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Caching territoriality and site preferences by a scatter-hoarder drive the spatial pattern of seed dispersal and affect seedling emergence

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Abstract

1. For plants with seeds dispersed by scatter-hoarders, decision-making by animals when caching determines the spatial pattern of seed dispersal and lays the initial template for recruitment, driving the regeneration of many species. However, the mechanism by which animal behaviour shapes seed distributions in spatially complex landscapes is not well understood. We investigated caching territoriality and site preferences to determine the spatial pattern of seed caching at different scales and whether scatter-hoarding behaviour drives the spatial distribution of seedling emergence.
2. We used radio-tracking and automatic wildlife cameras to monitor holm oak (*Quercus ilex*) acorn caching by Eurasian magpies (*Pica pica*), who are effective scatter-hoarders in agroforestry systems. We assessed the effect of caching territories, distance to seed source, habitat, sub-habitat, microsites, and caching material in the spatial pattern of acorn dispersal by magpies. In addition, we analysed the relationship between the density of cached acorns and of emerged seedlings in different habitats.
3. Breeding magpies cached the acorns inside their caching territories, where they preferred tilled areas over oak plantations and mostly avoided old fields. These differences in habitat preference were maximized at relatively short to medium dispersal distances, where most acorns were cached, and decreased or disappeared at long-distances. Within tree plantations, magpies preferred high plant-productivity sites over low productivity ones. At the finest spatial scale, magpies preferred structures built by animals, such as rabbit grit mounds and latrines and ant litter mounds, to cache the acorns. In many sites, magpies selected uncommon materials such as stones and litter to cover caches. In the subsequent spring, seedling emergence was positively correlated with acorn cache density.
4. *Synthesis.* Scatter-hoarding is a hierarchical process in which caching sites are selected using different criteria at different spatial scales driven by territoriality and site preferences. Territoriality constrained dispersal distance and the habitats available for acorn caching. Magpie territoriality therefore indirectly drives oak seedling emergence and can determine oak recruitment and forest regeneration.

Resumen

1. Para las plantas con semillas dispersadas por animales que hacen almacenes dispersos (*scatter-hoarders*), la toma de decisiones de los animales cuando almacenan las semillas determina el patrón espacial de dispersión y la plantilla inicial del reclutamiento, lo que dirige la regeneración

de muchas especies. Sin embargo, no se comprende bien el mecanismo por el cual el comportamiento animal da forma a la distribución de semillas en paisajes espacialmente complejos. En este estudio investigamos cómo la territorialidad para el almacenamiento de semillas y las preferencias espaciales del animal determinan el patrón espacial del almacenamiento de semillas a distintas escalas espaciales y si el comportamiento de realizar almacenes dispersos afecta a la densidad de plántulas emergidas.

2. Monitoreamos el almacenamiento de bellotas de encina (*Quercus ilex*) por la urraca (*Pica pica*), un dispersor efectivo en sistemas agroforestales, mediante radio-seguimiento y cámaras de fototrampeo. Evaluamos el efecto de los territorios de almacenamiento, la distancia a la fuente de semillas, el hábitat, el sub-hábitat, el micrositio y el material de almacenamiento en el patrón espacial de la dispersión de bellotas. Además, se analizó la relación entre la densidad de bellotas almacenadas y la de las plántulas emergidas en los distintos hábitats.
3. Las urracas reproductoras almacenaron las bellotas dentro de sus territorios de almacenamiento y prefirieron zonas abiertas aradas a plantaciones forestales de quercíneas, evitando generalmente el herbazal que rodea las plantaciones forestales. Estas diferencias en la preferencia por los distintos hábitats fueron máximas a distancias de dispersión relativamente cortas o medias, donde se almacenaron la mayor parte de las bellotas, y decrecieron o desaparecieron a distancias largas. Dentro de la plantación forestal, las urracas prefirieron los sub-hábitats de mayor productividad vegetal para almacenar bellotas. A escala de micrositio, prefirieron las estructuras hechas por animales, como escarbaduras y letrinas de conejos y hormigueros. En muchos lugares las urracas seleccionaron los materiales menos abundantes como piedras y hojarasca para ocultar las bellotas. En la primavera siguiente la densidad de plántulas recién emergidas en los hábitats se correlacionó con la densidad de bellotas almacenadas.
4. *Síntesis.* El proceso de toma de decisiones en el almacenamiento disperso de semillas es jerárquico dado que los lugares de almacenamiento se seleccionan a distintas escalas espaciales determinados por la territorialidad y las preferencias espaciales de almacenamiento. La territorialidad restringió la distancia de dispersión y la disponibilidad de hábitats y sub-hábitats para el almacenamiento de bellotas. En consecuencia, la territorialidad de las urracas determina indirectamente la emergencia de plántulas y puede determinar el reclutamiento de quercíneas y la regeneración del bosque.

Keywords: caching preferences, forest regeneration, gene flow, *Quercus ilex*, *Pica pica*, synzoochory.

1. INTRODUCTION

Seed dispersal is a central process in the plant life cycle that provides connectivity among populations, colonization of empty habitats, and range mobility in response to climate change (González-Varo et al., 2017). For zoochorous plants, animal behaviour drives seed fate because animals do not disperse seeds randomly in the landscape (Alcántara et al., 2000; Rodríguez-Pérez et al., 2012). Therefore, understanding the seed dispersal behaviour of animals is fundamental to unravel how seeds are distributed in space, the process which forms the initial template for plant recruitment (Nathan & Muller-Landau, 2000; Schupp & Fuentes, 1995) and forest regeneration (Leverkus & Castro, 2017).

Synzoochory is a special case of zoochory in which animals deliberately cache the seeds for later consumption (Gómez et al., 2019; Lichti et al., 2017). In scatter-hoarding animals, which superficially bury seeds in caches, the spatial pattern of seed dispersal results from a complex decision-making process (Lichti et al., 2017) aimed at maximizing retrieval of cached seeds (Pesendorfer et al., 2016; Waite & Reeve, 1992). Seed caching decisions involve trade-offs between seed caching effort and seed retrieval, risk of disperser predation, and avoidance of seed pilfering and damage (Clarkson et al., 1986; Lichti et al., 2017). From the plant perspective, the spatial distribution of individuals, reproductive success, and population genetic structure depend on the characteristics of seed caching sites, from the habitat to the microsite scale (García-Cervigón et al., 2018; Jordano, 2017; Scofield et al., 2010; Stiles, 2000).

Although synzoochory is context-specific and depends on animal and plant species' idiosyncrasies, several general features of the seed scatter-hoarding process may determine seed spatial pattern and, consequently, plant recruitment (Cousens et al., 2010; Scofield et al., 2010). For instance, several scatter-hoarding birds tend to cache food in the vicinity of their nests or inside their home ranges (Birkhead, 1991; DeGange et al., 1989; Jokinen & Suhonen, 1995; Tomback, 2016). However, little is known about the existence of "caching territories", i.e. areas where individuals cache seeds in exclusivity and that are defended to avoid seed pilfering (Lorenz et al., 2011). The existence of "caching territories" and their characteristics could determine the spatial pattern of seed dispersal, plant regeneration, and gene flow.

In spatially heterogeneous environments, scatter-hoarders often show strong preferences for sites with specific soil or vegetation characteristics to cache seeds (Gómez, 2003; Morán-López et al., 2015; Pons & Pausas, 2007b; Vander Wall, 1990). In this context, distance from seed sources to caching sites can affect the density and site preference of caches (Clarkson et al., 1986; Waite & Reeve, 1992). However, distance has been little considered in modelling site selection for food caching by scatter-hoarders. We also do not know whether caching territoriality constrains site preferences for seed caching.

Similarly, little is known about the variation of caching preferences at different spatial scales (Gómez, 2003) and whether these preferences drive the spatial pattern of seedling emergence (Lenda et al., 2012).

Here, we study the importance of caching territoriality, site preferences, and caching distance as drivers of 1) seed caching at different spatial scales and 2) subsequent seedling emergence at a coarse spatial scale. To address this goal, we used the interaction among Eurasian magpies (*Pica pica* L.) and holm oaks (*Quercus ilex* L.) as our study system. Magpies are massive acorn scatter-hoarders, i.e. disperse large number of acorns (Martínez-Baroja et al., 2019), and territorial breeders (Baeyens, 1981; Birkhead, 1991; Szala et al., 2020) that inhabit open landscapes. The holm oak is the most important tree in agroforestry systems in the western Mediterranean Basin (Pulido & Díaz, 2005). Acorn dispersal was monitored with radiotracking and cameras to address three objectives. First, we aimed to ascertain whether acorn caching in space is constrained by territorial behaviour of the scatter-hoarder. If magpies monopolised some areas for acorn caching, this would support our hypothesis of the existence of seed caching territories (H1). Our second objective was to investigate whether acorn-caching preferences occur at different spatial scales. If magpies cache acorns in specific sites after controlling for dispersal distance, this would support site preferences (H2). Third, our goal was to analyse whether oak seedling emergence matches the spatial pattern of acorn dispersal. Correspondence of emergence with cache distribution would support our hypothesis that caching preferences drive seedling emergence distributions (H3). The results of this study will contribute to the understanding of how scatter-hoarders shape the spatial pattern of natural forest regeneration. Further, they may provide practical lessons to assist in forest restoration.

2. MATERIAL AND METHODS

2.1 Study area

The study area is an agroforestry ecosystem in central Spain (40° 31' 0'' N, 3° 19' 55'' W), 605 m a.s.l. with continental Mediterranean climate. Mean annual temperature and precipitation are 13.8°C and 425 mm, respectively. The soil is alluvial and deep, with a silty loam texture and high proportion of gravel and pebbles (see Table S1 for stone cover) and a pH around 8.0 (Trueba et al., 1998). The area includes a 28.4 ha plantation of holm oak and Portuguese oak (*Quercus faginea* Lam.) planted in 1995, surrounded by old fields (Figure S1). Several firebreaks cross and surround the plantation and are ploughed at least once a year. Almond trees (*Prunus dulcis* (Mill.) D.A. Webb) have colonized some parts of the study area forming mixed almond tree and oak forest patches. Numerous potential acorn consumers such as rabbits (*Oryctolagus cuniculus* L.), magpies, common wood pigeons (*Columba palumbus* L.), and wood mice

(*Apodemus sylvaticus* L.), breed and feed in this area, while jackdaws (*Corvus monedula* L.) feed but do not breed there. Only magpies and mice are considered acorn scatter-hoarders. However, we believe that mice have a small impact on oak recruitment in the study area because their density is low due to the presence of feral cats and the role of mice as acorn dispersers has been argued (Gómez et al., 2019).

2.2 Spatial pattern of acorn dispersal

We studied the spatial pattern of acorn dispersal by magpies using radio-tagged acorns provided in six feeding stations (hereafter “feeders”) in 2015-2016. Feeders consisted of a colander fixed to the top of a 60-70 cm metal rod. Feeder positions were chosen to include a range of habitat types and distances from feeders to the old fields (Figure S1). From November to December 2015, the feeders were filled repeatedly to maintain 10 acorns per feeder to attract magpies. We monitored acorn removal by magpies with trail cameras (Moultrie MCG-12634; Moultrie Products, Alabama, USA), which recorded 1-minute videos when movement was detected. Once the magpies got used to the feeders, we regularly supplied radio-tagged and untagged acorns (Martínez-Baroja et al., 2019; Pons & Pausas, 2007b) from November 2015 to April 2016. Removed acorns were located on the same day to avoid post-dispersal predation or secondary dispersal. 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). We registered the type of habitat, sub-habitat, microsite, caching material, and coordinates of the cached acorns.

2.2.1 Delimitation of caching territories

To test whether magpies used caching territories, i.e. an area where only the pair that owns the territory caches acorns and prevents other magpies from caching and recovering acorns (H1), we constructed a Voronoi polygon (VP) around each active nest in the next spring to assess whether the distributions of cached acorns coincided with these polygons. VPs are often used as a model for bird territory estimations (Adams, 2001; Schlicht et al., 2014). In spring 2016, after monitoring acorn dispersal, we located all active magpie nests (Details in Supplementary Methods in Supporting Information; Figure S2 and S3). VPs were drawn using Quantum GIS (Quantum GIS Development Team, 2016) by establishing perpendicular bisectors of the lines connecting each active nest to the nearest neighbouring active nests in order to equally distribute all the available space among the active territories (Figure S4). Thus, any point within each VP is closer to the nest located inside the polygon than to any other nest. We applied a 5 m buffer around each VP for territoriality deviation and GPS errors.

To qualitatively validate the pattern of caching territoriality in time and space, we sampled 18 additional nests during the period 2016-2017. To do so, 1) we captured 33 breeding magpies from 24 active nests and 136 nestlings taken from 51 active nests from May to July 2016 (details in Supplementary Methods in Supporting Information). All individuals were individually marked with field-readable combinations of coloured metal rings to the tarsus for identifications purposes. 2) We installed 24 feeders close to the nests where breeders were ringed. From December 2016 to March 2017, magpies removed acorns from 14 of 24 feeders. Each active feeder was supplied with 2–11 radio-tagged acorns (mean = 5) to study the caching behaviour of ringed individuals as described before. Finally, 3) we located all active magpie nests in spring 2017 and delimited their VPs. For the 2016-17 season, activity of ringed individuals allowed us to assess the concordance between caching territories and breeding territories in the following breeding season.

2.2.2 Habitats, sub-habitats, microsites, and materials for acorn caching

We assessed site preferences for acorn caching at three spatial scales. At the coarsest spatial scale, we differentiated three habitats (Figure S1.C), which were: (1) Tree plantation, dominated by planted holm oaks, spontaneous almond trees, and some planted Portuguese oaks with herbaceous vegetation in the gaps; this habitat had not been ploughed for 10 years; (2) fields that were abandoned ca. 30 yr prior to the study (“old fields” from now on), dominated by an herbaceous community with a few abandoned olive trees (tree cover <1%); this habitat surrounds the tree plantation and has not been ploughed for 29 years; and (3) Tilled areas, which are 4-7.5 m wide firebreaks within the tree plantation and between the tree plantation and the old fields; this habitat was ploughed once or twice per year.

At an intermediate spatial scale, we distinguished two sub-habitats inside the tree plantation according to plant productivity: high and low plant productivity. This was determined by the mass and cover of herbs and trees, which were defined by the presence of a streambed (high plant productivity sub-habitat) that crosses the tree plantation longitudinally *versus* outside of the streambed (low plant productivity sub-habitat; details in Supplementary Methods in Supporting Information; Table S1, Figure S1, Figure S3). Additionally, we distinguished two sub-habitats according to tree cover in the tree plantation: beneath tree canopies *versus* in the gaps between canopies. Location, cover, and composition of habitats and sub-habitats were determined on digitized photos using Quantum GIS.

At a fine spatial scale, we distinguished three types of microsites made by two animal species: rabbit grit mounds and latrines and ant litter mounds. We estimated the cover of these microsites around each feeder using eight radial linear transects separated by 45°. Transect length in each feeder was

defined by the most remotely dispersed acorn from that feeder (mean = 83.3 m; range: 64-112 m). Microsite cover was calculated as the proportion of the transect overlapping each microsite. We also recorded three materials that magpies used to cover acorns: loose soil, plant litter, and stones. We estimated the cover of these three materials in 50 x 50 cm quadrats according to the following sampling design. We made three replicates, each one near each pair of feeders (feeders 1-2, 3-4 and 5-6; Figure S1C, Figure S3). Each replicate included four 40-m long transects: two transects in the tree plantation (one in the high and one in the low plant productivity sub-habitats), one transect in the old fields, and finally one transect in the tilled areas between the tree plantation and the old fields. Each transect was sampled using four quadrats that were regularly placed every 10 m along the transect (Table S1, Figure S3).

2.3 Seedling emergence in different habitat types

To evaluate whether the spatial pattern of acorn caching matched the distribution of seedling emergence by habitat, we compared the density of cached radio-tagged acorns with the density of emerged seedlings in each habitat type. First, we calculated acorn caching density in each habitat by territory using data of the 2015-2016 survey. Then, in July 2016, we counted the number of emerged oak seedlings in each habitat in 200-m² transects (length 30-65 m and width 3-10 m) to calculate the number of seedlings ha⁻¹. We sampled 12 transects, one in each combination of habitat and territory, in the four territories where all three habitat types occurred (three territories with feeders 2, 3 and 4 and one territory with feeders 5 and 6; Figure S1, Figure S3).

2.4 Data analyses

We constructed point process models with the R spatstat package to determine whether the territorial behaviour and site preferences of magpies explained the spatial distribution of cached acorns using the data of the 2015-2016 survey (Baddeley et al., 2015; R Core Team, 2018). A point process model is a dataset of observed spatial locations of points, represented by the acorns in our study, and their relationship with other layers of spatially-explicit variables (e.g. habitat type). Distance to feeders was included as a covariate. The dependence of acorn caching density on spatial covariates was modelled as an inhomogeneous Poisson process, where the intensity of the point pattern was a log-linear function of the predictor variables (Voronoi polygons, distance, habitat and sub-habitat types). Each of the six feeders had one point pattern, one Voronoi Polygon, one habitat or sub-habitat type and one distance layer. These layers were used to construct a “hyperframe” consisting of a collection of layers that provided analogous information for each feeder. The function “mppm” was used to fit six point process models simultaneously (i.e., one model for each feeder) to obtain parameter estimates for the combination of feeders (Baddeley et al., 2015).

We analysed the point pattern generated by caching events at two spatial scales, namely habitat (coarse) and sub-habitat (intermediate) scales. First, we considered the coarse habitat scale that included the six feeders and all the caching events and fitted models to assess whether the spatial pattern of dispersal from each feeder fitted within the caching territories defined by the VP in which the feeder was located, distance to the feeder, habitat type, and all possible interactions between the layers as explanatory variables for acorn caching density. The area for the analysis (window) of these models was the “radius of action of magpie dispersal”, which was defined as a circle centred at each feeder with a radius of the maximum registered caching distance from that feeder. Second, at an intermediate spatial scale, we fitted models to assess the effect of the two sub-habitat layers within tree plantation (high vs. low plant productivity, and beneath canopy cover vs. in open interspaces), distance to the feeder, and all possible interactions between layers as explanatory variables for acorn caching density. The window for the analyses of these models was the tree plantation habitat contained within each nest’s VP. The minimum adequate model was determined by model simplification, beginning with a global model that included all predictor variables (territory, habitat type and distance in the first model and sub-habitat type and distance in the second one), and their two- and three-way interactions. In each simplification step, the significance ($p < 0.05$) of the effect of each predictor was assessed using likelihood ratio tests until the minimum adequate model was produced, where each term was either significant or included within a significant higher-order interaction (Crawley, 2007).

We analysed magpies’ preferences for the microsites and caching material by comparing their use frequency against their abundance by chi-square tests. When expected counts were too small, we estimated p-values using a Monte Carlo simulation with the “simulate.p.value=TRUE” argument on the R function “chisq.test” to properly perform chi-square tests (Verzani, 2005). Spearman’s correlation was used to analyse the association between acorn caching density and seedling emergence density. All analyses were performed with R version 3.5.2 (R Core Team, 2018).

3. RESULTS

3.1 Spatial pattern of caches

We monitored 260 radio-tagged acorns in 2015-2016 and 77 acorns in 2016-2017, of which 178 (range 21-41 acorns feeder⁻¹) and 42 (2–11 acorns feeder⁻¹), respectively, were cached by magpies whereas the rest were pecked open for consumption. Across both study periods, distance of cached acorns to feeders ranged 1.4-210 m (mean \pm SE = 32.4 \pm 1.9 m; median = 23.5 m). All acorns were cached individually in the ground.

At the coarse scale, dispersal by magpies in 2015-2016 resulted in most cached acorns (89%) occurring inside the caching territories defined by the VPs where the acorns were removed in 2016 (Figure 1a). The effect of caching territories defined by the VPs on acorn cache density was significant after controlling for the effect of distance (Table 1, Figure 1). The distribution of the few cached acorns per feeder monitored in 2016-2017 also overlapped VPs of 2017, qualitatively supporting the territorial pattern observed in 2015-2016 (Figure S4). Between 2016 and 2017, nest displacement (several breeding magpies built new nests; 55% in 2016 and 69% in 2017) and the incorporation and disappearance of breeding pairs changed the number, size and location of VPs (Figure S5). Acorn cache density significantly differed (Table 1) among habitat types in 2015-2016 in the following order: tilled areas (100.7 acorns ha⁻¹, n = 40 acorns) > tree plantation (43.0 acorns ha⁻¹, n = 101) > old fields (10.8 acorns ha⁻¹, n = 18). These habitat differences in cache density depended on the distance to the feeders (habitat × distance interaction); thus, differences were greatest at short to medium-distances but decreased or disappeared at long-distances (Figure 2).

At the intermediate spatial scale, acorn cache density was significantly higher in the high plant productivity sub-habitat (50.8 acorns ha⁻¹, n = 93) than in the low plant productivity sub-habitat (13.8 acorns ha⁻¹, n = 8) (Table 1, Figure S6). Acorn cache density decreased with increasing distance to the feeder in these sub-habitats (Figure S7). There were no significant differences in acorn density under tree canopies and interspaces in the tree plantation (Table 1).

3.2 Microsite and materials preferences

Most acorns (92%) were cached in microsites unrelated to the activity of other animals. However, the remaining 8% (14 out of 178 acorns) were cached in structures built by animals other than magpies: rabbit grit mounds and latrines, as well as ant litter mounds. This frequency was significantly higher than expected by chance (Figure 3), even when all animal structures were grouped ($\chi^2_{178;0.95} = 35.11$; $p < 0.001$).

We analysed the materials used to cache the acorns in 159 out of 178 radio-tagged cached acorns. In 50% of the sites, magpies cached the acorns using the least abundant material in each site (Figure 4). In the high plant productivity sub-habitat, this corresponded to plant litter in feeders 5 and 6 and stones or litter in feeders 1 and 2. In the low productivity sub-habitat, more acorns were buried under soil than expected (feeders 5 and 6). In old fields, more acorns were cached under litter than expected (consistent for all feeders).

3.3 Emerged oak seedlings by habitat type

The density of emerged oak seedlings was 12 times greater in tilled areas than in the tree plantation and not a single seedling was recorded in old fields (Figure 5). Acorn caching density in the three habitat types in the fall-winter 2015-2016 was positively correlated with the density of emerged seedlings in early summer 2016 (Spearman's $\rho = 0.886$, $p < 0.001$, $n = 4$).

4. DISCUSSION

Acorn caching is a spatially structured process resulting from a hierarchical, top-down, and selective decision-making process where the features at a coarse spatial scale determine acorn caching decisions at finer spatial scales. Magpie territoriality was crucial for acorn caching at coarse and intermediate spatial scales (H1) because territoriality constrained dispersal distance and the habitats and sub-habitats available for caching. Magpies showed marked preferences for specific habitat and sub-habitat types, caching microsites, and materials to cache acorns (H2). Importantly, habitat preference matched the distribution of oak seedling emergence (H3), so seed dispersal lays the initial template for recruitment. This study illustrates how caching territoriality and site preferences of scatter-hoarders drive the spatial pattern of seed dispersal and can affect seedling emergence.

4.1 Caching territoriality

As hypothesized (H1), the distribution of cached acorns strongly coincided with the Voronoi polygons (VPs) around the nests of the next breeding season (2016), even after controlling for the effect of distance to feeders. This supports the hypothesis that breeding magpies establish acorn-caching territories, in which most (89%) removed acorns were cached (Figure 1). While other authors have suggested that breeding magpies cache food inside their nesting territories (Birkhead, 1991; Clarkson et al., 1986), to our knowledge our study is the first one to quantify such behaviour, a detailed adjustment of acorn caching patterns to territorial boundaries (VPs), and the exclusive use of such areas by breeding individuals. Consistent with this finding, Martínez-Baroja et al. (2019) determined that magpie breeding pairs removed 89% of the acorns from the feeders located within their territories, whereas the rest of removed acorns were taken by neighbouring breeding magpies or juveniles. These "thieves" moved and cached the stolen acorns in their own caching territories in the second study period (2016-2017) (Figure S4). This suggests that the cached acorns that do not match the territorial pattern in the first study period (2015-2016) could be the result of such "theft" and of the territorial behaviour of other breeding magpies.

Our study suggests that magpies have all-purpose territories for nesting, foraging, and food caching as other authors proposed previously for other scatter-hoarders (Maher & Lott, 1995; Scofield et

al., 2010). We observed that some magpies maintained their territories during the entire year, switching the territorial behaviour from caching seeds to nesting. Magpies usually remain in their nesting territory throughout the year but sometimes they move to other locations and return in spring (Birkhead, 1991; Szala et al., 2020). We showed that nest distribution varied between years, but the dispersal patterns matched the VPs derived from the nest distribution that appeared in the spring after the acorn dispersal season. Thus, food caching territories seem to affect nest location in the next breeding season (Figure 1a). Moreover, defence of seed caching territories could be a major mechanism to avoid seed pilfering by conspecifics when seed caching is massive, which would support the social context hypothesis, i.e. different behaviour in the presence or absence of conspecifics (Kalinowski et al., 2015; Beck et al., 2020). Keeping and defending an all-purpose territory throughout the year could motivate magpies to cache acorns not only for short-term recovery (the same day or a few days later; Birkhead 1991, Zinkivskay et al. 2009), but also for long-term storage (until spring or early summer), as reported for other corvids such as the Eurasian jay (Bossema, 1979). Future studies should address the temporal pattern of acorn recovery to assess this idea.

Acorn caching territories determined the spatial pattern of acorn dispersal. First, territoriality limits dispersal distance, which is constrained by the size and shape of the territory (Beck et al., 2020). The magpie is a medium-distance seed disperser (i.e. 25-250 m, Traveset et al. 2014) according to the acorn dispersal distances we found (mean of 32 m and maximum of 210 m). However, we observed a few long-distance dispersal events in two feeders in 2016-2017, likely resulting from acorn “theft” by breeding individuals from other territories (Figure S4). Long-distance dispersal events may also occur due to food removal by non-territorial individuals (Birkhead, 1991; DeGange et al., 1989; Scofield et al., 2010). Despite their low frequency, long-distance dispersal events can play an important role in gene flow among plant populations (Cain et al., 2000; Hampe et al., 2013). Additionally, long-distance dispersal by “thieves” could be highly relevant for oak forest expansion (Jordano, 2017) when caching territories are located outside oak forest patches and magpies nest in scattered non-oak trees (Figure S4).

Secondly, acorn caching territories can affect the direction in which acorns are dispersed (Scofield et al., 2010). For instance, acorns removed from feeder 1 were mainly cached westward, likely because most of the territory was located in that direction from the feeder (Figure 1 Feeder1). However, the number, size and shape of caching territories varied between years (Figure S5), which could be important for plant gene flow. Further, annual spatial dynamics of caching territories could decrease the rate of acorn retrieval of cached acorns and promote oak recruitment. Future studies should assess the generality of seed caching territories for other territorial scatter-hoarder and tree species.

4.2 Site preferences

Our results suggest that the spatial structure inside caching territories is important for the spatial pattern of seed dispersal in territorial scatter-hoarders. In accordance with our second hypothesis, magpies showed strong preferences for some habitats, sub-habitats and microsites for acorn caching. However, this site selection depended on their availability inside the caching territory. When several habitats were available inside a territory and distance to the feeder was controlled for, magpies selected mainly tilled areas, secondarily the tree plantation, and finally the old fields to cache the acorns. Habitat selection was negatively related to the time since last tilling of these habitats, which likely affects soil compaction. These findings suggest that ease of acorn caching into the ground could be an important factor for magpies. Other authors have also shown that habitat types with loose soils are highly selected by acorn scatter-hoarders (Bossema, 1979; Castro et al., 2017). The selection of specific places for acorn caching could aim to minimize the time investment, to improve efficiency of caching and subsequent retrieval, and to avoid pilfering (Bossema, 1979; Gómez, 2003; Pons & Pausas, 2007b).

The interaction between habitat type and dispersal distance found here could have implications for forest regeneration. Acorn dispersal into tilled areas and oak forest patches could contribute to increase tree density closer to the seed source because, within these two habitats, acorn caching density abruptly decreased with distance (Figure 2). This is usually interpreted in terms of minimized resource investment in dispersal and the natural geometric expansion of area as distance from a point-source increases (Lichti et al., 2016). However, density of caches in old fields decreased less with distance than in the other habitats, which could allow low but more homogeneous colonization in this habitat. This may be due in part to high soil compaction in the old fields that drives acorn caching mainly towards the scarce and homogeneously distributed animal structures with loose soil in this habitat (Figure 3 and Figure 4 d-f). Magpies with territories located entirely within oak-forest patches can only contribute to the regeneration and persistence of such patches (Figure 1). In contrast, magpies with territories spanning oak patches and old fields can contribute to oak forest expansion into the old fields. Tilling old fields right after abandonment or strategically placing nesting sites for magpies could increase acorn arrival and, consequently, oak colonization in these open areas.

At an intermediate spatial scale, all studied magpies preferred the high-productivity sub-habitat to the low-productivity one to cache acorns. This could be associated either with the higher number and diversity of spatial cues to cache seeds (Bennett, 1993; Bossema, 1979) or with the presence of other food sources, such as invertebrates and greater plant biomass, which allows magpies to feed extensively (Birkhead, 1991).

Some features of seed dispersal events at the fine scale emerged from individual behaviour. Magpies preferred structures built by animals to cache acorns, but these structures were relatively uncommon. Similarly, magpies preferred rare covering materials such as plant litter, stones or loose soil for this process. Preference for these materials differed among caching territories, suggesting that magpies are flexible in selecting materials for acorn caching. While low abundant structures and materials could serve as better cues for effective seed retrieval (Feenders & Smulders, 2011; Leverkus et al., 2016), they may also render the caches more conspicuous to potential competitors or seed predators. This disadvantage may be offset, however, by the placement within caching territories, which are defended against conspecifics. Additionally, magpies could select structures built by animals because they have loose soil, which could be important in compacted soils.

4.3 Seedling emergence

As hypothesized (H3), the density of emerged seedlings across habitats matched the spatial pattern of acorn dispersal (Figure 5). Thus, habitat preferences for acorn caching by magpies could have left an imprint on oak seedling emergence density (Lenda et al., 2012). The tight relation between the density of emerged seedlings and that of cached acorns suggests that the combined outcomes of post-dispersal predation and seedling emergence rate were similar among habitat types. In addition, the differences in these rates among habitat types may not have overcome the strong differences in caching. Further research is necessary to assess whether caching territory defence and strategies for cached-acorn recovery equalize post-dispersal acorn predation across habitats. Additionally, large-seeded species such as oaks tend to have higher seedling emergence rates than small-seeded species (Lavorel & Lebreton, 1992). The differences in seedling density among habitats could result in demographic conflicts in oak recruitment across different habitat features (Leverkus et al., 2016). For instance, tilled areas are more exposed to herbivores and solar radiation than other habitats, which strongly limit oak seedling survival (Gómez-Aparicio et al., 2008; Cuesta, Villar-Salvador, Puértolas, Rey Benayas, et al., 2010), but herb competition and soil compaction are low, which can increase root growth and seedling establishment (Cuesta, Villar-Salvador, Puértolas, Jacobs, et al., 2010; Kozłowski, 1999). Future studies should address the net outcome on oak recruitment of the positive and negative effects of environmental factors on diverse ontogenetic stages in tilled and non-tilled areas, since life stage conflicts are frequent and may ultimately define the spatial patterns of recruitment (Schupp, 2007).

5. CONCLUSIONS

This study shows that: 1) the scatter-hoarder responds to multiple environmental features for seed caching rather than just one feature; 2) these environmental choices are applied hierarchically; and 3) animal territories can be important constraints irrespective of the characteristics of the environment for the regeneration of zoochorous plants. Hierarchical behaviour of the caching animal will translate into structure in the plant population. This insight is demonstrated here by a territorial scatter-hoarder bird, but probably applies to a great range of other seed caching animals.

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AUTHORS' CONTRIBUTION

LMB, LPC, PVS, SR, MMM, ABL, JC, and JMRB conceived and designed the experiments. LMB, LPC, PVS and SR performed the experiments and collected the data. LMB and LPC reviewed the videos. LMB, ABL, LPC, and MP analysed the data. LMB wrote the first draft of the manuscript. All authors discussed the results and reviewed and approved the manuscript.

DATA AVAILABILITY STATEMENT

Data available via Figshare: <https://doi.org/10.6084/m9.figshare.14156705> (Martínez-Baroja, Pérez-Camacho, Villar-Salvador, Rebollo, Leverkus, Pesendorfer, Molina-Morales, Castro, Rey-Benayas, 2021)

6. REFERENCES

- Adams, E. S. (2001). Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics*, 32, 277–303. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114034>
- Alcántara, J. M., Rey, P. J., Valera, F., & Sánchez-LaFuente, A. (2000). Factors shaping the seedfall pattern of a bird-dispersed plant. *Ecology*, 81(7), 1937–1950. <https://doi.org/10.2307/177283>
- Baddeley, A., Rubak, E., & Turner, R. (2015). Replicated point patterns and designed experiments. In *Spatial point patterns: Methodology and applications with R* (pp. 661–708). Chapman & Hall/CRC Interdisciplinary Statistics.
- Baeyens, G. (1981). Functional aspects of serial monogamy: The Magpie pair-bond in relation to its territorial system. *Ardea*, 69, 145–166.
- Beck, K. B., Loretto, M.-C., & Bugnyar, T. (2020). Effects of site fidelity, group size and age on food-caching behaviour of common ravens, *Corvus corax*. *Animal Behaviour*, 164, 51–64. <https://doi.org/10.1016/j.anbehav.2020.03.015>
- Bennett, A. T. D. (1993). Spatial memory in a food-storing corvid. I. Near tall landmarks are primarily used. *Journal of Comparative Physiology A*, 173, 193–207. <https://doi.org/10.1007/BF00192978>
- Birkhead, T. (1991). *The magpies: The ecology and behaviour of black-billed and yellow-billed magpies*. T&AD Poyser.
- Bossemma, I. (1979). Jays and oaks: An eco-ethological study of a symbiosis. *Behaviour*, 70(1), 1–116. <https://doi.org/10.1163/156853979X00016>
- Cain, M. L., Milligan, B. G., & Strand, A. E. (2000). Long-distance seed dispersal in plant populations. *American Journal of Botany*, 87(9), 1217. <https://doi.org/10.2307/2656714>
- Castro, J., Molina-Morales, M., Leverkus, A. B., Martínez-Baroja, L., Pérez-Camacho, L., Villar-Salvador, P., Rebollo, S., & Rey-Benayas, J. M. (2017). Effective nut dispersal by magpies (*Pica pica* L.) in a Mediterranean agroecosystem. *Oecologia*, 184(1), 183–192. <https://doi.org/10.1007/s00442-017-3848-x>
- Clarkson, K., Eden, S. F., Sutherland, W. J., & Houston, A. I. (1986). Density dependence and magpie food hoarding. *Journal of Animal Ecology*, 55(1), 111. <https://doi.org/10.2307/4696>
- Cousens, R. D., Hill, J., French, K., & Bishop, I. D. (2010). Towards better prediction of seed dispersal by animals: Conceptual frameworks and process-based models. *Functional Ecology*, 24(6), 1163–1170. <https://doi.org/10.1111/j.1365-2435.2010.01747.x>
- Crawley, M. J. (2007). *The R book*. Wiley.

- Cuesta, B., Villar-Salvador, P., Puértolas, J., Jacobs, D. F., & Rey Benayas, J. M. (2010). Why do large, nitrogen rich seedlings better resist stressful transplanting conditions? A physiological analysis in two functionally contrasting Mediterranean forest species. *Forest Ecology and Management*, 260(1), 71–78. <https://doi.org/10.1016/j.foreco.2010.04.002>
- Cuesta, B., Villar-Salvador, P., Puértolas, J., Rey Benayas, J. M., & Michalet, R. (2010). Facilitation of *Quercus ilex* in Mediterranean shrubland is explained by both direct and indirect interactions mediated by herbs. *Journal of Ecology*, 98(3), 687–696. <https://doi.org/10.1111/j.1365-2745.2010.01655.x>
- DeGange, A. R., Fitzpatrick, J. W., Layne, J. N., & Woolfenden, G. E. (1989). Acorn harvesting by Florida Scrub Jays. *Ecology*, 70(2), 348–356. <https://doi.org/10.2307/1937539>
- Feenders, G., & Smulders, T. V. (2011). Magpies can use local cues to retrieve their food caches. *Animal Cognition*, 14(2), 235–243. <https://doi.org/10.1007/s10071-010-0357-2>
- García-Cervigón, A. I., Żywiec, M., Delibes, M., Suárez-Esteban, A., Perea, R., & Fedriani, J. M. (2018). Microsites of seed arrival: Spatio-temporal variations in complex seed-disperser networks. *Oikos*, 127(7), 1001–1013. <https://doi.org/10.1111/oik.04881>
- Gómez, J. M. (2003). Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography*, 26(5), 573–584. <https://doi.org/10.1034/j.1600-0587.2003.03586.x>
- Gómez, J. M., Schupp, E. W., & Jordano, P. (2019). Synzoochory: The ecological and evolutionary relevance of a dual interaction. *Biological Reviews*, 94(3), 874–902. <https://doi.org/10.1111/brv.12481>
- Gómez-Aparicio, L., Zamora, R., Castro, J., & Hódar, J. A. (2008). Facilitation of tree saplings by nurse plants: Microhabitat amelioration or protection against herbivories? *Journal of Vegetation Science*, 19, 161–172. <https://doi.org/10.3170/2008-8-18347>
- González-Varo, J. P., Carvalho, C. S., Arroyo, J. M., & Jordano, P. (2017). Unravelling seed dispersal through fragmented landscapes: Frugivore species operate unevenly as mobile links. *Molecular Ecology*, 26(16), 4309–4321. <https://doi.org/10.1111/mec.14181>
- Hampe, A., Pemonge, M.-H., & Petit, R. J. (2013). Efficient mitigation of founder effects during the establishment of a leading-edge oak population. *Proceedings of the Royal Society B: Biological Sciences*, 280(1764), 20131070. <https://doi.org/10.1098/rspb.2013.1070>
- Jokinen, S., & Suhonen, J. (1995). Food caching by willow and crested tits: A test of scatter hoarding models. *Ecology*, 76(3), 892–898. <https://doi.org/10.2307/1939354>

- Jordano, P. (2017). What is long-distance dispersal? And a taxonomy of dispersal events. *Journal of Ecology*, 105(1), 75–84. <https://doi.org/10.1111/1365-2745.12690>
- Kalinowski, R. S., Gabriel, P. O., & Black, J. M. (2015). Who's watching influences caching effort in wild Steller's jays (*Cyanocitta stelleri*). *Animal Cognition*, 18(1), 95–98. <https://doi.org/10.1007/s10071-014-0780-x>
- Kozlowski, T. T. (1999). Soil Compaction and Growth of Woody Plants. *Scandinavian Journal of Forest Research*, 14(6), 596–619. <https://doi.org/10.1080/02827589908540825>
- Lavorel, S., & Lebreton, J. D. (1992). Evidence for lottery recruitment in Mediterranean old fields. *Journal of Vegetation Science*, 3(1), 91–100. <https://doi.org/10.2307/3236002>
- Lenda, M., Skorka, P., Knops, J. M. H., Moron, D., Tworek, S., & Woyciechowski, M. (2012). Plant establishment and invasions: An increase in a seed disperser combined with land abandonment causes an invasion of the non-native walnut in Europe. *Proceedings of the Royal Society B: Biological Sciences*, 279(1733), 1491–1497. <https://doi.org/10.1098/rspb.2011.2153>
- Leverkus, A. B., & Castro, J. (2017). An ecosystem services approach to the ecological effects of salvage logging: Valuation of seed dispersal. *Ecological Applications*, 27(4), 1057–1063. <https://doi.org/10.1002/eap.1539>
- Leverkus, A. B., Rey Benayas, J. M., & Castro, J. (2016). Shifting demographic conflicts across recruitment cohorts in a dynamic post-disturbance landscape. *Ecology*, 97(10), 2628–2639. <https://doi.org/10.1002/ecy.1527>
- Lichti, N. I., Steele, M. A., & Swihart, R. K. (2017). Seed fate and decision-making processes in scatter-hoarding rodents. *Biological Reviews*, 92, 474–504. <https://doi.org/10.1111/brv.12240>
- Lorenz, T. J., Sullivan, K. A., Bakian, A. V., & Aubry, C. A. (2011). Cache-Site Selection in Clark's Nutcracker (*Nucifraga columbiana*). *The Auk*, 128(2), 237–247. <https://doi.org/10.1525/auk.2011.10101>
- Maher, C. R., & Lott, D. F. (1995). Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour*, 49(6), 1581–1597. [https://doi.org/10.1016/0003-3472\(95\)90080-2](https://doi.org/10.1016/0003-3472(95)90080-2)
- Martínez-Baroja, L., Pérez-Camacho, L., Villar-Salvador, P., Rebollo, S., Quiles, P., Gómez-Sánchez, D., Molina-Morales, M., Leverkus, A. B., Castro, J., & Rey-Benayas, J. M. (2019). Massive and effective acorn dispersal into agroforestry systems by an overlooked vector, the Eurasian magpie (*Pica pica*). *Ecosphere*, 10(12), e02989. <https://doi.org/10.1002/ecs2.2989>
- Martínez-Baroja, L., Pérez-Camacho, L., Villar-Salvador, P., Rebollo, S., Leverkus, A.B., Pesendorfer, M.B., Molina-Morales, M., Castro, J., Rey-Benayas, J.M. (2021). Data from: Caching territoriality and site

preferences by a scatter-hoarder drive the spatial pattern of seed dispersal and affect seedling emergence. *Figshare*. <https://doi.org/10.6084/m9.figshare.14156705>

Morán-López, T., Alonso, C. L., & Díaz, M. (2015). Landscape effects on jay foraging behavior decrease acorn dispersal services in dehesas. *Acta Oecologica*, *69*, 52–64.

<https://doi.org/10.1016/j.actao.2015.07.006>

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, *15*(7), 278–285.

[https://doi.org/10.1016/S0169-5347\(00\)01874-7](https://doi.org/10.1016/S0169-5347(00)01874-7)

Pesendorfer, M. B., Sillett, T. S., Koenig, W. D., & Morrison, S. A. (2016). Scatter-hoarding corvids as seed dispersers for oaks and pines: A review of a widely distributed mutualism and its utility to habitat restoration. *Condor*, *118*(2), 215–237. <https://doi.org/10.1650/CONDOR-15-125.1>

Pesendorfer, M. B., Sillett, T. S., & Morrison, S. A. (2017). Spatially biased dispersal of acorns by a scatter-hoarding corvid may accelerate passive restoration of oak habitat on California's largest island. *Current Zoology*, *68*, 363–367. <https://doi.org/10.1093/cz/zow075>

Pons, J., & Pausas, J. G. (2007a). Not only size matters: Acorn selection by the European jay (*Garrulus glandarius*). *Acta Oecologica*, *31*(3), 353–360. <https://doi.org/10.1016/j.actao.2007.01.004>

Pons, J., & Pausas, J. G. (2007b). Acorn dispersal estimated by radio-tracking. *Oecologia*, *153*(4), 903–911. <https://doi.org/10.1007/s00442-007-0788-x>

Pulido, F. J., & Díaz, M. (2005). Regeneration of a Mediterranean oak: A whole-cycle approach. *EcoScience*, *12*(1), 92–102. <https://doi.org/10.2980/i1195-6860-12-1-92.1>

Quantum GIS Development Team. (2016). *Quantum GIS Geographic Information System*. Source Geospatial Foundation Project. <http://qgis.osgeo.org>.

R Core Team. (2018). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.R-project.org/>

Rodríguez-Pérez, J., Wiegand, T., & Santamaria, L. (2012). Frugivore behaviour determines plant distribution: A spatially-explicit analysis of a plant-disperser interaction. *Ecography*, *35*(2), 113–123. <https://doi.org/10.1111/j.1600-0587.2011.06930.x>

Schlicht, L., Valcu, M., & Kempenaers, B. (2014). Thiessen polygons as a model for animal territory estimation. *Ibis*, *156*(1), 215–219. <https://doi.org/10.1111/ibi.12105>

Schupp, E. W. (2007). The suitability of a site for seed dispersal is context-dependent. In A. J. Dennis, E. W. Schupp, R. J. Green, & D. A. Westcott (Eds.), *Seed dispersal: Theory and its application in a changing world*. (pp. 445–462). CAB International.

Schupp, E W, & Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of plant population ecology. *Écoscience*, 2(3), 267–275.

<https://doi.org/10.1080/11956860.1995.11682293>

Scofield, D. G., Sork, V. L., & Smouse, P. E. (2010). Influence of acorn woodpecker social behaviour on transport of coast live oak (*Quercus agrifolia*) acorns in a southern California oak savanna. *Journal of Ecology*, 12. <https://doi.org/10.1111/j.1365-2745.2010.01649.x>

Stiles, E. W. (2000). Animals as seed dispersers. In M. Fenner (Ed.), *Seeds: The ecology of regeneration in plant communities* (2nd ed, pp. 111–124). CAB International.

Szala, K., Dylewski, Ł., & Tobolka, M. (2020). Winter habitat selection of Corvids in an urban ecosystem. *Urban Ecosystems*, 23(3), 483–493. <https://doi.org/10.1007/s11252-020-00942-2>

Tomback, D. F. (2016). Seed dispersal by corvids. In Ç. H. Şekercioğlu, D. G. Wenny, & C. J. Whelan (Eds.), *Why Birds Matter: Avian Ecological Functions and Ecosystems Services*. (pp. 196–234). University of Chicago Press.

Traveset, A., Heleno, R., & Nogales, M. (2014). The ecology of seed dispersal. *Seeds: The Ecology of Regeneration in Plant Communities*, 3, 62–93.

Trueba, C., Millán, R., Schmid, T., Roquero, C., & Magister, M. (1998). *Base de Datos de Propiedades Edafológicas de los Suelos Españoles. Vol. V. Madrid*. CIEMAT, Madrid, Spain.

Vander Wall, S. B. (1990). *Food hoarding in animals*. University of Chicago Press.

Verzani, J. (2005). *Using R for introductory statistics*. Chapman & Hall/CRC.

Waite, T. A., & Reeve, J. D. (1992). Gray Jay Scatterhoarding Behavior, Rate Maximization, and the Effect of Local Cache Density. *Ornis Scandinavica*, 23(2), 175. <https://doi.org/10.2307/3676446>

Zinkivskay, A., Nazir, F., & Smulders, T. V. (2009). What–Where–When memory in magpies (*Pica pica*). *Animal Cognition*, 12(1), 119–125. <https://doi.org/10.1007/s10071-008-0176-x>

TABLE

TABLE 1. Model selection from the global model to the minimum adequate models at the coarse (habitat) and intermediate (sub-habitat) spatial scales. Global model at the habitat scale: acorn caching density ~ territory x habitat x distance. Global model at the sub-habitat scale: acorn caching density ~ distance x plant productivity x tree cover.

Spatial scale	Parameters eliminated	Δ deviance	p-value
Coarse (habitat)	territory : habitat : distance	4.0154	0.1343
	territory : distance	2.6715	0.1022
	territory : habitat	4.9817	0.0828
	habitat : distance⁺	10.896	0.0043*
	territory⁺	61.571	< 0.001*
Intermediate (sub-habitat)	distance : plant productivity : tree cover	0.035255	0.8511
	distance : tree cover	0.26096	0.6095
	distance : plant productivity	0.50967	0.4753
	plant productivity : tree cover	0.36616	0.5451
	tree cover	1.3536	0.2446
	plant productivity⁺	16.2	< 0.001*
	distance⁺	77.6	< 0.001*

Note: ***parameters included in the minimum adequate model**, which were either significant or included within a significant higher-order interaction. ***significant p-value**, the removed variable or interaction should not be eliminated from the minimum adequate model.

FIGURES

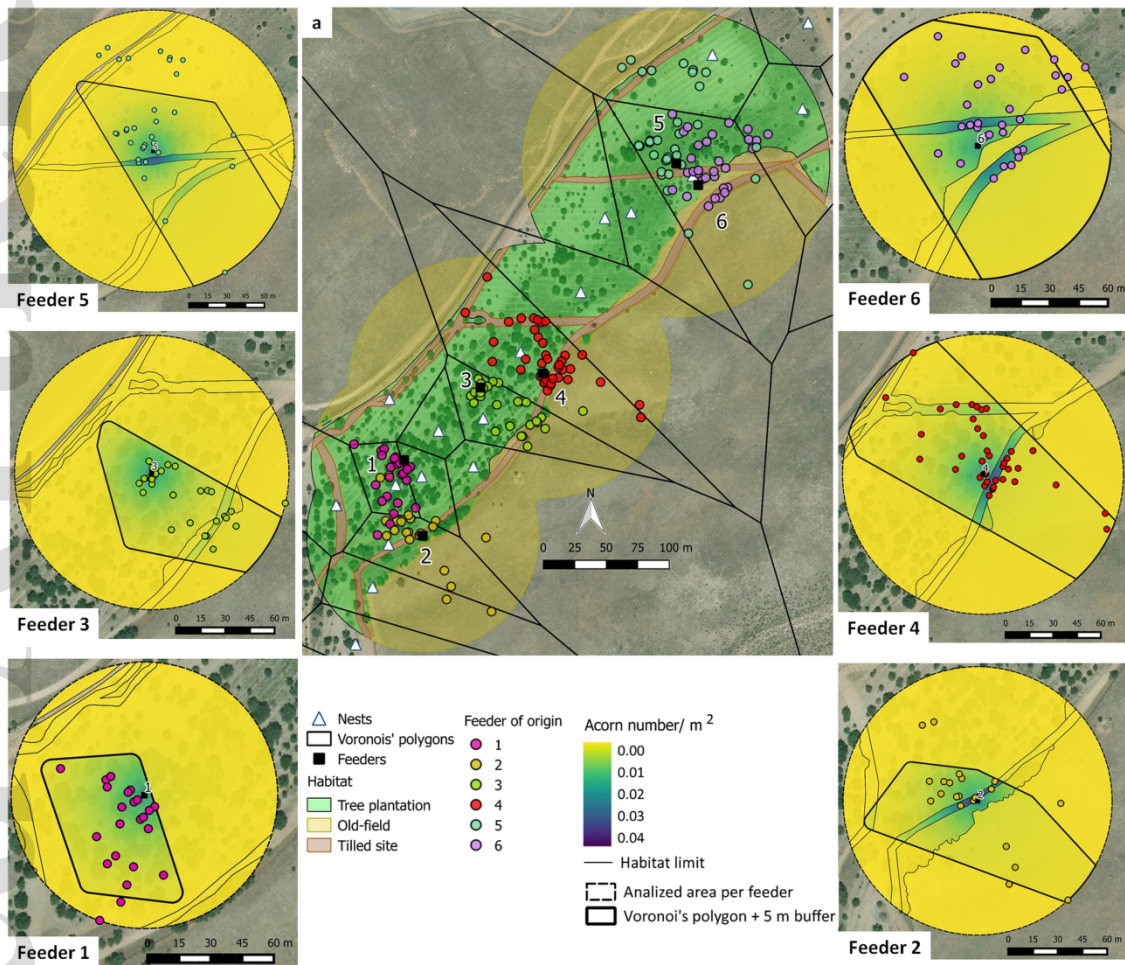


FIGURE 1. a) Voronoi polygons and dispersed acorns by magpies (dots) from the six feeders in 2015-2016. Three feeders were placed in the center of the tree plantation (numbers 1, 3 and 5) and another three at the tree plantation periphery (numbers 2, 4 and 6), near the old fields. Feeders 5 and 6 were located within the same territory. Proportions of tree plantation, old fields and tilled areas within the analyzed windows (colored circles) were 53.6%, 38.7% and 7.7%, respectively. The panels around panel a) are the spatially-explicit predictions for each feeder of acorn caching density at the habitat scale (models in Table 1). Note that the scale is different in each feeder because the radius of the maximum dispersal distance differed.

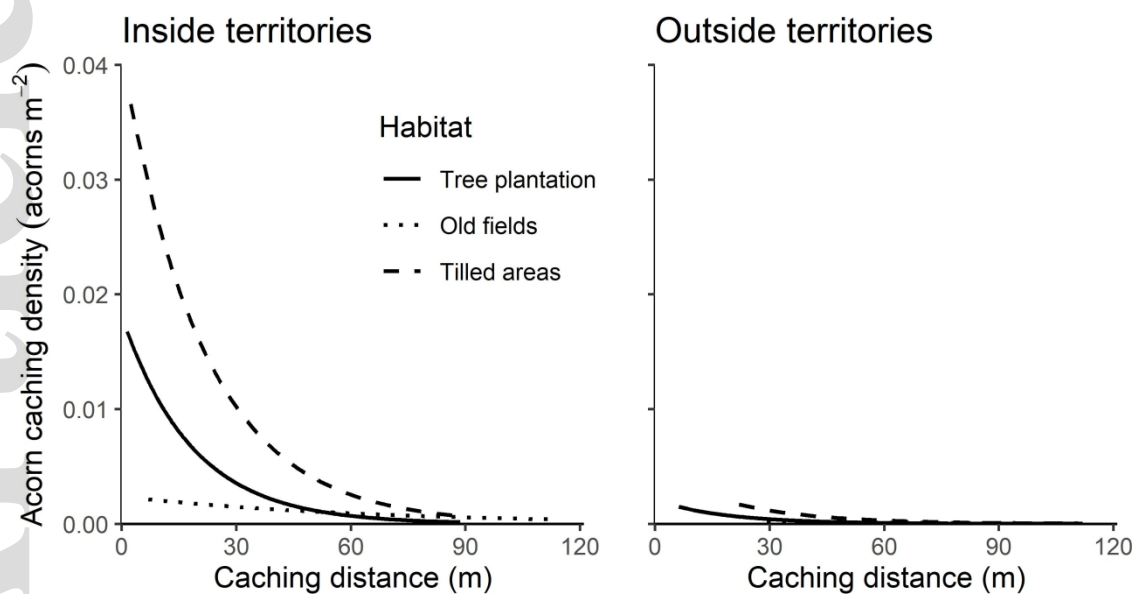


FIGURE 2. Interaction between habitat type and caching distance to the feeder on cached acorn density. Model: Acorn caching density \sim territory + habitat * distance. Model predictions for the acorns cached inside the territory (Voronoi polygon) where the feeder was (left graph) and for the acorns cached outside the territory (right graph).

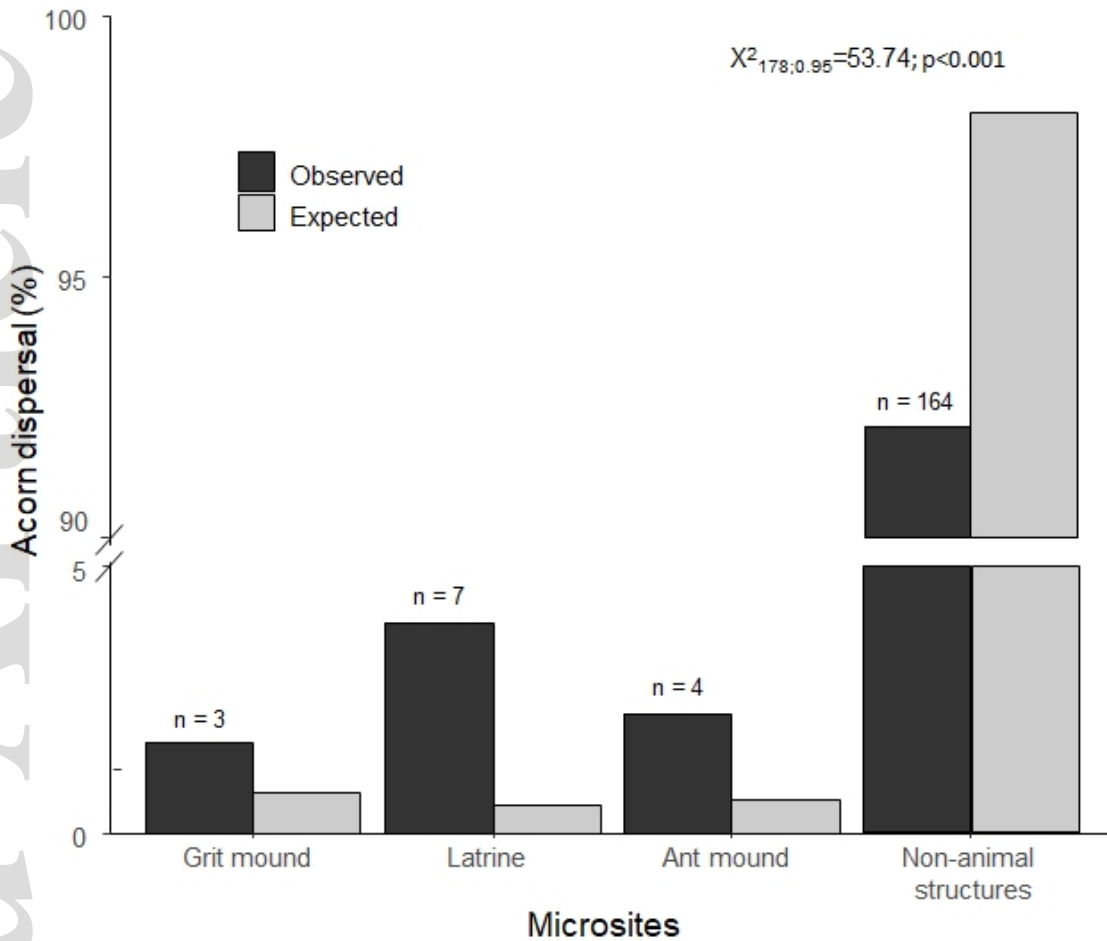


FIGURE 3. Relative frequency of observed (black) and expected (grey) cached acorns according to the microsites chosen by magpies to cache acorns. Grit mounds and latrines were made by rabbits. Total acorns n=178.

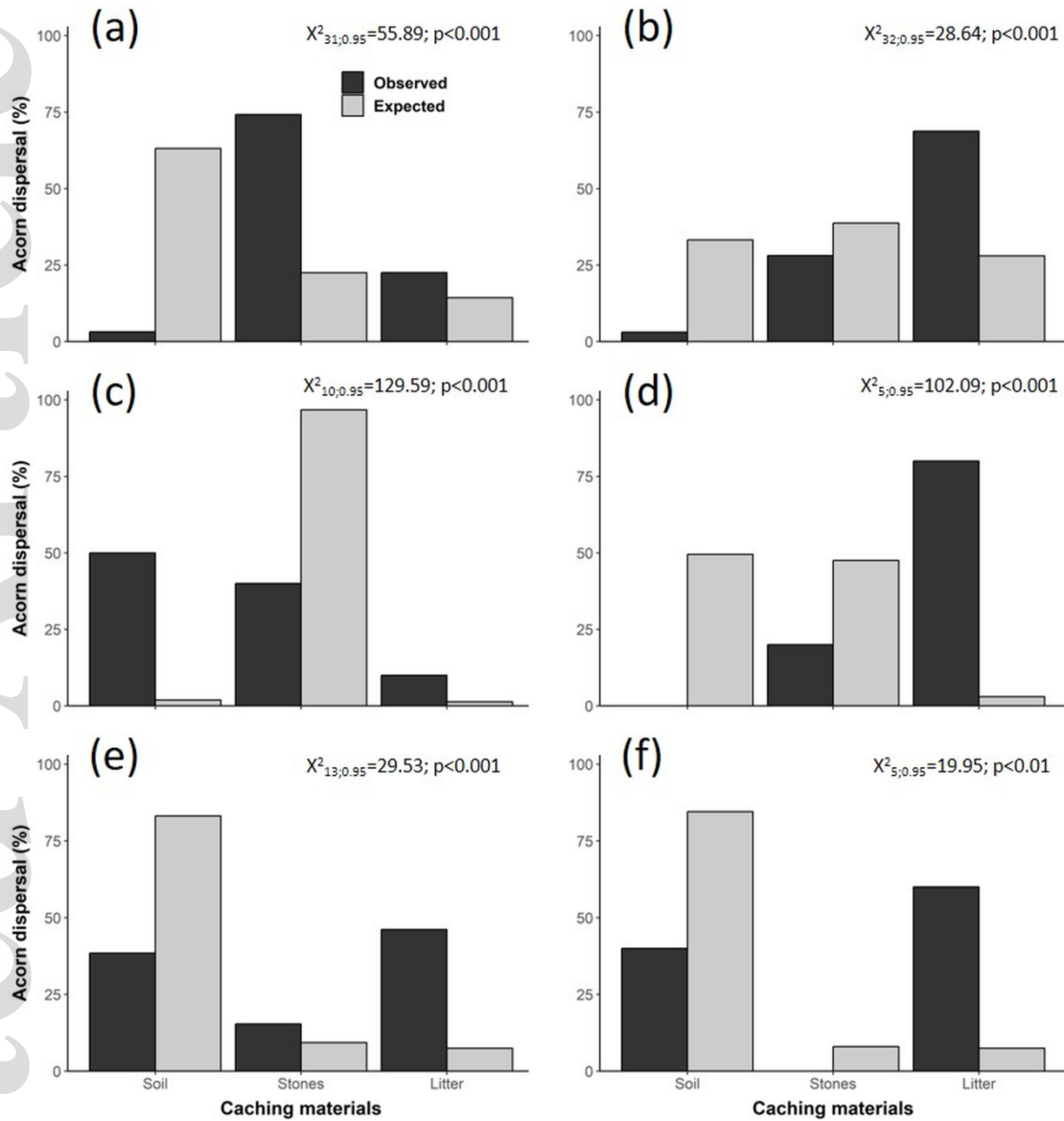


FIGURE 4. Relative frequency of observed (black) and expected (grey) cached acorns according to the caching material for the combinations of habitat or sub-habitat and feeder showing significant differences. High plant productivity sub-habitat of feeders 1 and 2 (a, n=31), and 5 and 6 (b, n=32); low plant productivity sub-habitat of feeders 5 and 6 (c, n=10) and old fields of feeders 1 and 2 (d, n=5), 3 and 4 (e, n=13), and 5 and 6 (f, n=5).

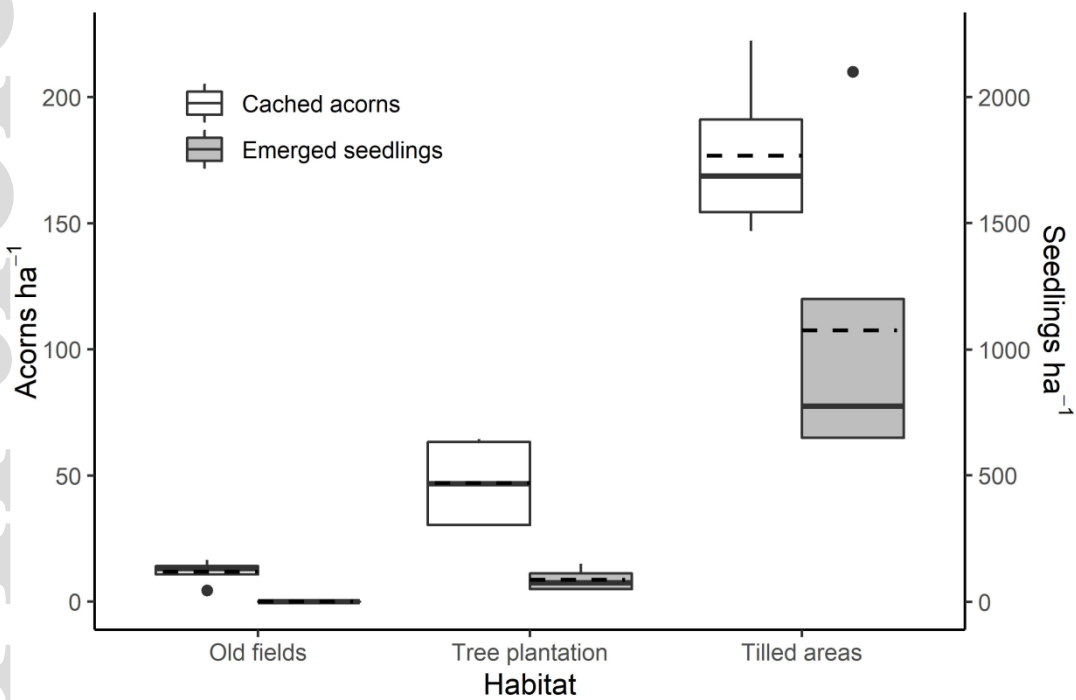


FIGURE 5. Density of cached acorns (white boxes) and emerged seedlings (grey boxes) in the three habitats ($n=4$). In the box plots, the solid and dashed lines are the median and mean, respectively. Boxes represent the first and third quartile. Whiskers represent the lowest and largest data point excluding outliers (points). Note that the density of cached acorns (left y-axis) is smaller than the density of emerged seedlings (right y-axis) because we used the density of cached radio-tagged acorns, which is a fraction of the cached acorn population.