dispersal legacy leaves footprints in the community assembly then: (a) intraspecific sapling–sapling and adult–adult spatial patterns should show similar complex cluster structures, (b) the network of interspecific spatial associations should show dominance of positive associations, especially in the case of bird-dispersed plants, (c) the community should be organized into multispecies clumps and (d) seed dispersal and spatial self-thinning (from seedling to adult stage) should be related to the weights of the emerging interspecific spatial association networks.

2 | MATERIALS AND METHODS

2.1 | Study systems

We conducted the study during the summer and autumn season of 2014 in two protected Mixed Pine–Oak forest communities in southeastern Spain, the Sierra de Jaén (37.38°N, −2.57°W; 850 m a.s.l.) and the Sierra de Segura (38.30°N, −2.55°W; 1,420 m a.s.l.) (MFJ and MFS, hereafter). Both communities show typical Mediterranean climate, with low rainfalls and high temperatures during the summer, and moderate rainfalls and mild temperatures during the winter. The two plots are old-growth forest stands, given the presence of many very old individuals of all the tree species, the abundant occurrence of individuals of all age classes. Aerial photographs show that both plots have been covered at least since the 1950s by forest, and the available evidence suggest that no recent fires occurred during the life span of the species that would have altered the emerging spatial patterns and their underlying mechanisms significantly.

We used in this study the most abundant plant species of the upper canopy (dry-fruited trees) and the understorey (fleshy-fruited shrubs). The upper canopy in the MFJ plot is dominated by Quercus faginea, Quercus ilex and Pinus halepensis, and the canopy at the MFS plot is dominated by Q. faginea, Q. ilex, Acer grani-
tense and especially Pinus nigra subsp. salzmannii. The understorey of both plots is composed of individuals of Crataegus monogyna mixed with other species such as Pistacia lentiscus, Phillyrea latifolia and Juniperus oxycedrus in MFJ, and with Crataegus laciniosa in MFS. While these species conform the core of these communities, other less common species occur at both sites, but due to their low abundance they were not included in the analyses (Supporting Information S1).

2.2 | Sampling design for point pattern analyses

At both communities, we set a plot of 50 × 50 m (small plot, hereafter) that was located concentrically inside a larger 100 × 100 m plot (large plot, hereafter). At both plots, we registered the X and Y coordinates (with a precision of 0.33 m) and DBH (diameter at breast height) for every adult tree of each upper canopy and understorey plant species. In the small plot, we registered the locations of saplings and measured their size as the basal diameter, and DBH when it was possible. We defined saplings as plants older than one year, having a basal diameter >1 mm, DBH <1 cm, and without showing evidence of being reproductive. Adults are defined as large individuals that showed evidence of being reproductive. A similar experimental design can be found in Perea et al. (2020). The plots correspond to old-growth forest stands, with homogeneous environments, and without evidence for recent disturbances. For this reason, no correction for heterogeneity was applied in the spatial point pattern analyses.

For analyses of adults we used the plants of the large plot, but for the analysis of saplings and saplings around adults we used only the plants of the small plot. The DBH threshold for adults was 8 cm for the upper canopy species (Pinus sp., Q. faginea, Q. ilex and A. granatense). Adults of understorey species (e.g. Crataegus spp., Juniperus oxycedrus, Phillyrea latifolia and Pistacia lentiscus) reach maturity with relatively small size, so no threshold was necessary to categorize adult individuals.

2.2.1 | Analysis 1: Intraspecific patterns and spatial self-thinning

To quantify the details of the intraspecific spatial patterns of saplings and adults and to assess their differences, we used a series of point process models with nested complexity (Supporting Information S2; Wiegand et al., 2009; Wiegand & Moloney, 2014). To fit the competing point process models to the data, we used the information of four summary functions, including the pair correlation function \( g(r) \), the distribution function \( D(r) \) of nearest neighbour distances, the spherical contact distribution \( H_s(r) \), and Ripley’s \( K(r) \) (Wiegand & Moloney, 2014). The summary functions \( g(r), D(r) \), and \( H_s(r) \) are the minimal set of summary functions able to capture the potentially complex intraspecific spatial structure (Wiegand et al., 2013), and adding the \( K \)-function is advantageous when fitting cluster point processes (Supporting Information S2, Wiegand et al., 2009).
The point process models showed two axes of complexity. The first involves clustering and was represented by complete spatial randomness (CSR) (i.e. no clustering), simple Thomas processes (i.e. randomly and independently distributed clusters of points), and nested double-cluster Thomas processes where the points of the simple Thomas process are replaced by small clusters of points. The parameters governing the number and size (typical radius) of clusters can be fitted using the observed K(r) and g(r). The second axis of complexity involves the distribution of the points over the clusters, governed by an aggregation parameter k: If it is aggregated (say k < 10) we have few clusters with many points and many clusters with few points, and if the distribution is not aggregated (say k = 1,000) the points are randomly distributed over the clusters. A heterogeneous distribution of points per cluster may arise if some perches or roosts are more used by seed dispersers (or provide more suitable microsites) than others, and in case of barochory, if some mother trees produce and disperse more seeds than others. The parameter k does not affect g(r) and K(r), but it can be fitted based on D(r) and H2(r) (Wiegand et al., 2009; Wiegand & Moloney, 2014).

Using Monte Carlo simulations, we generated 999 stochastic realizations of each point process model to obtain the mean and the covariance matrix of the summary functions g(r), K(r), D(r) and H2(r) for each distance radius r, given model parameters. This allowed us to build a ‘synthetic likelihood’ based on a multivariate normal distribution to assess model fit (Wood, 2010). We used the resulting log-likelihood to calculate the Akaike information criterion AIC that balances model fit and model complexity to identify the most parsimonious point process models (the ones with lowest AIC). Because the stochasticity in the 999 point process realizations introduced variability in the AIC values we used a conservative criterion of ΔAIC < 10 to exclude poorly supported models (SI 3 shows the AIC of all models). If more than one model showed a ΔAIC < 10, we used a stepwise approach. We first identified which model type (i.e. CSR, single cluster or double cluster) among the models with ΔAIC < 10 showed the highest R2 for the pair correlation function. If one model type was clearly better (i.e. ΔR2 > 0.1) we selected this model type, if not we looked in a similar way at the R2 of D(r) and H2(r). In the second step, we determined whether the best model type showed a heterogeneous distribution in the number of points. This was the case if none of the best models determined had parameter k = 1,000 associated with a random distribution of points over the clusters (we tested k = 1,000, 5, 1, 0.3, 0.1, 0.05, 0.03, 0.015, 0.0083, 0.0045).

Following Moeur (1997) and Getzin et al. (2008), the comparisons of clustering patterns among size classes can be used to explore whether self-thinning occurs. By using this approach, we assume that the current spatial pattern of saplings does not differ from the sapling patterns that gave rise to the current spatial structure of adults. To assess the degree of spatial self-thinning, we estimated for the saplings and adults of each species the mean density $O_9(r = 0)$ of points in the immediate neighbourhood of the points, which is given by

$$O_9(r = 0) = \lambda (1 + DC_3), \quad \text{double cluster} \quad (1a)$$

where $\lambda$ = number of points/area is the overall density of N points in a plot of area A, $DC_3$ describes the relative increase in neighbourhood density through small-scale clustering, and $DC_1$ the relative increase through an additional large-scale clustering (Wiegand et al., 2009; Wiegand & Moloney, 2014). $DC_3$ and $DC_1$ can be estimated from the fitted parameters of the cluster processes (see Supporting Information S2). Basically, they are the mean density of points per cluster area ($m^2$), estimated by dividing the number of large clusters by the approximate area of the clusters, and divided by the overall density $\lambda$ of points (Wiegand & Moloney, 2014). As the index of total self-thinning, we use the ratio of the neighbourhood densities of saplings and adults, that is, $O_3(r = 0)/O_3(r = 0)$.

2.2.2 | Analysis 2: Classification scheme of interspecific spatial association networks

To derive the interspecific spatial association networks of saplings, of adults and of saplings relative to adults we used a classification scheme (Wiegand et al., 2007, 2012) in the version of Getzin et al. (2014). We conducted these analyses for the bivariate patterns of adult–adult (large plot), adult–saplings (small plot) and sapling–saplings (small plot).

Our goal is to quantify how individuals of a species 2 are distributed within the neighbourhoods (with radius r) of individuals of a focal species 1. To quantify this spatial association between two patterns we used the bivariate version $K_{12}(r)$ of Ripley’s K and the bivariate distribution function $D_{12}(r)$ of nearest neighbour distances (Getzin et al., 2014). The bivariate $K_{12}(r)$ can be estimated as the mean number of trees of species 2 within distance r of the trees of the focal pattern 1, divided by $\lambda_1(r)$, is the proportion of trees of the focal species 1 (Getzin et al., 2014). To the bivariate $K_{12}(r)$ is the proportion of trees of the focal species 1 that have their nearest species 2 neighbor within distance r, the $D_{12}(r)$ and $K_{12}(r)$ will agree in a situation where all individuals of species 1 have more or less the same number of neighbors of species 2, but not in cases where some individuals of species 1 have many species 2 neighbors, but others very few.

To determine the strength and direction of the association network we compared the summary functions $K_{12}(r)$ and $D_{12}(r)$ of our observed patterns to patterns of a null model of independent placement. We used for this purpose the toroidal shift null model (Lotwick & Silverman, 1982; Wiegand & Moloney, 2014) that keeps the spatial pattern of species 1 and 2 largely unchanged, but breaks their potential association. This is accomplished by adding the same...
vector \((x_2, y_2)\) to the coordinates of each individuals of species 2. The vector is randomly drawn for each realization of the null model. If individuals of species 2 would be displaced to locations outside the study window, they are wrapped following torus geometry. The toroidal shift null model is appropriate here because the plots were placed into homogeneous environments. We then estimated standardized effect sizes (z-scores) of the summary functions \(D_{12}(r)\) and \(K_{12}(r)\) as

\[
P_{12}(r) = \frac{(D_{12}(r) - E[D_{12}(r)])}{SD[D_{12}(r)]},
\]

\[
M_{12}(r) = \frac{(K_{12}(r) - E[K_{12}(r)])}{SD[K_{12}(r)]},
\]

where the \(E[\cdot]\) and \(SD[\cdot]\) indicate the expectation and standard deviation of the summary statistics of the null model realizations at distance \(r\) respectively. Note that a low number of individuals will increase the standard deviations and therefore decrease the interaction strength (Wang et al., 2016). The standardized effect sizes have the convenient property that a significant departure from the null model with an error rate of 5% for a single distance \(r\) is indicated by values of \(<-1.96\) or \(>1.96\). Here, we combine the two summary function \(P_{12}(r)\) and \(M_{12}(r)\) and obtain therefore significant departures if at least one of the two values of \(P_{12}(r)\) or \(M_{12}(r)\) is higher than 2.24 or lower than −2.24 (Getzin et al., 2014).

The strength of the association between species 1 and 2 is given by the length of the vector \((P_{12}(r), M_{12}(r))\) in the two-dimensional P-M space (\(P\) is the \(x\)-axis and \(M\) the \(y\)-axis), that is, \((P_{12}(r))^2 + (M_{12}(r))^2)^{0.5}\). The direction of the interaction is then given by the \(M_{12}(r)\): positive values indicate a positive association and negative values, a negative association. This defines a weighted and directed network, where the species are the nodes of the network and the strength and direction of the pairwise spatial associations between species defines the weights of the edges.

### Analysis 3: Testing for multispecies clusters at the community level

To find out if species tend to form multispecies clusters we used the cumulative Simpson index \(\alpha(r)\), which estimates the probability that two randomly selected individuals located within distance \(r\) are heterospecific (Wiegand et al., 2017). This analysis summarizes the interaction networks described in analysis 2 at the community level, but includes also species with low densities. Species tend to form multispecies clusters if the observed \(\alpha(r)\) at small distances \(r\) is larger than the expectation for a community of independently placed species, and species tend to form single-species clusters if \(\alpha(r)\) is smaller than expected. As a null model we used, as in analysis 2, a toroidal shift null model for each species. We conducted 999 simulations of the toroidal shift null model, used the 25th highest and lowest values of the simulations as simulation envelopes, and tested significance of the observed summary function based on a global envelope test of the standardized effect size (Table 1).

### Analysis 4: Relating the interspecific spatial association networks and spatial self-thinning to seed dispersal

First, we investigated whether the strength of interaction is conditioned by the type of seed dispersal (fleshy-fruited or dry-fruited seed dispersal). To do that we used generalized linear models with normal distribution, using as dependent variable the strength of the pairwise interaction and as explanatory variables the type of seed dispersal and the life stage of each of the species interacting. Note that we included here also non-significant pairwise interactions, since they also affect the general pattern of the spatial community assembly. Significance of the differences between seed dispersal mechanisms across life stages were evaluated by post-hoc Tukey test across life stages for each community.

Second, we studied whether our measure of spatial self-thinning was influenced by the type of seed dispersal. Here we used the spatial self-thinning of each species as dependent variable and the type of seed dispersal as an independent variable. Community (MFJ and MFS) was introduced as a fixed effect.

### Statistical settings

Point statistical corresponding to the analyses 1, 2 and 3 were conducted by means of spatial point pattern analysis using Program 

### Results

#### Overall

A total of 3,074 individuals were mapped in MFJ, 83.4% were saplings and 16.6% adults. Abundance of individuals was slightly lower at MFS (1,824 individuals), where 74.6% were saplings and 25.4% adults. At MFJ, we could analyse adults and saplings of seven species, whereas at MFS, we did it for six species (Figure 1).

#### Intraspecific pattern of adults and saplings and thinning

Our model selection procedure revealed that all patterns of adults and saplings showed clustered spatial patterns. The only exception was a random (CSR) pattern of \(Q. faginea\) adults at the MFS plot. Spatial point processes that best described the spatial distribution pattern of the different species included Thomas cluster processes with one or...
two critical scales of clustering, often with a heterogeneous distribution of points over the clusters (see Table 2 and SI 3). In some cases, the number of individuals were low (i.e. <50; Table 2) and the spatial analyses less reliable. Nevertheless, the selected models fitted even in this case the observed pair correlation functions well (i.e. $R^2 > 0.6$; SI 3; except Q. ilex adults at the MFS site), and our model select method was able to differentiate among competing models (SI 3).

There were no indications of a simplification of the spatial patterns of adults compared to that of saplings as would be expected by conceptual models of old-growth forest development (Duncan, 1991; Moeur, 1997), in contrast, adult patterns with two critical scales of clustering were prevailing, especially at the MFJ plot. The analysis also revealed that the approximate size of the small clusters was very similar between life stages and plots (Table 2), with mean radius of 3.4 m and a coefficient of variation of 0.38. This is a hint of an underlying clustering mechanism that is similar for all species.

Comparison of the neighbourhood densities $O(r = 0)$ between saplings and adults shows that the neighbourhood densities of adults were generally smaller than that of saplings, with thinning factors ranging from 0.9 to 3.9 for C. monogyna at the MFS and MFJ plot, respectively, to 98.8 and 65 for Q. faginea respectively. Spatial self-thinning of dry-fruited species was on average five times higher than that of fleshy-fruited species (Table 2). Thus, both, the intraspecific spatial patterns of saplings and adults showed in general complex nested cluster structures that do not differ between life stages, despite substantial thinning in some dry-fruited species.

3.3 | Interspecific spatial network of interactions

The classification scheme at MFJ revealed several positive interactions between species, but no negative interaction. At the sapling stage, 35.7% of all possible combinations were significant and positive. Adult-sapling interactions were significant for 8.2% and 16.7% of all pairwise combinations respectively. Sapling-sapling interactions occurred with no general pattern, but adult-adult interactions happened mainly within the fleshy-fruited species (Figure 2). J. oxycedrus did not show any association during the adult stage, but facilitated conspecifics and P. lentiscus saplings. Adults of P. halepensis also facilitated C. monogyna and Q. faginea saplings. (Figure 2; see Supporting Information S4 for further details).

At the MFS site, we observed only one negative interaction (segregation), but the rest of interactions were positive. Positive interactions were particularly strong at the sapling stage, occurred exclusively between dry-fruited species of the upper canopy, and represented 20% of all possible pairwise combinations. At the adult stage, we only observed one positive interaction between the two fleshy-fruited species. We also observed a strong facilitation provided by P. nigra, which enhanced saplings of all dry-fruited species, representing 11% of the possible interactions. Additionally, C. laciniata also acted as a nurse plant for Q. ilex, but this species repelled the congeneric recruitment of C. monogyna (Figure 2).

Thus, the network of interspecific spatial patterns showed mainly positive associations, adults of several species facilitated saplings in
### TABLE 2

Results of the intraspecific spatial pattern analysis and assessment of self-thinning (Analysis 1) in the study plots (MFJ and MFS) (see Supporting Information S3 for additional results). $N_A$ and $N_S$ indicate the number of adults and saplings of each species in the plot. The table shows the most parsimonious point process (Double or Single cluster, DC and SC respectively) and distribution family (Poisson and Negative Binomial (NB)) of each species at each life stage, adults and saplings (Ad and Sap respectively). For each species, the analysis fits a cluster radius for large and small clusters for each life stage. Supporting Information S2 details estimation of the total neighbourhood density $\lambda (1 + DC_S + DC_L)$ and the neighbourhood density $\lambda_{DC_S}$ of small clusters. Total thinning was estimated as the ratio of the neighbourhood densities of saplings and adults. Seed dispersal mechanism of species are defined by F (fleshy-fruited species) and D (dry-fruited species). Last column represents the fit of pair correlation function for each cluster process. Note that, despite low number of individuals, most of species showed high values for $R^2$ indicating good adjustment to the null model.

| Plot and species | $N_A$ | $N_S$ | Point process and family distribution | Cluster radius (m) | Small cluster radius (m) | Total neighbourhood density (ind/m$^2$) | Neighbourhood density of small cluster (ind/m$^2$) | Total thinning | Seed dispersal | $R^2$ of g(r) |
|------------------|-------|-------|----------------------------------------|-------------------|----------------------------|------------------------------------------|-----------------------------------------------|----------------|---------------|----------------|
| MFJ              |       |       |                                        |                   |                            |                                          |                                               |                |               |                |
| C. monogyna      | 52    | 152   | DC                                     | 28.91             | 2.15                      | 0.258                                   | 0.184                                         | 3.9            | F             | 0.85           |
| J. oxycedrus     | 75    | 65    | DC–NB                                  | 16.41             | 2.75                      | 0.063                                   | 0.028                                         | 21.3           | F             | 0.67           |
| P. latifolia     | 47*   | 417   | DC                                     | 50.57             | 3.84                      | 0.157                                   | 0.119                                         | 7.8            | F             | 0.57           |
| P. halepensis    | 133   | 489   | DC–NB                                  | 30.02             | 4.36                      | 0.077                                   | 0.018                                         | 34.8           | D             | 0.61           |
| P. lentiscus     | 84    | 90    | DC–SC                                  | 16.44             | 3.15                      | 0.065                                   | 0.018                                         | 9.3            | F             | 0.61           |
| Q. faginea       | 91    | 1,304 | DC–NB                                  | 33.18             | 4.98                      | 0.073                                   | 0.028                                         | 64.7           | D             | 0.66           |
| Q. ilex          | 27*   | 48*   | SC–NB                                  | –                 | 3.29                      | 0.046                                   | 0.037                                         | 4.7            | D             | 0.71           |

| MFS              |       |       |                                        |                   |                            |                                          |                                               |                |               |                |
| A. granatensis   | 21*   | 518   | DC                                     | 42.26             | 2.81                      | 0.082                                   | 0.064                                         | 49.6           | D             | 0.80           |
| C. laciniata     | 20*   | 48*   | SC–NB                                  | –                 | 8.45                      | 0.080                                   | 0.073                                         | 2.3            | F             | 0.87           |
| C. monogyna      | 220   | 265   | DC–NB                                  | 30.05             | 5.39                      | 0.745                                   | 0.514                                         | 0.9            | F             | 0.96           |
| P. nigra         | 460   | 110   | SC–NB                                  | –                 | 45.38                     | 0.278                                   | 0.092                                         | 2.9            | D             | 0.75           |
| Q. faginea       | 22*   | 355   | CSR                                    | –                 | 7.93                      | 0.009                                   | 0.193                                         | 98.8           | D             | 0.91           |
| Q. ilex          | 21*   | 119   | SC                                     | 25.28             | 3.85                      | 0.034                                   | 0.138                                         | 10.3           | D             | 0.28           |

*Low number of individuals, results of cluster radii may be less reliable.
their proximity, and some simplifications occurred in the network of adults compared to that of saplings.

### 3.4 Testing for multispecies clusters

MFJ and MFS showed identical spatial pattern of the cumulative Simpson index for the sapling life stage, with significant and positive departures from the null model up to distances of some 2 m (Figure 3a). This result suggests that the small-scale clustering of individual species (with cluster radii somewhat larger than 2 m; Table 2) is organized at the community level into multispecies clusters. Adults at the MFS site showed only weakly significant positive effects just below 1 m according to pointwise test, and non-significant positive tendency over the entire range tested (i.e., $p > 0.05$ under the global envelopes test). However, for adults at MFJ, this tendency was significant for distances above 0.5 m, indicating a generally high spatial mixing of species (Figure 3b).

Finally, the bivariate Simpson index of adults around saplings shows that MFJ saplings tend to aggregate significantly in the immediate neighbourhood (<0.5 m) of heterospecific adults. In turn, MFS saplings show weak tendencies to aggregate at distances between 0.5 and 1.5 m of conspecific adults (Figure 3c), but global envelopes test was not significant.
3.5 | Seed dispersal mechanisms drive species interactions and spatial self-thinning

At MFJ, the strength of the interaction between saplings and between adults and saplings did not depend on the seed dispersal mechanism (Figure 4a). However, it was positive between adults and significantly stronger when both species had fleshy fruits. At MFS, interaction strength between saplings and between adults and saplings was positive and significantly stronger when both species were dry-fruited. However, when adults and saplings were fleshy-fruited, their interaction was negative and significant. On its part, adult–adult interactions were positive and significantly stronger when both species were fleshy-fruited (Figure 4b).

Finally, we observed that our surrogate of spatial self-thinning (i.e. the ratio of the neighbourhood densities of saplings and adults at small distances $r$, that is, $O_S(r = 0)/O_A(r = 0)$) was significantly affected by the seed dispersal mechanism ($z$-value $= -2.159; p = 0.0308$) and did not differ between study plots ($z$-value $= -0.052; p = 0.958$). Predictions of the spatial self-thinning of dry-fruited species was $38.39 \pm 12.36$, whereas spatial self-thinning of fleshy-fruited species was $7.83 \pm 14.16$.

4 | DISCUSSION

In this study, we conducted a detailed spatial analysis of mixed Pine–Oak forest communities to find out if and how the footprints of the seed dispersal process shaped the emerging spatial patterns across life stages and levels of organization (i.e. intraspecific, interspecific, community level). We found that saplings and adults of the different species showed complex intraspecific spatial patterns, mostly with two critical scales of clustering that did not change between life stages. Analysis of interspecific spatial associations revealed a dense network of positive associations, especially among saplings, and many of them remained in the adult stage. Adult spatial patterns reflected legacy effects, since the interspecific interactions between adult plants depended on the seed dispersal mechanisms.

All of these mechanisms created complex spatial structures that lead to communities where heterospecific adults co-occurred spatially in a well-mixed manner.

4.1 | Spatial legacy of early recruitment on the spatial structures of species

Double clustering of fleshy-fruited species may be created by specialist and generalist seed dispersal agents (Russo et al., 2006). For instance, frugivorous birds with variable body mass, such as *Turdus* spp., *Sylvia* spp. or *Erithacus rubecula* disperse seeds of *P. latifolia* or *P. lentiscus* relatively close to perches, which can promote the observed clustering of juveniles at one scale (González-Varo et al., 2014, 2021; Herrera, 1984), given that perches are not strongly aggregated themselves. However, clustered perches would lead to juvenile patterns with clustering at two critical scales, a pattern that may also arise if multiple seed dispersers imprint different spatial signatures (Wiegand et al., 2007, 2009). For example, species such as *C. monogyna* or *J. oxycedrus*, are additionally dispersed by other vertebrates such as foxes or wild boars (Matías et al., 2010), which can ingest a disproportionally high amount of seeds and deposit them highly aggregated (Fedriani & Wiegand, 2014).

Dry-fruited species at our study sites produce either winged seeds (dispersed by wind) or acorns. Wind dispersal is conditioned to wind pulses, so most of seeds appear highly aggregated (Gómez-Aparicio et al., 2007). On its part, acorn dispersal depends on gravity and hoarding by rodent and jays (Gómez, 2003). Similar to wind-dispersed seeds, acorns are highly aggregated along the plots, especially nearby conspecific adults (Axer et al., 2021). Indeed, the neighbourhood density of saplings of dry-fruited species was 2.3 times higher than that of fleshy-fruited species (Table 2). The sapling patterns of all dry-fruited species (except *Q. ilex* at the MFJ plot) was characterized by clustering at two critical scales, and interestingly, the radius of small sapling clusters showed very little interspecific variation (Table 2), which points to similar mechanisms of seed dispersal.
Interestingly, considering all species, the approximate radius of small-scale clustering of saplings and adults were similar with \(3.9 \pm 1.2\) m for adults and \(3.0 \pm 1.4\) m for saplings (Table 2). All these results clearly suggest that processes that drive recruitment leave a legacy on the spatial structure at the adult stage.

4.2 | Consequences of seed dispersal on the spatial self-thinning of species

Intraspecific processes, such as resource competition or density-dependent enemies, are weaker when densities are lower and when plants are farther away from conspecific adults (Bagchi et al., 2010; Connell, 1971; Janzen, 1970; Le Roux et al., 2013; Perea et al., 2020). Lower densities in seed clusters reduce distance- and density-dependent mortality, leading to weaker levels of spatial self-thinning. Dispersers of fleshy-fruit species tend to transport seeds away from conspecific adults, reducing the incidence of density-dependent agents of mortality or the intensity of competition between plants (i.e. foraging activity and scape hypothesis; Howe, 1989; Russo et al., 2006; Verdú & García-Fayos, 1996). Conversely, seeds of dry-fruit species are usually highly aggregated due to wind, gravity or scatter hoarding, which enhance the strength of density-dependent mechanisms and the spatial self-thinning, especially if they are deposited close to the mother plant (Beckman et al., 2012; Bell et al., 2006; Nathan & Muller-Landau, 2000; Perea et al., 2020). Indeed, we found that the neighbourhood density of saplings of fleshy-fruit species was on average 0.843 saplings/m², less than half that of dry-fruit species (1.958 saplings/m²), while thinning was on average five times stronger in dry-fruit than in fleshy-fruit species (Table 2). Thus, differences in the seed dispersal mechanisms promoted uneven densities of early life stage per cluster, and therefore, unequal strength of spatial self-thinning, possibly having consequences for intra- and interspecific interactions and demography of these species (Fedriani & Wiegand, 2014; Getzin et al., 2008; Howe, 1989). For instance, all other being equal, species experiencing stronger spatial self-thinning will likely reach lower adult densities and therefore lower population size and reduced chances of interacting with other plants.

4.3 | Consequences of early recruitment and spatial self-thinning on species interactions

Weak spatial self-thinning would favour the maintenance of many positive associations and that most of the spatial sapling interaction network could be conserved into the adult stage. Indeed, our results showed that adults of fleshy-fruit species conserves a considerable proportion of the positive spatial associations of the sapling network, whereas adults of the dry-fruit species lost almost all (Figure 2), thereby supporting the results of previous studies (Arnell et al., 2021). Nevertheless, all dry-fruit species belong to the upper canopy, therefore mechanisms related to their growth form may also contribute to the low neighbourhood densities of adults and their reduced spatial associations (Goldberg & Barton, 1992; Wang et al., 2018). Interspecific competition for light and nutrients between the larger adult individuals may lead to removal of spatial associations present at early life stages (Bigler, 2016; Jensen & Löf, 2017; Valladares & Niinemets, 2008).

Although seed dispersal and spatial self-thinning play a key role in structuring species spatial interactions (Chanthorn et al., 2018; Nathan & Muller-Landau, 2000; Timóteo et al., 2018; Wang et al., 2013), the interaction network of saplings does not translate directly via thinning into the adults network. Instead, cross-life stage spatial associations may appear at maturity (Le Roux et al., 2013). For example, frugivorous birds forage usually on several fleshy-fruit species and may deposit seeds of multiple species in the close vicinity of adult trees (Verdú & García-Fayos, 1996), leading to the observed positive adult–juvenile associations and multispecies clumps of saplings. Such a positive cross-life stage spatial association was very strong at MFS where adult P. nigra individuals showed positive spatial associations to saplings of all dry-fruit species (including conspecifics). At MFJ, we observed similar, but somewhat weaker, effect of the adult patterns of P. halepensis and J. oxycedrus that showed positive spatial associations with saplings of different species. Thus, at our sites such cross life stage effects were mostly driven by conifers, suggesting that the phylogeny of adult plants is involved in this process, as has been reported in other studies (Martins et al., 2018; Valiente-Banuet & Verdú, 2007, 2013; Verdú et al., 2009).

Adults can also exert competitive pressure on saplings (Alcántara et al., 2015; Perea, Garrido, et al., 2021) that may counteract initially positive associations mediated by animal seed dispersal. However, we found only one negative spatial association between adults and saplings of the two Crataegus species at the MFS plot. Moreover, for J. oxycedrus and P. nigra we even observed positive conspecific adult–sapling associations. This suggests that competition did probably neutralize some positive associations, but it was seldom strong enough to turn them into negative associations.

4.4 | Perspectives from community levels

Community-level patterns were similar between sites, but differed substantially among life stages. This suggests similar biotic controls of the dynamics and patterns emerging at our two mixed pine–oak forest communities. At both sites, the community level spatial patterns of saplings showed multispecies clumps of recruitment, which seems to be maintained up to 5 meters from each individual (Lan et al., 2012). However, MFS and MFJ differed in the spatial association patterns of saplings relative to adults. At MFJ, saplings tended to be surrounded by more heterospecifics, whereas at MFS saplings did not show a clear pattern (i.e. \(p > 0.05\) global envelopes test). These differences were caused by the strong positive conspecific adult–sapling association of P. nigra at MFS, and the more diverse interspecific associations at the MFJ plot. In any case, the community-level adult–sapling associations are, in contrast to the pairwise interspecific associations, only marginally
significant, given that they emerge as balance of positive intraspecific and interspecific associations. The adult community showed at both sites significantly elevated probabilities to be surrounded by heterospecifics, a pattern that was maintained at the MFJ site up to distances of at least 7 m, whereas it tended to disappear at MFS at distances >1 m. This suggests higher spatial heterogeneity at MFJ than at MFS, which may also be influenced by species richness of each place (29 and 15, respectively; Kumar et al., 2006). Similar patterns of positive interspecific associations of adults were found by Martínez et al. (2010) in a deciduous temperate forest in Northern Spain.

The almost complete lack of negative associations, especially for the adult community, is a rather unusual pattern in forest communities (Martínez et al., 2010). For example, Wang et al. (2010) found that 65 out of 210 species pairs at the temperate Changbaishan forest in north-eastern China showed negative small-scale associations, but only 10 pairs showed positive associations. Theoretical models suggest that spatial interspecific segregation together with intraspecific clustering can promote coexistence (Pacala, 1997; Wiegand et al., 2021) because both decrease the strength of interspecific interactions relative to intraspecific interactions. However, temperate forest communities composed of animal-dispersed species seem to follow different dynamics leading to species being distributed in clusters of different species and different life stages, with little importance of negative associations (Arnell et al., 2021; Martínez et al., 2010).

In contrast to harsh environments, where multispecies clumps are caused by facilitative interactions among stress-tolerant species (Losio et al., 2018; Maestre et al., 2009), we suggest that the multispecific seed rain by birds and mammals promotes the multispecies clumps in these Mediterranean forests.

5 | CONCLUSIONS

Spatial patterns of species can be shaped by several mechanisms associated to intra- or interspecific competition, such as density-dependent effects or resource competition (Lara-Romero et al., 2016). Changes of the spatial structure across plant life stages are driven by seed dispersal mechanisms and subsequent spatial self-thinning. Both factors generate a spatial footprint at the sapling stage that conditions the interactions between adult plants, and therefore local coexistence. The strength of these interactions was high among adults of the understorey dominated by fleshy-fruiting species, but disappeared for adults of the upper canopy dominated by dry-fruiting species. The dynamics of both strata seems to follow different paths, but they are connected through seed dispersal that configures positive cross-strata associations.

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AUTHORS’ CONTRIBUTION

A.J.P., J.L.G. and J.M.A. designed the study; J.M.A., P.J.R. collected the data; A.J.P. and T.W. analysed the data; A.J.P. led the writing of the manuscript with significant contribution of the rest of the authors. All authors gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data are available in the Dryad Digital Repository https://doi.org/10.5061/dryad.xwdbrv1dn (Perea, Wiegand et al., 2021).

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.
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