RESEARCH ARTICLE

Linking animal behaviour and tree recruitment: Caching decisions by a scatter-hoarder corvid determine seed fate in a Mediterranean agroforestry system

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Abstract

1. Seed dispersal by scatter-hoarder corvids is key for the establishment of important tree species from the Holarctic region such as the walnut (*Juglans regia*). However, the factors that drive animal decisions to cache seeds in specific locations and the consequences of these decisions on seed fate are poorly understood.

2. We experimentally created four distinct, replicated habitat types in a Mediterranean agricultural landscape where the Eurasian magpie (*Pica pica*) is a common scatter hoarder: soft bare soil; compacted bare soil; compacted soil with a dense herbaceous cover; and soft linear bare soil made up of the irrigation furrows that separated the rest of the treatments. We also experimentally placed visual landmarks (stones, sticks and bunches of dry plants) to test if magpies use them to place seed caches. Walnut dispersal from feeders to the habitats was monitored by radiotracking and camera traps.

3. A sowing experiment simulating natural caches tested the effect of caching type on seed germination and seedling emergence. Seed mass was controlled for the dispersal and sowing experiments.

4. Magpies selected the two habitats with soft soil, and avoided the one with compacted soil, to cache nuts. Seed mass did not affect dispersal distance, germination or emergence; however, heavier seeds were cached more often under litter and in the habitat with herbaceous cover, whereas lighter seeds were more often buried in the soft bare soil habitat. Seed burial under soil or litter determined

seed fate, as there was virtually no emergence from unburied nuts. There was no evidence of any effect of the visual landmarks.

5. *Synthesis*. The consequences of seed caching for seedling early establishment are driven by a fine decision-making process of the disperser. Magpies seemed to ponder the characteristics of the habitat and the seed itself to determine where and how to cache each nut. By doing so, magpies reinforced the quality of seed dispersal effectiveness, as they cached walnuts in locations that enhanced both seed survival and seedling emergence.

KEYWORDS

cache, camera trap, Eurasian magpie (*Pica pica*), radiotracking, seed dispersal, seedling emergence, walnut (*Juglans regia*)

1 | INTRODUCTION

Seed dispersal by scatter-hoarder vertebrates is a relevant process for the establishment and expansion of many tree species. These animals cache seeds for later consumption, but a fraction remains unrecovered providing the opportunity for seedling emergence and tree recruitment (Pesendorfer et al., 2016; Vander Wall, 1990). The decisions made by the animal to cache the seeds and to recover them later may have strong consequences for seed fate and seedling establishment. At the landscape scale, scatter hoarders cache seeds in a variety of habitat types that may affect seed survival and seedling establishment (Gómez, 2003; Martínez-Baroja et al., 2021; Morán-López et al., 2015; Pesendorfer et al., 2017; Vander Wall, 1990). At the microsite scale, seed burial or concealment under litter (a common caching behaviour in scatter hoarders; Vander Wall, 1990) may increase seedling establishment because seeds are better protected against pilfering and are less exposed to harsh environmental conditions (Briggs et al., 2009; García et al., 2002; Longland et al., 2001; Vander-Wall, 1990; Yi et al., 2013, and references therein). However, this behaviour may also reduce the success of plant establishment (Kuprewicz, 2015; Sipes Jr. et al., 2013; Zhang et al., 2013). Besides reducing pilfering by other individuals, a major goal of seed caching by scatter hoarders may be to reduce seed germination to protract the function of caches as food sources (Sipes Jr. et al., 2013). Thus, animals may cache seeds in dry places, reducing the probability of germination (Joët et al., 2013) and hence creating a conflict between dispersal and recruitment (Sipes Jr. et al., 2013 and references therein). Furthermore, the animal may discriminate between seeds for caching on the basis of particular traits such as seed mass, which in turn may affect dispersal distance, cache selection or cache recovery (Galetti et al., 2010; Gómez et al., 2008; Tamura & Hayashi, 2008; Theimer, 2003) and, consequently, seedling recruitment. In short, where, how and which seeds are cached is a context-dependent process with complex consequences for plant recruitment at different spatial scales (Aliyu et al., 2018; Schupp et al., 2010; Xiao & Krebs, 2015). Thus, understanding the factors that drive the selection of caching sites

by scatter hoarders is a key element to predicting seed dispersal effectiveness.

The studies addressing the role of scatter hoarders as vectors for seed dispersal in the wild have relied mostly on observational approaches in which seed dispersal is monitored from the source (either natural trees or feeder stations) to the caches (Gómez, 2003; Gómez et al., 2008; Kuprewicz, 2015; Martínez-Baroja et al., 2021). This procedure sheds light on the habitat and microhabitat selection by the animal. However, it precludes robustly inferring animal preferences because the distribution of habitats is neither random nor controlled by the researcher. The pattern of seed distribution might thus be mediated by other factors, such as the relative abundance of particular habitats, their spatial configuration, the distance from seed sources or the existence of particular landmarks to guide later seed recovery (Bennett, 1993; Bossema, 1979; Feenders & Smulders, 2011). Experimental manipulation of habitats, with proper replication and randomisation within a landscape, could help unravel the fine-grained drivers of cache site selection by scatter hoarders, but this has seldom been done in field studies to date (but see Castro et al., 2012).

In this study, we aim to experimentally determine the factors that drive cache site selection by a scatter-hoarder corvid and the implications of these decisions for the fate of the seeds and early seedling establishment. We used walnut (*Juglans regia* L., a tree secularly cultivated in western Europe) caching by the Eurasian magpie (*Pica pica* L., a common scatter-hoarder corvid in agroecosystems of Eurasia, Castro et al., 2017; Martínez-Baroja et al., 2019) as the study system. We created randomly distributed experimental habitat types of equal size but with contrasting soil compaction and grass cover, two features that determine cache site selection for this bird and corvids in general (Bossema, 1979; Martínez-Baroja et al., 2021). We also inserted landmarks that simulated local cues that could potentially guide cache site selection and cache recovery. Nut dispersal from feeders was sampled using radiotracking, and the fate of each seed was monitored until the period of seedling emergence. In addition, we conducted a seeding experiment to analyse the effect of cache type on seedling emergence in the different habitat types. Seed mass was controlled in both the

seed dispersal and seedling emergence experiments because it affects dispersal distance, seed storage decisions by scatter hoarders and seedling emergence (Johnson et al., 2004; Moore et al., 2007; Skarpaas et al., 2011; Xiao et al., 2004).

Given that the experimental habitat types substantially differed in herbaceous cover and soil compaction, we hypothesise that the disperser selects particular habitats for establishing caches (H1). As scatter hoarders use visual cues to facilitate seed recovery, we hypothesise that the experimental landmarks will influence the placement of caches (H2). Seed mass imposes restrictions for dispersal (heavier seeds may be more difficult to transport) and storage (heavier seeds may be preferred over lighter ones). Therefore, we hypothesise that seed mass will affect caching decisions (H3). Finally, we hypothesise that the interplay of decisions made by the animal for seed caching and the characteristics of the cache habitats will have contrasting effects on seedling emergence (H4). This study may provide insights into the functions of birds in agroecosystems, with relevance for ecosystem services related to forest regeneration and restoration.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The study was conducted in 'Vega de Granada', an area of small-sized farms located at 650 m a.s.l. in SE Spain (37°10′03.43″N, 3°36′57.80″W) and where the magpie is a common resident bird. The soil is deep and loamy, and climate is Mediterranean type, with hot dry summers and mild winters. The mean annual rainfall is $394 \pm 71 \, L \, m^2$ and the mean annual temperature is $15.3 \pm 0.1°C$ (Castro et al., 2017). Magpies arrived at the study site in 2002 as part of a process of local expansion within their regional distribution area, and are currently a common resident bird that acts as scatter hoarder of walnuts. Moreover, the magpie is the only scatter-hoarder bird

that disperses nuts in the area (Castro et al., 2017; Molina-Morales et al., 2019) and the only bird that has been recorded (Molina-Morales et al., 2020) or observed (JC and MMM personal observation) retrieving nuts from caches, providing an ideal system to study fine-grained details of the interaction between a scatter hoarder and a nut-producing tree. The common walnut (*Junglans regia*) is not a native tree in the area, but it is traditionally grown on farms, possibly since Roman times, as scattered trees close to houses to provide families with nuts (Castro et al., 2017).

At the study site, a field of *c.* 2000 m^2 was ploughed with a tractor using a rotovator (in July 2016 and again in July 2017) and split into 15 experimental plots of similar size (average surface of $152.17 \pm 6.37 \, m^2$ per plot). A total of 24 *c.* 2 m tall Aleppo pine (*Pinus halepensis*) saplings were in the field where the experiment was set up, and their presence was similarly distributed across the experimental treatments (see below; Figure 1). The plots were delimited by irrigation furrows of 90 cm width and 30 cm height, which were made with a single furrow ridge by the tractor. The 15 plots were randomly ascribed to three treatments that differed in soil compaction and cover (five plots per treatment, with no difference in surface across treatments; $F = 1.63$, df = 2, $p = 0.237$; Figure 1). In addition, the irrigation furrows resulted in a distinctive, linear visual structure that could guide caching site selection by the dispersers. Thus, they were considered ad-hoc in the analyses as an additional treatment. The treatments, hereafter termed habitat types, were the following:

1. **Soft bare soil (SBS)**, where no further action was taken except the application of herbicide (Roundup®, glyphosate at the dosage recommended by the manufacturer) to halt incipient herb growth, applied twice until the end of the period of seed dispersal monitoring (mid-October, see below).
2. **Compacted bare soil (CBS)**, where the soil was irrigated once by flooding the whole surface to compact the soil. The same herbicide and dosage were applied three times at regular intervals

FIGURE 1 Experimental design (area delineated by the blue line) to assess walnut caching sites by magpie at different habitat types. From the left to the right, the first plot in the picture corresponds to soft bare soil (SBS) followed by soft linear bare soil (SLBS)—which separates all the replicates of the other habitat types, compacted soil with dense herbaceous cover (CHC), and compacted bare soil (CBS). Green circles represent the experimental visual landmarks that were placed in the first year of the experiment. Orange triangles show the feeder locations. Pink circles represent the cached nuts. Trees in the upper, left corner of the experimental area are Aleppo pines (*Pinus halepensis*). Cached nuts beyond the blue line were not analysed in this study. Photo taken with a drone on 10 September 2016.

until the end of seed dispersal monitoring. This treatment created a habitat type whose main difference with respect to SBS was higher soil compaction (see soil density data below).

3. **Compacted soil with dense herbaceous cover (CHC)**, where the soil was irrigated three times as in CBS until the onset of the nut dispersal period (early September). No herbicide was applied and, hence, a dense herbaceous cover was present at the start of the seed dispersal study *c.* 1.5 months later.

4. **Soft linear bare soil (SLBS)**, which corresponds to the irrigation furrows that separated the experimental replicates and that created distinctive linear landscape features (Figure 1). The surface of the furrows that separated the different plots was on average $19.27 \pm 3.28 \, m^2$ (areas calculated with Quantum GIS from a photogrammetric flight with a drone; see below). These furrows were made up of soft bare soil like in the SBS treatment. The irrigation furrows were kept clean of herbs with the use of the same herbicide in the side delimitating replicates of the SBS and CBS habitats.

The distribution and size of the plots ascribed to each treatment was the same in the two study years (Figure 1), and therefore year is considered as a temporal replicate of the same experiment. Apparent soil density at 0–10 cm depth was sampled each year in early August, 3–4 weeks after treatment implementation, and used as a measure of soil compaction. Soil density differed among treatments; SBS ($0.88 \pm 0.016 \, g \, ml^{-1}$) and SLBS ($0.85 \pm 0.01 \, g \, ml^{-1}$) exhibited significantly lower density than CBS ($1.71 \pm 0.013 \, g \, ml^{-1}$) and CHC ($1.72 \pm 0.02 \, g \, ml^{-1}$; Supplementary Material S1).

Imbedded in this general design, we also placed 10 potential visual cues in each replicate of the experimental habitats at the onset of the experiment in 2016 to assess whether magpies cached nuts closer to them more often than expected by chance, those being four vertical wooden sticks, one concrete block, three stones and two bunches of dry maize plants (Figure 1; see Supplementary Material S2 for more details). These landmarks aimed to mimic the potential visual cues that animals can find in farmland-dominated landscapes. However, since the results of the first year (2016) showed that these visual cues had no effect on the pattern of nut dispersal (see Results below), they were excluded in the second year (2017).

No more actions were taken in the experimental habitats once the seed dispersal monitoring started (September 2016 and 2017). The habitats persisted during the period of seed dispersal, but winter and spring rains allowed grasses and forbs to grow in all plots. Consequently, the landscape changed during the period of seed recovery by magpies, and all habitat types showed a dense herbaceous cover at the end of each study year (May 2017 and May 2018; see Results).

A 5-cm pixel-resolution ortho-photo was constructed on 10 September 2016 (1 week after the beginning of the seed dispersal experiment) with a photogrammetric flight from a drone. This allowed to precisely locate each cached nut or point of interest in the experimental site (Figure 1), as well as to estimate the herbaceous cover of each habitat type at the beginning of the sampling period (Supplementary Material S3).

The Consejería de Medio Ambiente (Junta de Andalucía) provided fieldwork permission for capturing and ringing magpies (201699900084562-07/03/2016).

2.2 | Nut dispersal monitoring

Nut dispersal was investigated using radiotracking, as described in Castro et al. (2017). Two feeders separated by 100 m and placed at the border of the experimental area (Figure 1) were used as nut supply points. At each feeder, we placed groups of 9 to 12 nuts with an inserted radiotransmitter (PIP2 Tag Ag392; Biotrack; weight: 2.2 g; mean life span: 3 months; see Supplementary Material S4 for details of nut preparation). Each experimental nut was left with a similar weight as it had before transmitter insertion. The dispersed nuts were located 4–5 h after removal by means of a radiotracking receiver with an unidirectional Yagi antenna (Biotrack) plus a hand-held metal detector (White's Auto-Scan Personal Search Detector). Nuts were offered from 2 September to 20 October 2016, and from 14 September to 13 October 2017, coinciding with the period of natural dispersal in the study area. The identity of the seed dispersers (Supplementary Material S5) was assessed with video cameras placed at *c.* 1 m from the feeders (Moultrie M-990i; Moultrie Products, a movement-sensitive system with day and night vision). The mass of the nuts was positively correlated with their volume ($t = 9.66$; $R^2 = 0.582$; $N = 69$; $p < 0.001$, Supplementary Material S6).

Once a nut with a transmitter was located, the transmitter was recovered and a nonmanipulated nut was placed in the same location. The point where the nut was found was marked with a wooden stake (40 cm × 3 cm × 3 cm) placed 50 cm away from the nut, and a small metal rod was placed under the nut to allow cache relocation with the metal detector even if the nut was retrieved. This marking procedure does not affect the probability of cache recovery by magpies (Molina-Morales et al., 2019). Cache coordinates were also marked with a GPS, which allowed us to calculate dispersal kernels and distances using Quantum GIS version 2.18 and conduct spatial statistics (see below). In the last week of January 2017 and 2018, we estimated the recovery rate of cached nuts by sampling the status of all the cached nuts, considering the following categories: (i) recovered (nut absent from its caching site) or (ii) not recovered (nut present in its caching site).

2.3 | Cache types

For all dispersed nuts, the cache types were categorised as: (1) Superficial, nuts left visible on the ground; (2) Buried, nuts buried in bare soil; and (3) Under litter, nuts hidden under leaf litter or leaves of live vegetation. Ground cover (either of litter or live plants) for caches was calculated after taking a photograph

perpendicular to the ground for a circular area with a radius of 10 cm from the dispersed nut, which was delimited with a PVC collar. A 2×2 cm or 4×4 cm red square plastic piece was placed beside the collars to extract the exact circumference area based on pixel count of the squares (Supplementary Material S7). Images were later processed using a raster graphics editor software (Adobe Photoshop CS6) to accurately calculate the percentage of vegetation cover.

2.4 | Experimental test of habitat and caching type effects on seedling emergence

To test whether the experimental habitat types and caching type affected seed viability and seedling emergence, we conducted a sowing experiment during the first study year coinciding with the seed dispersal period. We established 10 sowing points in each of the five plots of SBS, CBS and CHC; at each point, one walnut was sown at 2 cm depth (i.e. 2 cm of soil above the nut in SBS and CBS and 2 cm of litter in the CHC habitat) and another paired nut was left on the surface (300 nuts in total). This procedure simulates the two main cache types under natural conditions: nuts left on the surface or concealed in the soil or the litter (Castro et al., 2017; Molina-Morales et al., 2019). Each sowing point was protected with a 15×15 cm, 8 cm tall cage made of 1.1 cm wire mesh, anchored to the ground with spikes. Sowing was conducted on 16–18 November 2016. From 29 April to 2 May 2017 (c. 5.5 months after sowing), coinciding with the onset of seedling emergence in the study area, we sampled the status of the sown nuts, which were categorised as: nongerminated and rotten (rotten, hereafter), nongerminated and healthy (nongerminated), germinated or emerged seedling. The status of nongerminated nuts (rotten vs. healthy) was assessed by opening the nut in situ. In the case of emerged seedlings, we also noted seedling height. At the time of sampling, herbaceous cover and height were measured in five 40×40 cm squares randomly located in each of the five plots per treatment. Herbaceous cover was 100% in all cases, with an average height of 116.2±5.1 cm in SBS, 120.9±4.0 in CBS and 135.6±5.1 in CHC. The SLBS habitat was not distinguished as an additional treatment in this sampling, but herbaceous cover was 100% in the whole plot.

2.5 | Data analysis

2.5.1 | Seed dispersal and habitat selection

The effects of habitat type, distance from the feeder and distance from the nearest visual cue on nut dispersal, as well as the concordance of these effects across feeders and years, were analysed with spatial statistics. For this analysis, we obtained four point patterns of dispersal events, one for each of the two feeders and years. We fitted point process models to all four point patterns simultaneously with the mppm function of the SPATSTAT R package version 1.64-1 (Baddeley et al., 2015). The models considered a nonhomogeneous Poisson process, with the density of dispersed nuts depending on three spatial and two nonspatial covariates. The spatially explicit variables were experimental habitat type, distance to the feeder from which each nut was dispersed, and distance to the nearest visual cue. The nonspatial factors were feeder and year. We fitted an initial model that included the three spatial and the two nonspatial factors as well as all possible interactions among them. The significance of each term was assessed through likelihood ratio tests during model simplification. All terms with $p > 0.05$ were excluded until the minimal adequate model was produced, in which each term was either significant or included within a significant higher-order interaction (Crawley, 2013). This analysis was restricted to the dispersal events into the experimental layout and run in R version 3.3.1 (R Core Team, 2016).

The effect of seed mass on dispersal distance was analysed using a linear mixed model (LMM) with Plot as a random factor to control for spatial autocorrelation. Dispersal distance was log-transformed for better adjustment of the residuals of the model to normality.

2.5.2 | Caching type

We ran three models to assess caching type. (1) To evaluate whether the proportion of cache types depended on habitat type, we used a multinomial logistic regression model with caching type as the response variable and habitat type as the explanatory factor (R package NNET version 7.3-14; Ripley et al., 2016). As we did not find any nut cached on the surface in the SBS habitat, we excluded it from the analyses. (2) To analyse whether habitat type affected ground cover around each cache, we ran a LMM in which ground cover (log-transformed) was the response variable, habitat type was the explanatory factor, and Plot was a random factor. And (3), to analyse whether nut mass was related to caching type, we used a linear model in which nut mass was the response variable (log-transformed) and caching type was the explanatory factor.

2.5.3 | Nut recovery

The probability of nut recovery in relation to habitat type was analysed with a generalised linear model (GLM) with a binomial error structure and a logit link function. Habitat type was included as a factor and the mass of the seed as a covariate. The CBS habitat was excluded because recovery there was 100%.

2.5.4 | Effect of habitat and caching type on seedling emergence

To evaluate whether seed fate depended on habitat or caching type, we used a multinomial logistic regression model with caching type

(nuts on the surface or buried in soil or litter) and habitat type as the explanatory factors (package NNET; Ripley et al., 2016). The relationship between nut mass and the probability of emergence of the experimentally sown nuts was analysed with a Gamma GLM. Nuts sown on the surface were excluded as only one germinated.

3 | RESULTS

3.1 | Seed dispersal and habitat selection

All nuts with an inserted radiotransmitter dispersed by magpies from the feeders were located by radio-tracking. A total of 80 and 81 nuts were dispersed into the experimental habitats in 2016 and 2017 respectively (350 additional nuts were dispersed outside the experimental treatments, both years pooled, but were not considered in this study). Of those, 92.5% (149) were cached, whereas the remaining were consumed immediately after removal from the feeder (these nuts were found open with the transmitter partially or entirely outside; one additional nut was cached in a tree hollow and was discarded for analyses). Pooling the data of both years, 31.5% of nuts were cached in SBS, 5.4% in CBS, 30.2% in CHC and 32.9% in SLBS (Figure 1). The disperser was recorded by the cameras in 151 of the 161 (93.9%) dispersal events. In all cases, the disperser was a magpie that transported a single walnut in each dispersal event. The herbaceous cover at the beginning of the sampling of nut dispersal was below 2.5% in SBS and CBS, and 95% in CHC (Figure 1; Supplementary Material S3).

The spatial analysis showed that the density of nuts decreased with increasing distance from the feeders (Figure 2). The slope was affected independently by the experimental habitat type and the identity of the feeder (i.e. significant distance × habitat type interaction: $\chi^2 = 8.55$, df = 3, $p = 0.04$, Figure 2a,c; and distance × feeder interaction: $\chi^2 = 5.79$, df = 1, $p = 0.02$). At short distances from the feeder, SBS yielded the highest nut densities, followed by SLBS and CHC. However, density decreased most steeply with distance in SBS, until equalling the density found in SLBS and CHC at about 40 m from the feeder (Figure 2a,c). The minimal adequate model did not include Year ($\chi^2 = 0.02$, df = 1, $p = 0.89$), distance to the nearest visual cue ($\chi^2 = 0.10$, df = 1, $p = 0.74$) or any interaction between distance to the nearest cue or Year and any other factor ($p > 0.05$ in all cases).

Dispersal distance within the experimental plots averaged 27.6 ± 1.26 m (mean SE hereafter; range = 5.05–84.95 m) and was independent of seed mass ($F = 1.101$; df = 1157; $p = 0.29$).

3.2 | Caching type

Of the 149 cached nuts, 5.4% were left on the ground surface, 33.6% were hidden under plant material, and 61.0% were buried in the soil. Caching type significantly differed among habitat types (Table 1); the proportion of buried nuts ranked SBS > SLBS > CBS > CHC. The proportion of nuts left on the surface was highest in CBS, whereas the proportion of nuts concealed under litter was highest in CHC (Figure 3).

Ground cover of litter and vegetation around the cached nuts differed considerably among the experimental habitat types ($F = 23.0$; df = 3136; $p < 0.001$). It was highest in CHC (65.7 ± 5.5%) followed by CBS (44.2 ± 15.8%), SBS (22.1 ± 5.2%) and SLBS (11.1 ± 2.9%; Supplementary Material S8). Note that cover refers both to live vegetation and litter, which explains the relatively high cover in the caches of CBS habitat where herbicide application at the early stage of herb growth produced dead plant material.

The mass of the cached nuts significantly differed between caching types ($F = 5.934$, df = 2146, $p = 0.003$): buried nuts were lighter (10.95 ± 0.17 g) than nuts concealed under litter (11.95 ± 0.27 g; nuts
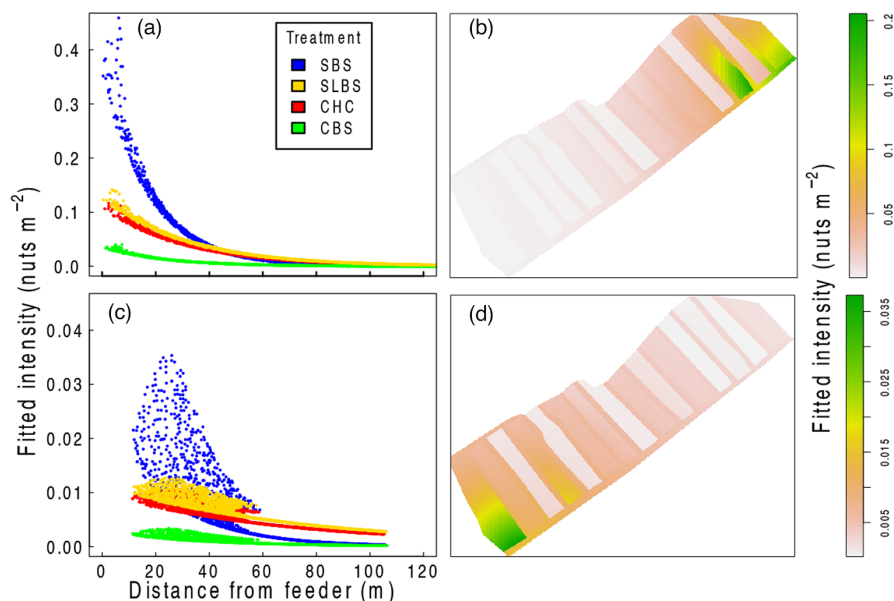
FIGURE 2 Predicted intensity (nut density) from point process models for (a, b) feeder 1 and (c, d) feeder 2. The predictions for the two feeders were generated with the same model. Two maps are provided because the model included differences between feeders in intensity and in the effect of distance. No effects were detected for year, so the density predictions apply to both years. Note that the intensities of the two feeders differ in an order of magnitude due to lesser dispersal from feeder 2. The location of the feeders and dispersed nuts is indicated in Figure 1.

TABLE 1 Results of nominal logistic regression on the relationship between habitat and caching types. Habitat types are CBS: Compacted bare soil and SLBS: Linear soft bare soil; the reference level for habitat type was CHC (compacted soil with dense herbaceous cover); soft bare soil (SBS) was excluded from the model because it did not contain nuts on the ground surface. Caching types are UL = nuts hidden under litter; superficial = nuts left on the ground surface; and buried nuts, which represents the reference level for caching type. Bold data indicate significant p-values

	Estimate	SE	Z value	p
Intercept	−0.0011	1.00	−0.001	0.99
Superficial - CBS	−0.692	1.323	−0.523	0.601
Superficial - SLBS	**−2.326**	**1.129**	**−2.060**	**0.039**
UL - Intercept	**3.020**	**0.724**	**4.171**	**<0.01**
UL -CBS	**−3.713**	**1.128**	**−3.289**	**0.001**
UL - SLBS	**−5.347**	**0.893**	**−5.984**	**<0.01**

TABLE 2 Results of GLM used to analyse the effect of experimental habitat types and seed mass on the probability of nut recovery. Habitat type: SBS = soft bare soil; SLBS = linear soft bare soil; reference level = CHC (compacted soil with dense herbaceous cover). Compacted bare soil (CBS) was not included in the analysis because magpies recovered 100% of the nuts in this habitat type. Bold data indicate significant p-values

Habitat type	Estimate	SE	Z value	p
Intercept	3.06	1.79	1.71	0.08
SBS	0.78	0.61	1.28	0.19
SLBS	**1.79**	**0.82**	**2.19**	**0.02**
Seed mass	−0.15	0.14	−1.06	0.28

registering 100% of recovery, followed by SLBS (95.9%), SBS (89.4%) and CHC (75.5%; significant differences between SLBS and CHC). The probability of recovery was not explained by nut mass (Table 2).

3.4 | Effect of habitat and caching types on seedling emergence

From the 300 experimentally sown nuts, 18.7% were rotten by the end of the experiment, 64.3% had not germinated but were healthy, 13.3% were germinated but still had not emerged and 3.7% rendered an emerged seedling. Among the nuts sown on the surface, only one germinated (Figure 4 left panel), whereas the remaining seeds that germinated or emerged (50 in total) were all from buried nuts (Figure 4). For the subset of buried nuts, there were significant differences in seed fate among habitat types; the CHC and SBS showed the highest and the lowest, respectively, proportions of emerged, germinated or healthy nuts (Table 3, Figure 4, right panel). Seed mass did not differ among categories of seed germination or emergence (Germinated and healthy, $E = -0.003 \pm 0.005$, $t = -0.53$, $p = 0.59$; Healthy not germinated, $E = -0.004 \pm 0.005$, $t = -0.79$, $p = 0.43$; Rotten, $E = -0.001 \pm 0.006$ $t = -0.24$ $p = 0.81$; only buried nuts considered and the three habitat types pooled).
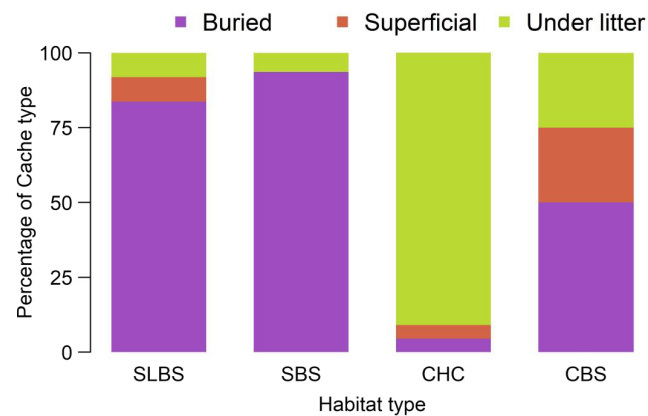

FIGURE 3 Distribution of cache types across experimental habitat types (SBS, soft bare soil; CBS = compacted bare soil; CHC = compacted soil with dense herbaceous cover; and SLBS = soft linear bare soil). Cache types are buried, superficial and under litter.

left on the surface [8] were eliminated from this analysis). This trend persisted consistently across habitat types ($F = 3.554$, df = 3, 145 $p = 0.016$): nuts dispersed to the CHC (where a higher proportion was concealed under litter) had higher mass (12.01 ± 0.26 g) than nuts dispersed to the SBS (11.14 ± 0.26 g; $W = 704$, $p = 0.02$), SLBS (11.06 ± 0.25; $W = 1454$, $p = 0.008$) and CBS (10.51 ± 0.62; $W = 94.5$, $p = 0.04$).

3.3 | Nut recovery

The recovery rate of cached nuts, measured in January following each study year, reached 89.5% in 2016 and 88.0% in 2017 (132 nuts recovered vs. 17 not recovered in total, both years pooled hereafter). Recovery rate differed among habitat types, with CBS

4 | DISCUSSION

Animal decisions to cache seeds may have strong implications for plant recruitment (Gómez et al., 2008; Pesendorfer et al., 2016), but a fine-grain knowledge of the factors that drive the selection of caching sites in scatter-hoarder corvids under natural conditions is not well understood. Our study using experimentally created habitat types and monitoring individual seed fate has demonstrated that the effect of a scatter-hoarder corvid on the early recruitment of a tree is a complex processes shaped by trade-offs between habitat selection, caching type, habitat suitability for seedling establishment and seed mass. All these actors set the template for recruitment success (Herrera et al., 1994).
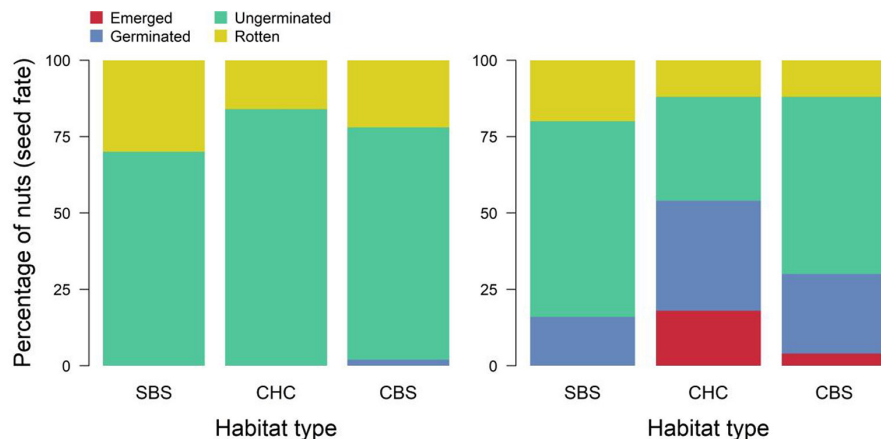
FIGURE 4 Proportion of emerged (E), germinated (G), healthy but not-germinated (HNG), and rotten (R) seeds at the beginning of the emergence season (May) from seeds sown on the surface (left panel) or at 2 cm depth (right panel) in different habitat types. Habitat nomenclature as in Figure 3. The soft linear bare soil (SLBS) was not included in this experiment, but the soil characteristics in this habitat type are similar to those in SBS.

TABLE 3 Results of nominal logistic regression model used to analyse the effect of habitat type on the fate of nuts that were experimentally buried. Reference level for seed fate: Rotten; habitat: CHC. Seed fate: E = emerged; GH = germinated healthy; HNG = healthy not-germinated. Habitat: CBS = compacted bare soil; SBS = soft bare soil. Bold data indicate significant p-values

	Estimate	SE	Z value	p
Intercept	0.405	0.527	0.768	0.442
E - CBS	−1.503	0.527	−1.546	0.122
E - SBS	−13.714	245.511	−0.056	0.955
GH - Intercept	**1.098**	**0.474**	**2.330**	**0.019**
GH - CBS	−0.325	0.682	−0.476	0.634
GH - SBS	**−1.322**	**0.668**	**−1.976**	**0.048**
HNG - Intercept	**1.042**	**0.475**	**2.193**	**0.028**
HNG- CBS	0.534	0.653	0.818	0.413
HNG - SBS	0.122	0.597	0.204	0.838

4.1 | Site selection for caching

As a first step in the dispersal process, magpies relied on certain habitat features to select caching sites (H1). They rejected habitats with compacted soil and selected habitats with loose soil where inserting a nut was easier and, secondarily, habitats with high herbaceous cover that provided loose plant material under which nuts could be concealed (Figure 5a). This agrees with most studies on seed caching by corvids (Bossema, 1979; Johnson et al., 2004; Lenda et al., 2012; Martínez-Baroja et al., 2021), and it is likely motivated by the need to easily conceal the seeds and reduce pilfering risk. Moreover, the way in which the nut was concealed was determined by the characteristics of the habitat. Most (*c*. 90%) of the nuts dispersed to the habitats with loose soil (SBS or SLBS) were buried, whereas the majority of nuts (*c*. 90%) transported to a habitat with dense herb cover were hidden below plant material. This suggests a fine decision-making process of the animal, as it changes caching behaviour according to habitat characteristics.

We did not detect any attraction of dispersal by the experimentally placed landmarks. This was unexpected (H2), as corvids use visual landmarks to guide caching site selection and recovery (Feenders & Smulders, 2011; Martínez-Baroja et al., 2021; Reichert et al., 2017). Nonetheless, we cannot discard that the birds used a combination of most reliable features for cache location different to those that we established. By contrast, magpies rely on linear landscape structures that guide their caching selection, such as the irrigation furrows (SLBS). The selection of linear landmarks such as edges, roads or forest tracks for caching has been documented for other corvids, both in the wild (Bossema, 1979; Johnson et al., 2004; Pons & Pausas, 2007; Woziwoda et al., 2018) and in captivity (Gould et al., 2010). Thus, our results support that magpies selected the places for seed caching according to characteristics that facilitated concealment (primarily soft bare soil but also areas with certain cover of vegetation) and/or guide spatial memory (e.g. linear structures).

4.2 | The importance of seed mass in caching decisions

Seed mass affected caching type (H3). Lighter nuts were more prone to being buried, whereas heavier nuts were cached proportionally more under plant material. This again suggests a precise decision-making process, as heavier seeds are more difficult to insert in the ground because magpies hammer nuts into the soil with the beak (Birkhead, 1991; Castro et al., 2017). It therefore seems that the magpie decides what to do with a dispersed nut depending on its mass, a pattern that has been previously reported for mammal scatter hoarders (Gómez et al., 2008; Tamura & Hayashi, 2008) but rarely for corvids. In contrast, the probability of seed recovery did not depend on seed mass, and therefore the template of seed mass distribution across habitat types translates to the following phase of establishment. Dispersal distance was unaffected by seed mass, despite widely reported relationships between these two variables in mammals (Brewer, 2001; Gómez et al., 2008; Jansen et al., 2004; Tamura & Hayashi, 2008; Xiao et al., 2013). An explanation for this
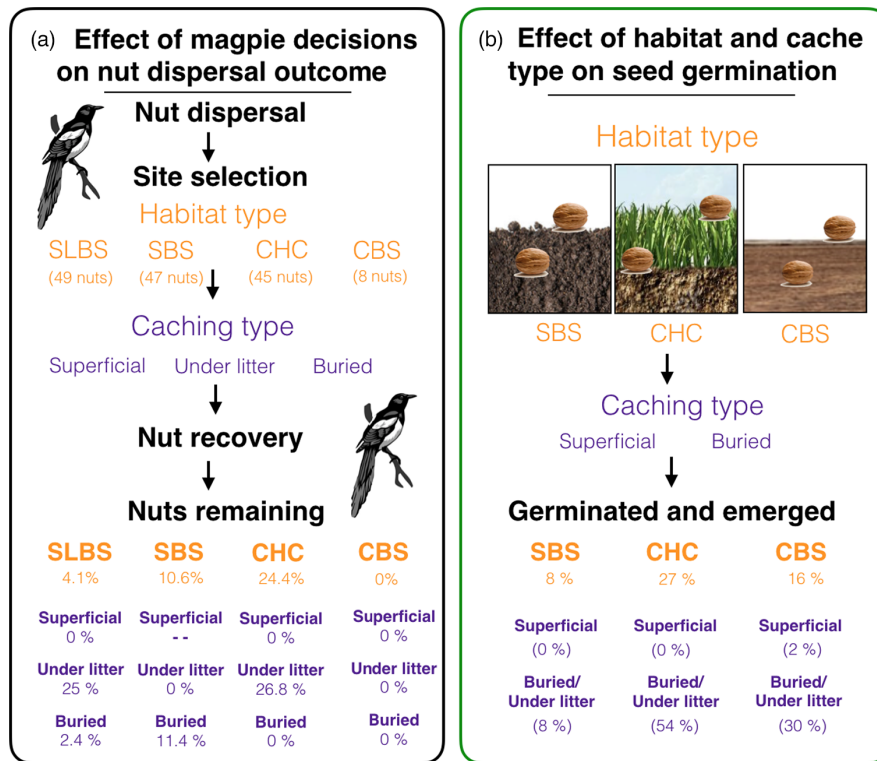
FIGURE 5 Summary of the consequences of walnut scatter hoarding by magpies for early seedling establishment. (a) Magpies disperse nuts selecting different habitats (SLBS = soft linear bare soil; SBS = soft bare soil; CHC = compacted soil with dense herbaceous cover; and CBS = compacted bare soil) and make different caching types (nuts cached on the ground surface, hidden under litter or buried in the soil) (site selection). A proportion of the nuts are recovered through the following months (nut recovery); all nuts left in the surface are recovered and only caches under litter or buried in the soil provide an opportunity for seedling emergence. (b) Seed germination of nuts placed experimentally in the surface is virtually null, while a high proportion of nuts buried below soil (buried) or placed under litter germinate and emerge. The scatter-hoarding behaviour of the magpies, concealing most nuts under litter or buried in the soil, promote therefore the qualitative component of seed dispersal. No nut was cached in the surface in the SBS treatment (–), and therefore 'nuts remaining' cannot be estimated in this case.

lack of effect is that the range of walnut sizes used in our experiment allowed the magpies to transport them with little differences in effort. Another possibility is that a relationship between nut mass and dispersal distance may appear if longer distances were considered (Bossema, 1979). Given that we restricted the study to an experimental set up that is close to the feeders, we artificially eliminated the episodes of long-distance dispersal that may be relevant for detecting a relationship between nut mass and dispersal distance (e.g. >100 m, which do occur in this system; Castro et al., 2017). We can thus not rule out that seed mass plays a relevant role in dispersal distance by magpies.

4.3 | Consequences of caching decisions for early seedling establishment

The initial walnut establishment was determined by a complex interplay of processes mediated by the animal's decisions, and that may create contrasting effects for subsequent phases of establishment (H4). Magpies preferred areas with loose soil (c. 65% of dispersal events pooling soft bare soil and SLBS), or with a dense herbaceous

cover (30%), and clearly rejected areas of compacted bare soil (5.4% of the nuts). In addition, all nuts dispersed into the compact bare soil habitat were recovered, rendering no chances for establishment (Figure 5a). Moreover, all nuts left in the surface were recovered, and in any case seed germination was almost restricted to nuts buried in the soil or under litter (Figure 5b). Therefore, magpies concealed the nuts in emplacements that increased the probability of seed germination and emergence and that may, additionally, enhance seedling performance (García et al., 2002; Gómez, 2004; Vander Wall, 1990). Thus, habitat selection by magpie had positive consequences for early seedling establishment.

The proportion of remaining, nonrecovered nuts was highest in the habitat with a dense herbaceous cover (Figure 5a), thereby changing the initial template of seed distribution. This habitat type also received seeds that were, on average, heavier than in the other treatments. Such processes are, again, mediated by animal decisions that can affect early seedling establishment and even filter genotypes, as heavier seeds usually render more competitive seedlings (Castro et al., 2006). Moreover, the habitat covered by herbs produced the highest proportion of germinated seeds and emerged seedlings (Figure 5b), hinting that those sites with dense herbaceous

cover could provide a particularly appropriate combination of conditions for early seedling recruitment. However, magpies reject areas once the herb cover or height reach a threshold that may hamper the access by the bird or increase their perceived risk of predation (reduced visibility or escaping possibilities; Johnson et al., 2004). In fact, the herbaceous cover in the 10-cm radius around the cached nuts in the CHC habitat (65.7%) is lower than the overall herbaceous cover estimated for this habitat at the plot scale (95%), suggesting that magpies preferred sites with a lower cover within this habitat type. In the same line, magpies never cached nuts in the neighbouring maize fields (except after harvest), despite it being an abundant habitat in the study area that could be considered as a dense, tall herbaceous cover (personal observations; Castro et al., 2017, Molina-Morales et al., 2019). In summary, the temporal and spatial patterns of different available habitat types for walnut dispersal and early seedling establishment are very dynamic in these systems.

5 | CONCLUSIONS

This study shows that the selection of caching sites by a scatter-hoarder corvid at the habitat scale (experimental plots) and cache types are factors that can benefit early seedling establishment. The magpies avoided areas with compacted soil lacking dense herbaceous cover, which are detrimental to seed viability and early seedling establishment. Contrarily, they selected places and produced cache types that would favour seed germination and seedling emergence. Thus, magpie caching behaviour increased the transition probability from seed to seedling. In fact, walnut seedling emergence in agricultural fields has been observed since the arrival of magpies to the study site, but not earlier (personal observations; see Lenda et al., 2012 for a similar pattern in Poland). This does not translate into walnut recruitment in these lands given that the area is intensively used for agriculture, but supports the role of magpies for the expansion of nut-producing trees described in other studies (e.g. walnuts and oaks; Lenda et al., 2012; Martínez-Baroja et al., 2021). Arable land is subjected to high levels of disturbance that result in areas of soft and bare soil and with incipient herbaceous cover. Ploughing produces a landscape where the scatter-hoarding behaviour of the magpie promotes tree seedling establishment. Thus, the magpie may act as a key vector that can foster forest colonisation of set-aside cropland, secondary succession or even active restoration plans in rural landscapes, as it has the capacity to provide relevant ecological benefits in the context of supporting ecosystem services.

AUTHOR CONTRIBUTIONS

Mercedes Molina-Morales and JC designed the experiment. Mercedes Molina-Morales, Jorge Castro and Gonzalo Albaladejo-Robles carried out the field work. Alexandro B. Leverkus and Mercedes Molina-Morales performed the statistical analyses. Mercedes Molina-Morales and Jorge Castro led the writing of the manuscript. All authors participated in the elaboration of the manuscript.

CONFLICT OF INTEREST

All authors declare that they have no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Analyses reported in this article can be reproduced using the dataset available from the Dryad Digital Repository https://doi.org/10.5061/dryad.fn2z34tz1 (Molina-Morales et al., 2022).

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SUPPORTING INFORMATION

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