Lasting effects of avian-frugivore interactions on seed dispersal and seedling establishment

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ABSTRACT

1. The consequences of plant-animal interactions often transcend the mere encounter stage, as those encounters are followed by a chain of subsequent stages on the plant's reproductive cycle that ultimately determine fitness. Yet, the dissemination and recruitment stages of animal-mediated seed dispersal are seldom analysed jointly, hindering a full understanding of the ecology of seed dispersal.
2. We analyse the dispersal and recruitment of a fleshy-fruited plant (*Pistacia lentiscus*), from fruit production to seedling survival up to their second year. We link early reproductive investment of individual plants to seedling recruitment and explore the role played by seed viability, the coterie of frugivores and microhabitat seed deposition.
3. The proportion of viable seeds was generally low (mean = 34%) but highly variable among individual plants (range: 0 - 95%). Seed viability did not seem to have a direct effect on individual plant's recruitment.
4. We recorded 28 bird species feeding on *P. lentiscus* fruits or seeds. Their contribution to plant recruitment was mainly determined by their intensity of fruit consumption and probability to disperse viable seeds. Most frugivores presented non-random microhabitat preferences, delivering uneven seed contributions to different sites.
5. Post-dispersal seed predation by rodents was the most limiting phase in *P. lentiscus* recruitment. Yet, microhabitats showing the lowest predation rates received the lowest seed rain. Hence, we found a decoupling of the dissemination and recruitment stages: most seeds do not arrive at the most suitable microhabitats.
6. We estimate *P. lentiscus* plants need to produce c. $5x10^5$ fruits to recruit a single seedling that survives to its second summer in our study site. Its success as a prevalent species in Mediterranean lowland landscapes relies on its high fecundity and thorough fruit removal and dispersal by a diversified frugivore assemblage, which compensates for the high seed unviability characteristic of this genus.

7. Synthesis - Measuring the delayed, post-dispersal outcomes of animal frugivory interactions may overturn inferences based on consumption observations only. Seed rain patterns are often decoupled from microhabitats' suitability for seedling recruitment. Hence, more integrative studies that encompass the entire plant reproductive cycle (from fruit production to seedling recruitment) are needed to fully understand frugivores' lasting contribution to plant regeneration in natural populations.

KEYWORDS

Doñana National Park, frugivory, microhabitat, *Pistacia lentiscus*, plant regeneration, plant-animal mutualisms, post-dispersal predation, seed viability, seedling recruitment, seedling survival.

INTRODUCTION

Plant population regeneration entails a series of demographic stages spanning flowering, fruiting, seed dispersal, seedling emergence, establishment, and subsequent growth (Harper, 1977; Wang & Smith, 2002). Each of these transition steps has the potential to limit recruitment and population growth (Nathan & Muller-Landau, 2000). Natural recruitment in plants can be restricted by two main mechanisms: (i) seed limitation, when not enough seeds arrive at sites suitable for seedling recruitment, and/or (ii) microhabitat suitability, if seeds arrive at sites where seedling recruitment is prevented by physical or biotic factors (Clark et al., 1999; Moore & Elmendorf, 2006). For animal-dispersed (zoochorous) plants, both the amount of seeds dispersed and the microhabitat where seeds arrive will be ultimately determined by their animal partners (Schupp et al., 1989). The arrival stage determines how many seeds reach a particular target microhabitat, depending on the consumption and movement of the different frugivore species. The recruitment stage determines the fraction of this seed rain that transitions to become established seedlings, saplings and, eventually, adults. Despite being crucially intertwined, frugivore studies typically examine just one of these two stages and thus we lack a full appreciation of the limiting transitions and bottlenecks throughout the regeneration process (Harms et al., 2000; Howe & Miriti, 2000).

Several ecological characteristics of frugivores will determine their effectiveness as seed dispersers and their net contribution to the plants' reproductive cycle: for example, variation in their consumption frequency and fruit handling behaviour, or in their habitat use preferences, which will influence the spatial pattern of seed deposition (Razafindratsima & Dunham, 2015; Schupp et al., 2010). Frugivores use the landscape heterogeneously (Wenny & Levey, 1998), thus determining non-random dispersal by depositing seeds in different microhabitats in proportions not directly determined by their availability in the landscape (e.g., Jordano & Schupp, 2000; Lázaro et al., 2005). The microhabitat where seeds are deposited is crucial for plant recruitment, since the deposition site often shows important differences in microclimatic conditions, such as soil moisture, nutrient availability, or seed predators' activity (Gómez-Aparicio, 2008). Frugivores providing high-quality dispersal will predominantly carry seeds to more suitable locations where seeds have greater probability of escaping predation or experience better microclimatic conditions for seedling establishment and subsequent growth. Hence, the set of animal frugivores with their characteristic feeding and movement behaviour, have lasting effects on individual plants recruitment (Wenny & Levey, 1998). Importantly, these effects are delayed relative to the actual occurrence of the plant-frugivore interaction, and probably this has hindered the joint treatment of the dissemination and establishment processes. Few studies have addressed how these sequential effects of animal frugivores (immediate contributions to the seed rain and delayed effects on recruitment) are intertwined during the seed dispersal process, i.e., how frugivore activity may link with the resulting recruitment patterns (e.g., Côrtes et al., 2009, Rey & Alcántara, 2000, Jordano & Schupp, 2000).

In addition to post-dispersal processes, the outcome of the mutualistic interactions in terms of plant recruitment may also be constrained by factors occurring prior to the establishment of the interaction itself. Many plants produce fully-developed fruits containing unviable seeds with no chances of recruitment, for example, due to pre-dispersal seed predation, seed abortion, or parthenocarpy (Jordano, 1989). Varying degrees of seed viability can thus determine the final probability of plant recruitment, beyond the number and location of dispersed seeds (González-Varo et al., 2019). In those situations, a complete evaluation of the outcome of mutualistic interactions and individual plants' reproductive, dispersal and regeneration success requires a comprehensive examination of both pre- and post-dispersal stages (Herrera et al., 1994; Yang et al. 2011).

Here we provide a comprehensive study of the regeneration cycle of *Pistacia lentiscus* L., a widespread plant species in the Mediterranean shrublands, aiming to disentangle the role of avian frugivores and variation in seed viability on early plant recruitment. This plant represents an interesting case study because, on the one hand, it produces an abundant fruit crop (thousands of fruits), interacts with a wide array of frugivores (supergeneralist), and can become locally very abundant, often being the dominant species in Mediterranean lowland shrublands. On the other hand, this species regularly produces relatively large percentages of unviable seeds within the fully-developed fruits (Grundwag, 1976), with considerable variation among individual plants, ranging between 10 and 40% (González-Varo et al., 2019; Jordano, 1989; Verdú & García-Fayos, 1998). This study seeks to elucidate what are the plant's demographic consequences of interacting with different assemblages of frugivores for reproductive success beyond the mere fruit-frugivore contact, and encompassing the following successive stages: fruit consumption (1), pre-dispersal avian predation on seeds (2), dispersal of viable seeds (3); the consequences of differential seed deposition in microhabitats through seed escape from rodent predation (4), seedling emergence (5) and seedling survival until its second summer (6) (Fig. 1).

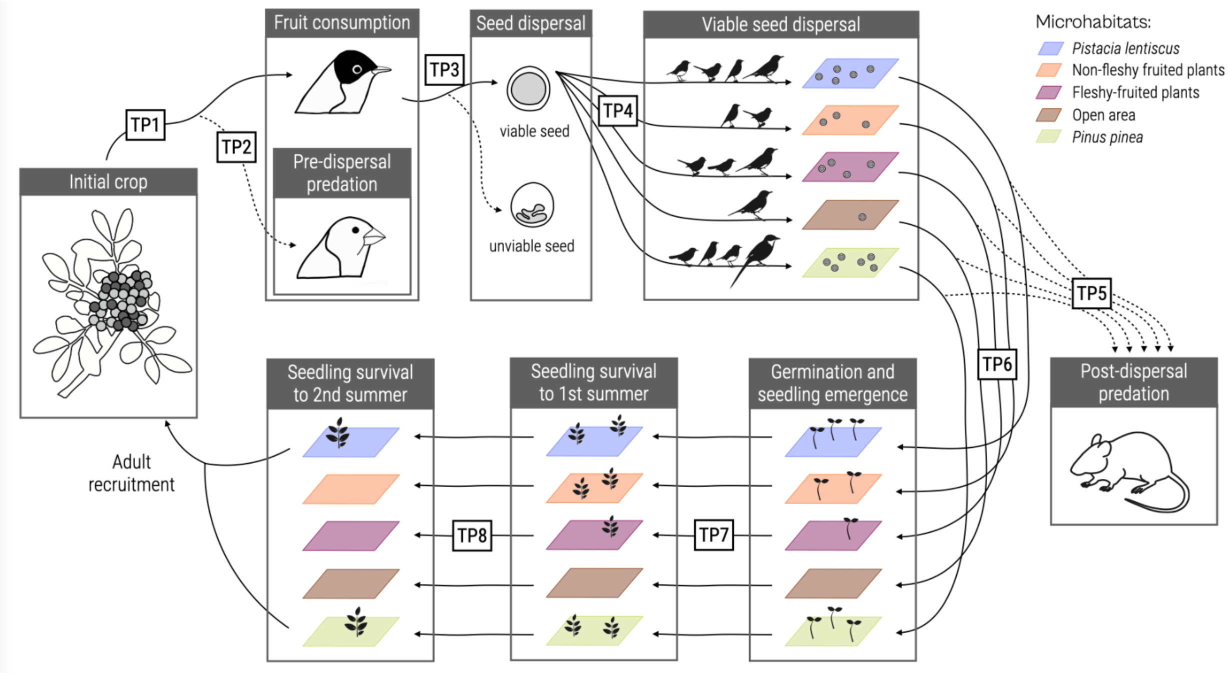

Figure 1. Simplified schematic view of the demographic cycle of *Pistacia lentiscus* focusing on its seed dispersal and recruitment stages. The figure shows demographic stages (rectangles) with their associated ecological processes. Continuous lines represent the contribution of propagules to the next demographic phase while dashed lines indicate the loss of propagules. The derived effects of each demographic stage results in variable transition probabilities (TPs) between the successive demographic stages considered in this study. TP1: prob. of fruit consumption, TP2: prob. of seeds escaping finch predation, TP3: prob of dispersing a viable seed; TP4: prob. of viable seed being dispersed to a certain microhabitat, TP5: prob. of dispersed seeds escaping rodent predation, TP6: prob. of seedlings emerging from surviving seeds, TP7: prob. of seedling surviving its 1st summer and TP8: prob. of seedling surviving its 2nd summer. Coloured rectangles represent distinct microhabitat types that differ in arrival of seeds and recruitment probabilities. Different avian assemblages disperse seeds to different microhabitats as a result of foraging preferences (in TP3). The product of the successive TP values determines the overall probability of recruitment (OPR) for the plant.

Specifically, we address the following main questions: (1) Does a remarkably high incidence of seed unviability combine with high dispersal success and establishment for the (few) viable seeds produced in the demographic cycle of a dominant plant species? In other words, are frugivores, through their consumption, able to compensate for the high unviability rates of *P. lentiscus* seeds and disperse enough viable seeds for plant regeneration? (2) Do frugivores, with their non-random patterns of foraging and heterogeneous landscape use, limit seed arrival to potentially suitable microhabitats? That is, do viable seeds predominantly reach certain microhabitats as a result of differential dispersal mediated by specific frugivore species, and does seed fate differ in these microhabitats? Finally, (3) which are the main limiting demographic transitions in the seed dispersal and recruitment cycle of *P. lentiscus,* and do frugivores, through their direct (dispersal) and indirect (pre- and post-dispersal) effects, play different roles in the plant's demographic stages, beyond their consumption frequencies?

We expect birds will provide complementary dispersal services attending to their different use of the landscape (González-Castro et al., 2015; Lavabre et al., 2016) leaving a distinct spatial signal that will serve as the starting template for population recruitment to follow (Howe & Miriti, 2004; Perea et al., 2021). Similarly, we expect microhabitats will differ in their suitability for seed survival, emergence and growth into seedlings (Gómez-Aparicio, 2008). This spatial pattern in the seed rain is expected to vary for individual plants depending on the assemblage of frugivore species consuming their fruits and their non-random dispersal service. Understanding the role of frugivorous species on the limitation of plant recruitment will be useful to predict the consequences of the increasingly omnipresent environmental changes and animal fluctuations, driven by anthropogenic impact, for plant regeneration and distribution in nature.

METHODS

Study species

Pistacia lentiscus L. (Anacardiaceae) is an evergreen shrub species widely-distributed in the Mediterranean basin (Martínez-López et al., 2020; Verdú & García-Fayos, 2002). It is found in low and medium altitude Mediterranean shrublands, where it can become dominant, acting as a foundation species (Ellison 2019). This species is dioecious (i.e., separate male and female individuals) and wind-pollinated but relies on animals for the dispersal of its seeds that are covered with a thin fleshy mesocarp forming a drupe. The pulp is very rich in lipids (Herrera, 1992) and heavily consumed by frugivorous birds during the fruiting season, from September to March, spanning late summer, autumn and winter. A significant number of the seeds produced are unviable as a result of parthenocarpy (i.e., fruit development without fertilisation), embryo abortion or pre-dispersal seed predation by wasps (Grundwag, 1976; Jordano, 1989). The wasp *Megastigmus pistaciae* of the superfamily Chalcidoidea oviposits on the fruit, where the larvae will consume the endosperm from within, rendering the seed unviable (Traveset, 1993; Verdú & García-Fayos, 1998). The frequency of empty seeds varies from year to year, as well as among *P. lentiscus* populations (Jordano, 1988, 1989; Verdú & García-Fayos, 1998). Fruits have a red colour when unripe that turns into black when fully ripe (Jordano, 1989). Frugivores show a strong preference for black ripe fruits over red fruits (Jordano, 1989), since black fruits have a higher percentage of lipids (Trabelsi et al., 2012). Fruits that turn black also present significant higher chances of having filled, viable seeds (Jordano, 1989). Thus, frugivores are expected to disperse a higher amount of viable seeds but together with a variable fraction of empty seeds. The proportion of unviable seeds dispersed appears to increase along the fruiting season (González-Varo et al., 2019). *Pistacia lentiscus* is considered mainly a bird-dispersed plant (Herrera, 1989; Suppl. Mat. A), although fruit consumption by carnivores and ungulates has been reported (Perea et al., 2013). Yet, mammal fruit consumption is rare and their contribution to dispersal is probably negligible since they break most seeds during consumption, acting mostly as seed predators (Mancilla-Leytón, 2013; Perea et al., 2013). In addition, no mammal consumption of *P. lentiscus* fruits was detected in our study sites, hence here we focus on frugivory and seed dispersal by birds.

Sampling design and estimation of initial (pre-dispersal) seed viability

We conducted fieldwork in Doñana National Park, southern Spain, between the years 2019-2021. We monitored a total of 80 female *Pistacia lentiscus* plants along the fruiting season at two Mediterranean scrubland sites: El Puntal (EP; 36° 57' 54.3816" N, 6° 26' 47.1588" W) and Laguna de las Madroñas (LM; 37° 1' 49.2312" N, 6° 28' 19.1604" W) (Quintero et al., 2023a).

For each individual plant we measured its cover area, counted the initial crop size with the help of a hand counter (at the beginning of the fruiting period, i.e., September 2019) and estimated the proportion of viable seeds found in their crop. Seed viability was estimated through floatation/sink experiments (Albaladejo et al. 2009, González-Varo et al. 2019). We bagged branches at individual plants with a mesh fabric to prevent fruit consumption by birds before sampling for viability analysis. This was necessary to avoid biassed viability estimates caused by birds' selective consumption of ripe black fruits (Jordano, 1989). At EP site, branches were bagged in three consecutive periods along the season: early (bagged 21st August and collected 25th September), mid (bagged 25th September and collected the 7th-11th November) and late period (bagged 11th November and collected 23rd December). The amount of fruits per branch was variable (mean number of fruits per plant = 146, range = 13-595; see grouped sample size for each plant on top of Fig. 2). Differences in viability between periods were not significant (Suppl. Mat. B). At LM site, bags were placed once on individual plants' branches on the 29th August, and collection date varied between plants (between 2nd October and 25th November), depending on when fruits ripened. At the LM site, the mean number of seeds collected per plant was 131 (range = 12-503; see Fig. 2). We aggregated fruits collected in the different sampling periods to calculate seed unviability of each plant. In addition, to determine the causes of seed unviability (i.e., parthenocarpy, abortion or wasp predation), we dissected a minimum of 30 floating (unviable) seeds of each plant (mean number of seeds per plant = 47). We modelled the proportion of viable seeds produced by each plant using a Bayesian logistic regression where the logit probability of producing viable seeds had a wide prior Normal(0, 2) (Quintero et al. 2023b).

Frugivory interaction sampling

To estimate the number of fruits consumed by different avian species from individual plants we combined two non-invasive techniques: DNA-barcoding and video footage (Quintero et al., 2022). For the first method, we collected faecal samples and regurgitated seeds by placing seed traps beneath *P. lentiscus* plants at both sites. One to two seed traps of 0.22 m2 were installed per individual plant and operated during the full fruiting season (September 2019 to February 2020). We extracted animal DNA present on the samples' surface, amplified and sequenced it to determine the avian species identity (for a detailed protocol see González-Varo et al., 2014 and Quintero et al., 2023a for modifications). A total of 2691 faecal and regurgitated samples were collected for DNA-barcoding, of which 93% were analysed with a 94% identification success rate.

In addition, we installed continuous recording cameras in front of 40 focal plants at EP site to record avian visitation and consumption behaviour. Each plant was recorded 9 times over the course of the fruiting season from September to January, rendering 19 hours recorded per plant on average (range = 18-20). Cameras recorded 3970 animal visits; with species reliably identified for 91% of the visits.

Combining data extracted from both methodologies we calculated the total number of fruits consumed by avian frugivores on individual plants during the entire fruiting season (see Quintero et al. 2023a for details). Briefly, we multiplied the posterior distributions obtained from four Bayesian models of: (1) the total number of bird visits (using DNA-barcoding data), (2) the probability of each bird species visiting individual plants (using both DNA-barcoding and camera data), (3) the probability that a bird visit involves fruit or seed consumption (using camera data), and (4) the number of fruits or seeds consumed per visit with feeding event (using camera data). Additionally, the proportion of fruits consumed was calculated by dividing the estimated number of fruits that birds consumed by the plants' crop size.

The number of fruits consumed by frugivores was corrected by pre-dispersal seed predation, since four bird species (finches from Fringillidae family) were observed acting mainly as seed predators, breaking the seed coat in half and feeding on the embryo. By relating the number of predated and undamaged seeds found in seed traps and attributed to granivores, we estimated that c. 0.14% of the seeds consumed by these granivores actually escaped predation (80% CI = 0.08 - 0.2%; Quintero et al. 2023a).

Bird dispersal of viable seeds

Dispersed seed viability was estimated during the DNA extraction phase for frugivore identification (González-Varo et al., 2019). After adding the extraction buffer mix to the samples and incubating them at 50ºC for 75 minutes, we checked the seed floatability in the supernatant inside the microcentrifuge tubes. We used a hierarchical Bayesian logistic regression to estimate the proportion of viable seeds consumed by each bird species (Quintero et al. 2023b). The probability of birds dispersing viable (versus unviable) seeds had an informative prior based on the fact that birds consume mostly black fruits (98% of the consumed fruits versus 2% of red fruits) and black fruits are generally more viable (75% viable compared to 27% viable red fruits) (Quintero et al. 2023a, b and Suppl. Mat. B; see also Jordano 1989, González-Varo et al. 2019). We used a Normal(1, 1) prior distribution on the logit scale, corresponding to c. 0.73 probability that bird-dispersed seeds are viable.

We estimated the number of viable seeds dispersed by each bird species from each plant as the product of each bird's posterior probability of dispersing viable seeds and the estimated total number of fruits consumed from each plant by each bird species. In a few cases (n = 7 out of 80 plants) the estimated number of viable fruits consumed by birds surpassed the estimated amount of viable seeds produced by the plant. The viable fruit consumption surplus was then redistributed between the other plants based on their availability of viable seeds and bird consumption intensity at each plant (Quintero et al. 2023b).

Post-dispersal seed fate and seedling recruitment

To assess the subsequent consequences of seed dispersal by different frugivores on plant recruitment, we selected five microhabitats at EP site that were deemed to potentially differ in seed deposition and fate (Jordano & Schupp, 2000; Lavabre et al., 2016): under *P. lentiscus* female conspecifics (PL), under other fleshy fruited species (FR), under non-fleshy fruited species (NF), under pine trees (*Pinus pinea*; PP) and open ground areas (OA). We estimated the cover of each microhabitat using ten 30-m long vegetation transects randomly distributed across the EP site. Microhabitat cover percentages were calculated using the R package 'vegetools' (Rodríguez-Sánchez 2016).

To estimate the density of *P. lentiscus* seed rain we placed seed traps in all microhabitats except in open area (OA), where we used 17 1-m wide transects that we monitored weekly (biweekly in 5 out of 17 censuses) adding up to 3506 m in length. For the PL microhabitat we used the 40 seed trays of 0.22 m^2 located beneath the 40 focal plants at EP site, while for FR, NF and PP microhabitats we placed two seed trays totalling 0.168 m^2 at 15 sampling points per microhabitat. The identity of the animal disperser from collected seed samples was inferred using DNA-barcoding, using the same protocol as above. We estimated the number of *P. lentiscus* seeds dispersed by each frugivore species to each microhabitat in two steps (Quintero et al. 2023a). First, we used a Bayesian Negative Binomial regression to estimate the total number of *P. lentiscus* seeds arriving at each microhabitat. We used an offset to account for different sampling areas across microhabitats, and considered the total extent of each microhabitat at the EP site (4.1 ha) to estimate the total seed rain per microhabitat. Second, we used a Bayesian binomial model to estimate the proportion of seeds dispersed by each frugivore at each microhabitat, based on frugivore assignments derived from DNA barcoding. Finally, the number of *P. lentiscus* seeds dispersed to each microhabitat by each frugivore was obtained as the product of both posterior distributions (number of seeds arriving at each microhabitat, and the estimated proportion of seeds brought by each frugivores to each microhabitat).

To assess the intensity of post-dispersal seed predation by rodents in each of the five microhabitats we performed seed-offering experiments at EP site starting in January of 2019. We located six replicated seed predation stations per microhabitat, where each replicate consisted of a petri dish containing 10 viable seeds that were monitored daily and then gradually spaced over time. We estimated the probability of dispersed seeds to escape rodent predation during the first 30 days, when seedlings start emerging, through a Bayesian binomial model (Quintero et al. 2023a).

Finally, we measured seedling emergence and survival for two years using seed sowing experiments at EP site. We conducted this experiment twice, one starting in January 2019 and the other in October 2019. At each microhabitat we installed six germination stations the first season (2018-19), and seven the second season (2019-20). In each station we sowed 16 viable *P. lentiscus* seeds protected with wire mesh to prevent predation, herbivory, debris and trampling. The experimental stations were monitored approximately every fortnight for the first four months and monthly thereafter.

We modelled separately seedling emergence and seedling survival after their first and second summer using a hierarchical Bayesian model with Bernoulli distribution (Quintero et al. 2023b). Sample sizes were: 1040 seeds for the seedling emergence model, 126 seedlings for the model of seedlings survival through the first summer, and 32 seedlings for modelling survival up to the 2nd summer. All models had microhabitat and fruiting season as fixed effects while germination station was set as a random factor to account for lack of independence within sowing units. We used relatively informative priors for the average seedling emergence and survival on the logit scale: for emergence we used a Normal(-1.8, 2) prior centred around ~15% emergence, for seedling survival through the first summer a Normal(-1.4, 2) prior corresponding to 20% survival, and for seedling survival through the second summer a Normal(-0.8, 2) prior corresponding to 30% survival (based on information from Amat et al., 2015; Trubat et al., 2011). Other parameters had large prior distributions: Normal(0, 2) for the microhabitat and season effects, and half-Normal(0, 1) prior for the germination station random effect.

Diversity analysis of seed rain

To evaluate the seed dispersal service performed by each frugivore species we performed diversity analyses of the spatial seed rain deposition. For each bird species we considered the number of seeds collected at each of the $n = 102$ sampling units at EP site and calculated diversity using Hill numbers for the first three orders (Chao et al., 2014; Jost, 2007). Diversity in this case translates into the effective number of sites receiving seeds brought by a given frugivore species. First order ($q = 0$) Hill number indicates the site richness (i.e., the number of sites that received at least one seed), second order ($q = 1$) is the exponential Shannon diversity index which not only accounts for the number of sites receiving seeds but also for the relative abundance of seeds across sites; and third order ($q = 2$) is the inverse of the Simpson's diversity index, which places higher weight to the evenness of seed relative abundances across sites.

Bottlenecks in transitions between demographic stages and total recruitment

Finally, we reconstructed the complete recruitment cycle of individual *P. lentiscus* plants, from fruit production up to 2nd-year seedling recruitment, to identify the major demographic bottlenecks as well as the contribution of different frugivores and microhabitats at the scale of individual plants. In particular, we calculated the following transition probabilities (TPs): (TP1) probability of fruit consumption by birds, (TP2) probability of seeds escaping bird predation and being dispersed, (TP3) probability of a dispersed seed being viable, (TP4) probability of seeds arriving at specific microhabitats, (TP5) probability of seeds escaping rodent predation, (TP6) probability of seedling emergence at each microhabitat, (TP7) probability of seedlings surviving their first summer and (TP8) probability of seedlings surviving their second summer (Fig. 1). When estimating the number of propagules arriving at each demographic stage for the five distinct microhabitats, we directly started after TP2 (seeds that escaped bird predation and got dispersed). The overall probability of recruitment (OPR) at each microhabitat was calculated as the product of the full posterior distributions of the step-specific probabilities for seed/seedling transitions after seed arrival (TP5 to TP9).

Data Analysis

We performed all analyses with R version 4.3.0 (R Core Team, 2023). For the Bayesian analyses we used Stan (Stan Development Team, 2023) and brms v. 2.19.0 (Bürkner, 2017). For model checking we used DHARMa v. 0.4.6 (Hartig, 2022) and DHARMa.helpers v. 0.0.1 (Rodriguez-Sanchez, 2023). For the diversity analyses we used hillR v. 0.5.1 (Li, 2018) and vegan v. 2.6.4 (Oksanen et al., 2022). For data management and visualisation we used tidyverse v. 2.0.0 (Wickham et al., 2019) combined with ggdist v. 3.3.0 (Kay, 2022). For a complete list of all packages used please refer to Suppl. Mat. H.

RESULTS

Pre-dispersal seed viability

The viability of the seeds produced by *P. lentiscus* plants was generally low (mean = 34%; SD = 19%) in congruence with previous studies (Jordano, 1988; Verdú & García-Fayos, 1998). There was strong variation in seed viability between individual plants, LM population being more variable than EP (Fig. 2, Table S1). Unviability causes also varied substantially between individual plants, with abortion having the highest incidence (38%), followed by parthenocarpy (25%) and wasp predation (2-4%) (Table S1).

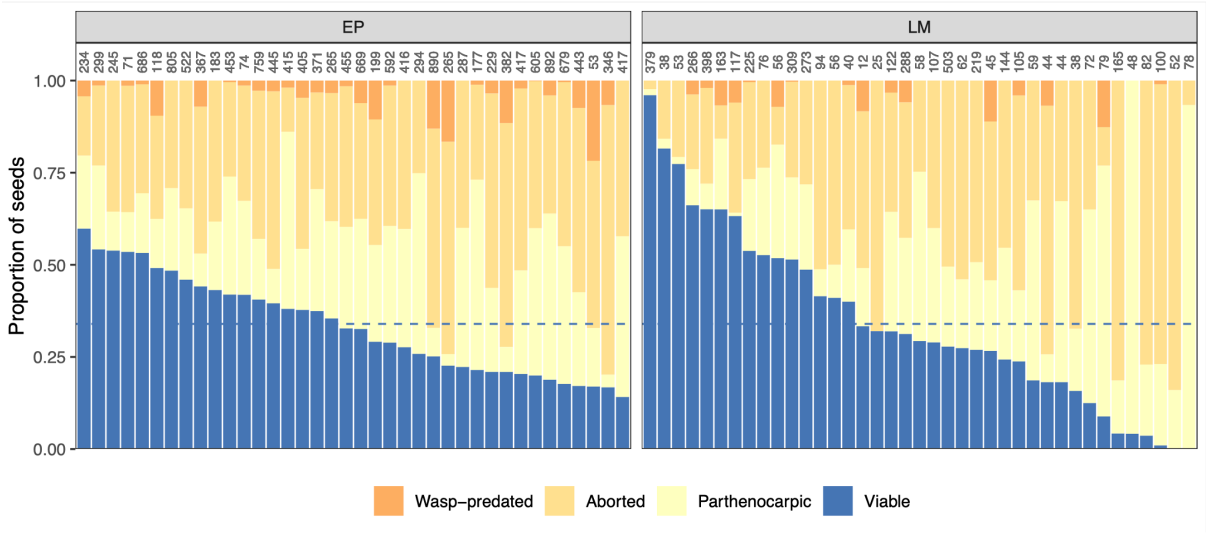

Figure 2. Bar graph showing the proportion of the four types of seeds found in individual plants. The two panels represent two *Pistacia lentiscus* populations (EP, LM) and each bar represents an individual plant. Numbers above indicate sample size (number of fruits sampled) and dashed lines represent mean seed viability at each population.

Viable fruit consumption and dispersal

We recorded a total of 28 bird species consuming *P. lentiscus* fruits. Five of the bird species detected were new in respect to previous literature (Suppl. Mat. A). Birds consume both unripe and ripe fruits, yet with marked preference for ripe ones, and thus may disperse either viable or unviable seeds. We detected 526 unique pairwise interactions between frugivores and individual plants, which represent 24% of all the potential connections. Most interactions, however, were dominated by just three species, *Curruca melanocephala, Erithacus rubecula* and the seed predator *Chloris chloris*. These three species were responsible for more than 85% of all the fruits consumed (see Quintero et al., 2023a for more frugivory interaction details).

Overall, *P. lentiscus* seeds represented 70% of the fruits consumed by birds during the study period of 2019-2020 (Table 1). Birds in which the prevalence of *P. lentiscus* seeds was highest (>85%) were mostly partial frugivores or seed predators, denoting a higher preference for *P.*

lentiscus in their fruit diet. On the other hand, species such as *Cyanopica cooki* or *Sylvia atricapilla* showed lower prevalence of *P. lentiscus* seeds in their diets, indicating reliance on other fruiting resources.

The viability of dispersed seeds found in the seed traps was 29.5% (n = 1892 dispersed seeds). The estimated probability of a dispersed seed being viable was highest when fruits were consumed by summer migrants (median = 0.57, 80% CI = 0.34 - 0.80) and lowest when consumed by winter migrants (median = 0.46, 80% CI = 0.22 - 0.84) (Table 2, Suppl. Mat. C). Plants with larger crops dispersed more seeds, regardless of their viability. In other words, large crop sizes did not favour the dispersal of more viable over unviable seeds (Suppl. Mat. D).

Seed rain among microhabitats

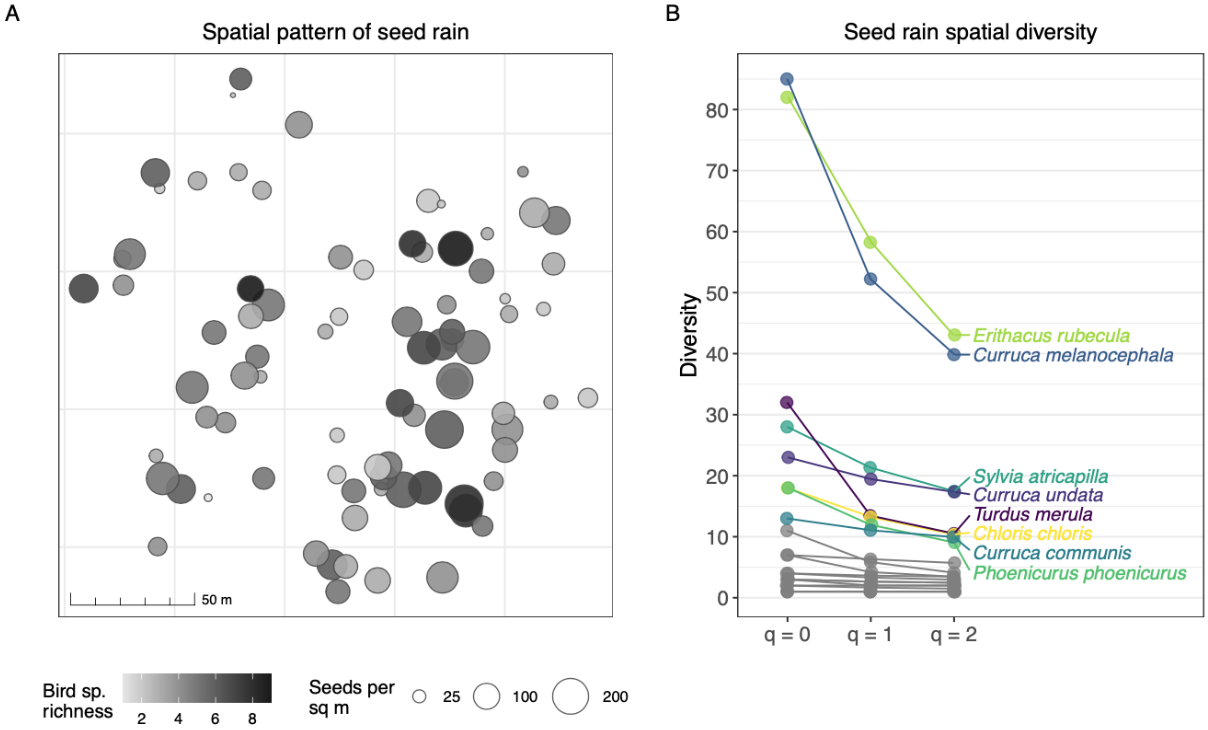

Figure 3. A) Spatial pattern of *P. lentiscus* seed rain performed by birds. Dots indicate locations of seed traps monitoring seed rain in the El Puntal study plot. Shading intensity in points denotes bird species richness found at each sampling point and circle size denotes seed rain density (seeds per m^2). Open area (OA) microhabitat is not

represented in this figure as it was sampled using transects rather than fixed seed trays (see Methods). B) Diversity profile of the spatial pattern of seed rain generated by each bird species. Diversity is estimated using Hill numbers which represent the effective number of sites receiving seeds (out of 102 sampling points in total), i.e., a proxy of the spatial "spread" of dissemination performed by the frugivore assemblage. When q = 0, diversity is equal to the number of sites receiving at least one seed dispersed by that bird species (richness); q = 1 is the exponential Shannon's index and q = 2 is the inverse Simpson's index. The higher the q value, the more weight given to the evenness of seed abundances across sampling points.

All sampling points at EP received at least one seed of *Pistacia lentiscus*, indicating seed dispersal was widespread and abundant. The spatial distribution of seed rain was however uneven, with seed abundance differing by two orders of magnitude across sampling points (Fig. 3A). Seed rain density was positively related with the number of frugivore species contributing seeds to each location ($r = 0.71$, p-value < 0.001).

Different bird species produced contrasting patterns of seed rain (Fig. 3B; Suppl. Mat. E). The most abundant bird species (*Curruca melanocephala* and *Erithacus rubecula*) ensured widespread seed rain across the landscape, contributing seeds to more than 80% of all seed traps. The following three most consuming species (*Sylvia atricapilla*, *Turdus merula* and *Curruca undata*) dispersed seeds to more than 20% of the sampling points (Fig. 3B, Table 1). Considering the evenness in their seed deposition pattern revealed further differences among bird species. Diversity (D) scores for each bird species in Fig. 3B represent the effective number of sites receiving seeds, and the higher the degree (q), the higher the importance of evenness in seed relative abundances across sampling points. Therefore, the more pronounced the slopes in Fig. 3B, the more uneven the relative seed contribution across sites for that bird species. Thus, *E. rubecula* and *C. melanocephala* disperse seeds to a large number of sampling points (>80%) but some sites receive much fewer seeds than others, causing the drop in their respective diversity for $q > 0$. Likewise *T. merula* is the third species contributing seeds to more sites ($D = 32$ for $q = 0$) but its seed deposition was markedly concentrated at certain sampling sites leading to low diversity (D = 10.5) for q = 2. In contrast, *Curruca undata* and *Sylvia atricapilla*, which disperse seeds to fewer sites than *T. merula*, achieve a more even, widespread seed rain than the latter species (Fig. 3B).

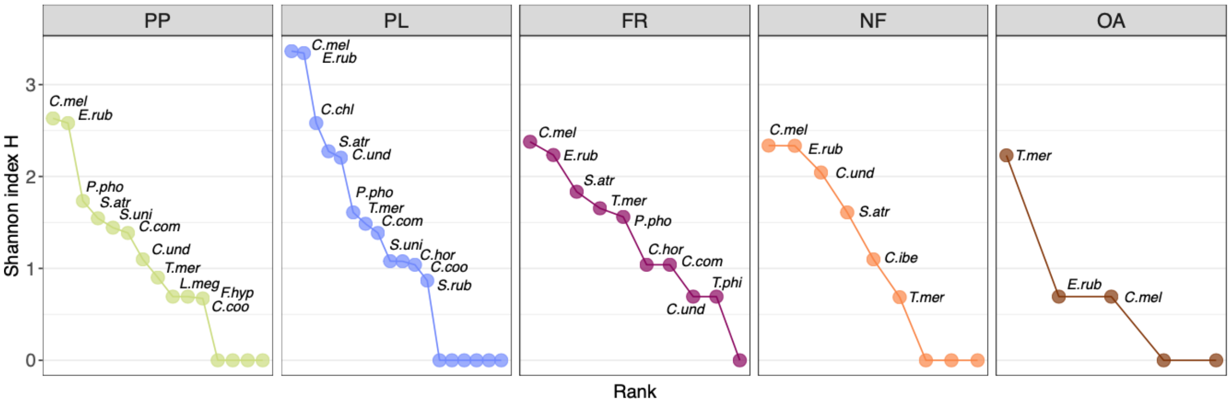

Figure 4. Cumulative contribution of birds to the diversity (Shannon index) of *Pistacia lentiscus* seed rain across sampling points for each microhabitat. Higher diversity values indicate higher spread of the seed dissemination among sites (more even distribution), while lower values suggest higher concentration of seeds across fewer sites. Panels are ordered by decreasing probability of bird's depositing seeds at each specific microhabitat. Microhabitats codes: PL = under female *Pistacia lentiscus* plants, FR = under other fleshy fruited species, NF = under non-fleshy fruited species, PP = under pine trees, OA = open areas. Animal species codes in alphabetical order: *C.chl = Chloris chloris, C.com = Curruca communis, C.coo = Cyanopica cooki, C.hor = Curruca hortensis, C.ibe = Curruca iberiae, C.mel = Curruca melanocephala, C.und = Curruca undata, E.rub = Erithacus rubecula, F.hyp = Ficedula hypoleuca, L.meg = Luscinia megarhynchos, P.pho = Phoenicurus phoenicurus, S.atr = Sylvia atricapilla, S.rub = Saxicola rubicola, S.uni = Sturnus unicolor, T.mer = Turdus merula, T.phi = Turdus philomelos*. Unlabelled points indicate other avian species in the frugivore assemblage contributing to just one site in that specific microhabitat in which case Shannon index is 0.

The analysis of seed rain across microhabitats also revealed contrasting differences in seed abundance and frugivores' contributions. Sites covered by *Pinus pinea* (PP) and *P. lentiscus* (PL) received the largest seed densities (122 seeds/m^2, 80% CI = 98 - 158, and 88 seeds/m^2, 80% CI = 79-101, respectively), also contributed by the largest number of frugivores (15 and 18 species, respectively) (Fig. 4, Suppl. Mat. E). In contrast, open area (OA) received very low seed densities (median 0.08 seeds/m^2, 80% CI = 0.069-0.083) brought by only three bird species, with most seed rain contributed by *T. merula* (Fig. 4). The most frequent consumers (*C. melanocephala* and *E. rubecula*) were the main contributors of seed dispersal to all microhabitats, except open areas. Some species also showed marked preference for specific microhabitats, such as *Sturnus unicolor* for pine trees, or *Curruca undata* for non-fleshy plants or *Chloris chloris* for *P. lentiscus* plants.

Bird species	**P of fruits consumed**	**P of seeds dispersed**	**P of viable seeds dispersed**	**P of seedlings recruited**	**Traps with seeds (%)**	**Prevalence of *P. lentiscus* in seed rain (%)**
Curruca melanocephala	0.3 [0.1–0.5]	0.5 [0.5–0.5]	0.5 [0.5–0.6]	0.5 [0.4–0.6]	85.0	65.5
Erithacus rubecula	0.2 [0.09–0.4]	0.3 [0.3–0.3]	0.2 [0.2–0.3]	0.2 [0.2–0.4]	82.0	85.0
Sylvia atricapilla	0.04 [0.02–0.1]	0.03 [0.02–0.04]	0.03 [0.02–0.05]	0.08 [0.05–0.1]	28.0	37.5
Turdus merula	0.04 [0.01–0.1]	0.06 [0.05–0.07]	0.04 [0.03–0.05]	0.04 [0.03–0.05]	32.0	71.2
Phoenicurus phoenicurus	0.01 [0.005–0.04]	0.02 [0.01–0.02]	0.02 [0.01–0.03]	0.03 [0.01–0.05]	18.0	94.4
Curruca communis	0.008 [0.003–0.02]	0.009 [0.006–0.01]	0.02 [0.01–0.03]	0.03 [0.02–0.04]	13.0	45.9
Sturnus unicolor	0.004 [9e-04–0.01]	0.01 [0.007–0.01]	0.03 [0.02–0.04]	0.02 [0.008–0.06]	11.0	41.5
Cyanopica cooki	0.005 [0.002–0.02]	0.005 [0.003–0.008]	0.008 [0.004–0.01]	0.02 [0.01–0.03]	7.0	16.0
Curruca undata	0.009 [0.004–0.02]	0.03 [0.02–0.04]	0.03 [0.02–0.04]	0.01 [0.007–0.02]	23.0	100.0
Curruca hortensis	0.003 [0.001–0.01]	0.006 [0.004–0.01]	0.01 [0.006–0.02]	0.009 [0.005–0.02]	7.0	66.7
Saxicola rubicola	0.002 [9e-04–0.007]	0.003 [0.002–0.005]	0.007 [0.003–0.01]	0.009 [0.003–0.02]	4.0	87.5
Luscinia megarhynchos	0.001 [4e-04–0.005]	0.001 [4e-04–0.003]	0.002 [5e-04–0.005]	0.004 [0.002–0.009]	3.0	100.0
Ficedula hypoleuca	4e-04 [1e-04–0.001]	0.001 [4e-04–0.003]	0.002 [6e-04–0.005]	0.001 [5e-04–0.003]	3.0	100.0
Turdus philomelos	4e-04 [1e-04–0.002]	0.001 [5e-04–0.003]	0.002 [5e-04–0.005]	0.001 [4e-04–0.002]	3.0	50.0
Sylvia borin	3e-04 [8e-05–0.001]	0.001 [5e-04–0.003]	0.002 [6e-04–0.005]	7e-04 [2e-04–0.002]	1.0	60.0
Chloris chloris	0.3 [0.08–0.6]	0.02 [0.01–0.02]	0.02 [0.01–0.03]	7e-04 [1e-04–0.002]	18.0	85.7
Curruca iberiae	5e-05 [1e-05–2e-04]	0.004 [0.002–0.01]	0.008 [0.003–0.02]	1e-04 [5e-05–2e-04]	4.0	66.7
Muscicapa striata	3e-05 [5e-06–2e-04]	4e-04 [8e-05–0.001]	7e-04 [1e-04–0.003]	8e-05 [3e-05–2e-04]	1.0	100.0
Fringilla coelebs	0.002 [6e-04–0.006]	8e-04 [3e-04–0.002]	0.001 [3e-04–0.003]	6e-06 [2e-06–2e-05]	2.0	100.0
Pyrrhula pyrrhula	7e-05 [2e-05–3e-04]	5e-04 [1e-04–0.001]	8e-04 [2e-04–0.003]	3e-07 [9e-08–7e-07]	1.0	100.0

Table 1. Metrics defining frugivores' role in *Pistacia lentiscus* seed dispersal and recruitment. First four columns refer to P (proportion) indicating the relative contribution of that bird species to the total service provided by all birds at EP site. Bird species are listed in descending order by the proportion of seedlings recruited. Numbers indicate the median of the corresponding posterior distributions while numbers in brackets indicate 80% credible interval. The last two columns refer to the general role of birds in the population. 'Traps with seeds (%)' indicates the percentage of seed traps receiving at least one *P. lentiscus* seed dispersed by a bird species. 'Prevalence of *P. lentiscus* in seed rain (%)' indicates the percentage of *P. lentiscus* seeds found in bird droppings out of the total number of different seeds dispersed by bird species.

Subsequent consequences of seed dispersal

Post-dispersal seed fate (Fig. 1) varied among microhabitats, however these differences were not pronounced (Table 2; Fig. S4). TPs refer to the probabilities that a propagule reaching a specific demographic stage will survive the ecological process acting at that stage; thus, these are stage-specific transition probabilities. First, the probability of surviving post-dispersal rodent predation was very low in all microhabitats (median = 0.008; 80% CI = 0.001 – 0.07), but slightly higher under pine trees (median = 0.02) and open areas (median = 0.01). Seedling emergence for viable seeds was around 8% (80% CI = 0.04 – 0.18). Seeds arriving to open areas had the highest probability of emergence (median = 0.17) and seeds falling under fleshy-fruited species the lowest (median = 0.05). Seedling survival through their first summer was slightly higher than the previous transition stages (median = 0.25; 80% CI = 0.09 – 0.53), being highest under non-fleshy fruited plants. Lastly, the probability of surviving until their second summer was around 20% (80% CI = 0.02 – 0.54), being significantly lower in open areas (median = 0.02). In the end, the overall probability of recruitment (OPR) after seed arrival was similar among microhabitats (median = 1.9×10^{-5}; 80% CI = $1.3 \times 10^{-6} – 2.6 \times 10^{-4}$), as the effects of different post-dispersal stages partially cancelled each other. Seeds arriving under pine trees had the highest probabilities of recruitment, yet these probabilities considerably overlap with those of seeds arriving under fleshy-fruited species, the lowest quality microhabitat (Table 2).

Table 2. Transition probabilities (TPs; see Fig. 1) and overall probability of recruitment (OPR) in different microhabitats. Numbers in brackets denote 80% credibility intervals. TP is the probability that a propagule gets from the previous stage to the subsequent stage (e.g., probability that a seed that escaped seed predation emerges as a seedling). The OPR is the cumulative probability of recruitment across all successive stages; it was calculated by multiplying the full distribution of the posterior probabilities at each demographic stage after seed arrival (i.e., not considering the first row).

	Fleshy-fruited species (FR)	**Non fleshy-fruited species (NF)**	**Open ground areas (OA)**	***Pistacia lentiscus* female plants (PL)**	**Pine trees (PP)**
P seed arrival at EP site (TP4)	0.19 [0.15 – 0.24]	0.5 [0.44 – 0.58]	0.00018 [0.00015 – 0.00022]	0.28 [0.24 – 0.33]	0.019 [0.015 – 0.026]
P escape seed predation (TP5)	0.0068 [0.0012 – 0.034]	0.0054 [0.00051 – 0.042]	0.013 [0.0015 – 0.096]	0.0037 [0.00036 – 0.029]	0.023 [0.0023 – 0.15]
P seedling emergence (TP6)	0.051 [0.027 – 0.086]	0.091 [0.05 – 0.16]	0.17 [0.094 – 0.25]	0.087 [0.049 – 0.15]	0.052 [0.028 – 0.097]
P seedling survival to 1st summer (TP7)	0.12 [0.085 – 0.21]	0.52 [0.32 – 0.73]	0.3 [0.21 – 0.42]	0.26 [0.14 – 0.38]	0.14 [0.061 – 0.26]
P seedling survival to 2nd summer (TP8)	0.16 [0.048 – 0.34]	0.11 [0.019 – 0.34]	0.023 [0.0064 – 0.069]	0.45 [0.26 – 0.63]	0.4 [0.18 – 0.65]
Overall Probability of Recruitment	5.5×10^{-6} [6.5×10^{-7} – 4.1×10^{-5}]	2.3×10^{-5} [1.1×10^{-6} – $3.3\ 10^{-4}$]	1.3×10^{-5} [9.8×10^{-7} – 1.4×10^{-4}]	3.4×10^{-5} [2.7×10^{-6} – 3.1×10^{-4}]	5.3×10^{-5} [4.2×10^{-6} – 4.7×10^{-4}]

Transitions between demographic stages and total recruitment

Seedling recruitment experienced a 6-order magnitude decay from ripe fruit production stage to the seedling survival through their second summer stage. From nearly a million fruits initially produced by the 40 studied plants at EP site, we estimate that only a few seedlings (median = 1.6, 80% CI = 0.2 – 10.1) were recruited and survived through their second summer (Suppl. Mat. F and G). Individual plants' probability of recruitment was quite even, although four individual plants had 2-3 times higher probability of recruiting than the others (Suppl. Mat. F). Recruitment of individual plants was not correlated with the proportion of viable seeds found in the crop (r = 0.16, p = 0.32), suggesting that higher plant investment in viable seeds does not directly translate into higher recruitment. Overall, we estimate that the median number of fruits required to recruit a 2-year-old seedling was 514,000 fruits. For context, crop sizes in our focal plants ranged from 3,500 to 119,000 fruits.

Of all the demographic transitions studied, post-dispersal predation by rodents was the most limiting stage, followed by seedling emergence (Fig. 5 and Table 2). With the exception of Fringillidae (mainly *Chloris chloris,* which destroyed almost all seeds consumed), bird species' contribution to recruitment was directly related to their fruit consumption intensity (r = 0.81, p-value < 0.001 for all birds species, r = 0.99, p-value < 0.001 for only legitimate dispersers, Fig. 5A and Table 1).

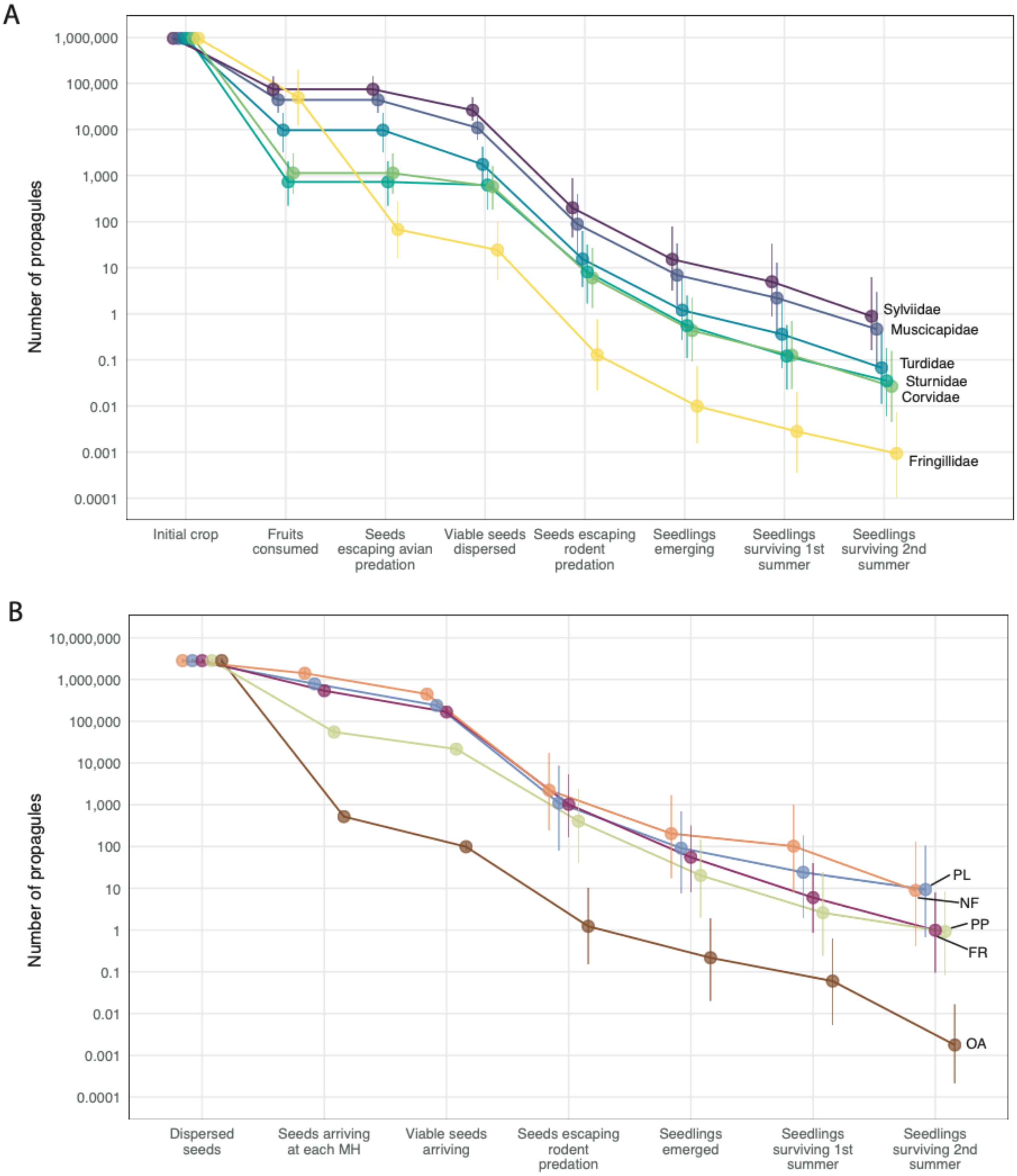

Figure 5. Decline in the number of propagules of *Pistacia lentiscus* (fruits or seeds depending on the demographic stage) along the seed dispersal and recruitment process. Panel A shows the contribution of different bird families along the recruitment process for the 40 plants studied at EP site. Panel B shows the demographic transition for seeds dispersed at different microhabitats for the whole *P. lentiscus* population at EP site. Each point represents the median of the posterior distributions and bars represent 80% CI. Note the log-scale in y-axis.

When examining total recruitment at EP site, based on seed rain density at the population level rather than crop production of the 40 focal plants, *Pistacia lentiscus* (PL) and non-fleshy fruited species (NF) emerged as the microhabitats where most seedlings were recruited (median number of seedlings in PL = 11, 80% CI = 1 – 98; median number of seedlings in NF = 10, 80% CI = 1 – 119; Fig. 5B). This is largely explained by the large area covered by both microhabitats at EP site (45% NF and 22% PL) and their good overall quality in terms of recruitment probabilities (Table 2). Open area, despite being potentially suitable, showed virtually no recruitment (median number of seedlings = 1.3×10^{-3}; 80% CI = 1×10^{-4} – 0.02, Fig. 5B) because of the limited arrival of seeds. Pine trees (PP) are very scarce in our study site (1% cover) and received relatively few seeds, yet the lower rodent predation in this microhabitat led to relatively high recruitment considering its reduced extent. We estimate that for every million seeds arriving to pine trees, this microhabitat would be able to recruit 15 seedlings (80% CI = 1.4 –123), while fleshy fruited plants would roughly manage to recruit 2 seedlings (80% CI = 0.2 –14). Overall, we estimate the total number of recruits surviving the second summer was 47 (80% CI = 9 – 249), coming from ~2.8 million seeds dispersed (80% CI = 2.5 - 3.3 million) for a total area of 4.1 ha.

DISCUSSION

Here we examine the sequential stages from fruit production to seedling recruitment of a fleshy-fruited plant to obtain an integrative view of plants' reproductive cycle (Schupp & Fuentes, 1995). This integrative approach enabled us to disentangle the role of frugivores, seed dispersal, and microhabitat deposition along the demographic transitions of a seed until establishing as a second-year seedling. We have found a decoupling of the dissemination and recruitment processes: despite the overall high fecundity of *P. lentiscus* plants and the large array of frugivores dispersing its seeds, which ensure a widespread and relatively abundant seed rain, most seeds arrive at suboptimal microhabitats for seedling recruitment. As a result, individual plants must produce large amounts of fruits to ensure minimal recruitment.

Causes and consequences of seed viability on plant recruitment success

Plants widely differed in the amount of viable seeds they produced. The causes for this variation are not clearly understood, however they seem to be related to a combination of plants' individual life history, pollen limitation and water allocation (Jordano, 1988; Verdú & García-Fayos, 1998). Higher investment in viable seeds did not seem to directly increase individual plant's recruitment, probably because other factors and processes are also mediating in recruitment success. Having unfilled seeds is hypothesised to have evolved to reduce seed lost to pre-dispersal predation (Fuentes & Schupp, 1998; Traveset, 1993; Verdú & García-Fayos, 2001). The production of large fruit crops, even if unviable, can also contribute to attracting higher amounts of dispersers, which also explains the benefit of retaining parthenocarpic and aborted fully-developed fruits in the crop. Yet we found no evidence in the two study populations that larger fruit crops resulted in an increased percentage of viable seeds dispersed relative to unviable seeds dispersed. Noteworthy, this study did not follow the identity of individual plants' seeds after dispersal, but inferred average seed fate at the population-level. Besides seed viability, individual differences in seed size likely affects post-dispersal success (predation, germination and seedling survival; Alcántara & Rey, 2003). Further research that tracks maternal seed identity through post-dispersal stages will help to understand the effect of seed viability investment on recruitment.

We found slightly lower viability in seeds dispersed compared to the initial viability of plants' crop. This was unexpected as bird species positively select black fruits of *P. lentiscus* that have higher viability rates than red fruits (see also Jordano, 1989). This preference may be offset by the fact that birds consume both the more abundant, unripe fruits and the fully ripe fruits (either with viable seeds or not). It is also possible that dispersed seeds decrease their viability when exposed to harsh climatic conditions such as marked changes in temperature, moisture and heat exposure (Franchi et al., 2011). *Pistacia lentiscus* seeds are sensitive to very high temperatures (Salvador & Lloret, 1995) and rarely form seed banks because of their short seed longevity (García-Fayos & Verdú, 1998). This explanation is consistent with the fact that seeds dispersed by *Turdus merula*, which deposit most seeds at exposed open areas, showed the lowest viability (Suppl. Mat. B).

Frugivore and microhabitat roles in seedling recruitment

Pre- and post-dispersal processes of plants are often studied in isolation. Integrative studies that connect frugivore consumption with seedling recruitment are much less frequent (e.g., Côrtes et al., 2009; Donoso et al., 2016; Herrera et al., 1994; Jordano & Herrera, 1995; Jordano & Schupp, 2000; Rey & Alcántara, 2000; Schupp, 1995). Here we managed to estimate the recruitment success of individual plants from seed production to seedling survival, assessing the delayed consequences of pre-dispersal (e.g., seed viability, frugivore predation) and post-dispersal stages (frugivore-mediated seed rain, microhabitat-associated rates of seed predation or seedling survival) on plant overall recruitment success. Moreover, our analysis allowed assessing the contribution of each frugivore species to final recruitment.

Our results suggest that bird species' contribution to *P. lentiscus* recruitment is stable along demographic transitions. The number of seedlings recruited through the interaction with birds was directly related to their quantity of fruit consumption. The major exception are Fringillids, which shifted from playing an important role in fruit removal to destroying nearly all the seeds consumed, contributing only marginally to recruitment (Heleno et al., 2011). The fact that animals’ recruitment service is mainly guided by consumption (the frequency component) indicates redundancy in their dispersal service (Quintero et al., 2023; Rehling et al., 2023).

Despite ample functional redundancy among frugivores, their dispersal services were complementary in some important aspects, such as temporal and spatial patterns. Birds present at the beginning of the fruiting season (trans-Saharan migrants) dispersed a greater amount of viable seeds than summer migrants (in congruence with González-Varo et al., 2019), thus increasing their relative contribution to recruitment (Table 1, Fig. S1). In addition, although the main disperser species deposited seeds in all microhabitats, bird species differed in their contribution to different microhabitats most likely as a consequence of preferences for good perching sites for resting (Athiê & Dias, 2016). These bird preferences translated into microhabitat differences in the amount of seed rain and the diversity of bird species contributing to it. For example, most of the (few) seeds arriving at open areas are brought by a single bird species, *Turdus merula*. Hence, this disperser must play an important role in colonising new spaces, and its eventual local disappearance could have important consequences on *P. lentiscus’* colonisation ability and plant community structuring (Campo-Celada et al., 2022; González-Varo et al., 2017; Isla et al., 2023). The overall spatial clumping of the seed rain was concordant with many previous studies (e.g., Arnell et al. 2021; Clark et al. 1998). The unevenness found in seed deposition sites together with microhabitat preferences illustrate how bird species’ differences in site fidelity and landscape use generate a patchy template on which plant regeneration takes place. This heterogeneous and non-random seed deposition leads to the creation of orchards (aggregation clusters of heterospecific seeds and seedlings; Lázaro et al. 2005), having lasting consequences on local plants’ recruitment. We expect the spatial and temporal complementary role of frugivores' on dispersal will be differently manifested in other plant populations and habitats with varying animal-disperser abundances and microhabitat compositions (García-Rodríguez et al. 2022).

Differences in microhabitat quality for arriving seeds along the regeneration cycle were discordant; high-quality patches in some stages became low-quality patches in others, as previously reported in several studies (Clark et al., 1999; Gómez-Aparicio, 2008; Herrera et al., 1994; Jordano & Herrera, 1995; Schupp, 1995). These differences have been attributed to both biotic and abiotic factors such as plant-plant competition/facilitation, fungal pathogens, insects, temperature, humidity or soil nutrients (Fricke et al., 2014; Traveset et al., 2003). High seed densities at fleshy-fruited microhabitats may enhance the call-effect for rodent predation and increase plant-plant competition. In contrast, open areas, a microhabitat typically avoided by birds (Alcántara & Rey, 2003; Jordano & Schupp, 2000), lead to low seed predation due to lack of shelter for rodents (Fedriani & Manzaneda, 2005), but high seedling mortality due to higher water and irradiance stress (Amat et al., 2015).

Spatial discordance between seed rain and recruitment has been repeatedly reported (Houle, 1992; Jordano & Herrera, 1995; Rey & Alcántara, 2000; Schupp & Fuentes, 1995; but see García et al., 2005). In this study we found that microhabitat differences in the transition probabilities between demographic stages partially cancelled each other, leading to small differences in the overall probability of recruitment (OPR) among microhabitats. However, variations between microhabitats were large enough to detect small spatial discordances, depicted by the differences in the shape and crossings of the decaying cumulative curves among microhabitats (Fig. 5B, Fig. S4). In the end, recruitment was mostly determined by the initial number of seeds arriving at each microhabitat, which was again determined by the microhabitat preferences of bird frugivores.

Demographic bottlenecks and recruitment success

Post-dispersal seed predation emerged as the main limiting demographic transition in *P. lentiscus* regeneration (also reported in González-Varo et al., 2019), followed by seedling emergence, in congruence with similar studies carried out in Mediterranean species (Gómez-Aparicio, 2008).

The overall probabilities of recruitment (OPR) for *P. lentiscus* at our study site were similar, although a bit lower, than those found for other Mediterranean plants (Gómez-Aparicio, 2008; Herrera et al., 1994; Jordano & Herrera, 1995; Rey & Alcántara, 2000; Traveset et al., 2003). Even if the OPR were low and overlapped between microhabitats, some microhabitats differed in their median probability by as much as 10-fold, with pine trees (PP) showing considerably larger suitability for recruitment than fleshy-fruited (FR) or open areas (OA). These differences, if accumulated over time, can have important consequences for landscape regeneration. In fact, evidence from the literature supports significantly lower recruitment of *P. lentiscus* in open areas compared to beneath tree canopies (García-Fayos & Verdú 1998), including pine trees (Maestre et al. 2004). Additionally, recruitment can be dependent on population maturity and establishment. Our study site is a densely vegetated shrubland, dominated by reproductive adults of *P. lentiscus*, while young saplings of this plant are harder to find. García-Fayos & Verdú (1998) also found recurrent low densities of *P. lentiscus* seedlings in closed shrublands.

The quantity of avian fruit consumption was the key determinant of plants' recruitment success, while qualitative differences among frugivores and microhabitats played a minor role. This underscores the importance of a reliable and abundant seed dispersal service for recruitment, and its susceptibility to eventual fluctuations in frugivore abundances. We anticipate that the identity of frugivores and their seed deposition patterns will become important in different habitats, under natural succession or anthropogenic disturbances scenarios, where recruitment success will be dependent on the distribution of available microhabitats in the landscape (García-Rodriguez et al. 2022, Rost et al., 2009; Wenny & Levey, 1998).

CONCLUSION

Our investigation of the recruitment process of *Pistacia lentiscus*, from fruit production to seedling recruitment, unveiled a key role of frugivores and their non-random microhabitat use on individual plant recruitment success. Frugivore effects include both immediate interaction outcomes during fruit consumption and, importantly, delayed effects lasting after seed dissemination.

Pistacia lentiscus overcomes its high seed unviability by investing in large crops and representing a staple nutritious resource to many bird species, which disperse vast amounts of seeds. We found that different bird species provide largely overlapping, but also complementary, dispersal services. Bird species markedly differ in the amount of fruits they consume and in the proportion of viable seeds they disperse, related to the timing of their arrival during the fruiting season. Functional redundancy in birds' overall post-dispersal quality makes *P. lentiscus* particularly robust to the loss of minor consuming species and therefore more resilient to ecosystem disturbances (Loiselle et al., 2007).

This study supports previous literature highlighting the importance of consumption frequency for plant recruitment (e.g., Rehling et al., 2023; Vázquez et al., 2005). However, behind the major effects of interaction frequency, the differences detected in spatial patterns of seed deposition by birds and the suitability of microhabitats for future plant recruitment underscore the importance of evaluating post-dispersal consequences of plant-animal frugivory interactions. Our results illustrate the complexity of the recruitment process in which there is an interplay between plants' investment in viable seeds, bird consumption and dispersal service, and the suitability of the microhabitat to which seeds arrive. The loss of certain avian species with specific phenologies (e.g., frugivorous wintering migrants; see Campo-Celada et al., 2022) and preferences for fruit consumption and land-use may impact plant recruitment in the most suitable microhabitats, having lasting consequences in plant regeneration and vegetation physiognomy.

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AUTHOR CONTRIBUTIONS

Following the CRediT author statement, the contributions for this manuscript are E.Q.: conceptualization, data curation, software, investigation, visualisation, writing—original draft, writing— review and editing; P.J.: conceptualization, data curation, project administration, software, visualisation, supervision, writing—original draft, writing— review and editing; J.M.A.: investigation, data curation; R.D.: conceptualization, supervision, writing— review and editing; F.R.S.: conceptualization, data curation, software, validation, visualisation, supervision, writing—original draft, writing— review and editing.

DATA AVAILABILITY STATEMENT

Data and code for the analyses are available at the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.8289087 (Quintero et al. 2023b) and the GitHub repository (https://github.com/elequintero/MS_P.lentiscus_demography).

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