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Research Article

Seed co-occurrence caused by shared frugivores leaves a long-lasting signal in the spatial co-occurrence among plants

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By dispersing seeds, frugivorous animals affect spatial co-occurrence of plants, ultimately influencing plant community dynamics. Frugivorous animals are intrinsically involved in plant community dynamics, by dispersing seeds of fleshy-fruited plants and influencing their spatial co-occurrence. Particularly, generalist avian frugivores forage on them, co-dispersing and co-disseminating their seeds. This dispersal process often promotes spatial clumping and sets the initial spatial template on which subsequent ecological processes operate. Despite this mutualism is key at the early stages of fleshy-fruited species, it remains unknown whether these co-dispersed and co-disseminated plant species maintain their initial pairwise seed co-occurrence along their demographic cycle. If so, this would reflect a lasting signal of these early mutualistic interactions in the plant community assembly. We investigated whether plant species that share avian seed dispersers also co-occur spatially across different life stages, from seed to adult individuals. We combined data on seed rain from nine fleshy-fruited species, dispersed by a community of 21 bird species identified through DNA-barcoding, with spatial co-occurrence patterns among these plant species at the sapling and adult stages, using point pattern analyses. From this, we built matrices showing: 1) the number of frugivore species shared between each pair of plant species, and 2) their spatial co-occurrence at different life stages: seeds (seed–seed), saplings (sapling–sapling and sapling–adult), and adults (adult–adult). We then used structural equation modelling to test whether the level of shared avian frugivores predicts the spatial co-occurrence among adult plants, while also assessing the indirect effects of processes occurring at intermediate demographic stages. Our results revealed both direct and indirect effects of frugivore sharing during the fruit removal and seed dissemination stage on the spatial assembly of established adult species. Specifically, we found that higher levels of shared frugivores increased the co-occurrence among plant species in

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seed rain (seed–seed), apparent facilitation (sapling–adult) and adult community (adult–adult), but not within the sapling bank (sapling–sapling). Frugivorous birds drive the co-occurrence among fleshy-fruited plant species, from seed to adult stages, although their influence decreases as the plant demographic cycle advances. However, the co-occurrence at adult stages is exclusively achieved when adults apparently facilitate sapling establishment. This reinforces the key role of the plant–plant facilitation in Mediterranean systems, and the deterministic role of mutualistic avian frugivores as drivers of spatial assembly in plant communities.

Keywords: frugivory, seed dispersal, plant community, plant-animal interactions, facilitation, plant demography, plant-plant interaction, structural equation models, point pattern analyses

Introduction

The seed dispersal mechanism of plant species determines their spatial distribution (Nathan and Muller-Landau 2000) and dispersed seeds constitute the first spatial template on which subsequent ecological processes operate in the assembly of local plant communities, influencing community dynamics, diversity and ecosystem functions (Levine and Murrell 2003, Beckman and Sullivan 2023). In particular, frugivory is one of the mechanisms that can lead to the dissemination of seeds of zoochoric species away from the parent plant, reducing their loadings of antagonists in the seedscape (Beckman and Sullivan 2023, Perea et al. 2025) and enhancing plant establishment (Janzen 1970, Connell 1971). These indirect effects of seed dispersal operate during the entire plant life cycle and shape spatial interactions among plant species (Harper 1977, Wang and Smith 2002, Gómez-Aparicio 2008, Adler et al. 2018).

However, frugivorous birds also influence subsequent plant–plant interactions in a more direct way. When two plant species share interactions with the same frugivorous species (or with a large proportion of them), co-dispersal of their seeds (i.e. seeds being ingested during a given feeding bout and transported together in the animal digestive tract) and co-dissemination (i.e. seeds disseminated at the same microsite in different dispersal events) occur very frequently (Jordano 1988, Schaefer et al. 2014). Thus, if two plant species (whether at seed, sapling or adult stage) co-occur in space, it might be determined by the early sharing of frugivores. The foraging patterns of frugivores (movements among fruiting plants where they feed on fruits), and their microhabitat preferences (non-random use of habitats depending on the resources and protection they provide) represent two key elements that shape the composition patterns of the seed rain of animal-dispersed plants (Jordano and Schupp 2000, Tewksbury et al. 2002, Rey and Alcántara et al. 2000, Isla et al. 2024, Quintero et al. 2024). Driven by variations in the way frugivores use the landscape , dispersed seeds reach their final deposition sites, where they may co-occur with conspecific and/or heterospecific seeds (Loiselle 1990, González-Varó et al. 2022). This process implies a direct effect of frugivores shaping the spatial structure of the seed rain by enhancing the seed co-occurrence, which may persist and ultimately have a lasting indirect signal on the spatial structure of the assembled plant community. However, these effects remain poorly known (but see Houle 1992, Jordano and Herrera 1995, García et al. 2005).

As a consequence of the temporal and spatial overlap of seed co-dispersal and co-dissemination processes, plant species that share more frugivore species (higher overlap in frugivore species partners) should also co-occur more frequently in the seed rain (Herrera 1984, Verdú and García-Fayos 1996). Therefore, the spectrum of interactions that an individual plant establishes with the rest of the plants in its community (plant–plant interactions) is determined a step earlier (plant-animal interactions in the seed stage). This co-occurrence at the dispersed-seed stage caused by temporal overlap in seed co-dispersal and co-dissemination could persist throughout the demographic cycle of the plant species (Schupp and Fuentes 1995, Ramachandran et al. 2023), whenever successive regeneration stages are effectively coupled (Jordano and Herrera 1995).

The majority of studies on plant interactions in a demographic context usually refers to temporal subsets of the life cycle, such as seed dispersal (Jara-Guerrero et al. 2020) and the transition from seed to seedling (García et al. 2005, Donoso et al. 2016). Similarly, other studies have focused on the transition from seedling to sapling, and from juvenile to adult (Zhu et al. 2015). The study of longer plant life cycles and demographic stages has been focused on single species (Godínez-Álvarez et al. 2002, Rey and Alcántara 2000, Horvitz et al. 2015, Rehling et al. 2023 Quintero et al. 2024). The approaches of temporal subsets create gaps between consecutive stages, and species-specific studies lack the full context to understand the demography of plant communities. Specifically, plant–plant interaction studies are usually focused on the establishment and recruitment processes, typically evaluating facilitation, habitat filtering or competition (Kraft et al. 2015, O'Brien et al. 2017, Alcántara et al. 2019a). In contrast, seed dispersal studies usually cover shorter periods; from the pre-dispersal stages to early seedling establishment (Schupp et al. 2010). For example, previous studies in Mediterranean forests have shown that the spatial co-occurrence of fleshy-fruited saplings persists across demographic stages (Perea et al. 2021). However, the role of seed co-dispersal and co-dissemination as early catalytic processes in plant–plant interactions and subsequent assembly of the community remains to be understood.

One reason for the aforementioned gaps between life stages is likely to be the commonly long lifespan of fleshy-fruited plants, combined with the difficulties in obtaining the necessary data to analyse demographic processes at the community level across extended timescales. Here, the cumulative spatial footprints of saplings and adults can provide important insights into the underlying processes and mechanisms that shaped spatial patterns during earlier life stages (Wiegand and Moloney 2014). For example, clumped seed dispersal underneath specific fleshy-fruited adults can result in the aggregation of seedlings from multiple species by nucleation (Verdú and García Fayos 1996, Clark et al. 2004, Lázaro et al. 2005). This high co-occurrence of seeds generated by frugivores may persist through later stages under weak mortality and competition, as expected close to heterospecific individuals (Janzen 1970, Connell 1971, Adler et al. 2018), leading to apparent facilitation (Levine 1999). The resulting pattern, described as 'taxonomic contagion' (Clark et al. 2004), has been evidenced by the presence of recurrent spatial clustering of specific groups of fleshy-fruited plant species (Tewksbury et al. 1999, Lázaro et al. 2005).

Here, we assess the effect of frugivore sharing on the co-occurrence of dispersed seeds, and whether this pattern persists into the sapling and adult stages (see Fig. 1 for a conceptual framework). To this end, we first assess the fine-scale composition of the seed rain resulting from seed co-dispersal and co-dissemination events mediated by avian frugivores in a Mediterranean shrubland community. Next, we describe

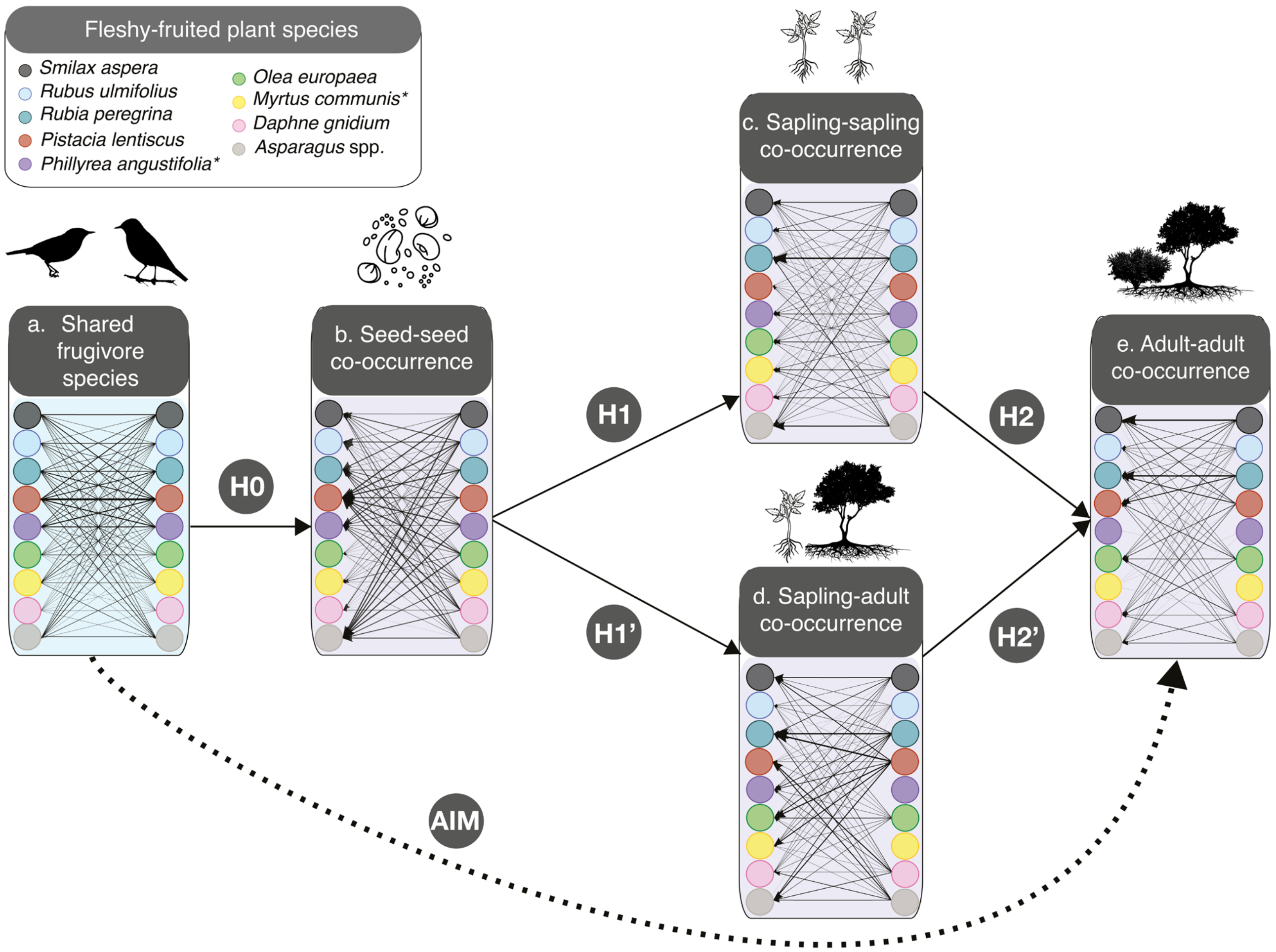

Figure 1. Conceptual diagram of this study. Co-occurrence patterns of fleshy-fruited plant species (coloured circles within boxes) at different demographic stages spanning the dispersal process, from early interactions with frugivorous birds at the fruit removal stage (a) to final recruitment of adult plants (e). Lines between circles represent the co-occurrence between plant species, with thickness proportional to the frequency of co-occurrence. In (a) the links represent the number of shared frugivores between the two plant species; in (b) the (asymmetric) co-occurrence of focal species *i* with an associated species *j* at the same target microsite in the seed rain; (c), (d) and (e) illustrate the (asymmetric) spatial co-occurrence of a focal species *i* with an associated species *j*, where the focal and associated species were plants at the sapling–sapling (c), sapling–adult (d) and adult–adult (e) life stages. Solid black arrows between boxes represent the tested direct effects between the co-occurrences at subsequent life stages (H0, H1, H1’, H2 and H2’). The dashed black arrow between (a) and (e) represents our primary hypothesis (Aim) of identifying a lasting signal of the early stage of fruit removal/frugivory on the final pattern of spatial co-occurrence between adults. *, not enough adults to include the species in the analyses.

the spatial co-occurrence patterns of plant species at the same spatial scales along different life stages of their demographic cycles (from seeds to adults). The aim of this work is to disentangle whether plant species sharing more frugivores also co-occur more often at adult stages. More specifically, we tested whether (Fig. 1): (H0) frugivore sharing by plant species determines their co-occurrence at the seed stage (seed–seed co-occurrence). Following this, we explored whether (H1) the co-occurrence at the seed stage persists into the sapling stage (sapling–sapling co-occurrence), and also whether (H1') the early co-occurrence of seeds is associated with the pattern of co-occurrence between saplings and adults (sapling–adult co-occurrence). Finally, we also tested if (H2) the observed spatial sapling-sapling co-occurrences persist into the adult stage (adult–adult co-occurrence), and whether (H2') the observed spatial sapling–adult co-occurrences persist into the adult stage (adult–adult co-occurrence).

We hypothesize that the co-occurrence of plant species at the early stage of active seed dispersal by frugivores (co-dispersal and co-dissemination) will be higher when the pair of plant species shares a higher proportion of frugivore-species. Similarly, we expect that the pairwise co-occurrences of species at the sapling–sapling, adult–sapling and adult–adult stages would be influenced by the co-occurrences at the seed stage. These seed co-occurrences include seed–seed presence either due to active dispersal (co-dispersal in the same dispersal event) or due to co-dissemination (seed–seed co-occurrence in a specific microsite resulting from cumulative dispersal events reaching that specific microsite). The outcome of these mechanisms would be a long-lasting spatial signature of the activity of frugivorous birds in the spatial structure of plant communities.

Material and methods

Study site

The study was conducted in a Mediterranean shrubland located in the El Puntal area in Doñana National Park (SW Spain) (36°57′54.381″N, 06°26′47.158″W). The area has a typical Mediterranean climate, with mild winters, warm summers, and soft spring and autumn. Rainfalls are scarce, and most of them concentrate during autumn and winter. The plant community in our study site is dominated by *Pistacia lentiscus*, co-occurring with other low-shrubland species such as *Erica arborea*, *Cistus salviifolius*, *Halimium halimifolium* and *Ulex parviflorus*, and some scattered *Pinus pinea* trees. The interest of this place resides in the large number of co-occurring fleshy-fruited species such as *Asparagus* spp., *Chamaerops humilis, Daphne gnidium, Myrtus communis, Olea europaea var. sylvestris, Phillyrea angustifolia, Rubia peregrina, Rubus ulmifolius, Smilax aspera, Osyris alba, Lonicera periclymenum* and *Solanum nigrum*. These fruit resources make the El Puntal area crucial for both local and migrant frugivorous bird species such as *Curruca melanocephala, Erithacus rubecula, Sylvia atricapilla* and *Turdus merula* (Quintero et al. 2023, 2024).

Frugivore assemblage and co-occurrences in the seed rain

We sampled the seed rain generated by frugivorous birds using seed traps and transects between September 2019 and February 2020 covering the main fruiting peak of the fleshy-fruited plant species in the area, which occurs during the winter season (Herrera 1984). We placed 85 seed traps (hereafter, traps) in a replicated, randomly-stratified design among five distinct microhabitat types that characterize the physiognomy of the site and are relevant to avian microsite preferences (Jordano and Schupp 2000). The five microhabitats were considered based on the influence of the adult plant canopy on seed dispersal (frugivores' habitat use and perching preferences) and on seedling recruitment: 1) under female *P. lentiscus*, 2) under other fleshy-fruited species, 3) under pine trees (*P. pinea*), 4) under non-fleshy-fruited species and 5) open areas (no canopy above) (Quintero et al. 2023). *Pistacia lentiscus* and *P. pinea* had their own microhabitat due to their dominance in the community, and their potential for bird perching, respectively. Open areas were sampled through 17 linear transects (1-m wide, mean transect length ± SD = 227 ± 97 m), which is an effective sampling method for microhabitats receiving very low seed density. Seed trap contents (bird droppings) were collected weekly during the full fruiting season. Plant species were identified based on seed morphology and the frugivore species that dispersed each seed was identified through DNA-barcoding (see Quintero et al. 2023 for laboratory procedures). Seed–seed co-occurrence was assessed at the seed trap level, representing co-dissemination events. These may result from actual co-dispersal events or from cumulative dissemination to the same seed trap by different individual frugivores. Previous work analysed in detail actual co-dispersal based on combinations of seed species found within individual scats (Jordano 1988, Schaefer et al. 2014).

Once all dispersed seeds and their corresponding frugivorous seed dispersers were identified, we constructed a matrix $SF_{i,j}$ in which the elements i–j represent the number of frugivore species shared between plant species *i* and *j* (Fig. 1a).

Next, we calculated the co-occurrence of seeds SC_{ij} of species *j* with seeds of species *i* (Fig. 1b). This metric represents the average number of times a seed of a focal species *i* co-occurred with seeds of species *j* in the same trap, reflecting co-dispersal and co-dissemination events. This method accounts for the asymmetry of interactions between species pairs, so the co-occurrence of species *i* with species *j* may differ from that of species *j* with species *i* (as illustrated by the directed arrows in Fig. 1b). The estimation of SC_{ij} requires scaling up from the seed trap level to the microhabitat level to the community level. Thus, we first estimated the pairwise seed co-occurrence ($SP_{i,j,t}$) between seeds of species *i* and *j* at the trap level by summing the number of times that the seeds of the species *i* co-occurred with seeds the species *j* in the tray *t*. Next, we estimated the pairwise seed-seed co-occurrence $SP_{i,j,m}$ between species *i* and *j* at the microhabitat level by summing up the pairwise co-occurrences $SP_{i,j,t}$ at all traps *t* in a given microhabitat *m*. Once a pairwise occurrence matrix was built, we estimated at the microhabitat level the overall frequency of seed co-occurrence by dividing $SP_{i,j,m}$ by the number of seeds of species *i* in the microhabitat *m* ($N_{i,m}$). Finally, to combine the co-occurrences from different microhabitats, we estimated the microhabitat relative cover in the study area by using ten 30 m long vegetation transects randomly distributed across the study site. This allowed us to include the natural heterogeneity in seed composition by using a weighted mean of the seed co-occurrence $SP_{i,j,m}$ over all microhabitats *m* to finally get the average spatial co-occurrence SC_{ij} of seeds of species *i* and *j* at the community level:

$$SC_{ij} = \sum^{m} c_m \frac{SP_{ij,m}}{N_{i,m}}, \tag{1}$$

where $SP_{i,j,m}$ is the number of times seeds of species *i* co-occurred with seeds of species *j* in microhabitat *m*, $N_{i,m}$ the total number of seeds of species *i* in microhabitat *m*, and c_m the relative cover of microhabitat *m*. Thus, the average co-occurrence SC_{ij} between species *i* and species *j* at the community level has the interpretation of the average number of times where a seed of species *i* co-occurs with a seed of species *j* (see the Supporting information for further details).

The information encapsulated in the microhabitat-level co-occurrence $SP_{i,j,m}$ between seeds of species *i* and *j* allows us to assess if the frugivorous bird species dispersed seeds at different microhabitats in a similar way. In this case the two matrices $SP_{i,j,m}$ and $SP_{i,j,l}$ of microhabitats *m* and *l* would be correlated (Supporting information). We assess this by using a Mantel test based on the method of Kendall-τ (Supporting information). Indeed, the seed co-occurrence was significantly correlated between all microhabitats around plants, but that of open area was slightly weaker compared to those around plants (Supporting information). The significant positive correlations support the pooling of seed co-occurrence data across microhabitat types for subsequent analyses.

Also, to assess the complementary effect of fruit size on frugivore sharing between plant species pairs, we used non-metric multi-dimensional scaling (NMDS) (Supporting information). Data on fruit size were obtained from Valido et al. (2011). Finally, we conducted a Spearman rank correlation to test whether fruit size similarities between plant species drives the frugivore sharing degree, and seed co-occurrence.

Spatial co-occurrence of saplings and adults

In the same study site where the seed rain was characterised, we conducted in 2023 a fully-mapped survey of saplings and adult individuals in a plot of 75 × 75 m (Fig. 2). For this survey, we recorded the x- and y-coordinates of all individuals of each fleshy-fruited plant species. We considered an individual as sapling if it was non-reproductive, showed less than 25% of the typical adult size for its species, and had survived from the previous year (i.e. seedlings were excluded) (Perea et al. 2021, Alcántara et al. 2025). We considered an individual as adult if it showed evidence of flowering or, and, fruiting that is a priori expected to contribute substantially to the species demography (i.e. juveniles were excluded).

Co-occurrence of saplings and adults

To quantify, similarly to the co-occurrence of seeds in traps, how individuals of species *j* are distributed within the neighbourhoods of individuals of a focal species *i*, we measured the spatial co-occurrence of individuals within a defined radius r. Studying the legacy of seed dispersal on later life stages requires choosing an optimal neighbourhood distance r. Thus, the most appropriate distance (r) was given by the average distance of the seed tray to the centre of the plant (main stem) where it was located. (i.e. r < 1 m).

To obtain a measure of spatial co-occurrence between pairs of plants, we used techniques of spatial point pattern analysis (Wiegand and Moloney 2014, Getzin et al. 2014, see also interaction strength index in Perea et al. 2021). We conducted this analysis for the co-occurrence patterns between saplings (sapling–sapling), saplings and adults (sapling–adult), and between adults (adult–adult). We used the bivariate version $K_{ij}(r)$ of Ripley's K and the bivariate distribution function $D_{ij}(r)$ of nearest neighbour distances, which capture different aspects of the spatial co-occurrence (Wiegand et al. 2007, 2012, Wiegand and Moloney 2014, Getzin et al. 2014). $K_{ij}(r)$ is the expected number of individuals of species *j* within distance *r* of the individuals of the focal pattern *i*, divided by the mean density λ_j of individuals of species *j* in the study plot. The bivariate $D_{ij}(r)$ is the proportion of individuals of the focal species *i* that have their nearest species *j* neighbour within distance r.

To determine the degree of co-occurrences between species *j* and *i* we compared the observed summary functions $K^0_{ij}(r)$ and $D^0_{ij}(r)$ (superscript '0' for observed) with that of the realizations $K^k_{ij}(r)$ and $D^k_{ij}(r)$ of a suitable null model (below). The superscript '*k*' indicates the *k*th realization of the null model. We then estimated standardized effect sizes as:

$$Pij(r) = \Big[D0ij(r) - \mathrm{E}\big[Dkij(r)\big]\Big) / \mathrm{SD}\big[Dkij(r)\big] \tag{2a}$$

$$Mij(r) = \Big[K0ij(r) - \mathrm{E}\big[Kkij(r)\big]\Big) / \mathrm{SD}\big[Kkij(r)\big] \tag{2b}$$

where E[.] and SD[.] are the expectation and standard deviation of the 999 null model summary functions, respectively. The standardized effect size indicates a significant departure from the null model with an error rate of 5% at a single distance r if its value is smaller than −1.96 (less co-occurrence than expected by the null model) and if its value is greater than 1.96 (more co-occurrence than expected by the null model) (Martínez et al. 2010). To obtain a measure of the overall degree of spatial co-occurrence $IS_{ij}(r)$ (interaction strength, Perea et al. 2021), we rescaled the values of $P_{ij}(r)$ and $M_{ij}(r)$ in a way that they show their minimal values at $P_{ij}(r) = 0$ and $M_{ij}(r) = 0$ (i.e. by adding appropriate constants) and used the length of the vector ($P_{ij}(r)$, $M_{ij}(r)$) in the two-dimensional P–M space (P is the x-axis and M the y-axis), that is,

$$IS_{ij}(r) = \sqrt{P_{ij}^2(r) + M_{ij}^2(r)}. \tag{3}$$

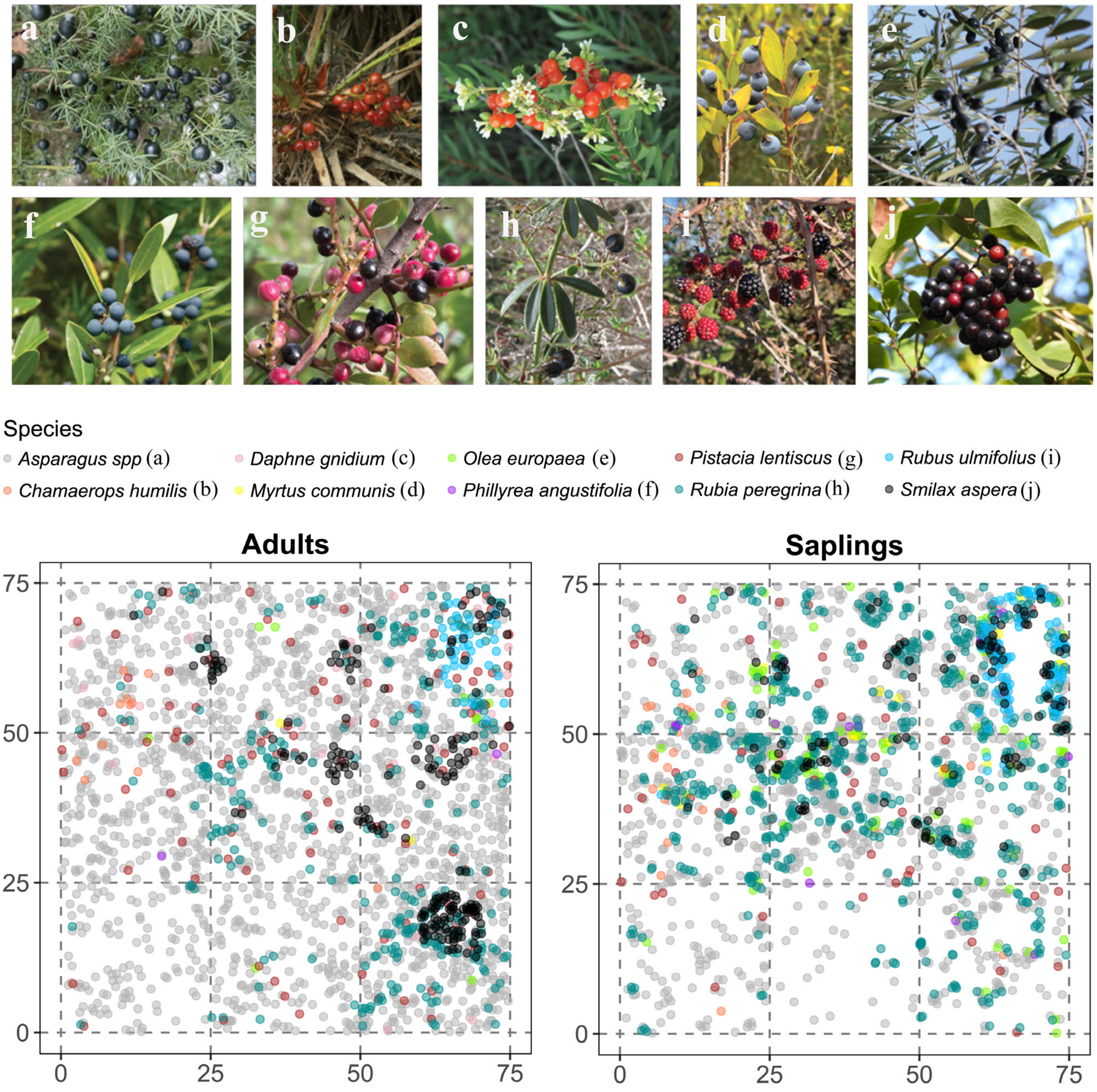

Figure 2. Spatial locations of adults and saplings of the studied fleshy fruited species in the 75 × 75 m plot. Each colour represents a different plant species. Note that although *Chamaerops humilis* was present in the plot, no dispersed seeds were found in the traps (this species is mostly dependent on mammals for dispersal).

Thus, a value of $IS_{ij}(r) = 0$ indicates the lowest co-occurrence and the larger $IS_{ij}(r)$, the larger the co-occurrence of species *j* within the neighbourhoods of species *i*. Note that this approach also considers asymmetry between species, co-occurrence of species *i* with species *j* does not need to be the same as co-occurrence of species *j* with species *i*.

Null model for saplings and adults co-occurrence

To assess the degree of spatial co-occurrence between the individuals of two species *i* and *j* we contrasted the observed values of $P_{ij}(r)$ and $M_{ij}(r)$ with that arising from the null model of spatial independence between the patterns of species *i* and *j* (Getzin et al. 2014, Wiegand and Moloney 2014). To this end, we randomized the locations of species *j*, while keeping the locations of the focal species *i* unchanged. Realisations of spatial independence need to conserve the observed spatial aggregation of species *j* and account for possible effects of the environment on the placement of species *j*. Null model realisations meeting these conditions can be generated using nonparametric techniques of heterogeneous pattern reconstruction (Wiegand and Moloney 2014). For each life stage (i.e. sapling and adult) we conducted 999 null model reconstructions of the pattern of each species, conditioned by a non-parametric intensity function that accounts for the larger scale pattern of adults (Supporting information). Null model pattern reconstructions were made by means of the software 'Pattern reconstruction' (Wiegand et al. 2013, Wiegand and Moloney 2014) and the standardized effect sizes were obtained by means of software 'Programita' (Wiegand and Moloney 2014).

Integrating pairwise co-occurrence along plant species demography.

Once we obtained the asymmetric co-occurrences between species pairs at the seed, sapling and adult stages, we studied the persistence and the pathway of the co-occurrences from the initial level of frugivore species sharing until the adult stage. To do that, we divided our analyses into three steps (Fig. 1). First, we tested whether the number of shared frugivorous bird species between plant species determined the seed co-occurrence of these plant species by co-dispersal and co-dissemination (H0). Second, we investigated if the seed–seed co-occurrence determined the spatial co-occurrence between saplings (i.e. sapling–sapling; H1) or the co-occurrence among saplings and adults (H1'). Third, we determined whether the spatial co-occurrence observed at the saplings stage (H2), and between saplings and adults (H2´), were maintained into the adult stage.

To assess the cascades and correlations of the co-occurrences at a given life stage on the subsequent life stages, we used structural equations models (hereafter SEM) (see Jordano and Herrera 1995 for a similar approach). Response variables were seed–seed co-occurrence (H0), sapling–sapling co-occurrence (H1), sapling–adult co-occurrence (H1') and adult–adult co-occurrence (H2 and H2'). Predictor variables were the number of shared species of frugivorous birds (H0), seed–seed co-occurrence (H1 and H1'), and sapling–sapling and adult–sapling co-occurrence (H2 and H2', respectively) (Fig. 1). Due to the asymmetric co-occurrence among species (Supporting information), the focal plant species was included as a random covariate in the SEM. Finally, to test the main hypothesis of our study, we analysed the association between the first (observed level of frugivore sharing) and the last step of the plant demographic cycle (adult–adult co-occurrence). This was modelled as a correlation between the two variables in the SEM, rather than as a direct causal path, allowing us to capture their relationship without assuming one causes the other (Fig. 1). The structure of the causal models allows us to account for asymmetric co-occurrence along all the stages of the demographic cycle of the plant species.

Finally, some species were not considered in the analysis due to missing information in the seed co-occurrence (*C. humilis* and *S. nigrum*), or because they show too few individuals to reliably estimate their spatial pattern (i.e. n < 20, adults of *M. communis* and *P. angustifolia,* Supporting information). Note that, although three plant species had few individuals (n ~ 20, i.e. *D. gnidium*, *O. europaea* or *R. ulmifolius*), their consistent spatial patterns allowed for pattern reconstruction and its incorporation to the subsequent analyses (Supporting information).

Statistical settings

To assess the goodness of fit of the SEM model we used Fisher's C statistics as:

$$C = -2\sum_{i=1}^{k} lnln\ (p_i) \tag{4}$$

where k indicates the number of all the independent claims (variables with no causal arrows pointing to them from within the model) in the basis set, i the number of a particular claim, and p_i the p-value from the corresponding test. Basically, this statistic is similar to the χ^2 statistic but incorporates all the p-values of the different tests, meaning a global estimation. Fisher's C with p-value > 0.05 indicates that the structure of the SEM is supported by the data, without missing key paths (see Shipley and Douma 2020 for further details).

To allow meaningful comparisons, all variables included in the SEM were scaled (mean = 0, SD = 1). We tested for normality and homogeneity of variance of all co-occurrences by means of ANOVA and Levene tests (bootstrap method with 999 simulations), using the 'stat' and 'lawstat' R packages, respectively (www.r-project.org, Hui et al. 2008). ANOVA and Levene tests revealed homoscedasticity and normality among all scaled variables. Structural equation coefficients, path coefficients and effects were obtained by using the 'piecewiseSEM' R package (Lefcheck 2016) in R ver. 4.3.1 (www.r-project.org) by using 'R-markdown' (Xie et al. 2018). The equations within the SEM were estimated with linear mixed-effect models using the 'nlme' R package (Pinheiro and Bates 2006), previously checking the adjustment of each model by using 'DHARMA' R package (Hartig and Hartig 2017).

Results

Frugivore assemblage and co-occurrences in the seed rain

We detected 21 different frugivore bird species, generating the seed rain composed of 3240 seeds of 12 fleshy-fruited plant species. The assemblage of frugivorous birds consisted of species from seven different families and was mainly dominated by small and medium-sized birds. The two dominant frugivore species were *Sylvia melanocephala* (926 dispersed seeds from eight plant species) and *Erithacus rubecula* (593 dispersed seeds from seven plant species), two subdominant frugivore species were *Turdus merula* and *Sylvia atricapilla* (630 dispersed seeds in total), while other 17 avian seed dispersers accounted for the dispersal of the rest of seeds. In terms of frugivore sharing, we found a large variability among pairs of plant species, which ranged between 0 to 10 shared frugivore species (mean = 3.7 shared birds).

The species composition in the seed rain was strongly dominated by two species, *P. lentiscus* (1888 seeds, 58%) and *Asparagus* spp. (629 seeds, 20%) (Supporting information). In this regard, both were the most abundant plant species (in terms of cover), showing also the highest rate of co-occurrence in seed rain with other species (0.92 ± 0.07, and 0.77 ± 0.08, mean ± SD, respectively). Overall, seed co-occurrence among species showed mean values of 0.44 ± 0.29. Results also revealed that fruit size similarity among plant species correlates positively with frugivore sharing (Spearman-rho = 0.27, p = 0.02), but not with the seed co-occurrence (Spearman-rho = 0.23, p > 0.05).

Plant species co-occurrence at sapling and adult stage

We found a total of 4671 individual plants of 13 species in our 75 × 75 m plot, with 51.5% being adults and 48.5% saplings (Fig. 2). The most abundant species were *Asparagus* spp. with 2771 individuals (~ 50%), whereas the least abundant species was *Phillyrea angustifolia* with 23 individuals. At considering the conspecific cases, our spatial analyses revealed that the interaction strength (proxy of co-occurrence) was generally stronger among saplings than among sapling and adults and among adults (respectively 13.5 ± 6.71, 6.07 ± 3.89, 10.13 ± 7.03, mean and SD, see the Supporting information for each pairwise species values), whereas at heterospecific co-occurrence among adults was the strongest (respectively, 3.90 ± 2.72, 3.88 ± 2.78, 5.89 ± 2.50 mean and SD). For heterospecific cases, the maximum interaction strength among saplings, saplings and adults, and among adults was respectively 12.35, 13.76 and 12.24 (representing the maximum values of co-occurrence at each life stage = 1). Remember that analyses are focused on disentangling differences of co-occurrences among life stages, but not among conspecific and heterospecific cases, since the method to obtain the interaction strength slightly varies among them (not comparable), and also that co-dissemination of species requires heterospecificity.

Combining seed dispersal with plant community assembly

The model structure to conduct the path analyses was fitted to data (Fisher C = 3.976, p = 0.859, df = 8. Partial χ^2 = 8.992, p = 0.109, df = 5), without any significant missing path (independent claims: p > 0.05).

We found significant correlation between the level of frugivore sharing and the co-occurrence of plant species at the adult stage, both directly and indirectly (Table 1). First, the direct effect followed the pathway from frugivore sharing to the seed–seed co-occurrence to adult–sapling co-occurrences to co-occurrence at the adult stage (see Table 1 for all the results, and Fig. 3 for diagram results). Specifically, the level of frugivore sharing had a large and positive effect on the co-occurrence of plant species at seed stage (H0, R^2conditional = 0.58, Est. = 0.78). Second, our results showed that the observed species co-occurrence at the seed stage was not maintained for sapling-sapling co-occurrence (H1, R^2 conditional = 0.02, Est.= 0.13), but interestingly, the observed species co-occurrence at the seed stage propagated into the co-occurrence of saplings around adults (H1', R^2 conditional = 0.27, Est.= 0.47) (Fig. 3). Third, the observed adult–sapling co-occurrence (H1') significantly influenced the spatial co-occurrence at the adult stage (H2', R^2 conditional = 0.16, Est.= 0.30) (Fig. 3). Since the last path (H2') showed to be determinant in the demographic cycle, we additionally evaluated whether co-occurrence values in apparent facilitation (sapling–adult co-occurrence) strengthen or weaken the co-occurrence at adult stages for each (asymmetric) specific pairwise. The two-sided paired t-test revealed a strengthening of the co-occurrences, manifesting now the success of facilitation (t = 3.75, Mean difference = 1.93, p-value < 0.005). Finally, we observed that all indirect paths were not significant, apart from that going from the level of frugivore sharing to the co-occurrence at the adult stage (Est. = 0.39, p-value < 0.01), our primary aim or hypothesis of interest (Table 1, Fig. 3).

Discussion

In this study, we investigated whether pairs of plant species that share seed dispersers co-occurred spatially in the seed rain and

Table 1. Results of the path diagram testing all indirect effects (from H0 to H2'), and whether the level of frugivore sharing between plant species determines the adult–adult co-occurrence of these plant species directly ('Aim'). The independent claims show that no missing path was present in the analysis. Significant paths are in bolds, and p-values are indicated with *, ** and ***, corresponding to p-values lower than 0.05, 0.01 and 0.005, respectively.

Hypothesis path	Response	Predictor	Est.	SE	df	Crit. value	p-value	
H0	**seed–seed co-occurrence**	**shared frugivores**	**0.78**	**0.15**	**34**	**5.11**	**< 0.005**	***
H1	sapling–sapling co-occurrence	seed co-occurrence	0.13	0.15	34	0.85	0.403	ns
H1'	**sapling–adult co-occurrence**	**seed co-occurrence**	**0.47**	**0.14**	**34**	**3.51**	**0.013**	**
H2	adult–adult co-occurrence	sapling–sapling co-occurrence	−0.23	0.14	33	−1.63	0.112	ns
H2'	**adult–adult co-occurrence**	**sapling–adult co-occurrence**	**0.30**	**0.14**	**33**	**2.18**	**0.036**	*
Aim	**adult–adult co-occurrence**	**shared frugivores**	**0.39**	**-**	**42**	**2.61**	**0.006**	**
Independent claims								
Sapling–sapling co-occurrence		shared frugivores	-	-	33	−0.044	0.970	ns
Sapling–adult co-occurrence		shared frugivores	-	-	33	0.943	0.350	ns
Adult–adult co-occurrence		seed–seed co-occurrence	-	-	31	−0.723	0.475	ns
Sapling–adult co-occurrence		sapling–sapling co-occurrence	-	-	33	−0.1941	0.847	ns

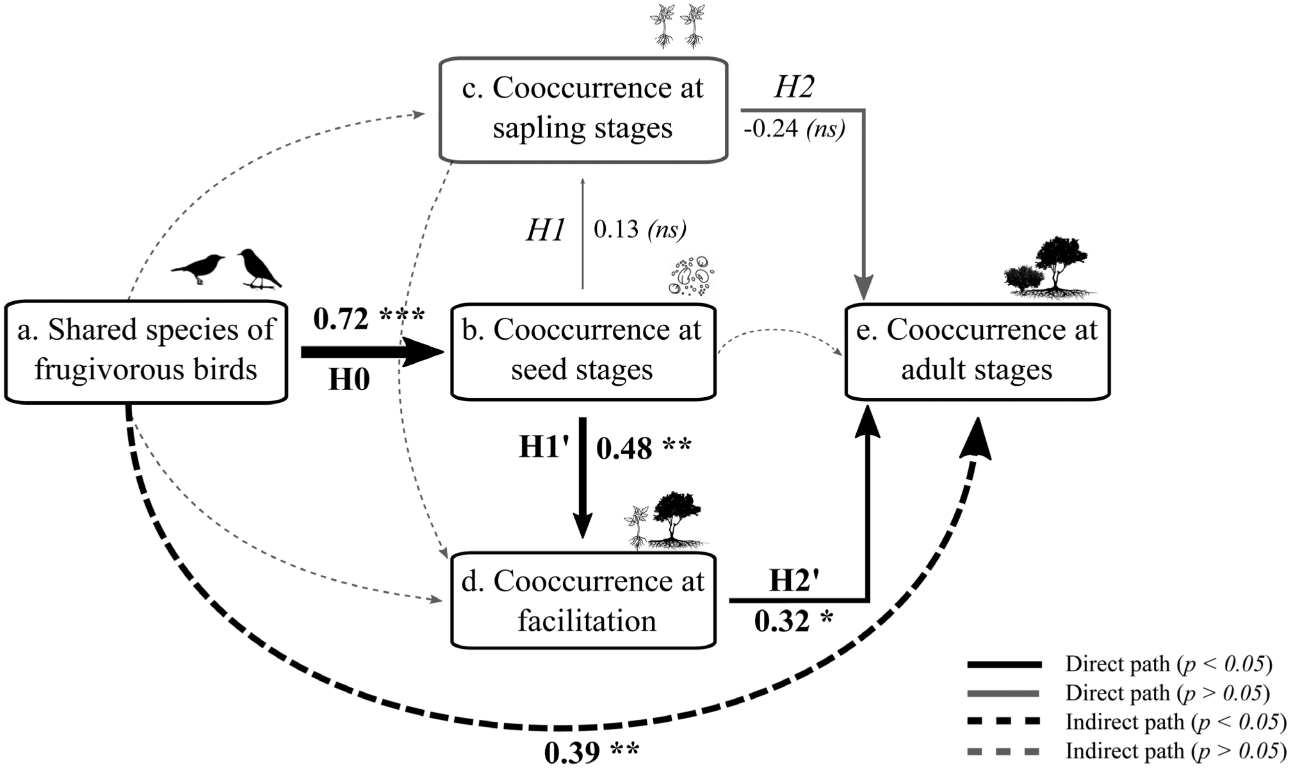

Figure 3. Path diagram and results of the structural equation model (SEM) that shows the sequential effects of shared frugivorous seed dispersers on spatial community assembly of fleshy-fruited plant species (see also Table 1). Directed and solid arrows for each step of the path show direct effects (from H0 to H2/H2'), while dashed lines show the correlated error among non-consecutive (indirect) steps of the path. All paths considered in the model (both direct and indirect) are labelled with the standardized path coefficient (standardised estimates), which indicates the magnitude of change in the predictor variable with one std. deviation unit change in the response variable (in std. deviation units). Significant paths are represented by black lines, together with their significance level, with *, **, and *** indicating p-values < 0.05, 0.01 and 0.005, respectively. The tested non-significant (*ns*) paths are showed in grey colour. Models were fitted using the maximum likelihood.

in subsequent life stages. Frugivore sharing left a long-lasting signature on the spatial structure of the plant community, which lasted up to the adult stage. This influence propagated across demographic stages, from the co-occurrence of seeds, to the aggregation of saplings around adults, and ultimately to the spatial association among adult individuals. Thus, the greater the number of shared frugivore species, the higher the likelihood of seed co-occurrence between plant species, as well as adult–sapling and adult–adult co-occurrence (Fig. 3). These findings indicate that shared dispersal agents, which co-disperse seeds and influence spatial patterns across successive stages of plant life cycle, have a lasting signal as early drivers of the co-occurrence among fleshy-fruited plants.

Note that the results presented assume that seed rain is relatively consistent across years, as our seed co-occurrence data represent a snapshot from a single fruiting season. Further sampling across years and ideally, monitoring individual woody plants throughout their full demographic cycle, from seed to adult, would help overcome this limitation. While interannual variation in seed rain may occur and could influence the patterns observed, we expect it will not be strong enough to substantially alter the overall trends detected in our results. This study offers a first approximation to understand the causes and consequences of plant–frugivore mutualistic interactions, fulfilling the gap among pre- and post-dispersal stages of seeds at the community level.

Determinants of seed co-occurrence; the first legacy (H0)

Through the identification of the dispersal agents using molecular techniques, we show that the co-occurrence of seeds of pairs of plant species is higher when both plant species share more frugivore species (Fig. 3). This result highlights a strong effect of the foraging pattern of frugivores and of their microhabitat preferences on the spatial structure of the seed rain of fleshy-fruited species (Lázaro et al. 2005, García et al. 2005, Isla et al. 2024). Previous studies (Jordano 1988, Schaefer et al. 2014) have documented, for example, that some *Sylvia* warblers may mix up to seven different fruit species in a meal, with frequent use of 2–3 fruit species during short feeding bouts. In addition, microhabitat preference patterns by avian frugivores tend to be species-specific (Jordano and Schupp 2000) meaning recurrent use of certain microhabitat types and high concentration of seed deposition. Thus, we revealed a strong deterministic role of frugivorous birds as drivers of plant community assembly in the Mediterranean region.

The species *P. lentiscus*, *Asparagus* spp., *R. peregrina, D. gnidium* and *P. angustifolia* produce smaller fruits, which makes them more prone to co-occur with other species in the community (Supporting information). It is likely that the high co-occurrence between these species stems from their high overlap in frugivorous bird assemblage composition, since their fruits can be consumed by birds with small and large beaks. It is noteworthy the case of *R. ulmifolius*, with poly-drupes that can be fully or partially consumed, respectively, by birds with large and small beaks, increasing the co-occurrence chances with heterospecifics (Supporting information). In contrast, plant species with larger fruits, such as *M. communis, O. europaea* or *S. aspera*, have only a reduced frugivore assemblage because only a subset of the bird species present at the study area can consume their fruits, which may reduce their co-occurrence with other plant species at the seed stage.

Indeed, co-occurrence at seed stages is driven mainly by frugivore sharing among the co-occurred plant species (Fig. 3), adding values to previous studies (Albrecht et al. 2015). Similarly, trait-matching between the gape width of birds and the fruit size of plants has been noted by González-Varo et al. (2022), which shows that these mutualistic and specific plant–animal interactions are strongly influenced by fruit sizes. Our results also support that fact, showing that similarity in fruit size among species drives frugivore sharing. Nevertheless, this similarity did not determine the seed co-occurrence given that seed stage collapses multiple plants and frugivores phenological processes Thus, other mechanisms may still have a weight in the seed co-occurrence, like plant abundance and avian diet-preference (Albrecht et al. 2015). In fact, the small-fruited species, *P. lentiscus* and *Asparagus* spp., are the most abundant (in terms of cover) and productive in terms of fruiting in the study site (Quintero et al. 2024), suggesting that the species cover may play a significant role in shaping the co-occurrence patterns of plants during the seed stage. This complements previous findings that emphasize its role in processes relative to later life stages, such as plant facilitation (Alcántara et al. 2019a).

Seed co-occurrence and plant recruitment; the second legacy (H1 and H1′)

The SEM analysis revealed that the observed co-occurrence pattern of plant species at the seed stage can persist during the recruitment of plants, but depending on the life stages of the plant species). Interestingly, and somewhat unexpectedly, the co-occurrence at the seed stage did not translate into the co-occurrence at the sapling stage, but into the co-occurrence of saplings around adults. It is likely that several ecological processes counteract a direct transfer of the spatial co-occurrence from the seed to the sapling stage (Donoso et al. 2016). For example, abiotic factors like climatic conditions, which can be quite severe in the Mediterranean region, may affect the early life stages of plant species differently (Acevedo-Limón et al. 2024), causing a lack of correlation in the co-occurrence pattern found between seed and sapling stages (Rey and Alcántara 2000, Sánchez-Gómez et al. 2006). Additionally, conspecific density-dependence mortality and competition (Johnson et al. 2014, Adler et al. 2018) or microsite suitability (Sánchez-Gómez et al. 2006, Mendoza et al. 2009) may remove the co-occurrence signal in the seeds at the transition to saplings. These are the type of effects driving the decoupling between successive recruitment stages, as documented in previous research (Schupp 1995, Jordano and Herrera 1995).

Our study shows that apparent facilitative adult-sapling interactions are a key process in this shrubland community, as has been repeatedly reported from other Mediterranean study sites (Arroyo et al. 2015, Alcántara et al. 2019b, Andivia et al. 2017). Furthermore, our results suggest that these 'facilitative' interactions may be promoted by animal-mediated seed co-dissemination of fleshy-fruited plant species early in the dispersal process, supporting the results of Albrecht et al. (2015). Frugivorous birds consume fruits, and defecate or regurgitate the seeds mostly underneath adult plants (i.e. foraging activity and perching). Consequently, the diet of birds and the co-dissemination of seeds may enhance reciprocal facilitation and nucleation processes among the species pairs from which they consume the fruits (Loiselle 1990, Verdú and García-Fayos 1996, Albrecht et al. 2015). Interestingly, this opens two possible scenarios where the growth rate and plant size of the interacting individual plants become key.

First, dispersal events may occur underneath some adult plants which are already established, receiving seeds from other species that will reach the sapling stage, a direct effect of structural physiognomic diversity and complexity of plant cover (McDonnell and Stiles 1983). In our study, we cannot assume that all the facilitative pairwise interactions come straightaway from the co-occurrence in the seed rain of both interacting plant species. To fully determine whether seed co-occurrence determines apparent facilitation, we need to attend complementarily to the second scenario. Here, a positive adult–sapling co-occurrence can also be generated by different growth rates of the plant species. Even when two seeds are co-disseminated and established during the same fruiting period, they may grow at different rates or follow divergent developmental paths. For example, a fast-growing species (e.g. *Asparagus* spp.) may facilitate a slow-growing species (e.g. *P. lentiscus*) and/or a species with strong seed dormancy (e.g. *Olea europaea*) in just a few years, but not the other way around. This mechanism will promote a strong asymmetry in the adult–sapling co-occurrence.

Which of the two mechanisms creates the apparent facilitation will be context-dependent, but since it occurred in both directions (e.g. from *P. lentiscus* to *Asparagus* spp., and the other way around) (Fig. 1, Supporting information), both scenarios seem complementary. However, the footprint of the foraging activity of shared dispersers that shapes the seed co-occurrence among plant species (H0) persists during the plant recruitment stages when at least an adult is involved (H1'). Yet, the strength of the co-occurrence fades away regarding the lasting effects of the early seed-seed co-occurrence (i.e. the first legacy, Fig. 3), so other ecological processes (and stochasticity) likely influenced this weakening such as abiotic factors, other non-avian dispersers, pathogens or herbivores (Beckman and Sullivan 2023).

Apparent facilitation and community assembly; the third legacy (H2′)

The spatial co-occurrence among adult plant species is influenced by combined effects of their shared avian frugivores, their seed co-occurrence and their mutual pairwise apparent facilitation. Note that we cannot fully prove a direct facilitation, since we are analysing the spatial outcome of all the mechanisms that shape spatially the early life stages, so maybe the co-occurrence among species is the results of an over-abundant seed dispersal (bird-perching preferences), density dependent mortality, or a species-specific boosting of saplings. Thus, apparent facilitation becomes more suitable in our context than facilitation per se (Levine 1999). The outcome of the apparent facilitation leads to two possible scenarios; not co-occurrence, when adults inhibit or depress the sapling growth, or co-occurrence, if adult allows or boosted it (Yu et al. 2024). Thus, based on our results ($t = 3.75$, mean difference $= 1.93$, $p < 0.005$) we evidenced that apparent facilitation of fleshy-fruited species enhances the co-occurrence at adult stages, likely by boosting the sapling growth (Yu et al. 2024). This has been also documented in previous studies in forest communities which showed that interactions among fleshy-fruited plant species are maintained along the plant demographic stages (García et al. 2005, Perea et al. 2021). However, our study spans a larger range of life stages, and additionally provides the number of shared frugivores among plant species and the co-occurrence of these species at the seed stage, thus filling important gaps along the plant demographic cycle (by spanning from ripe fruit throughout the adult plant).

We provide evidence for a cascading effect that builds up early from the fruit removal/seed dispersal stage up to mature plants. More specifically, we show that the effects of early co-occurrence at the seed dispersal stages among plant species is maintained along the species demographic stages, and that the spatial assembly of fleshy-fruited plant communities is achieved through apparent facilitation that is enhanced by the early effects of foraging patterns of frugivorous birds. Although several processes operating across sequential life stages could reduce species co-occurrence, the initially high spatial co-occurrence observed at the seed stage persists – albeit diminished – throughout the plant life cycle, remaining significant even in the assembled adult community. The legacy observed here highlights the importance of conserving these frugivores, as they play a key role in the assembly and maintenance of plant communities (Morán-López et al. 2018, Mendes et al. 2024). Also, these results underscore the need to consider these animals when modelling plant community regeneration dynamics.

Concluding remarks

Previous studies outlined the key role of bird dispersal on recruitment of fleshy-fruited species (Jordano and Herrera 1995), as well as the importance of plant recruitment and plant–plant facilitation in plant community assembly (Alcántara et al. 2018). Furthermore, others documented the legacy effects of species co-occurrence from recruitment to adult stages (Perea et al. 2021). By taking an ecological step backwards, our study links the process of animal-mediated seed dispersal almost from the early fruit removal, where mutualistic interactions with frugivores take place, to the spatial assembly of plant communities, thus spanning the whole sequence of plant demographic stages. These lasting effects of frugivores can be probably generalized to other systems where frugivorous animals constitute a key element for the forest regeneration: their use of food resources (fruits) and foraging patterns pervade the spatial co-occurrence of plant species from the early disseminated seed to the adult stage through plant–plant apparent facilitation. Our findings shed light on the mechanisms determining the spatial structure and assembly of natural plant communities where animal mutualists mediate in seed dispersal.

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Author contributions

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Data availability statement

Data are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.15873224 (Perea et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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Supporting information

Seed co-occurrence caused by shared frugivores leaves a long-lasting signal in the spatial co-occurrence among plants.

Authors

Affiliations

Supporting information 1

Calculations and correlations of seed dispersal among Microhabitat.

1. *Estimations of pairwise seed co-occurrence* $Sp_{i\text{-}j\text{-}t}$ *(at tray scale)*

   a) First: we calculated at tray levels the seed co-occurrence between species *i* and species *j* (or *i*) by applying the next formula:

<u>Conspecific cases:</u>

$$\boldsymbol{SP_{i\text{-}i\text{-}n} = SP_{i\text{-}i}\ \text{€}\ Tray_t} = ((N_i\ \text{€}\ Tray_t) - 1)\ x\ (N_i\ \text{€}\ Tray_t)$$

where N_i is the number of seeds of species *i* in (**€**) *Tray t*. Note that we subtract one (-1) seed from the focal species, since the focal seed cannot co-occur with itself. This, allows to account for lack of conspecific co-occurrence (despite conspecific cases were not included in this study). Examples:

if species *i* owns 1 seed, *then co-occurrence times i-i is 0:*
if species *i* owns 2 seeds, *then co-occurrence times i-i is 1.*
if species *i* owns 10 seeds, *then co-occurrence times i-i is 90*

<u>Heterospecific cases</u>

$$\boldsymbol{SP_{i\text{-}j\text{-}t} = SP_{i\text{-}j}\ \text{€}\ Tray_t} = (N_i\ \text{€}\ Tray_t)\ x\ (N_j\ \text{€}\ Tray_t)$$

For example, if species *i* has 5 seeds and species *j* has 3 seeds, species *i* co-occur 15 times with species *j*. $SPi\text{-}j\text{-}t = 15$ in (**€**) the *Tray t*.

2. *Estimations of pairwise seed co-occurrence SP_{i-j-m} (at the microhabitat scale)*

Once we obtained all the SP_{i-j-t} values, we grouped them at Microhabitat levels (MH, hereafter) by summing all the co-occurrence in their corresponding trays (i.e. MH_{PL}, MH_{FR}, MH_{NF}, MH_{PP}, MH_{OA}, see methods in Main text).

$$SP_{i-j-m} = \sum SP_{i-j-t} \text{ € } MH_{xx}$$

(Once obtained SP_{i-j-m} we proceed to equation 1 in the main text)

Microhabitat encompasses PL, FF, NF, PP and OA, corresponding to *Pistacia lentiscus*, Fleshy-fruited, Non-Fleshy-fruited, *Pinus pinea* and Open Areas, respectively.

Table S1

Table S1. Results of the estimations of the asymmetric seed co-occurrence frequency (seed_) among species 2 and species 1 in the five studied microhabitat (MH): under adults of *Pistacia lentiscus*, fleshy-fruited, non-fleshy-fruited, *Pinus pinea*, and open area, namely respectively as PL, FR, NF, PP and OA. Seed_overall (SC_{ij}) represents the average across MH of the asymmetric seed co-occurrence of each species i with species j pair (SP_{i-j-m} / N_{im}), weighted by the relative cover (c_m) of each MH. Species (ASPSPP, DAPGNI, MYRCOM, OLEEUR, PHIANG, PISLEN, RUBPER, RUBULM and SMIASP, correspond to *Asparagus* spp*., Daphne gnidium, Myrtus communis, Olea europaea, Phillyrea angustifolia, Pistacia lentiscus, Rubia peregrina, Rubus ulmifolius* and *Smilax aspera*).

sp1	**sp2**	**seed_PL**	**seed_FR**	**seed_NF**	**seed_PP**	**seed_OA**	**seed_overall**
ASPSPP	ASPSPP	0.883	0.865	0.859	0.871	0.000	0.722
ASPSPP	DAPGNI	0.000	1.000	1.000	1.000	0.000	0.618
ASPSPP	MYRCOM	1.000	0.909	0.500	1.000	0.000	0.592
ASPSPP	OLEEUR	1.000	1.000	1.000	1.000	0.000	0.834
ASPSPP	PHIANG	0.968	1.000	1.000	1.000	0.000	0.827
ASPSPP	PISLEN	0.969	0.943	0.963	1.000	0.000	0.802
ASPSPP	RUBPER	0.957	1.000	1.000	1.000	0.000	0.825
ASPSPP	RUBULM	1.000	1.000	1.000	1.000	0.000	0.834
ASPSPP	SMIASP	1.000	1.000	1.000	1.000	0.000	0.834
DAPGNI	ASPSPP	0.000	0.048	0.065	0.017	0.000	0.037
DAPGNI	DAPGNI	0.000	0.500	0.500	0.000	0.000	0.303
DAPGNI	MYRCOM	0.000	0.000	0.000	0.000	0.000	0.000
DAPGNI	OLEEUR	0.000	0.000	0.000	0.000	0.000	0.000
DAPGNI	PHIANG	0.000	0.000	0.111	0.275	0.000	0.054
DAPGNI	PISLEN	0.006	0.013	0.147	0.133	0.000	0.071
DAPGNI	RUBPER	0.021	0.000	0.000	0.042	0.000	0.005
DAPGNI	RUBULM	0.000	0.091	1.000	0.286	0.000	0.472
DAPGNI	SMIASP	0.000	0.000	0.200	0.158	0.000	0.093
MYRCOM	ASPSPP	0.249	0.317	0.217	0.345	0.000	0.205
MYRCOM	DAPGNI	0.000	0.000	0.000	0.000	0.000	0.000
MYRCOM	MYRCOM	0.647	0.545	0.000	0.200	0.875	0.370
MYRCOM	OLEEUR	0.500	0.200	0.500	0.000	0.000	0.366

MYRCOM	PHIANG	0.419	0.091	0.111	0.400	0.000	0.159
MYRCOM	PISLEN	0.323	0.338	0.052	0.292	0.401	0.215
MYRCOM	RUBPER	0.277	0.538	0.143	0.208	0.000	0.209
MYRCOM	RUBULM	0.611	0.485	0.000	0.262	0.000	0.208
MYRCOM	SMIASP	0.591	0.357	0.000	0.316	0.464	0.262
OLEEUR	ASPSPP	0.145	0.183	0.261	0.103	0.000	0.179
OLEEUR	DAPGNI	0.000	0.000	0.000	0.000	0.000	0.000
OLEEUR	MYRCOM	0.059	0.091	0.500	0.000	0.000	0.254
OLEEUR	OLEEUR	0.000	0.600	0.000	0.000	0.000	0.091
OLEEUR	PHIANG	0.097	0.000	0.111	0.025	1.000	0.238
OLEEUR	PISLEN	0.136	0.140	0.115	0.088	0.030	0.109
OLEEUR	RUBPER	0.000	0.231	0.214	0.042	0.500	0.216
OLEEUR	RUBULM	0.611	0.333	0.000	0.190	0.421	0.255
OLEEUR	SMIASP	0.000	0.214	0.000	0.105	0.071	0.045
PHIANG	ASPSPP	0.435	0.587	0.609	0.552	0.000	0.466
PHIANG	DAPGNI	0.000	0.000	1.000	1.000	0.000	0.466
PHIANG	MYRCOM	0.353	0.455	0.500	0.800	0.000	0.382
PHIANG	OLEEUR	0.500	0.000	0.500	1.000	1.000	0.513
PHIANG	PHIANG	0.516	0.364	0.222	0.750	0.000	0.276
PHIANG	PISLEN	0.490	0.535	0.534	0.718	0.030	0.443
PHIANG	RUBPER	0.340	0.385	0.357	0.458	0.500	0.383
PHIANG	RUBULM	0.611	0.242	1.000	0.940	0.421	0.704
PHIANG	SMIASP	0.591	0.571	0.400	0.526	0.071	0.414
PISLEN	ASPSPP	1.000	1.000	1.000	1.000	0.000	0.834
PISLEN	DAPGNI	1.000	1.000	1.000	1.000	0.000	0.834
PISLEN	MYRCOM	1.000	1.000	0.500	1.000	0.946	0.763
PISLEN	OLEEUR	1.000	1.000	1.000	1.000	1.000	1.000
PISLEN	PHIANG	1.000	1.000	1.000	1.000	1.000	1.000
PISLEN	PISLEN	0.954	0.934	0.921	0.951	0.950	0.935
PISLEN	RUBPER	1.000	1.000	1.000	1.000	1.000	1.000
PISLEN	RUBULM	1.000	1.000	1.000	1.000	1.000	1.000
PISLEN	SMIASP	1.000	1.000	1.000	1.000	1.000	1.000
RUBPER	ASPSPP	0.543	0.519	0.717	0.784	0.000	0.531
RUBPER	DAPGNI	1.000	0.000	0.000	1.000	0.000	0.227
RUBPER	MYRCOM	0.412	0.636	0.500	0.800	0.000	0.422
RUBPER	OLEEUR	0.000	1.000	1.000	1.000	1.000	0.784
RUBPER	PHIANG	0.774	0.364	0.556	0.875	1.000	0.651
RUBPER	PISLEN	0.636	0.531	0.555	0.851	0.184	0.510
RUBPER	RUBPER	0.468	0.462	0.429	0.500	0.000	0.372
RUBPER	RUBULM	0.000	0.909	0.000	0.952	0.421	0.218
RUBPER	SMIASP	0.727	0.929	0.600	0.842	0.071	0.592
RUBULM	ASPSPP	0.250	0.065	0.586	0.000	0.097	0.097
RUBULM	DAPGNI	1.000	1.000	1.000	0.000	0.618	0.618
RUBULM	MYRCOM	0.182	0.000	0.800	0.000	0.049	0.049
RUBULM	OLEEUR	0.200	0.000	1.000	1.000	0.316	0.316
RUBULM	PHIANG	0.182	0.111	0.825	1.000	0.275	0.275
RUBULM	PISLEN	0.250	0.147	0.617	0.033	0.145	0.145
RUBULM	RUBPER	0.692	0.000	0.417	0.500	0.192	0.192
RUBULM	RUBULM	0.848	0.917	0.905	0.895	0.885	0.885
RUBULM	SMIASP	0.857	0.200	0.789	0.071	0.241	0.241
SMIASP	ASPSPP	0.327	0.348	0.750	0.000	0.284	0.284
SMIASP	DAPGNI	0.000	1.000	1.000	0.000	0.466	0.466
SMIASP	MYRCOM	0.182	0.000	0.600	0.768	0.353	0.353
SMIASP	OLEEUR	1.000	0.000	1.000	1.000	0.329	0.329
SMIASP	PHIANG	0.364	0.222	0.575	1.000	0.447	0.447
SMIASP	PISLEN	0.338	0.461	0.692	0.679	0.470	0.470
SMIASP	RUBPER	0.615	0.429	0.542	0.500	0.474	0.474
SMIASP	RUBULM	0.727	1.000	0.833	0.421	0.645	0.645
SMIASP	SMIASP	0.643	0.200	0.474	0.714	0.420	0.420

3. Testing for correlations of seed-dispersal among microhabitats

To do that, we conducted Mantel tests, by using the method of Kendall-τ, being this the most suitable (robustness and accuracy) for not-large databases (i.e. 81 observations, nine by nine plant species matrix).

Figure S1

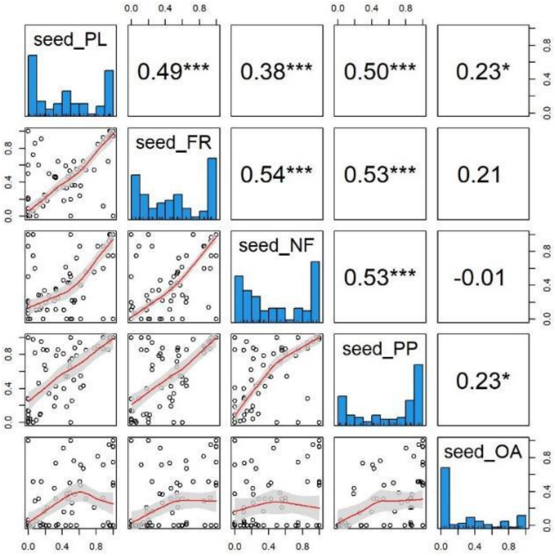

Figure S1. Results of the Mantel tests testing correlations. Data showed that all the micro-habitats (MH) had a correlated seed co-occurrence (i.e. PL *Pistacia lentiscus*, FR fleshy-fruited, NF Non fleshy-fruited & PP *Pinus pinea*). Open area (OA) was correlated with PP and PL.

Supporting information 2.

Exploration of shared bird-dispersed species among plant species; Fruit size

The frugivorous bird assemblage of each plant species can be determined by the complementarity between the size of the bill and the size of the fruit (i.e. trait matching) (Wheelwright 1993, Pegman et al. 2017, Escribano-Ávila et al. 2018). Furthermore, birds tend to optimize fruit removal by selecting specific fruits traits (e.g. maximum fruit-size), therefore determining the frugivorous assemblage of each plant species (Sallabanks 1993, Schupp et al. 2019). Different frugivore assemblages may differently condition the seed co-occurrence and later processes. Thus, first, we need to explore this fact.

To do that, we conducted a Non-Multi-Dimensional-Scaling (NMDS) based on the dissimilarity of the frugivorous bird species shared among plant species. Dissimilarity was calculated by means of Morisita-Horn index. This index accounts for Simpson diversity index, which in turn accounts for the abundance of species. Note that this index ranges from 0 to 1, being 0 the least dispersed and 1 the highest dispersion of bird assemblages among plant species. In terms of overlapping, becomes easier to use "1 – Morisita-Horn index", meaning 1 the strongest overlapping. *Ordenation distance* and *Observed similarity* showed a linear response for both Non-Metric fit (R^2 = 0.99) and Linear fit (R^2 = 0.93), based on Convex-Hull models, reaching solution at 20 runs with 0.1 of stress (Figure S2). Note that the number of bird species shared by plant species is the exogenous variable in the SEM analyses, but not this dissimilarity index.

Figure S2

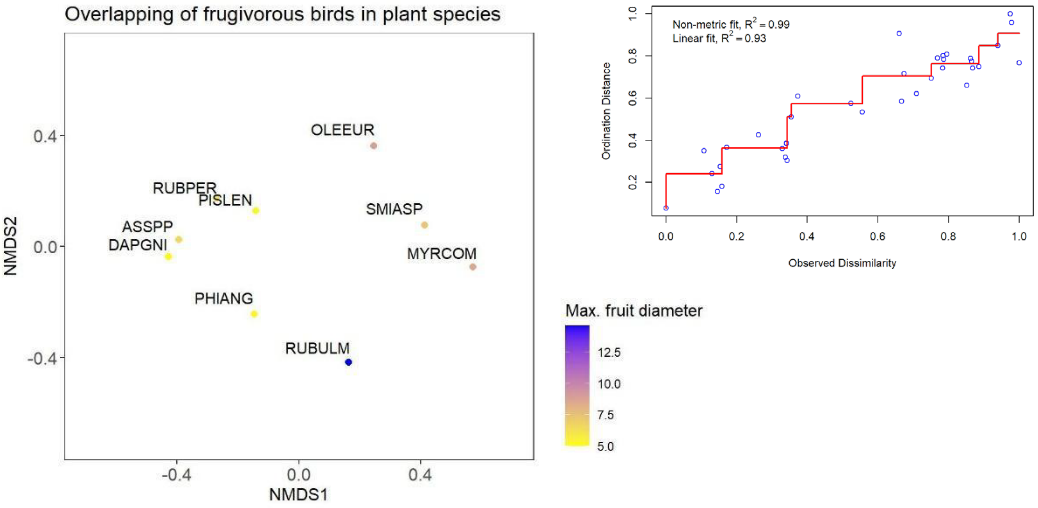

Figure S2. Structure of the bird-dispersal communities among plant species. *Olea europaea*, *Smilax aspera, Myrtus communis* and *Rubus ulmifolius* have a fruit average between 7.3 and 14.6 mm. On its part, *Pistacia lentiscus, Asparagus* spp., *Rubia peregrina, Daphne gnidium* and *Phillyrea angustifolia*, have a fruit average between 5- and 6.5-mm. Data of fruit size was obtained from Valido et al. (2011). Species (ASPSPP, DAPGNI, MYRCOM, OLEEUR, PHIANG, PISLEN, RUBPER, RUBULM and SMIASP, correspond to *Asparagus* spp., *Daphne gnidium, Myrtus communis, Olea europaea, Phillyrea angustifolia, Pistacia lentiscus, Rubia peregrina, Rubus ulmifolius* and *Smilax aspera*).

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Supporting information 3.

Conspecific interactions of saplings and adults

The interaction strength between conspecific adults, or between conspecific saplings was also calculated as a complement for our analyses (but not included in the study). In this case, we did not simulate null model patterns based on pattern reconstruction, since we would obtain in this case very similar values of $K(r)$ and $D(r)$ between observed and simulated patterns. To estimate the conspecific interaction strength, we conducted a Heterogeneous Poisson Process (Wiegand et al. 2007). The main difference to the heterospecific cases is that the spatial structure of each pattern (i.e. clustering) is broken, but points are randomized following the intensity function (obtained previously by *Pattern reconstruction*). Once $K(r = 1\text{m})$ and D ($r = 1\text{m}$) were obtained, estimations of the interaction strength were done by using their standardized effects sizes (P and M, and applied to *eq. 2* in the main text). Note that, we did not test whether the interaction strength is significant or not (i.e. $IS > 2.24$ or < -2.24, see Martinez et al., 2010 and Perea et al. 2021).

Overall details of Point Pattern analyses

Table S3a. Number of individuals

Table S3a. Number of individuals of each species at each life-stage. As mentioned in the main text, some species showed low number of individuals, nevertheless some species showed a consistent pattern for which was possible to apply *Pattern reconstruction* (i.e. adults of *Olea europaea,* saplings of *P. angustifolia, M. communis, and D. gnidium;* in **bold**). In contrast, for others species with more individuals it was not possible to fit the model (*italic* and crossing typo). Note that despite fitting simulated and observed data, fewer individuals partially decrease the reliability of the reconstruction, but see figure S3 as example. *Indicates the species for which path analyses was conducted. We excluded the non-fleshy fruited species (*Pinus pinea* and *Erica arborea*) from the spatial analyses, since it was not of our interest in this study. **included in the analyses*

Species	**Ad**	**Sap**
*Asparagus spp**	1613	1158
Chamaerops humilis	~~*11*~~	~~*24*~~
*Daphne gnidium**	32	**7**
Erica scoparia	88	~~*0*~~
*Myrtus communis**	~~*2*~~	**22**
*Olea europaea**	**9**	97
*Phillyrea angustifolia**	~~*3*~~	**20**
Pinus pinea	3	20
*Pistacia lentiscus**	117	54
*Rubia peregrina**	291	625
*Rubus ulmifolius**	36	98
*Smilax aspera**	199	119
Solanum nigrum	~~*0*~~	~~*23*~~

Figure S3. Pattern reconstruction

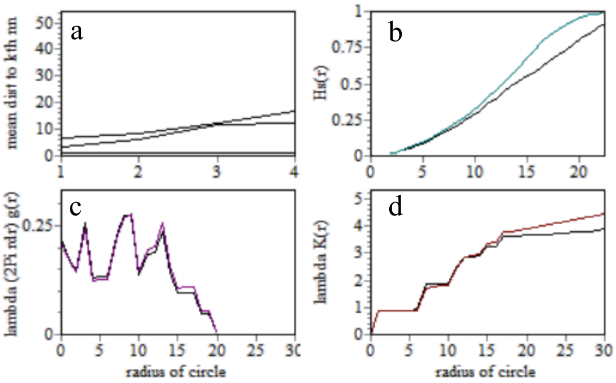

Figure S3. Results of simulations of saplings of *D. gnidium* (7 individuals). Despite of having only few individuals, simulated (coloured lines) fit well enough to observed data (black lines) at the first meters (< 3 m) for the mean distance to the kth neighbour (Panel a), empty space function (Panel b), pair correlation function (Panel c) and Ripleys' K (Panel d). These cases could be included for the subsequent analyses. However, we should remark that we are not testing for significant effects when using the spatial tools, rather we are just interested in mimicking the observed patterns for our null model analysis. Otherwise, larger amount of points may be required.

Table S3b. Results of spatial analyses

Table S3b. Results of the spatial analysis, obtaining the Interaction Strength (*IS*), among species, based on the Standardized Effect Sizes (*SES*) of the bivariate (*Heterospecifics*) and univariate (*Conspecifics*) $K_{12}(r)$ and $D_{12}(r)$ summary functions up to $r = 1$ m. These results are rescaled and the minimum of $IS = 0$. See main text for further info, and Perea et al. 2021 for more details. Species (ASPSPP, DAPGNI, MYRCOM, OLEEUR, PHIANG, PISLEN, RUBPER, RUBULM and SMIASP, correspond to *Asparagus* spp., *Daphne gnidium, Myrtus communis, Olea europaea, Phillyrea angustifolia, Pistacia lentiscus, Rubia peregrina, Rubus ulmifolius* and *Smilax aspera.* Note that *IS* is the *Interaction Strength* (endogenous variables in the path analyses). Bold rows indicate conspecific cases, whereas cursive and bold numbers indicate higher *IS* among heterospecifics than among conspecifics of sp1.

			Sapling-Sapling			**Sapling-Adult**			**Adult-Adult**		
Case	**sp1**	**sp2**	(*D*)	(*K*)	IS	(*D*)	(*K*)	IS	(*D*)	(*K*)	IS
Con	**ASPSPP**	**ASPSPP**	**10.98**	**17.65**	**20.79**	**4.39**	**4.11**	**6.02**	**6.84**	**6.07**	**9.14**
Het	ASPSPP	DAPGNI	1.85	1.10	2.15	4.32	3.46	5.54	4.04	5.19	6.58
Het	ASPSPP	MYRCOM	3.63	5.51	6.60	1.12	1.07	1.55	NA	NA	NA
Het	ASPSPP	OLEEUR	4.78	4.46	6.54	2.49	3.07	3.96	2.63	3.15	4.11
Het	ASPSPP	PHIANG	2.56	2.56	3.62	2.18	2.04	2.99	NA	NA	NA
Het	*ASPSPP*	*PISLEN*	*0.81*	*1.13*	*1.39*	*6.41*	*5.39*	***8.37***	*3.99*	*4.64*	*6.11*
Het	ASPSPP	RUBPER	8.17	9.27	12.35	2.39	5.34	5.85	3.82	4.84	6.17
Het	ASPSPP	RUBULM	3.51	2.28	4.19	1.94	1.66	2.55	2.44	2.78	3.70
Het	ASPSPP	SMIASP	4.64	4.17	6.23	1.55	1.69	2.29	1.24	2.16	2.50
Het	*DAPGNI*	*ASPSPP*	*1.47*	*0.97*	*1.76*	*3.46*	*4.39*	***5.59***	*4.80*	*5.15*	***7.04***
Con	**DAPGNI**	**DAPGNI**	**7.04**	**7.46**	**10.26**	**1.78**	**1.42**	**2.28**	**4.01**	**4.71**	**6.18**
Het	DAPGNI	MYRCOM	3.41	5.89	6.81	1.44	1.12	1.82	NA	NA	NA
Het	DAPGNI	OLEEUR	0.94	0.66	1.15	0.99	0.62	1.17	5.86	6.84	***9.01***
Het	*DAPGNI*	*PHIANG*	*0.38*	*0.47*	*0.60*	*3.21*	*2.31*	***3.96***	*NA*	*NA*	*NA*
Het	*DAPGNI*	*PISLEN*	*4.09*	*3.56*	*5.42*	*6.37*	*7.16*	***9.58***	*2.96*	*4.41*	*5.32*
Het	DAPGNI	RUBPER	0.00	0.39	0.39	1.30	1.67	2.11	3.15	3.84	4.96
Het	DAPGNI	RUBULM	0.85	0.16	0.87	1.89	1.48	2.40	2.01	2.56	3.25
Het	*DAPGNI*	*SMIASP*	*3.20*	*1.85*	*3.70*	*4.00*	*2.12*	***4.53***	*3.49*	*4.15*	*5.42*
Het	MYRCOM	ASPSPP	2.51	6.10	6.60	NA	NA	NA	NA	NA	NA
Het	MYRCOM	DAPGNI	6.12	5.03	7.92	NA	NA	NA	NA	NA	NA
Con	**MYRCOM**	**MYRCOM**	**10.76**	**6.49**	**12.57**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Het	MYRCOM	OLEEUR	4.33	5.11	6.70	NA	NA	NA	NA	NA	NA
Het	MYRCOM	PHIANG	0.31	0.36	0.48	NA	NA	NA	NA	NA	NA
Het	MYRCOM	PISLEN	2.13	1.85	2.82	NA	NA	NA	NA	NA	NA
Het	MYRCOM	RUBPER	0.07	0.77	0.77	NA	NA	NA	NA	NA	NA
Het	MYRCOM	RUBULM	0.75	1.37	1.56	NA	NA	NA	NA	NA	NA
Het	MYRCOM	SMIASP	0.21	0.09	0.22	NA	NA	NA	NA	NA	NA
Het	OLEEUR	ASPSPP	3.95	4.69	6.13	1.27	2.98	3.24	1.74	3.01	3.47
Het	OLEEUR	DAPGNI	0.89	0.59	1.07	2.11	1.73	2.73	5.85	7.06	9.17
Het	OLEEUR	MYRCOM	2.74	4.85	5.57	NA	1.53	2.45	NA	NA	NA
Con	**OLEEUR**	**OLEEUR**	**9.77**	**8.12**	**12.70**	**4.19**	**3.08**	**5.20**	**6.88**	**7.34**	**10.06**
Het	OLEEUR	PHIANG	4.36	5.37	6.92	1.97	1.63	2.56	NA	NA	NA
Het	OLEEUR	PISLEN	1.98	1.58	2.53	1.83	1.44	2.33	5.78	5.87	8.23
Het	OLEEUR	RUBPER	3.60	3.60	5.09	1.51	1.69	2.26	2.06	3.24	3.84
Het	OLEEUR	RUBULM	4.07	3.05	5.08	1.07	1.23	1.63	4.59	4.87	6.69
Het	OLEEUR	SMIASP	4.11	4.51	6.10	2.28	2.05	3.06	2.61	3.29	4.20
Het	PHIANG	ASPSPP	2.66	2.63	3.74	NA	NA	NA	NA	NA	NA
Het	PHIANG	DAPGNI	0.43	0.47	0.64	NA	NA	NA	NA	NA	NA
Het	PHIANG	MYRCOM	0.27	0.36	0.44	NA	NA	NA	NA	NA	NA
Het	PHIANG	OLEEUR	3.45	5.93	6.86	NA	NA	NA	NA	NA	NA
Con	**PHIANG**	**PHIANG**	**10.50**	**6.13**	**12.16**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Het	PHIANG	PISLEN	2.67	4.30	5.06	NA	NA	NA	NA	NA	NA
Het	PHIANG	RUBPER	4.22	3.46	5.45	NA	NA	NA	NA	NA	NA
Het	PHIANG	RUBULM	1.00	0.84	1.31	NA	NA	NA	NA	NA	NA
Het	PHIANG	SMIASP	4.05	5.56	6.88	NA	NA	NA	NA	NA	NA
Het	*PISLEN*	*ASPSPP*	*0.88*	*1.02*	*1.35*	*5.06*	*1.95*	***9.18***	*3.52*	*4.75*	***5.91***
Het	*PISLEN*	*DAPGNI*	*5.65*	*4.12*	***6.99***	*1.43*	*7.30*	*2.42*	*2.90*	*4.32*	***5.20***
Het	*PISLEN*	*MYRCOM*	*1.33*	*1.79*	***2.23***	*5.13*	*7.17*	***8.92***	*NA*	*NA*	*NA*
Het	*PISLEN*	*OLEEUR*	*2.49*	*1.57*	***2.94***	*6.99*	*4.13*	***10.01***	*6.29*	*6.16*	***8.81***
Het	*PISLEN*	*PHIANG*	*1.50*	*4.11*	***4.37***	*4.57*	*11.18*	***6.16***	*NA*	*NA*	*NA*
Con	**PISLEN**	**PISLEN**	**0.84**	**1.72**	**1.92**	**3.65**	**2.69**	**4.54**	**1.28**	**0.00**	**1.28**
Het	*PISLEN*	*RUBPER*	*1.13*	*2.10*	***2.39***	*8.02*	*0.50*	***13.76***	*8.47*	*8.83*	***12.24***
Het	*PISLEN*	*RUBULM*	*3.76*	*1.28*	***3.97***	*0.63*	*5.64*	*0.80*	*2.81*	*4.76*	***5.53***
Het	*PISLEN*	*SMIASP*	*0.54*	*0.15*	*0.57*	*5.59*	*4.53*	***7.94***	*5.27*	*7.01*	***8.77***
Het	RUBPER	ASPSPP	7.39	9.04	11.68	3.92	1.61	5.99	3.95	4.51	5.99
Het	RUBPER	DAPGNI	0.62	0.42	0.75	2.44	2.21	2.92	3.58	3.97	5.34
Het	RUBPER	MYRCOM	0.34	0.66	0.74	2.93	4.15	3.67	NA	NA	NA
Het	RUBPER	OLEEUR	3.15	3.57	4.76	5.45	4.16	6.85	2.23	3.27	3.96
Het	RUBPER	PHIANG	3.75	3.35	5.03	4.04	0.95	5.80	NA	NA	NA
Het	RUBPER	PISLEN	2.29	2.04	3.07	1.08	2.18	1.44	8.46	8.82	12.22
Con	**RUBPER**	**RUBPER**	**16.92**	**19.65**	**25.93**	**9.06**	**9.48**	**13.11**	**12.83**	**13.35**	**18.52**
Het	RUBPER	RUBULM	2.76	2.57	3.77	2.37	3.47	3.22	2.02	3.62	4.15
Het	RUBPER	SMIASP	3.46	3.98	5.27	4.32	0.00	5.54	6.16	5.95	8.57
Het	RUBULM	ASPSPP	1.92	2.33	3.02	0.00	1.21	0.00	1.51	1.44	2.09
Het	RUBULM	DAPGNI	0.57	0.48	0.75	1.55	1.32	1.96	1.88	2.43	3.07
Het	*RUBULM*	*MYRCOM*	*1.97*	*2.04*	*2.83*	*2.01*	*0.58*	***2.40***	*NA*	*NA*	*NA*
Het	RUBULM	OLEEUR	2.55	2.80	3.79	0.95	1.02	1.11	4.35	4.54	6.29
Het	RUBULM	PHIANG	1.39	1.64	2.15	1.31	0.94	1.65	NA	NA	NA
Het	*RUBULM*	*PISLEN*	*1.88*	*1.57*	*2.45*	*1.37*	*0.24*	*1.66*	*2.70*	*4.63*	***5.36***
Het	RUBULM	RUBPER	2.53	1.93	3.18	0.73	1.50	0.77	1.36	3.22	3.50
Con	**RUBULM**	**RUBULM**	**7.50**	**8.59**	**11.40**	**1.59**	**1.61**	**2.26**	**3.31**	**4.04**	**5.22**

Het	*RUBULM*	*SMIASP*	*5.18*	*5.78*	*7.77*	*2.20*	*4.35*	***2.66***	*4.02*	*5.10*	***6.49***
Het	SMIASP	ASPSPP	3.43	3.94	5.23	2.72	1.26	5.13	0.00	1.03	1.03
Het	SMIASP	DAPGNI	2.06	1.77	2.72	1.60	1.47	2.04	3.17	4.36	5.39
Het	SMIASP	MYRCOM	0.10	0.00	0.10	1.83	2.63	2.34	NA	NA	NA
Het	SMIASP	OLEEUR	5.28	4.24	6.77	2.70	2.20	3.77	2.56	3.17	4.07
Het	SMIASP	PHIANG	4.14	5.34	6.76	3.09	0.26	3.79	NA	NA	NA
Het	SMIASP	PISLEN	0.37	0.22	0.43	0.66	4.32	0.71	6.29	7.62	9.88
Het	SMIASP	RUBPER	4.99	4.18	6.51	3.43	1.60	5.51	5.23	5.29	7.44
Het	SMIASP	RUBULM	4.20	5.32	6.77	2.29	6.01	2.80	3.43	5.10	6.15
Con	**SMIASP**	**SMIASP**	**10.98**	**8.36**	**13.80**	**6.85**	**6.01**	**9.11**	**12.81**	**15.98**	**20.48**

Supporting information 4

Integrating pre-dispersal and post-dispersal

Table S4. Exploratory results checking for homoscedasticity and normality of the variance of responses and predictors.

	Homogeneity of variance		**Normality of variance**		
	Levene		ANOVA		
Variable	*F-value*	*p-value*	*F-value*	*p-value*	
Shared dispersed (just predictor)	0.929	0.500	4.78	< 0.005	***
Seed cooccurrence	0.329	0.952	0.39	0.92	
Sapling - sapling cooccurrence	0.603	0.772	0.77	0.63	
Sapling - adult cooccurrence	1.210	0.320	0.63	0.75	
Adult - adult cooccurrence (just response)	0.570	0.745	1.30	0.29	