



Spatial decision-making in acorn dispersal by Eurasian jays around the forest edge: Insights into oak forest regeneration mechanisms

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ABSTRACT

Seed dispersal is key to forest regeneration and often depends on the behavior of seed scatter-hoarding animals. However, our understanding of the decision-making of scatter-hoarders and how vegetation structure at different spatial scales affects dispersal patterns remains limited. We studied seed dispersal at the forest edge across multiple spatial scales (habitat, sub-habitat, microsites) between and within habitats with distinct vegetation structure. Our model system is a mixed-oak forest dominated by holm oak (*Quercus ilex*) and an adjacent shrubland dominated by the shrub *Retama sphaerocarpa*. For three years, we tracked the movement of acorns by a keystone scatter-hoarder, the Eurasian jay (*Garrulus glandarius*). At the coarse scale, jays did not show a preference for caching acorns either in the forest or in the shrubland when the source tree was within the forest. However, when the source tree was on the forest edge or was an isolated oak tree in the shrubland at < 200 m from the forest, jays showed a preference for caching in the forest. Conversely, when isolated oak trees were > 200 m from the forest, all acorns were dispersed in the shrubland. Dispersal distances were shorter within the forest than within the shrubland. At an intermediate scale, within the shrubland jays preferred to cache acorns under large retamas while avoiding gaps. In the forest, jays also avoided gaps and preferred certain woody species and vertical vegetation structures, although these preferences varied across feeders. At the finest scale, jays selected stones as cache microsites. Thus, the selection of acorn caching sites followed a hierarchical and selective top-down process across different spatial scales. The position of the source trees in the landscape determined habitat preference and dispersal distance. We detected different preferences in response to similar vegetation structure and composition, indicating that the decision-making process is flexible at an intermediate scale that generates diverse spatial patterns of dispersal. This study sheds light on the intricate decision-making process of seed caching by scatter-hoarders, and the consequences for the spatial patterns of seed dispersal as well as the expansion and regeneration of oak forests.

1. Introduction

Forest regeneration and expansion begin with seed dispersal, which links adult plants with offspring recruitment places. The spatial pattern of dispersal has profound effects on the probability of successful recruitment, and the dynamics, structure and gene flow of plant populations (Schupp and Fuentes, 1995; Bohrer et al., 2005). However, unravelling the mechanisms by which seed dispersal causes these effects has proven to be a challenge (Cousens et al., 2010).

Zoochory is driven by animal behavior (Alcantara et al., 2000; Rodríguez-Pérez et al., 2012), especially when seed carrying and scatter

dispersing is deliberate, namely scatter-hoarding (Hulme, 2002; Vander Wall and Beck, 2012). Scatter-hoarders move seeds away from the mother plant; cache them separately or in small groups mostly in the ground, reducing seed predation and desiccation, in places generally suitable for seed germination and seedling establishment; and fail to recover a variable fraction of the cached seeds (Pesendorfer et al., 2016; Lichti et al., 2017; Gómez et al., 2019). Many of the dominant woody species in Holarctic temperate forests rely on scatter-hoarders for dispersal (Pesendorfer et al., 2016; Kurek et al., 2019; Wróbel et al., 2022). However, the general principles of decision-making in scatter-hoarders for seed caching and their consequences for the spatial

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pattern of plant dispersal and recruitment remain little known (Gómez, 2003; Lichti et al., 2017; Martínez-Baroja et al., 2021).

Seed dispersal and caching imply economic decisions by the animal, i.e., choices regarding investment of time and energy, and minimizing predation risk to make some profit in the future (Lichti et al., 2017). Success in recovering seeds dispersed in the fall is critical to winter survival of many scatter-hoarders from temperate and cold biomes (Bossema, 1979; Bennett, 1993). The profitability of seed caching, i.e., the proportion of cached food recovered, depends on trade-offs among scatter-hoarder predation risk, pilfering risk of the cached seed, the probability of finding cached seeds and the dispersal distance, among others (Clarkson et al., 1986; Lichti et al., 2017). Predation risk is heterogeneously distributed through the landscape and influences the way in which scatter-hoarders use their habitat. Consequently, predation risk can regulate the interactions between scatter-hoarders and the plants that they disperse (Laundré et al., 2014). Predation risk of scatter-hoarders seems to be driven mainly by the vegetation structure of their habitat, which provides concealment and refuge (Caraco et al., 1980; Verdolin, 2006). Conversely, pilfering of cached seeds is higher under plant canopy than in open areas because small post-dispersal seed predators are also potential preys preferentially foraging in protected areas (Perea et al., 2016). Seed recovery effectiveness by scatter-hoarders also depends on the ability to create mental maps of caching sites (Feenders and Smulders, 2011; Källander, 2007). For this purpose, scatter-hoarders select elements of the landscape as landmarks to cache and recover seeds (Bossema, 1979; Gómez, 2003; Morán-López et al., 2015). Dispersal distance is a result of all these economic decisions, but also a decision in itself by the effort and time spent in covering that distance (Gómez, 2003; Morán-López et al., 2015; Lichti et al., 2017).

Three main seed dispersal decisions by scatter-hoarder, namely selection of foraging trees, seed transport to caching areas and caching seeds in specific sites, affect the performance of plants by changing the likelihood of seed survival and subsequent seedling establishment (Pesendorfer et al., 2016). First, scatter-hoarders select the seeds that they cache (Bossema, 1979; Lichti et al., 2017). For example, compared to trees in forest patches, isolated trees frequently produce more and healthier seeds (Pausas et al., 2009; Bogdziewicz et al., 2018), which can drive foraging by scatter-hoarders (Christensen and Whitham, 1993, 1991). Second, some highly mobile scatter-hoarders, such as corvids, often transport seeds between habitats (Gómez, 2003; Gómez et al., 2008; Martínez-Baroja et al., 2021). However, we still have a limited knowledge of how scatter-hoarders move seeds across the landscape. To do this it is necessary to track the movement of seeds under natural conditions, linking mother plants with seed caching sites. While several studies have shown that habitat preferences by scatter-hoarders can increase long-distance dispersal events (Gómez, 2003; Lenz et al., 2011), it is less known whether the type of foraging habitat and its structure affect dispersal distances and why. Third, the caching site determines seed fate, such as seed recovery by the scatter-hoarder or seed pilfering (Gómez et al., 2008).

We studied holm oak (*Quercus ilex* L.) acorn dispersal throughout the landscape by the Eurasian jay (*Garrulus glandarius* L.), a key scatter-hoarder, by tracking acorn movements. We focused on the holm oak because it is the dominant tree in many forests of the western Mediterranean basin (Kappelle, 2006; Pesendorfer et al., 2016). Our study system is a mixed oak forest adjacent to a shrubland dominated by the pioneer shrub *Retama sphaerocarpa* (L.) Boiss (hereafter retama) with several large, isolated holm oak trees. Specifically, we assess whether: 1) acorn dispersal pattern depends on the location of the source oak tree in the landscape (within the forest, forest edge or shrubland) and the distance of the tree to the forest edge. We hypothesized that acorn dispersal would be disproportionately towards the forest, due to the forest habit of the jay (Gianpasquale and Alberto, 2019; Pons and Pausas, 2008), but that the preference for forest would be reduced as the distance of isolated oak trees in the shrubland to the forest edge increases due to increased transportation costs among others (H1). 2) Dispersal distances

depend both, on the location of the source tree and on the acorn caching habitat (i.e., inter-habitat, intra-forest or intra-shrubland dispersions). We hypothesize that dispersal distance will be greater when acorn caching involves habitat change, especially from shrubland towards the forest, due to forest preference of jays (Gómez, 2003; Morán-López et al., 2015); jays may forage far from the forest for high value resources, but they are expected to return to the forest for caching while there is no incentive for making long distance dispersal events from the forest into the shrubland (Caraco et al., 1980; Verdolin, 2006). With respect to within-habitat dispersal events, we predict distances will be greater in the shrubland than in the forest due to the lower density of landmarks, e. g. woody vegetation (H2). And 3) acorn dispersal pattern depends on the sub-habitats pattern, i.e., woody vegetation vs. gaps, and the microsites pattern. We hypothesize that certain sub-habitats (as woody vegetation), and microsites (as some vertical structures, volumes or discrete individuals of woody species or stones), drive acorn dispersal as they may constitute landmarks that facilitate the recovery of the cached seed (Bossema, 1979; Gómez, 2003; Morán-López et al., 2015) (H3).

2. Material and methods

2.1. Study area

The study area is an agroforestry ecosystem in Uceda, Central Spain (UTM X: 462 830; UTM Y: 4 524 000; ETRS89 30N), 730 m a.s.l. The climate is continental Mediterranean and mean annual temperature and rainfall are 13 °C and 500 mm (Torero Sánchez, J., 1998). According to IGN (2006) and following Soil Taxonomy (Soil Survey Staff, 2003), Haploxeralfs-Calcixerepts/Haploxerepts soil associations are found in the area, with silt loam to loam textures. The study area has two main habitats (Figs. S1 and S2): 1) forest, ca. 166 ha, dominated by holm oak and Portuguese oak (*Quercus faginea*), accompanied by terebinth (*Pistacia terebinthus*), cade juniper (*Juniperus oxycedrus*), hawthorn (*Crataegus monogyna*), jasmine (*Jasminum fruticans*), gum rockrose (*Cistus ladanifer*) and wild rose (*Rosa* spp.). Shrub species abundances vary among the three forest sampling sites (Fig. S3). Forest management ceased in 1984 except in a few small sites where some coppice thinning has been made. 2) Shrubland, ca. 106 ha, dominated by retama (*Retama sphaerocarpa*) with a mean cover of 9.5%, and with sparse isolated holm oaks, most of them of large size, Portuguese oak, terebinth, cade juniper, wild rose and hawthorn. Most shrubland is located on a flat riverbank with an average width of 467 m, but it also occupies several plains within the forest. Cereal farming in the plains ceased in 1984, although occasional sheep and goat grazing has remained in the area. Since 1985, the fields have progressively changed to a retama shrubland, which is progressively being colonized by oaks (Cruz-Alonso et al., 2020).

2.2. Experimental design for seed dispersal

An acorn dispersal experiment was replicated in three zones, separated between 900 and 1500 m from each other (Fig. S1). Seed dispersal assessment in each zone lasted from January to early April 2009–2011. We installed the acorn feeders and began feeding them in late October and November coinciding with the beginning of holm oak acorn dispersal. However, jays did not visit the feeders while natural acorns were available in the landscape. To our knowledge, there are no studies showing seasonal variation in jay dispersal behavior. Therefore, research is needed to elucidate this point. Each zone consisted of three feeders installed in large holm oaks located: 1) within the forest (F); 2) in the forest edge (FE); and 3) in the shrubland (S) in isolated trees (henceforth feeder location). The feeders within the forest and shrubland were located at different distances from the forest edge, depending on the overall forest structure and the locations of suitable trees (Table S1). An additional feeder (S0) was installed in the shrubland between the first and second zone to expand the range of distances from the feeders to the forest edge (S0 was designated as the farthest feeder

from the forest; Fig. S1 and Table S1). Feeders consisted of 2.5 m long wooden slats or straight oak branches, with a basket fixed at the end. To prevent rodents from accessing the baskets, a funnel was attached in the middle of the slat or branch (Fig. S4). The feeders were installed horizontally in the tree crown leaving the basket outside, 3–5 m high from the ground. In the trees of the forest edge, feeders were orientated towards the shrubland. Feeders were weekly filled with holm oak acorns each fall-winter to attract jays, which were identified by cameras (Bushnell Trail Scout-119800, Busnell Company, Overland Park, KS, EEUU) fitted on the feeders, which recorded 15 sec. videos when movement was detected. Cameras were placed at four feeders covering all zones and feeder locations (Fig. S1), remaining active for at least one month in each feeder while the dispersal experiment was being conducted. The information obtained from the videos was used to confirm the exclusive involvement of Eurasian jays in acorn removal and to characterize their acorn removal behavior. However, no data from the videos were used in the data analyses.

To locate caching sites, we inserted radio-transmitters (PIP21LL, Biotrack, Wareham, Dorset, UK; weight: 2.2 g) inside the acorns (Pons and Pausas, 2007; Martínez-Baroja et al., 2019). We transversally cut the acorns and emptied part of the cotyledons to fit the radio transmitter with the antenna rolled up. Then, we closed the acorns with instantaneous cyanoacrylate adhesive (Fig. S5). When we detected acorns disappearing from the feeders, we placed batches of 8–15 radio-tagged acorns per feeder, mixed with approximately the same number of untagged acorns to minimize possible acorn rejection by jays. One week later, caches of radio-tagged acorns were located in two steps. First, the caching vicinity was determined with a Yagi antenna connected to a radio receiver (Biotrack SIKA Radio Tracking Receiver, Wareham, Dorset, UK). Finally, precise locations were determined using a metal detector (White's Auto-Scan Personal Search Detector, Tulsa, Oklahoma, USA). Once a tagged acorn was found, we registered if it was predated or cached intact, cache location using a GPS, distance to the feeder, habitat type, i.e., forest or shrubland, and sub-habitat and microsite type (see below). Only cached intact acorns were used for statistical analyses. Intact acorns and transmitters of predated acorns, which were reinserted into new acorns, were replaced in the feeders in repeated batches until the end of the study period. We could not estimate acorn recaching by jay. However, we believe that recaching did not bias our results as it is not a common process among birds (Vander Wall, 1990; Waite and Reeve, 1995) and rodents are mainly larder-hoarders and predate most of the handled acorns (Gómez et al., 2019; unpublished data).

2.3. Assessment of sub-habitats and microsities used for seed caching

To analyze whether jays showed preferences for caching acorns in some sub-habitats and microsities, we quantified their cover around each feeder. The sampled area was decided after the dispersal experiment, when we knew the area used by jays to cache acorns around each feeder. We used four radial linear transects using tapes separated 90° and departing from each feeder. In the forest edge feeders, three transects were made in the forest and one in the shrubland. Transect length was defined as the distance that contained 85% of the cached acorns for a given feeder. Because dispersal distance varied among feeders, transect lengths varied accordingly. In both the shrubland and the forest, the sub-habitats were the sites beneath the canopy of woody vegetation (shrubs and trees) and the gaps (spaces covered by herbs, chamaephytes and bare ground); and the microsities were the species identity of the woody vegetation above a given cached acorn (Table S2). Additionally, in the forest, other caching microsities were stones and three types of forest vegetation categorized by vertical structure: 1) shrubs with no trees in the overstory; 2) trees with no shrubs in the understorey; and 3) trees with shrubs in the understorey. Neither stones nor the tree + shrub category were estimated in the shrubland due to their virtual absence. We considered a tree as any individual of a tree species taller than 3 m

and a shrub as any individual smaller than 3 m of any woody species, including small trees. The cover of species and of categories of vertical forest structure were calculated as the proportion of the transect overlapped by these microsities. Stone cover in the forest was sampled every 5 m in the transects by the point-quadrat method (Levy and Madden, 1933). Only stones that protruded out of the ground more than 3 cm and larger than 25 cm² approximately were considered. To assess the size distribution of the retamas we measured the canopy size of the individuals that overlapped the transects in a subset of five FE and S feeders in zones 1, 2 and feeder S0. We measured canopy height and its width as two diameters, maximum and perpendicular to the maximum, and then calculated canopy volume assuming the canopy to be a semi-ellipsoid. Canopy size of all retamas used by jays to cache acorns in zones 1, 2 and feeder S0 was also measured in the same way.

2.4. Data analyses

To determine whether jays show a preference to cache acorns in the forest, we used generalized linear models (GLMs) with a binomial distribution and a logit-link function. We modelled the probability of acorns being cached in the forest with respect to the distance of the feeders to the forest edge, the feeder location (forest, forest edge or shrubland) and their interaction. Model selection was done using the AIC indicator (Akaike, 1987) and we used ΔAIC values < 2 units relative to the model with the lowest AIC scores to identify the best explanatory models (Crawley, 2013). We subsequently assessed whether the 95% confidence interval of the predictions of the selected model overlapped with the values of the null model. The null model represents the expected proportion of acorns cached in the forest when the jays do not exhibit a preference for any specific habitat for caching. To simulate the null model, we used the proportion of forest within a buffer zone with a radius equal to the mean dispersal distance of the jays in the experiment (41 m) at each distance from the forest edge (Fig. 1). To test the effects of feeder location (forest, forest edge and shrubland), the habitats where the acorns were cached (forest and shrubland) and their interaction on the dispersal distance, we used a GLM with a gamma distribution and an inverse-link function. To analyze the preference of jays for different sub-habitats and microsities to cache acorns, we used chi-square tests following the Monte Carlo method when necessary to compare the number of observed acorns in each sub-habitat and microsite with the number of expected acorns based on the abundance of each sub-habitat and microsite from the transect data. For each caching habitat, we used data: 1) for the forest, three F feeders and three FE feeders; and 2) for the shrubland, four S feeders. For simplicity in the analyses, we pooled the cover of isolated tree species in the shrubland (holm oak and Portuguese oak) and the cover of the less abundant shrub species in the forest and in the shrubland (*Rosa* spp., *Crataegus monogyna* and *Artemisia campestris*). To assess whether jays selected retamas of specific sizes to cache acorns, we compared the canopy volume distribution in the population of retamas with the canopy volume distribution in the subset of retamas selected by jays to cache acorns by chi-square tests using the Monte Carlo method. All analyses were performed with R version 4.1.0 (R Core Team, 2021).

3. Results

3.1. Identification and behavior of the scatter-hoarders

Cameras provided more than 600 videos showing six bird species, five of them with a single visit. The rest of the videos (99,2%) showed Eurasian jays, which was the only species that manipulated, ate, and removed acorns from the feeders. In 25% of the videos, jays selected an acorn, picked it up with the beak and dropping it until finally choosing one. In 4% of the videos chosen acorns were eaten in situ; and 35% showed flights where jays carried intact acorns away from the feeder. In 66% of those flights, jays carried a single acorn in the beak; in 3%, a

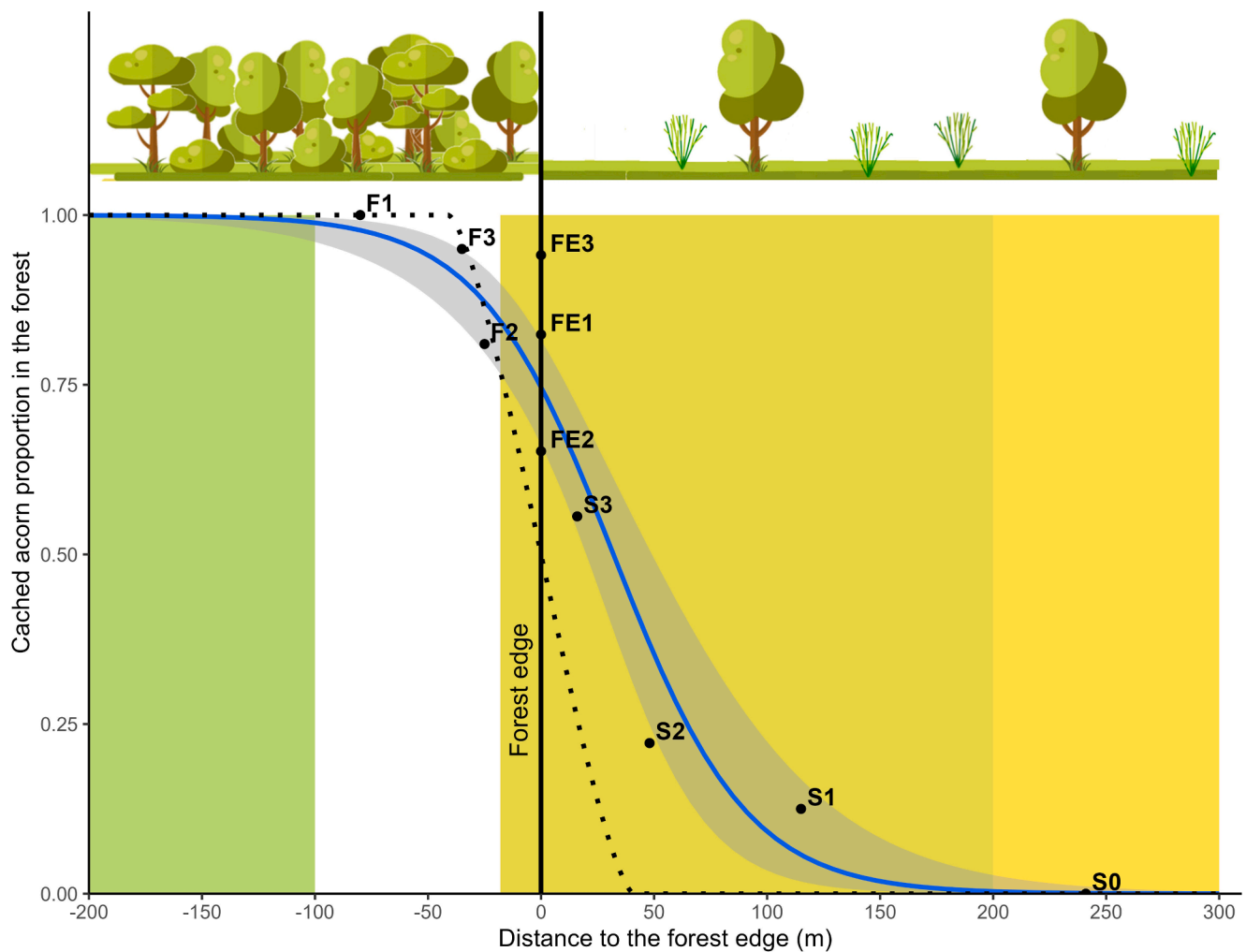


Fig. 1. Observed proportion of cached acorns in the forest with respect to the distance from each feeder (labeled points) to the forest edge (black vertical solid line). Letters of the labels represent: (F) forest, (FE) forest edge, and (S) shrubland; and numbers indicate the studied zone (Fig. S1). Adjusted logistic model to the data (blue solid line) with the 95% confidence interval (grey shadow). Null model (dot line) shows the expected proportion of cached acorns in the forest if acorns were randomly dispersed using the mean dispersal distance (41 m) of jays, that is, in the proportion to forest habitat abundance in the dispersal area. Four habitat strips parallel to the forest edge were distinguished depending whether caching behavior differed from the expected (logistic model *versus* null model): 1) in the forest at distances > 100 m from the forest edge, where jays exclusively cache acorns in the forest (dark green strip, distances where the blue line reaches $y = 1$); 2) in the forest at distances between 100 m and approximately 20 m from the forest edge, where jays show no preference for the forest to cache acorns, (white strip, when grey shadow mostly overlap dot line); 3) a strip that goes from sites in the forest at 20 m approximately from the forest edge to sites in the shrubland at < 200 m from the forest edge, where jays show high preference for caching acorns in the forest (light green strip, when grey shadow do not overlap dot line); and 4) in the shrubland at > 200 m from the forest edge, where jays show exclusive preference for the shrubland to cache acorns (yellow strip). Tree and shrubland composition were created using “Tree vector” created by macrovector – www.freepik.com. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

single acorn in the crop; and in 31%, two acorns simultaneously, one in the crop and one in the beak. In the three study years, 299 tagged acorns removed from the feeders were found, 192 of which were found cached, and the rest were found predated. Jays always cached a single acorn in a caching site. We never found any dispersal event between the different zones of the study area (Fig. S1).

3.2. Habitats and distances of seed dispersal

Of all cached acorns, 120 were cached in the forest and 72 in the shrubland (Table S1), but the proportion of acorns cached in the forest varied with the distance of the feeder to the forest edge, with the feeder location and their interaction (Table 1).

In the forest feeders, the proportion of acorns cached inside the forest decreased with the proximity to the forest edge, while the opposite occurred in the shrubland feeders (Fig. 1). When acorns came from

Table 1

Model selection for the probability of dispersed acorns to be cached in the forest considering the distance from each feeder to the forest edge, feeder location (forest, forest edge and shrubland) and their interaction. Global model (proportion of acorns to the forest \sim Distance \times feeder location) were one of two best models selected (**bold**), with a McFadden deviance of 40.94%.

Model parameters	df	AICc	Δ AICc
Distance	2	159.36	0.00
Distance \times Feeder location	5	160.36	1.00
Distance + Feeder location	4	161.51	2.15
Feeder location	3	178.43	19.07
Null model	1	256.06	96.70

inside the forest, the proportion of cached acorns in the forest was the expected, i.e., the dispersal was randomly distributed between the two habitats. However, when acorns were dispersed from shrubland feeders,

they were cached in the forest more than expected by random. In the forest edge feeders, where forest and shrubland are equally represented in our system, a higher-than-expected proportion of acorns were cached in the forest. No acorn reached the forest when acorns were removed from the farthest feeder from the forest (S0: 241 m).

Mean dispersal distance was affected by the interaction between the feeder location and the habitat where the acorn was cached (Table 2, Fig. 2). Mean dispersal distance was greatest when the dispersal involved a habitat change, i.e., from the forest to the shrubland and *vice versa*, intermediate when dispersal was entirely within the shrubland and the least when dispersal was entirely within the forest.

3.3. Seed dispersal in sub-habitats and microsites

All cached acorns were found in the ground but two acorns, which appeared in branches of the tree canopy. Acorns were usually cached at the base of a grass tussock and other herbs, within a tussock, or placed under leaf litter or mosses. They were rarely exposed above the ground or even semi-hidden, and no acorns were buried in the soil.

At all feeders in the shrubland, acorns were cached in the gap sub-habitat less than expected by chance, despite gaps constituting the most represented sub-habitat (Fig. 3). Inversely, the proportion of cached acorns in the sub-habitat beneath the canopy of woody vegetation was far higher than expected, but preferred woody species varied among feeders, rejecting completely the rest of woody species: in three of the four shrubland feeders (S0, S1 and S2), 74% of the acorns were cached under retama (Fig. 3a) while in the remaining feeder (S3), 50% of the acorns were cached under isolated trees and 13% under shrubs other than retama (Fig. 3b).

The proportion of cached acorns under retamas with canopy volumes < 25 m³ was less than or similar to the expected. In contrast, the proportion of cached acorns under retamas > 25 m³ was greater than expected (Fig. 4).

In the forest, 87% of the cached acorns were found under the vegetation canopy sub-habitat (i.e., under trees and/or shrubs), which is more than expected by chance (Fig. 5a), considering the data of all feeders grouped. Acorns were cached beneath a wide range of woody species (Fig. 5b; also see material and methods). Microsite preferences for caching acorns beneath specific woody species and beneath categories of vertical structure of the vegetation were detected, but these preferences varied among the three zones and even among feeders within the same zone. Only around feeder F1 were significant plant species preferences detected, with more acorns than expected being cached under terebinths and jasmine and fewer than expected being cached under holm oak (Fig. 5b). In three of the six feeders placed inside the forest and in the forest edge, jays showed preferences for specific vertical vegetation structure (tree, shrub, or tree + shrub). In two of these feeders, more than twice as many acorns as expected were cached under shrubs, either in sites only with shrubs or sites with tree + shrub (Fig. 5c and 5d). In the remaining feeder, frequency of acorns cached under the trees was three times greater than expected by chance (Fig. 5e). Finally, more acorns than expected were cached under or next to stones when all zones were considered together (Fig. 5f), and this pattern was observed separately in each zone.

Table 2

Model selection for the dispersal distance considering the habitat of feeder location (forest, forest edge and shrubland), the habitat of cached acorns (forest and shrubland) and their interaction. Global model (dispersal distance ~ Feeder location × Caching habitat) was the best model selected (**bold**) with R² = 0.181.

Model parameters	df	AICc	ΔAICc
Feeder location × Caching habitat	7	1715.1	0
Feeder location + Caching habitat	5	1758.2	43.03
Feeder location	4	1759.3	44.17
Caching habitat	3	1790.3	75.2
Null model	2	1793.3	78.2

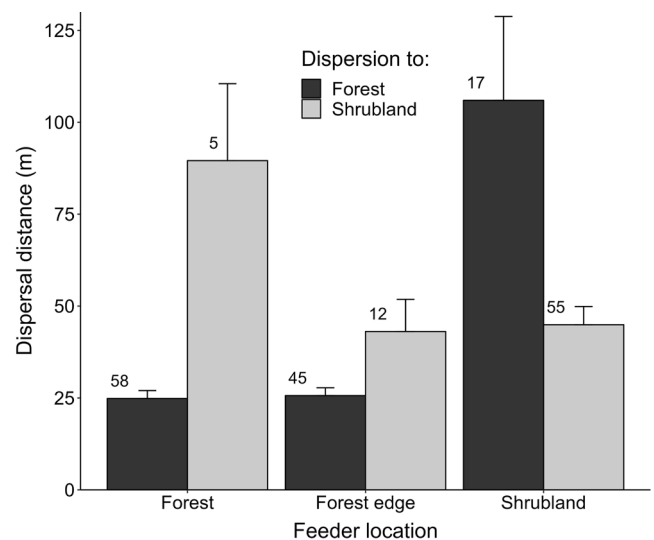


Fig. 2. Mean dispersal distances of acorn depending on the habitat of the feeder and the caching habitat. Error bars show the standard error and numbers show the number of dispersed acorns.

4. Discussion

The Eurasian jay was the sole avian scatter-hoarder observed, exhibiting compulsive caching behavior similar to previous findings in jays and other corvid scatter-hoarders across Eurasia and North America (Pesendorfer et al., 2016; Gómez et al., 2019; Martínez-Baroja et al., 2019). Jays showed a complex acorn caching process that varied with the position of mother trees in the landscape and habitat structure, with subtle differences among sites that suggested individual differences. In the following sections, we discuss the relationship between acorn caching by jays and site structure, and its implications for oak regeneration in Mediterranean forests.

4.1. Seed source location drives habitat destination and dispersal distance through the landscape

Selection of the habitat to which seeds were dispersed was conditioned by the location of the seed source tree, i.e., habitat type and distance to the forest edge (H1). Jays did not show habitat preferences for dispersal when the source trees were in the forest, including trees in the forest > 100 m from the forest edge where all dispersal events ended within the forest (Fig. 1). Dispersal towards the forest was prioritized over the shrubland when the acorn source was in the forest edge or in the shrubland < 200 m from the forest edge. When choosing the dispersal habitat, jays must weigh their own predation risk, the time and effort to transport acorns and the risk of cached acorns being pilfered to maximize caching profitability (Lichti et al., 2017). Our results suggest that jays prioritize their security over reducing pilfering of cached acorns while weighing transport costs, because: 1) jay predation risk is lower in the forest than in shrubland (Caraco et al., 1980; Verdolin, 2006); 2) post-dispersal predation of acorns is greater in the forest than in the shrubland (Kennedy, 2005; González-Rodríguez & Villar, 2012; pers. observation); and 3) in isolated trees at < 200 m to the forest edge, preference for caching inside the forest was a function of the distance from the tree to the forest (Fig. 1). Such behavior is spatially (between zones), and accordingly temporally (between years), concordant, despite spatial differences in vegetation structure and composition, which suggests that it is a characteristic of jay idiosyncrasy, possibly due to its marked forest habit (Pons and Pausas, 2008). However, when isolated trees in the shrubland were at > 200 m from the forest, acorn dispersal occurred only within the shrubland. In this later case, the cost of transporting acorns from the shrubland to the forest (e.g., higher time,

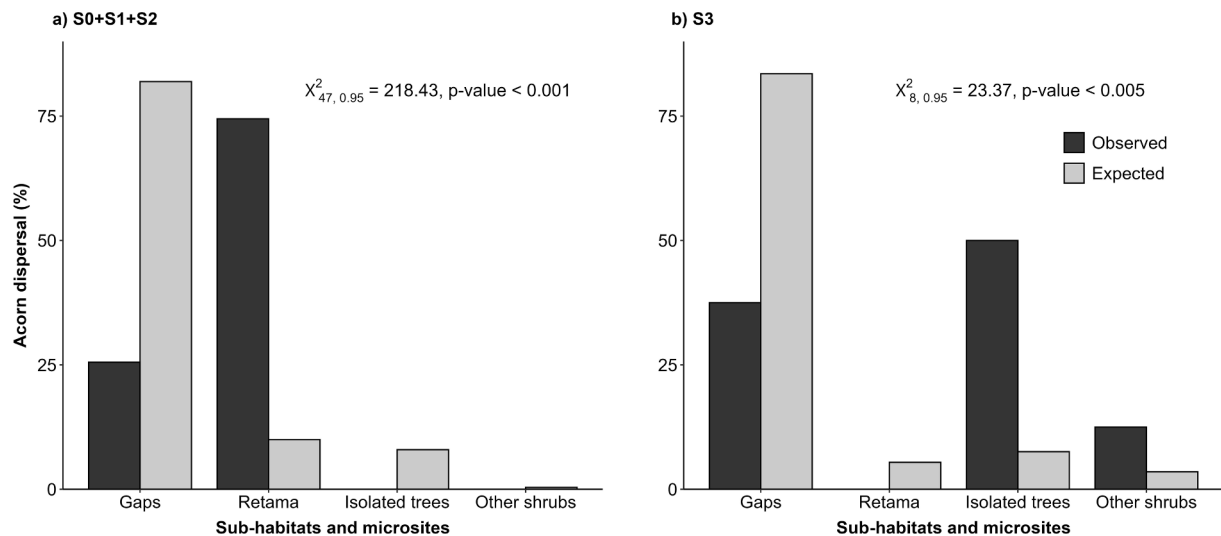


Fig. 3. Proportion of cached acorns in the shrubland sub-habitats (gaps vs. under woody vegetation), where woody vegetation was differentiated in: retama, isolated trees and other shrubs. We show results for a) feeders S0, S1, S2 together where the abundance of sub-habitats and microsities around them was similar, and b) S3 feeder.

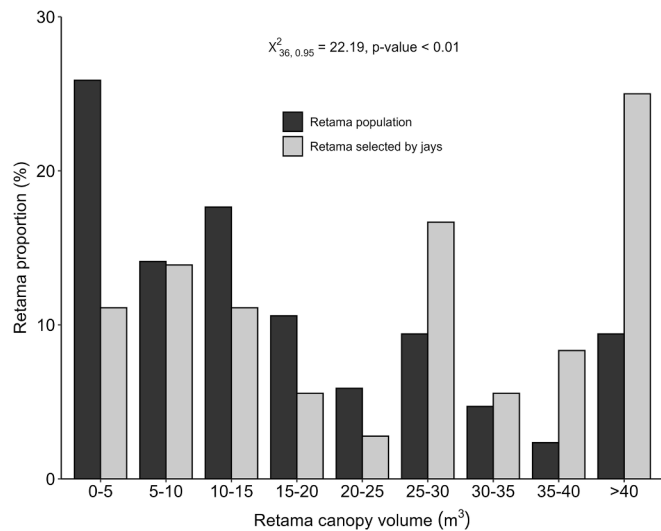


Fig. 4. Canopy volume distribution in the population of retamas (black) and in the subset of retamas selected by jays to cache acorns (grey). Data are from feeders S0, S1, S2, FE1 and FE2.

energy expenditure and predation risk during transport) probably does not compensate for the lower jay predation risk provided by the forest to hide acorns. As shown for other forest frugivorous species (García and Ortiz-Pulido, 2004; Albrecht et al., 2012), acorn dispersal in the shrubland by jays may be driven by acorn production because isolated trees usually have higher seed production than forest trees (Pausas et al., 2009; Morán-López et al., 2015). It is possible that habitat selection by jays and the spatial dispersal pattern observed in this study can also be influenced by acorn caching territories, mainly in the forest around their nests, as demonstrated in another corvid, the magpie (Martínez-Baroja et al., 2021). Research is needed to elucidate this point.

Dispersal distance varied depending on the origin and the destination habitat of the cached acorns (H2). Dispersal distance between main habitats (forest and shrubland), in both directions, was similar and it was greater than the dispersal distances within habitats. Habitat preferences by scatter-hoarders can increase long-range dispersal events (Gómez, 2003; Lenz et al., 2011), but this has not resulted in increased mean dispersal distances in our study system, probably because we have

only two contiguous habitats. Dispersal distances were greater in the shrubland than in the forest (Fig. 2), probably because the shrubland has a lower density of suitable landmarks for jays to use when caching acorns (Bossema, 1979).

4.2. Landmarks drive acorn dispersal into the habitats and at small scale

Woody species drove the specific sites of acorn dispersal in both habitats (H3), expanding our scarce knowledge on the subject (Vander Wall, 1990; Gómez, 2003; Pons and Pausas, 2007; Morán-López et al., 2015) and reinforcing the documented importance of woody vegetation as perches for seed dispersion by frugivorous birds (Duncan and Chapman, 1999; Jordano and Schupp, 2000; González-Varo et al., 2017). Woody species could be landmarks to facilitate finding the cache (Bossema, 1979), while shade reduces the visual information to potential conspecific thieves (Dally et al., 2004). Our results show that the simpler the woody vegetation structure is (shrubland vs. forest) the greater importance the woody species have as landmarks likely to attract acorn dispersal, because most cached acorns were concentrated under these low-cover structures (Fig. 3 vs. Fig. 5a).

Different sites within each habitat type resulted in different spatial patterns of dispersal despite having similar structure and woody species composition. In the shrubland, jays generally preferred the retama to cache acorns in zones 1, 2 and feeder S0, but other shrubs and tree species were preferred over the retama in zone 3 of the shrubland. This suggests that jays use global landmarks, such as shrubs, to cache seeds, but they may restrict caching to a particular subset of species of shrubs as local landmarks as a strategy to simplify the search when retrieving cached seeds. In addition, woody species, especially shrubs, can also shelter jays from predators in open areas (Caraco et al., 1980; Verdolin, 2006), which agrees with the preference of jays for large retamas (Fig. 4). Similar to shrublands, jays did not use vegetation homogeneously in the forest, preferring different woody species and vertical structures of the forest in the different zones and forested sites within zones. For example, jays preferred terebinth to cache acorns harvested from feeder F1 (Fig. 5b), but not for acorns harvested from FE1, 80 m far from the former and with a similar terebinth cover and size (Fig. S3). Similarly, jays preferred trees in the feeder F3 and shrubs in FE3, despite these feeders were only 35 m from each other (Fig. 5d and 5e). This suggests: 1) behavioral differences between jay individuals, as other studies have shown (Cheke and Clayton, 2012) or 2) their behavior is flexible, resulting in choosing different local landmarks at different sites.

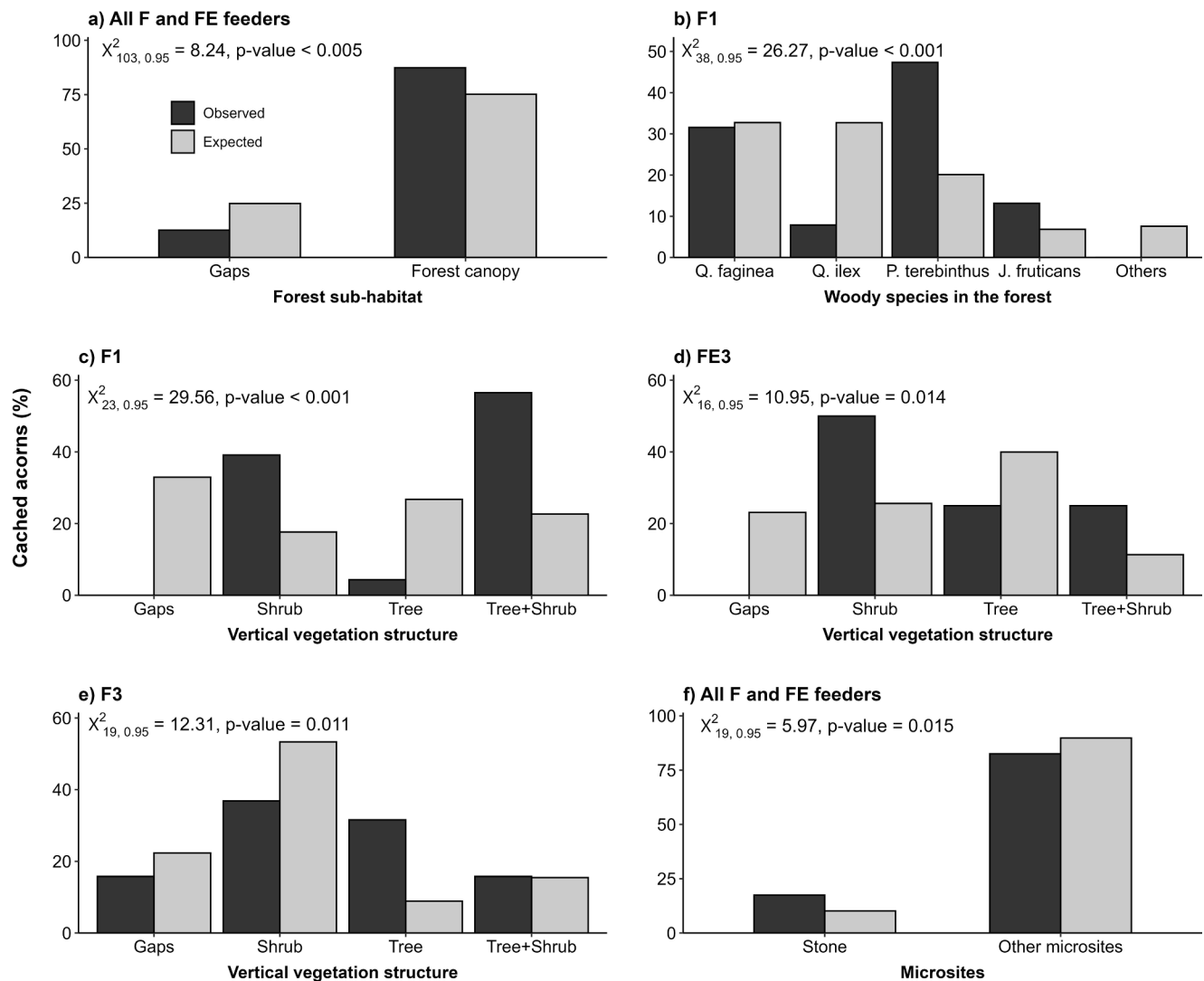


Fig. 5. Proportion of cached acorns in: a) each forest sub-habitat (gaps vs. under forest canopy), coming from all the forest and forest edge feeders; b) under the different woody species in the forest in feeder F1; and c), d) and e) under the different categories of vertical vegetation structure in the forest, coming from feeder F1, FE3 and F3, respectively; f) under or right next to stones taller than 3 cm vs. other microsites than stones, coming from all forest and forest edge feeders. Figures a) and f) show a single graph for all feeders because the abundance of their sub-habitat or microsites does not differ.

Both options lead to the notion that a single scatter-hoarder species might function analogously to multiple species (Zwolak and Sih, 2020). Experiments with marked individuals should be conducted to elucidate these points. Overlapping caching strategies of different individuals or the use of triangulation between nearby landmarks for caching and retrieving seeds by some scatter-hoarder species could also explain difficulties of finding a clear caching dispersal pattern in some areas (Waisman and Jacobs, 2008; Raby and Clayton, 2010). Our study provides a good example of how the diversity of strategies within a scatter-hoarder population in the same environmental context can translate into a diverse spatial seed dispersal pattern. All this, points to a maintenance of the dispersion function in the face of certain disturbances that could affect woody vegetation, but not against others, which could affect key landscape elements for dispersion, such as isolated trees in the shrubland.

Jays must presumably develop a caching strategy for any given habitat and location. Apparently, the different strategies coincide in preferring a type of woody vegetation with an intermediate cover in the caching area, avoiding the very frequent and very scarce elements (Figs. 3 and 5). It is possible that achieving a high density of cached acorns in restricted microsites could later lead to effective acorn

retrieval without requiring jays to spatially memorize each caching location. This hypothesis should be tested in subsequent experiments. Other scatter-hoarding corvids, such as magpies, use olfaction to find cached seeds (Molina-Morales et al., 2020), which might direct the search within the landmarks with high seed density. This hypothesis should also be tested in subsequent experiments on more scatter-hoarder bird species.

Stones were the predominant caching landmark at the smallest scale detected (H3). Bossema (1979) emphasized the importance of rough terrain and the presence of both vertical and lying sticks to hide acorns by jays at the finest scale. Our results contrast with those of Bennett (1993) in which he concludes that jays avoided short landmarks and mainly used vertical landmarks at least 20 cm tall.

4.3. Implications for oak forest management and regeneration

Understanding the caching behavior of scatter-hoarders would allow predicting seed dispersal patterns and understanding gene flow at landscape level. This knowledge is important to develop management strategies to facilitate forest regeneration. The estimated economic value of oak reforestation made by a pair of jays in Sweden was 1600–7000 €

$\text{ha}^{-1} \text{ year}^{-1}$ (Hougnier et al., 2006).

The acorns dispersed from the forest into the shrubland came from a 100 m wide band close to forest edge. This means that only a limited fraction of the area of the oak forest patches harboring jays contribute to oak forest expansion. This is important to refine models of oak expansion (Axer et al., 2021). Although the proportion of acorns coming from the forest that were cached in the shrubland was low, i.e., 8% (range 1–25%) of dispersed acorns from the forest outer band (Fig. 1), the absolute number of acorns cached in the shrubland is high enough to trigger oak colonization of the retama shrubland near de forest, i.e., < 60 m (Cruz-Alonso et al., 2020). Notably, acorn caching behavior of jays from isolated trees far away from the forest (> 200 m) seems to contribute almost exclusively to forest expansion, highlighting their potential to drive forest expansion dynamics as demonstrated for other frugivorous animals (Hampe et al., 2008; González-Varo et al., 2017). This highlights the importance of conserving isolated trees for shrubland colonization by oaks. Moreover, planting isolated oaks or oak islets in the shrublands > 200 m away from the forest edge will speed the colonization of the shrublands by oaks (Rey-Benayas et al., 2015; Martínez-Baroja et al., 2022); planting them < 200 m from the forest edge additionally will accelerate colonization of the forest by oaks, which may be interesting for increase the diversify forest tree species, e.g. in forest of other oaks; finally, planting them in the forest gaps will accelerate only colonization of the forest, not of the shrubland, by oaks. Using different species of oaks for this task can increase the tree diversity in the forest, for example in monospecific forests.

The preference of jays for caching acorns under retama shrubs coupled with the direct facilitation capacity of this shrub (Cuesta et al., 2010) triggers recruitment of holm oak in shrublands (Andivia et al., 2017; Cruz-Alonso et al., 2020). Consequently, conservation and plantation of retama shrublands next to the oak forests is crucial for oak forest expansion (Andivia et al., 2017; Cruz-Alonso et al., 2020; Morán-López et al., 2015). Acorn dispersal to shrublands would be expected to increase sharply when there is an increase in retamas with canopy volume > 25 m³ (Fig. 4). Consistent with our result, holm oak colonization under retama is only appreciable under medium and large shrubs older than 7 years (Cruz-Alonso et al., 2020).

Preference for the forest habitat to cache acorns suggests that the contribution of jays to the closure and regeneration of oak forest stands is greater than their contribution to the colonization of forest gaps and to expand the oak forest into the shrubland. Management directed to enhance shrub and tree and vertical vegetation diversity in the forest will allow scatter-hoarders more options to cache acorns. As jays are the most efficient holm oak acorn dispersers (Gómez et al., 2019) conserving and promoting jay populations must be a priority for oak forest regeneration and expansion, especially with the foreseeable population reduction in Mediterranean forests due to climate change (Villén Pérez et al., 2022).

Both pollen flow and seed flow contribute substantially to genetic diversity through the gene flow (Kremer et al., 2012). Our results suggest that the holm oak gene flow linked to acorn dispersal by jays occurs in three ways: 1) a two-way acorn flow between the forest and shrubland habitats with isolated oak trees within an asymmetrical strip around the forest edge, twice wider in the shrubland than in the forest (Fig. 1). The acorn flow came from a greater variability of holm oaks from the forest to the shrubland, but it is quantitatively greater per holm oak from the shrubland to the forest. 2) On both sides of that strip, the acorn flow occurred primarily intra-habitat and at a greater distance in the shrubland than in the forest (Fig. 2). 3) In the shrubland acorn flow was restricted to the vicinity of isolated trees and nucleated mainly under the shrubs, but in the forest a complex pattern of acorn flow was performed due to multiple overlapped shadows of seeds from different trees. As climate changes globally, seed dispersal will emphasize its crucial role in oak forest ability to displace the altitude and latitude of their ranges and to adapt to the new climate by increasing genetic diversity (Kremer et al., 2012).

5. Conclusions

Acorn dispersal by jays was a spatially structured process resulting from: 1) a top-down hierarchical and selective decision-making process across spatial scales, in which decisions at a coarse scale conditioned decisions at finer ones; and 2) the vegetation structure at the landscape scale and within the habitats. Spatial patterns of acorn dispersal at the landscape scale were the result of the different contributions of individual trees mediated by jays preference for woody vegetation at different spatial scales. Acorn spatial dispersal patterns were also the result of how jay individuals used the habitat with an overall similar dispersal pattern at the landscape scale but with a variety of patterns within the habitats linked to different strategies of individuals. Our findings contribute valuable insights into the factors influencing acorn dispersal behavior by Eurasian jays and its implications for oak forest regeneration. This knowledge is crucial for the development of mechanistic models aimed at predicting seed dispersal by scatter-hoarders across diverse landscapes. These implications are particularly significant considering that Eurasian jays disperse a wide variety of seeds, including various acorns of several oak species, nuts of beech and hazel, among others (Bossema, 1979; Rolando, 1998). Moreover, Eurasian jays are abundant corvids, and their distribution overlaps extensively with that of oaks throughout Eurasia. Protection and promotion of the three species involved in this study, namely isolated oaks in the shrubland, nurse shrubs like the retama, jay populations; and enhancement of the forest diversity of woody species has been recommended in different situations to trigger oak colonization in the retama shrublands, forest regeneration of oaks or both.

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Author contributions

PVS, LPC and JC designed the experiment. TGS, PVS, LPC and JC carried out the field work. LMB, LPC, PVS, and TGS performed the statistical analyses. LPC and TGS led the writing of the manuscript. All authors participated in the correction and approval of the manuscript.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121291>.

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