Massive and effective acorn dispersal into agroforestry systems by an overlooked vector, the Eurasian magpie (*Pica pica*)

LORETO MARTÍNEZ-BAROJA [ID],[1,†] LORENZO PÉREZ-CAMACHO [ID],[1] PEDRO VILLAR-SALVADOR [ID],[1]
SALVADOR REBOLLO [ID],[1] PABLO QUILES [ID],[1] DANIEL GÓMEZ-SÁNCHEZ,[1] MERCEDES MOLINA-MORALES [ID],[2]
ALEXANDRO B. LEVERKUS [ID],[1,3,4] JORGE CASTRO [ID],[4] AND JOSÉ MARÍA REY-BENAYAS [ID][1]

[1]*Forest Ecology and Restoration Group, Departamento de Ciencias de la Vida, Universidad de Alcalá, 28805 Alcalá de Henares, Madrid, Spain*
[2]*Departamento de Anatomía, Biología Celular y Zoología, Universidad de Extremadura, Badajoz, Spain*
[3]*Department of Animal Ecology and Tropical Biology, University of Würzburg, Würzburg, Germany*
[4]*Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain*

Abstract. Oak regeneration and the expansion of forested sites in Eurasia rely on acorn dispersal by animals, especially the Eurasian jay (*Garrulus glandarius*). However, in open agroforestry systems where jays are absent, such as old fields far from acorn sources, oak recruitment still occurs. We hypothesize that the Eurasian magpie (*Pica pica*), an abundant corvid in this system, substitutes the jay in its seed dispersal function. By ringing 169 magpies, video recording >7500 acorn removal events with trail cameras, and radio-tagging 337 acorns, we quantified that (1) magpies cached 41–56% of the annual acorn production of *Quercus ilex* trees in single caches on the ground; (2) breeding pairs, and especially males, were the main acorn dispersers; (3) each breeding magpie cached 169–1372 acorns in 6 weeks; and (4) the effectiveness of dispersal (percentage of cached acorns resulting in seedlings) was 0.6–2.4%, which (5) yielded a high density of emerged seedlings (56–439 seedlings/ha). We evidence that magpie could be a key species in the regeneration of oak agroforestry mosaics because they massively and effectively dispersed acorns. However, in our particular study site, effectiveness was low probably due to herbivory and summer drought stress (i.e., a context limitation rather than an intrinsic limitation of the disperser). As the distributions of magpies and oaks overlap widely in Eurasia, effective acorn dispersal by magpies could have a significant role in large-scale oak forest recovery in strongly fragmented landscapes.

† **E-mail:** loretomabavi@outlook.es

INTRODUCTION

Forest regeneration is paramount to counteract centuries of land degradation (Chazdon 2017), combat climate change (Nabuurs et al. 2007), and attain the Sustainable Development Goals (U.N. 2017). However, natural forest regeneration is limited by the ability of tree species to spread naturally (Rey Benayas et al. 2008, 2015). Animal-mediated seed dispersal of large-seeded

trees, like acorns, constitutes a major ecosystem service that allows the regeneration, densification, and expansion of forests (Whelan et al. 2008). More than 60% of tree species in communities of temperate biomes are zoochorous (Howe and Smallwood 1982). Synzoochory, seed dispersal by seed-caching seed predators (Gómez et al. 2019), is especially relevant in *Quercus* species (henceforth "oaks") and other large-seeded trees (Pesendorfer et al. 2016a). Oaks include

more than 400 species widely distributed in the Northern Hemisphere (Denk et al. 2017). The strong fragmentation and degradation of oak forests, coupled with the usually slow recruitment of oaks, have transformed many of those landscapes into cropland and agroforestry mosaic systems with few scattered oak remnants (Rey Benayas et al. 2015). The holm oak (*Quercus ilex*) is an abundant oak in the Mediterranean Basin. It dominates many forests and agroforestry mosaics such as the *dehesas*, which are savannah-like ecosystems of great ecological, economic, and historical importance (Pulido and Díaz 2005).

Corvids are the main dispersers of acorns (Vander Wall 1990, Whelan et al. 2008, Gómez et al. 2019). Several corvid species are key for medium and long-distance oak dispersal (Pesendorfer et al. 2016*a*). In Eurasia, only two corvids are known as major acorn dispersers, namely the Eurasian jay (*Garrulus glandarius*) and, to a lesser degree, the rook (*Corvus frugilegus*; Källander 2007, Pesendorfer et al. 2016*a*). These corvids usually make scattered caches of food, which allows them to store resources that are abundant for short periods, like acorns in autumn, for later consumption (Bossema 1979, Clarkson et al. 1986, Vander Wall 1990). However, many acorns remain unrecovered and can develop into seedlings (Vander Wall 1990, Whelan et al. 2008, Pesendorfer et al. 2016*a*). This behavior has additional benefits for oaks. First, corvids usually select sound acorns, that is, the biggest and healthiest (Bossema 1979, Pons and Pausas 2008, Pesendorfer et al. 2016*a*). Second, they carry acorns away from mother trees, reducing kin competition. Third, they make single-acorn caches, which reduces post-dispersal predation, desiccation, and competition and increases seedling emergence and survival (Vander Wall 1990, Pesendorfer et al. 2016*a*, Kurek et al. 2018).

The Eurasian jay plays a central role in acorn dispersal dynamics of oak forests (Bossema 1979, Gómez 2003, Pons and Pausas 2007*b*, 2008, Morán-López et al. 2015, Leverkus et al. 2016). However, in strongly deforested farmland of the Mediterranean landscapes where jays are very scarce or absent (Bossema 1979, Pons and Pausas 2008, Gianpasquale and Alberto 2019), recruitment of oak juveniles has often been observed at long distances (above several tens of meters) from remnant oak trees and small forest patches (Andivia et al. 2017 and authors' observations). Such recruitment cannot be attributed to dispersal by rodents as these disperse acorns at small distances (Pons and Pausas 2007*a*, Morán-López et al. 2018). The long-distance disperser(s) of acorns in open systems thus remains to be unveiled.

The Eurasian magpie (*Pica pica*; henceforth "magpie") abounds in open landscapes (Kryukov et al. 2017). Several lines of evidence suggest that magpies might act as the unknown acorn dispersers in these open landscapes: (1) They cache a wide variety of food types (Waite 1985, Vander Wall 1990, Birkhead 1991); (2) they disperse and promote the recruitment of the common walnut (*Juglans regia*; Castro et al. 2017), and some authors suggested that they disperse other large-seeded trees such as the almond tree (*Prunus dulcis*; Homet-Gutiérrez et al. 2015) and the chestnut tree (*Castanea sativa*; Gómez et al. 2019); and (3) several authors have pointed out that magpies occasionally cache acorns of some oaks (Waite 1985, Clarkson et al. 1986, Birkhead 1991, den Ouden et al. 2005). However, despite magpies being among the most common corvids in Eurasia (Birkhead 1991, Kryukov et al. 2017) and their distribution largely overlapping with that of the *Quercus* genus (Kappelle 2006, Pesendorfer et al. 2016*a*, Denk et al. 2017; Fig. 1), neither the potential of magpies as acorn dispersers nor the effectiveness of such dispersal for oak seedling recruitment has been quantified yet. We hypothesized that magpies are effective and long-distance dispersers of acorns in open agroforestry systems and thus contribute to the natural regeneration of Mediterranean oak forests. Moreover, differences between individuals, that is, sex and reproductive status, could affect acorn dispersal, due to the different role in food provision among sex and territoriality (Birkhead 1991). For example, if mortality differs between sexes or reproductive status (Birkhead 1991), the amount of abandoned cached acorns could be different. These aspects have been little studied in scatter-hoarding corvids (DeGange et al. 1989), and they may affect oak regeneration.

In this study, we analyzed the role of magpies as dispersers of oaks by assessing several quantitative and qualitative aspects of holm oak acorn
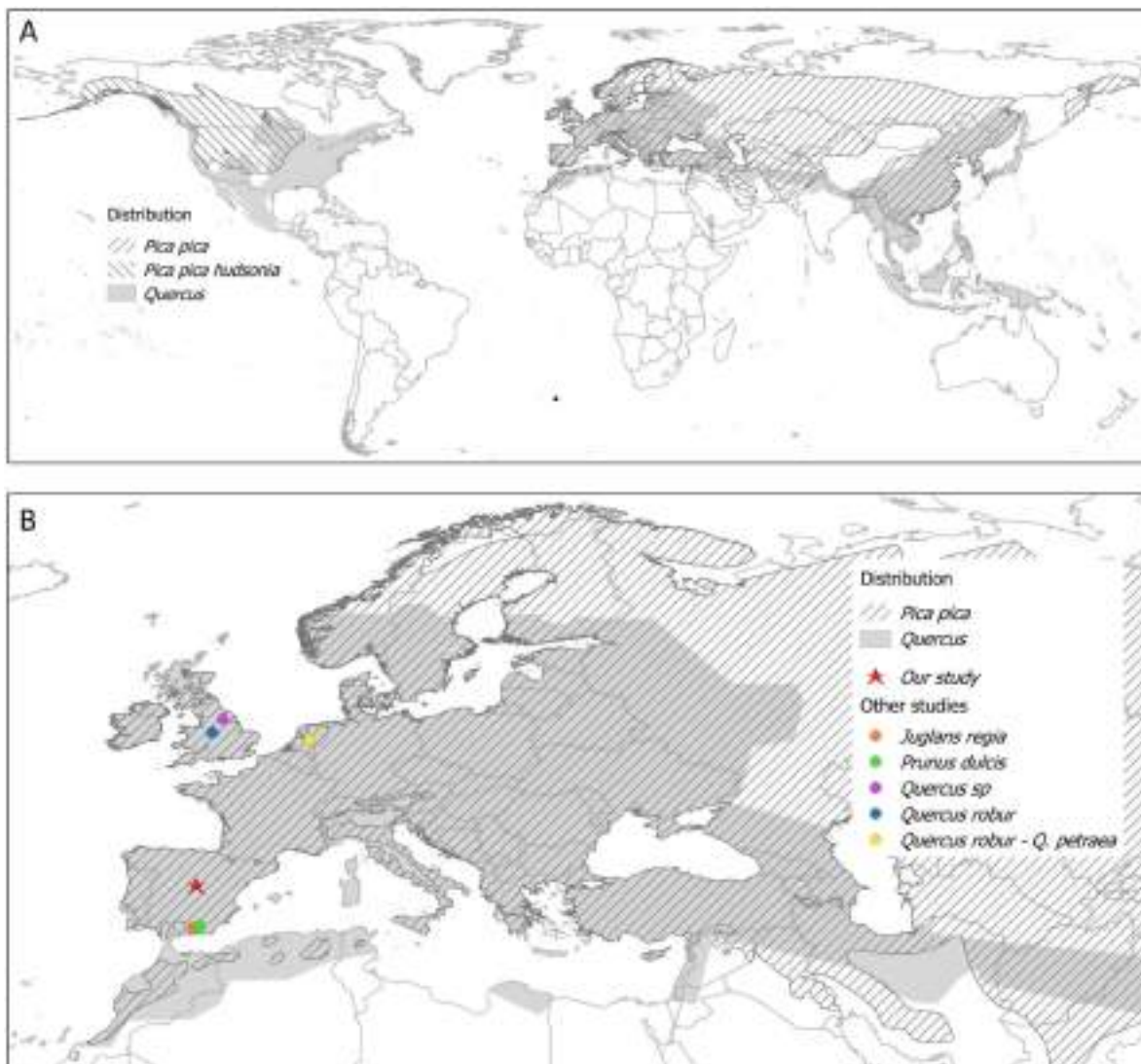
Fig. 1. Distribution of magpies (*Pica pica*) and oaks (*Quercus* spp.) in the world (A) and in Europe (B). The red star shows the location of our study site. The color dots show the location of studies on dispersal of acorns and other nuts by magpies (Waite 1985, Clarkson et al. 1986, Birkhead 1991, den Ouden et al. 2005, Homet-Gutiérrez et al. 2015, Castro et al. 2017). Source of bird distribution: BirdLife International and Handbook of the Birds of the World 2017. Sources of oak distribution: Kappelle 2006, Pesendorfer et al. 2016a, Denk et al. 2017.

dispersal in a Mediterranean agroecosystem in central Spain. We quantified acorn dispersal of the holm oak and the effectiveness of dispersal (measured as seedling emergence, sensu Schupp et al. 2010) of oaks. Our specific aims were to (1) quantify acorn dispersal (removal and caching) by magpies directly from the oak trees; (2) quantify the proportion of removed acorns that are cached and assess whether magpies are acorn

scatter hoarders; (3) quantify the amount of cached acorns per individual throughout the dispersal season; (4) assess acorn dispersal effectiveness; and (5) determine whether sex and reproductive status (i.e., breeders vs. juveniles) determine acorn dispersal. Bearing in mind the wide distribution of magpies and oaks, demonstrating that magpies are effective acorn dispersers can open a new perspective in the

ecology, regeneration, and restoration of Eurasian oaks in sparsely forested agroforestry mosaics, which may change our vision of the ecological role of magpies in agroforestry systems.

MATERIALS AND METHODS

Study site

To test our hypotheses, we selected a study site located in an open agroforestry system in an alluvial terrace of the Henares River (central Spain 40°31′0″ N, 3°19′55″ W, elevation 605 m) where jays are absent. The climate is continental Mediterranean, with dry and hot summers and cold winters. The mean annual temperature is 13.8°C, and the annual rainfall is 425 mm. The study site comprised a 28.4-ha plantation of holm oaks and some Portuguese oaks (*Quercus faginea*) established in 1995, surrounded by abandoned cereal fields. Cereal cultivation in the old fields ceased in 1990, and the fields are currently dominated by annual herbaceous vegetation. The oak plantation also included dispersed almond trees and a few Siberian elms (*Ulmus pumila*), olive trees (*Olea europea*), common figs (*Ficus carica*), common walnuts, white mulberries (*Morus alba*), and black locusts (*Robinia pseudoacacia*). A diverse community of vertebrates thrives in the area. Noteworthy is the high density of magpies and rabbits (*Oryctolagus cuniculus*), which are potential acorn predators. Other present acorn consumers were common wood pigeons (*Columba palumbus*), jackdaws (*Corvus monedula*), wood mice (*Apodemus sylvaticus*), and European roe deer (*Capreolus capreolus*). Potential magpie predators included several raptors (e.g., booted eagles (*Aquila pennata*) and Eurasian eagle–owls (*Bubo bubo*), red foxes (*Vulpes vulpes*), European polecats (*Mustela putorius*), and domestic cats (*Felis silvestris catus*)).

Magpies are relatively short-lived (mean life expectancy of 1.2–3.5 yr in the wild for adults) and medium-sized (170–270 g; various races) corvids (Birkhead 1991). They display territorial behavior in the breeding season, and breeding pairs remain together during the autumn and winter (Birkhead 1991). The holm oak is an evergreen tree up to 25 m high, very long-lived (up to hundreds of years), and mainly distributed around the central-western Mediterranean basin.

The fresh weight of holm oak acorns varies between 2 and 10 g (Villar-Salvador et al. 2013); they mature in autumn, and the seedlings emerge in late spring.

Identification of acorn dispersers from the trees and acorn caching

To investigate whether acorn removal from oak tree canopies is a common behavior of magpies and the species that remove or predate acorns, we installed motion-sensor trail cameras (Browning Dark Ops HD Elite, Browning Trail Cameras, USA). Five holm oaks were recorded in 2016, and a different set of nine trees was recorded in 2017. In both years, we installed the trail cameras on the ground at 5.5 m from the target tree, pointing up toward the crown, in mid-October, when the acorns were almost ripe but still green (emergence rate was >80%, see Results). Our trail cameras were not capable of capturing small animals such as mice at the distance they were placed. Cameras recorded videos for 30 s whenever they detected animal motion until removal of all acorns of the tree crowns (by early November). We viewed the recorded videos to estimate the percentage of removed or predated acorns by each animal species.

We assessed whether magpies cached acorns from holm oaks by means of radio-tracked acorns. The size and shape of the radio-tracked acorns were similar to those of the unmanipulated acorns because the both groups of acorns were a random sample from the same acorn crop. We inserted a radio transmitter (PIP2 Tag Ag392; Biotrack, Wareham, Dorset, UK; weight: 2.2 g) inside acorns following the methodology of Pons and Pausas (2007b). We transversally cut the acorns and emptied a part of the cotyledons to fit the radio transmitter with the antenna rolled up (the weight of the acorn with the transmitter was similar to that of the non-manipulated acorn; data not shown). Finally, we closed the acorns with instantaneous cyanoacrylate adhesive (Appendix S1: Fig. S1). To assess acorn removal from the oak trees, we glued 1–3 radio-tracked acorns per tree with cyanoacrylate adhesive onto acorn caps of the current year still attached to the branches of five trees. This manipulation was done during 10 d in November 2017 when there were few acorns left in the

crowns. Once magpies removed radio-tagged acorns, they were re-located on the same day to avoid predation by rodents and rabbits or possible secondary dispersal by magpies. We located the radio-tagged acorns using a unidirectional Yagi antenna connected to a radio receiver (Biotrack SIKA Radio Tracking Receiver, Wareham, Dorset, UK). Once the general caching vicinity was detected, the precise location of the acorns was found using a hand-held metal detector (White's Auto-Scan Personal Search Detector, Tulsa, Oklahoma, USA). Then, we assessed whether the acorns were predated or cached intact. We considered an acorn to be predated when we found the radio transmitter on the ground or hanging from branches, without the acorn or with the acorn partially consumed.

To identify the species that consumed or removed acorns from the ground below trees, we positioned 100 acorns inside a camouflaged shallow plate on the ground below six holm oaks in December 2018 (600 acorns in total). We installed trail cameras at 1 m from the plate that recorded videos for 1 min whenever they detected animal motion. We viewed the recorded videos to estimate the percentage of consumed or removed acorns by each animal species. Complementarily, we assessed detectability of

the consumed or removed acorns by the different species in the videos. In both cases, either the oak canopy or the ground, trees were the sample unit, because acorns between different trees were more independent than acorns within the same tree.

Proportion of active feeders by magpies

To experimentally quantify acorn removal and dispersal by magpies, in November 2015 we installed 14 feeders with 10 acorns each, which were monitored until December 2015–April 2016 (Fig. 2A). We worked on this relatively late period to encourage magpies to remove acorns from the feeders and then tracked the radio-tagged acorns. The feeders consisted of a domestic colander attached to a metallic rod (60–70 cm high) to avoid acorn predation by rabbits and mice and were placed below the crown edge of holm oak trees (Appendix S1: Fig. S2). We then installed trail cameras (Moultrie MCG-12634; Moultrie Products, Alabama, USA) on the ground, pointed at the feeders, to record videos for 1 min whenever motion was detected. We viewed the recorded videos to know the bird species that removed each acorn and to estimate the percentage of feeders used by magpies (active feeders).
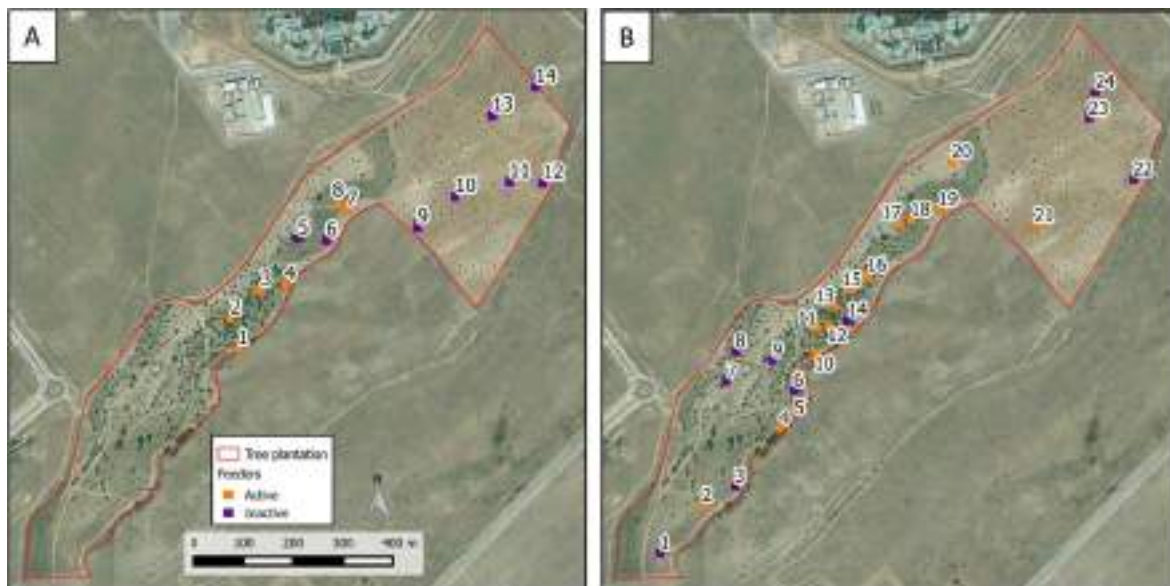

Fig. 2. Location of active and inactive feeders in the study site in 2015–2016 (A) and 2016–2017 (B). Trees on the image are mostly holm oaks and almond trees.

The type of feeders, their position and materials, and the surveillance method were key aspects for magpies to use them. Preliminary observations revealed that magpies avoided auto pet feeders ($n = 24$) or colanders with large mesh size (≥ 0.6 cm; $n = 2$), and hardly used feeders placed in the oak crowns ($n = 6$; Appendix S1: Fig. S3). Moreover, watching from hides or cars ($n = 9$) interrupted dispersal from previously active feeders surveyed by trail cameras. For this reason, we only used trail cameras to quantify acorn removal. Other authors have made direct observations to quantify the dispersed acorns by less skittish corvids (Darley-Hill and Johnson 1981, Pesendorfer et al. 2016c).

Quantification of acorn dispersal

We assessed the proportion of cached acorns with respect to the removed acorns from the feeders, and the characteristics of caches, through radio-tracked acorns (method described above; Pons and Pausas 2007b) in the 2015–2016 period. When the feeders were visited by magpies in 2015–2016, we placed 15 acorns per trial (3–10 trials per feeder), 5–10 of which had a radio transmitter (260 radio-tagged acorns in total); the remaining were non-manipulated acorns with a scratch imitating the scar produced after inserting the radio transmitters. Previous trials showed the importance of scratching non-manipulated acorns to minimize the rejection of acorns containing transmitters (L. Martínez-Baroja et al., *unpublished data*).

To quantify the acorn removal rates per individual magpie, we color-banded 33 breeders of 24 active nests out of 53 active nests and 136 nestlings in 51 active nests in the spring of 2016. We ringed nestlings when they were at least 15 d old and thus could thermoregulate (Molina-Morales et al. 2012). Birds were tarsus-ringed with a standard ornithological ring of stainless steel with a unique identifier number and two or three colored aluminum rings; thus, each magpie had a different color combination for later identification. To capture breeding magpies, we placed a Sherman trap with a caged magpie as decoy under all trees with active nests. In December 2016, we placed a feeder under the crown of each tree with active nest where at least one adult of the breeding pair was ringed (Fig. 2B). To minimize the territorial disputes between neighboring

magpies for the use of the feeders, we placed them under the tree with active nest or under a nearby tree that was in a central point of the magpies' territories. For 6 weeks, we continuously refilled the feeders, which held up to 300 acorns, mimicking their availability in oak ecosystems (Pulido and Díaz 2005). We placed motion-sensor trail cameras to record the feeders and later identify the individuals that removed and dispersed acorns. We analyzed the data of the feeders where ringed magpies removed acorns for more than 20 d to calculate daily acorn removal rates (males $n = 7$ and females $n = 4$).

Similarly, in one magpie territory, we monitored one Portuguese oak tree and one feeder with its acorns for 10 d to assess whether the magpies removed and cached acorns of this oak species. In this study and only for illustrative purposes, we just show that magpies did remove and cache Portuguese oak acorns from feeders and trees and almonds from the ground (Videos S1–S5).

To check whether the acorns removed by magpies were cached in the 2016–2017 sampling period, we radio-tracked one to nine acorns from each feeder following the previously described methodology (77 radio-tagged acorns in total). However, this small sample did not allow to accurately calculate the proportion of removed acorns that were cached and predated.

Effectiveness of acorn dispersal

In both feeder experiments (i.e., 2015–2016 and 2016–2017), the cached radio-tracked acorns found intact were replaced with unmanipulated acorns, trying not to disturb the micro-site and using latex gloves to avoid impregnating the acorns with human smell. We tested emergence rate of brown fully ripened acorns in the laboratory, resulting in an average of 95.0% and 83.3%, respectively, for years 2015–2016 and 2016–2017. The acorns were harvested from the holm oak canopy as most of the acorns dispersed by magpies. We monitored the replaced acorns to know if they remained in situ and eventually produced a seedling or they were removed and consequently subjected to post-dispersal predation or secondary dispersal. As we did not follow the fate of the acorns removed from caches, we assumed that all disappeared acorns were predated. Cached acorns were geopositioned, and

we buried a 2-cm long nail under them to facilitate their relocation with a hand-held metal detector. We checked the acorns every week during the first month after acorn dispersion and every other week until the end of the experiment in mid-June.

To complement the results of seedling emergence from the monitored acorns, we sampled the abundance of holm oak and Portuguese oak emerged seedling in 200-m^2 transects in July 2016 and July 2017. Each year we surveyed the same 18 transects, nine of them next to three feeders (three transects per feeder 1, 4, and 7; Fig. 2A) and nine of them farther away from these feeders (mean = 39.3 m, range = 26.8–48.6 m). If there were trees in the set transects, we circumvented the area below tree crowns to avoid the dispersion by gravity. We attributed most of the emerged oak seedlings to acorn dispersal by magpies as seedling emergence due to acorn dispersal by wood mice in Mediterranean environments is very low (Gómez 2003, Gómez et al. 2019).

Characteristics of the magpie individuals that dispersed acorns

To identify breeding magpie adults and juveniles that removed acorns, we watched all the videos taken in the feeders in 2016–2017; juveniles were the ringed nestlings in the previous breeding season. We sexed breeding magpies by drawing a drop of blood from each trapped individual with standard molecular procedures (Fridolfsson and Ellegren 1999). Of the ringed breeding magpies, 19 were females and 14 were males. We captured both individuals of the breeding pairs for nine out of the 24 territorial breeding pairs. We never captured two individuals of the same sex in these territories. Later, to verify whether the ringed individuals were the breeding magpies of the territories, we installed trail cameras below the nest trees. We frequently observed ringed individuals in the breeding territories where they had been trapped. Additionally to the ringed breeding magpies, we were able to identify some un-ringed individuals as breeding magpies due to their cooperative behavior with the ringed breeding individual of the territory (for instance, an un-ringed magpie often offered acorns to a ringed female and, often, both individuals of the territorial breeding

pairs defended together the feeder against other magpies). Moreover, some of these un-ringed individuals had a body mark or distinctive behavior (e.g., a small crest or stain, and turning around itself before getting on the feeder).

Statistical analyses

We used generalized linear mixed-effects model with a Poisson error distribution and a log-link function to analyze differences in the number of acorns removed by magpies depending on sex, feeder, and time (days) as fixed effects (package lme4; Bates et al. 2015). Individuals were the random effect. We performed two analyses using the data from feeders where magpies removed acorns for 42 d. In the first analysis, we only used the feeders where both sexes from the same breeding territory removed acorns (both males and females $n = 3$). In the second analysis, data from all feeders where at least one of the sexes removed acorns were analyzed (males $n = 6$, females $n = 3$). The variable time was standardized by rescaling to a mean of 0 and standard deviation of 1. Akaike's information criterion (AIC) was calculated for each model; a smaller AIC indicates a better-fitting model as determined from the parsimony in the number of parameters. We used the cutoff of ΔAIC < 2 units to differentiate models with better explanatory power (package MuMin; Barton 2019). The analyses were performed in R (R Core Team 2018).

Results

Identification of acorn dispersers from the trees and acorn caching

Trail cameras detected three bird species, namely magpie, wood pigeon, and jackdaw, removing or consuming acorns from the crown of the holm oaks. The magpie was the species that removed most acorns from the 14 studied holm oaks (65%; Appendix S1: Table S1). We recorded 93 removal events by magpies from all the five studied holm oaks in 2016 and 174 removal events from the nine studied holm oaks in 2017. The acorns that were consumed or removed from the crown (Video S6) before falling to the ground were mostly green but already ripe and sound (emergence rate >80% according to our lab tests). Therefore, we observed that most of the acorn production was removed from

the tree crowns, while only a small proportion of acorns ended on the ground. The magpie was the only detected species that cached acorns after taking them from the oaks. Jackdaws removed acorns but we did not observe any single caching event, which is in accordance with Waite's (1985) study. We found seven radio-tagged cached acorns that were directly removed by magpies from five trees. We recorded five species consuming or removing acorns placed on the ground, in the following order of frequency: magpie (48%) > rabbit > wood mouse > wood pigeon > red-legged partridge (*Alectoris rufa*; Appendix S1: Table S2).

Proportion of active feeders by magpies and quantification of acorn dispersal

We recorded acorn removal by magpies in six out of 14 (43%) feeders in 2015–2016 and 14 out of 24 (58%) feeders in 2016–2017 (Fig. 2). Magpies also removed most acorns from the feeders (84% of 694 acorns recorded in 2015–2016). The majority (>90%) of acorns removed by magpies was taken one by one, carrying the acorns in their bills. Occasionally, they carried two or three acorns at the same time, one of them in the enlarged buccal cavity, partially swallowed, and the rest in the bill (Videos S7–S9).

Magpies were also the only species that cached acorns once taken from feeders. They cached 178 radio-tagged acorns in 2015–2016 (Table 1) and 42 in 2016–2017; the dispersal distance ranged between 1.4 and 210 m (mean 32.5 ± 23.5 m;

$n = 220$; Fig. 3). Each cache always contained a single acorn. Videos showed that magpies usually flew and walked testing different sites before selecting the final caching site; then, the acorn was inserted into the ground and hammered with the bill until it was totally or partially cached into the ground. The cached acorn was often covered with small stones (43.7%), litter or leaves (36.1%), or buried (20.2%) at a depth of 1–2 cm (Videos S10–S11). We also watched magpies recovering acorns from the caches in some videos (Video S12); however, we do not know if the recovered acorns were consumed or recached. To produce conservative estimates, we considered that acorns that disappeared had been predated.

During 2016–2017, 1214 ± 280 (mean $\pm$ SE) acorns per feeder ($n = 6$; range 409–2165) were removed over 6 weeks by one or two individuals of the breeding pairs. Of the four feeders from where only magpies removed acorns in 2015–2016, 86% (134 of 159) of the removed acorns were cached and the remaining were consumed immediately after removal (Table 1). Therefore, we estimate that one or two magpies could cache a mean of 1044 ± 240 (86% of 1214) acorns per feeder (range 352–1862 acorns) in 6 weeks.

Effectiveness of acorn dispersal

Just one seedling emerged each year out of all cached acorns that were located using radio tracking in the two studied years (emergence was 0.6% and 2.4% in 2015–2016 and 2016–2017,

Table 1. Number of acorns with radio transmitter that were cached by magpies, consumed by magpies or jackdaws, or lost, and the species that removed acorns from each feeder in 2015–2016.

| Number of active feeder (2015–2016)	Number of removed acorns with transmitter							Species that removed acorns
	Total Number	Cached acorns		Consumed acorns		Lost acorns		
		Number	%	Number	%	Number	%	
1	46	21	45.7	22	47.8	3	6.5	Magpie and perhaps jackdaw
2	55	23	41.8	31	56.4	1	1.8	Magpie and perhaps jackdaw
3	29	29	100	0	0	0	0	Magpie
4	52	41	78.9	11	21.1	0	0	Magpie
7	38	32	84.2	6	15.8	0	0	Magpie
8	40	32	80.0	8	20.0	0	0	Magpie
Summary of all feeders	260	178	71.7	78	30.0	4	1.5	
Summary of feeders from which only magpies removed acorns	159	134	85.8	25	14.2	0	0	
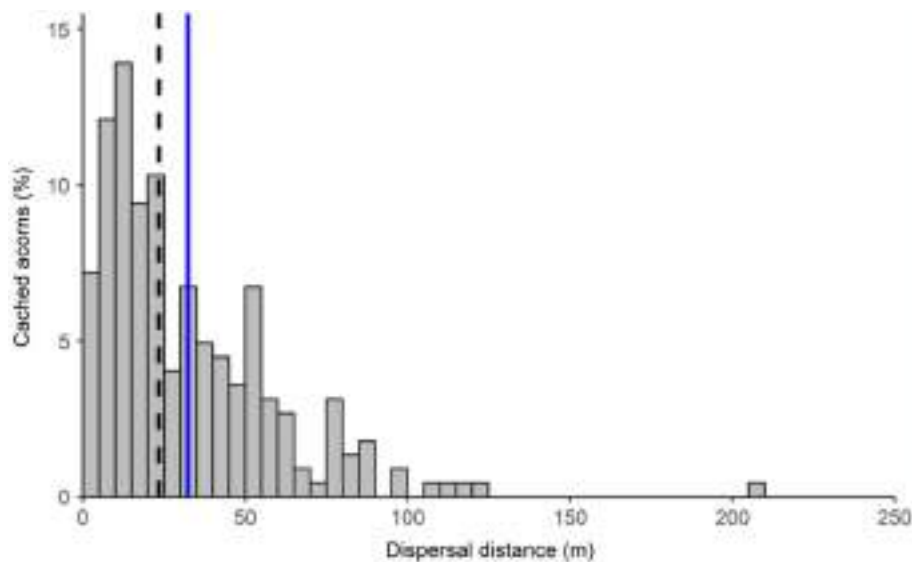
Fig. 3. Frequency of dispersal distances of cached radio-tagged acorns in 2015–2016 (n = 178) and 2016–2017 (n = 45). The blue line represents the mean (32.4 m), and the dashed black line is the median (23.5 m).

respectively). The remaining acorns were either removed or consumed (99.4% and 85.7% in 2015–2016 and 2016–2017, respectively) or dried out (0% and 11.9% in 2015–2016 and 2016–2017, respectively).

Our surveys in the transects revealed that, in 2016, 439 ± 234 and 289 ± 141 (mean ± SE) oak seedlings/ha emerged in sites near and far away from the feeders, respectively, while in 2017, the density was 56 ± 23 and 56 ± 21 seedlings/ha, respectively. No trace of the seedlings located in 2016 was found in 2017, suggesting strong predation by rabbits.

Characteristics of the magpie individuals that dispersed acorns

Acorns were removed from the feeders mainly by breeding magpies. We detected 14 out of the 33 ringed breeding magpies but only one out of the 136 ringed nestlings removing acorns from the feeders. Breeding magpies removed acorns regularly and mainly from the feeder located in their territory (6515 or 89.4% of the removed acorns); they seldom removed acorns from feeders located in other territories (four acorns or 0.1%). Occasionally, juveniles and unidentified magpies removed acorns from the feeders (213 acorns or 2.9% and 551 acorns or 7.6%, respectively). Magpie behavior was different when they

removed acorns from the feeders in their own territory (normal behavior) than when they did it in other territories (skittish behavior). When both sexes of the same breeding territory removed acorns from the feeders, males removed significantly more acorns (61.6%) than females (38.4%). The number of removed acorns decreased slightly with time and differed among feeders (Table 2 and Fig. 4). Similar results were observed in the feeders where at least one of the sexes removed acorns (Appendix S1: Fig. S4 and Table S3).

Table 2. Model selection for generalized linear mixed-effects model of acorns removed by magpies in the feeders where both sexes removed acorns (both males and females n = 3).

Model parameters	df	AICc	ΔAIC	Weight
Sex + feeder + time	6	3944.3	0	0.997
Feeder + time	5	3956.6	12.31	0.002
Time	3	3960.6	16.37	0
Sex + time	4	3961.1	16.86	0
Feeder + sex	5	4085.8	141.49	0
Feeder	4	4098.1	153.82	0
Null model	2	4102.2	157.91	0
Sex	3	4102.6	158.38	0

Notes: Global model, number of acorns removed ~ sex + feeder + time + (1|individual), was the best model (marginal pseudo-R^2 = 0.818). Degrees of freedom, AICc, ΔAIC, and model weight are shown.
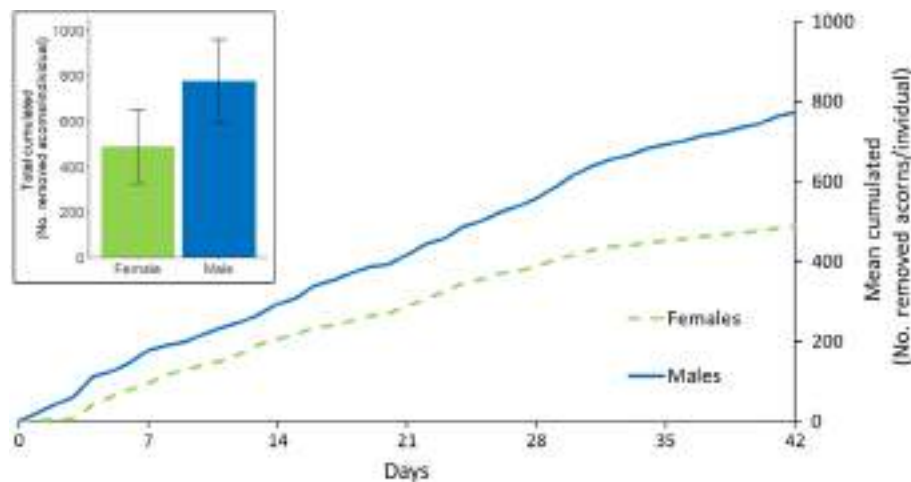
Fig. 4. Mean number of daily-cumulated acorns removed by females (*n* = 3) and males (*n* = 3). Data from feeders where both sexes from the same breeding territory removed acorns for at least 42 d during 2016–2017. Inset figure shows the mean total cumulated number of removed acorns per individual at the end of the studied period, and error bars represent one standard error of the mean.

Considering the data of all feeders, breeding males (*n* = 7) removed 17.5 ± 4.3 (mean ± SE) acorns per day (range 5.2–38.0 acorns) and 805 ± 199 acorns (*n* = 6) in 6 weeks (range 219–1595 acorns). Breeding females (*n* = 4) removed 13.3 ± 3.2 acorns per day (range 4.7–18.6 acorns) and 487 ± 159 acorns (*n* = 3) in 6 weeks (range 197–747 acorns; Appendix S1: Fig. S5 and Table S4). Daily removal rates were calculated based on eight feeders, six with at least 42 d of acorn removal activity plus two feeders with at least 20 d of activity.

Since 86% of the acorns removed by magpies were cached, we estimate that a breeding male cached 15 acorns per day and 692 acorns during the 6-week period of dispersal on average. Similarly, a breeding female cached 11.4 acorns per day and 419 acorns in 6 weeks on average.

DISCUSSION

This study confirms our hypothesis that magpies, one of the most common corvids in Eurasia, are effective and long-distance dispersers of acorns in open agroforestry systems. Acorn dispersal by magpies was massive and not just an occasional activity as previously considered (Waite 1985, Clarkson et al. 1986, Birkhead 1991, den Ouden et al. 2005). Magpies produced hundreds to thousands of scattered caches of one single acorn. This resembles the strategy shown by the Eurasian jay, which maximizes the potential for seedling emergence (Kurek et al. 2018), among other reasons. Our data revealed that a yearly average of 1.5% of the cached acorns resulted in emerged seedlings. The breeding status and gender of the magpies determined acorn dispersal propensity, and adult magpies were the dominant hoarders. Thus, acorn dispersal by magpies may have important implications for the recovery of oak forests in open agroforestry systems and abandoned croplands, where these birds are very abundant. Considering that magpies disperse other large seeds in Europe (Waite 1985, Clarkson et al. 1986, den Ouden et al. 2005, Castro et al. 2017, Gómez et al. 2019), we suggest that this process could occur in large areas of Eurasia. Besides its ecological and practical ramifications, the results from this study should improve the tarnished reputation of magpies, which persists due to misconceptions about their adverse effects on crops, small game animals, and songbirds (Madden et al. 2015).

Magnitude of acorn dispersal by magpies

The magpie was the bird species that removed the greatest number of acorns from experimental feeders and tree crowns, and the only bird

species that cached acorns (169–1372 acorns per individual in 6 weeks). Our estimates of the amount of acorns removed and cached from the feeders are highly conservative because (1) we observed that many magpies noticeably suspected the feeders; (2) magpies only used the feeders when acorns in trees disappeared, that is, the amount of removed acorns from the feeders was only a fraction of the total removed acorns; (3) some acorn removal events were not recorded by trail cameras, particularly when magpies removed acorns very quickly; and (4) acorn handling to insert the radio transmitter may have increased acorn predation rate by magpies suspecting the cutting marks. All these pieces of evidence suggest that the number of dispersed acorns per individual could be higher with a more protracted acorn supply. For instance, Pulido and Díaz (2005) determined that holm oak acorn supply lasted for 13–20 weeks in oak agroforestry systems (*dehesas*) in central-western Spain. Previous studies suggest magpie-mediated dispersal of almonds and chestnuts (Homet-Gutiérrez et al. 2015, Gómez et al. 2019) or study acorn and walnut dispersal from feeders by magpies (Waite 1985, Castro et al. 2017). However, no study had previously quantified the magnitude of acorn dispersal by magpies.

A better understanding of the ecological relevance of the interaction between magpies and oaks requires estimating the intensity of such interaction (see Wootton and Emmerson 2005 for other animal–plant interactions). Gómez et al. (2019) suggested that the most reliable estimate of the quantity component of synzoochory effectiveness is the proportion of the seed crop that is dispersed by the hoarding animal, irrespective of the final fate of the seed after dispersal. In our study, as magpies removed 65% of acorns from the holm oak crowns and cached 86% of the removed acorns, we estimated that they cached 56% of all acorns from the oak crowns (Fig. 5A). Other studies have reported cached proportions of removed walnuts by magpies of 89.4% (Castro et al. 2017) and 64% of removed acorns by Eurasian jays (Pons and Pausas 2007*b*). The fate of crown acorns was likely representative of what happened to most of the acorn production of trees in our study area because acorns were mostly removed or consumed before falling to the ground. Moreover, we estimated that magpies cached 41% of all acorns from the ground (Fig. 5B). These values from oak crowns and ground of our study coincide with the value found, pooling many studies of synzoochory, by Gómez et al. (2019), who reported that 48% of the seed crop was harvested and dispersed by corvids.

In short, our data suggest that the interaction between magpies and holm oaks is likely a major mean by which this tree species disperses in open landscapes. Magpies are thus likely to have a strong ecological and evolutionary impact on their interacting tree partners, and vice versa. However, this massive acorn dispersal behavior by magpies has remained undetected, likely due to the birds' mistrust of humans. Only the combination of trail cameras and radio tracking allowed us to discover this behavior in our study site (see *Material and methods* for effective and ineffective methodology).

Magpies can be considered effective acorn dispersers (sensu Schupp et al. 2010) because a fraction of cached acorns became seedlings. We estimated that 0.8% of all acorns from the holm oak crowns and 0.6% of all acorns from the ground below oaks resulted in emerged seedlings in early summer (Fig. 5). Despite these relative low proportions of emerged oak, we observed a high seedling density in the study site because of the high absolute magnitude of the acorn crops. We attribute most of these emerged oak seedlings to acorns that were dispersed by magpies, since the other potential acorn disperser in the study site—the wood mice—consumes nearly all the acorns they disperse (Gómez 2003, Gómez et al. 2019). In an experiment that we conducted in a site close to our study area, none of the 809 acorns of holm and Portuguese oaks removed by wood mice became a seedling because all were consumed (L. Martínez-Baroja et al., *unpublished data*).

Seedling emergence was possibly favored by several reasons, namely (1) a portion of the acorns was not recovered because magpies forgot them after being cached; (2) magpies did not need to recover all cached acorns due to excess of acorns or other food types; and (3) dispersers died or lost their territory (Bossema 1979, Darley-Hill and Johnson 1981, Schupp et al. 2010). Some facts support these reasons, including that our study area had plenty of food for magpies
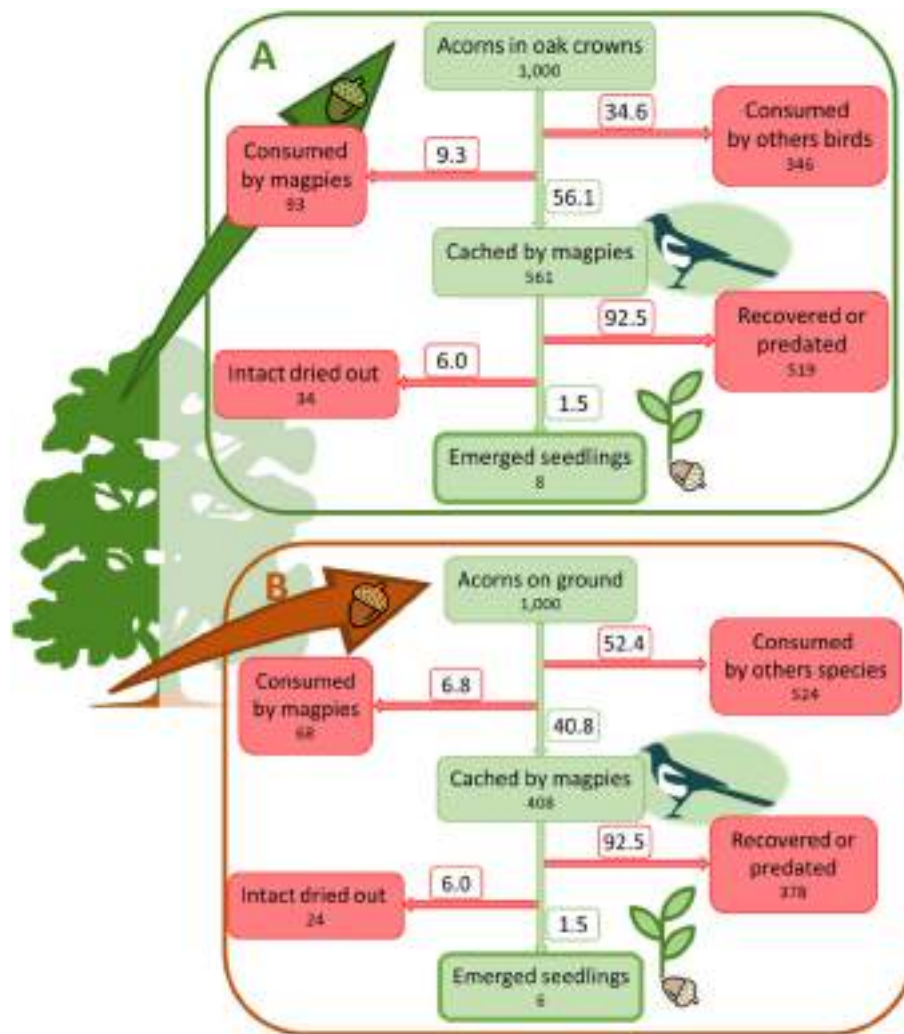
Fig. 5. Path diagrams of acorn fate after acorn removal. Numbers inside the boxes indicate the standardized number of acorns in every stage with a starting amount of 1000 acorns. (A) Removal from the holm oak crowns by birds and (B) from the ground by all species until seedling emergence. The numbers associated with the arrows indicate the percentage of available acorns for the next stage (arrows pointing to the green boxes) or lost acorns (arrows pointing to the red boxes). Cached acorns by magpies that were recovered or predated could be also secondary dispersal.

(acorns, almonds, walnuts, rabbit carrion, etc.) and a great diversity of magpie predators. However, the presence of rodents, high density of rabbits that consumed both acorns and seedlings, and strong drought stress were important bottlenecks for oak recruitment in our study area. These context-dependent factors might also explain the lower dispersal effectiveness compared with a previous study of walnut dispersal by magpies (Castro et al. 2017). Consistently

with this pattern, Pesendorfer et al. (2016b) reported a significant recovery of oak species with the presence of an acorn disperser corvid when herbivores were removed in a Californian island.

Comparison with the dispersal capacity of other corvid species

The number of acorns removed and cached by magpies was lower than the values reported

for other corvids. Pesendorfer et al. (2016c) estimated that Island scrub jays (*Aphelocoma insularis*) cached between 3500 and 5000 acorns per individual in a dispersal period of 110 d, with a rate of 7.2 acorns per hour. DeGange et al. (1989) estimated that Florida scrub jays (*Aphelocoma coerulescens*) cached about 5000 acorns per dispersal season of four months. Bossema (1979) reported that Eurasian jays could cache about 4600 acorns per dispersal season. Four reasons could explain the lower estimated dispersal by magpie individuals compared with other corvids, including the (1) different quantification methodology; (2) different length of the dispersal period; (3) fear of removing acorns from the feeders by some magpies; and (4) more generalist diet of magpies than of the other corvids (Birkhead 1991).

Differences in dispersal behavior between individual magpies

Non-breeding individuals removed few acorns from the feeders with respect to the breeding pairs, probably due to the magpie territorial behavior, who forced their offspring to leave. However, this scarce acorn dispersal by non-breeding individuals could be qualitatively relevant for oak regeneration because they could be dispersed over longer distances than the ones dispersed by breeding individuals (Birkhead 1991). Despite low replication, breeding male magpies dispersed around twice as many acorns as breeding females. Future studies should confirm this result and elucidate the ecological implications of differences in dispersal behavior among sex or reproductive status on oak regeneration. It is possible that if mortality differs between sexes or reproductive status (Birkhead 1991), this could affect also the amount of abandoned cached acorns, leading to different amount of seedling emergence.

We detected acorn removal by magpies only in half of the feeders we installed. Some explanations for this are (1) the above-mentioned fear of some magpies to the feeders; (2) the death or loss of territories by some individuals (territory tenure by magpies was 1.7 yr at our study site, $n = 33$; calculated following Birkhead 1991); and (3) territories with low primary productivity in autumn–winter may have been abandoned during this period.

Ecological implications of acorn dispersal by magpies

Our study shows for the first time a strong interaction between oaks and magpies. As a result, we hypothesize that the massive behavior of acorn dispersal by magpies could be a common behavior where its distribution overlaps with that of oak species (Fig. 1). Several lines of evidence support this hypothesis: (1) Magpies are known to cache food (Birkhead 1991); (2) acorn dispersal in our study was massive despite the existence of other food sources; (3) we recorded magpies caching acorns of two oak species and almonds; (4) magpies have been found to cache other large seeds too (Homet-Gutiérrez et al. 2015, Castro et al. 2017, Gómez et al. 2019); and (5) other authors occasionally detected magpies caching acorns of oak species other than holm oak and Portuguese oak such as pedunculate oak (*Q. robur*) and sessile oak (*Q. petraea*; Waite 1985, Clarkson et al. 1986, Birkhead 1991, den Ouden et al. 2005). This hypothesis should be tested in other areas with different landscape structure and where other oak species and magpie species coexist, opening a research field that could have deep implications for forest restoration in strongly deforested landscapes (Andivia et al. 2017). Moreover, the habitat complementarity between the Eurasian jay and the magpie suggests broad biogeographical implications throughout Eurasia mediated by extensive acorn dispersal.

Magpies have traditionally been considered a pest by farmers and hunters (Madden et al. 2015). It is our hope that this view progressively changes as we increase our understanding of the ecological role of magpies in the provision of ecosystem services such as acorn dispersal. This ecosystem service could have strong implications in the current context of farmland abandonment across Eurasia (Verburg and Overmars 2009). Analyzing the spatial pattern of acorn dispersal by magpies and oak recruitment would help further understand how magpies may transform open habitats into woodlands, as has previously been assessed for other corvids (Waite 1985, Gómez 2003, Pesendorfer et al. 2016b). Taking all these ideas together, our study suggests that magpies could be a key species, as major acorn dispersers in open agroforestry systems and in landscapes with remnants of small oak patches or scattered oaks.

ACKNOWLEDGMENTS

LITERATURE CITED

Andivia, E., P. Villar-Salvador, L. Tovar, S. Rabasa, and J. M. Rey Benayas. 2017. Multiscale assessment of woody species recruitment in Mediterranean shrublands: facilitation and beyond. Journal of Vegetation Science 28:639–648.

Barton, K. 2019. MuMIn: multi-Model Inference. R package version 1.43.6. https://cran.r-project.org/web/packages/MuMIn/index.html

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Birkhead, T. 1991. The magpies: the ecology and behaviour of black-billed and yellow-billed magpies. T&AD Poyser, London, UK.

Bossema, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70:1–116.

Castro, J., M. Molina-Morales, A. B. Leverkus, L. Martínez-Baroja, L. Pérez-Camacho, P. Villar-Salvador, S. Rebollo, and J. M. Rey-Benayas. 2017. Effective nut dispersal by magpies (Pica pica L.) in a Mediterranean agroecosystem. Oecologia 184:183–192.

Chazdon, R. L. 2017. Landscape restoration, natural regeneration, and the forests of the future. Annals of the Missouri Botanical Garden 102:251–257.

Clarkson, K., S. F. Eden, W. J. Sutherland, and A. I. Houston. 1986. Density dependence and magpie food hoarding. Journal of Animal Ecology 55:111.

Darley-Hill, S., and W. C. Johnson. 1981. Acorn dispersal by the blue jay (Cyanocitta cristata). Oecologia 50:231–232.

DeGange, A. R., J. W. Fitzpatrick, J. N. Layne, and G. E. Woolfenden. 1989. Acorn harvesting by Florida Scrub Jays. Ecology 70:348–356.

den Ouden, J., P. A. Jansen, and R. Smit. 2005. Jays, mice and oaks: predation and dispersal of Quercus robur and Q. petraea in North Western Europe. Pages 223–239 in P.-M. Forget and Association for Tropical Biology and Conservation, and Smithsonian Tropical Research Institute, editors. Seed fate: predation, dispersal and seedling establishment. CABI Publishing, Wallingford, Oxfordshire, UK.

Denk, T., G. W. Grimm, P. S. Manos, M. Deng, and A. L. Hipp. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. Pages 13–38 in E. Gil-Pelegrín, J. J. Peguero-Pina, and D. Sancho-Knapik, editors. Oaks physiological ecology. Exploring the functional diversity of genus Quercus L. Springer International Publishing, Cham, Switzerland.

Fridolfsson, A.-K., and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Biology 30:116–121.

Gianpasquale, C., and M. Alberto. 2019. The occurrence and density of three sympatric corvids in a Mediterranean agroecosystem explained by land use. Journal of Ornithology 160:1133–1150.

Gómez, J. M. 2003. Spatial patterns in long-distance dispersal of Quercus ilex acorns by jays in a heterogeneous landscape. Ecography 26:573–584.

Gómez, J. M., E. W. Schupp, and P. Jordano. 2019. Synzoochory: the ecological and evolutionary relevance of a dual interaction. Biological Reviews 94:874–902.

Handbook of the Birds of the World and BirdLife International. 2017. Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 9.1. http://datazone.birdlife.org/species/taxonomy

Homet-Gutiérrez, P., E. W. Schupp, and J. M. Gómez. 2015. Naturalization of almond trees (Prunus dulcis) in semi-arid regions of the Western Mediterranean. Journal of Arid Environments 113:108–113.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 1:201–228.

Källander, H. 2007. Food hoarding and use of stored food by Rooks *Corvus frugilegus*. Bird Study 54:192–198.

Kappelle, M., editor. 2006. Ecology and conservation of neotropical montane oak forests. Springer, Berlin, Germany.

Kryukov, A. P., L. N. Spiridonova, S. Mori, V. Yu. Arkhipov, Y. A. Red'kin, O. A. Goroshko, E. G. Lobkov, and E. Haring. 2017. Deep phylogeographic breaks in magpie *Pica pica* across the Holarctic: concordance with bioacoustics and phenotypes. Zoological Science 34:185–200.

Kurek, P., D. Dobrowolska, and B. Wiatrowska. 2018. Dispersal distance and burial mode of acorns in Eurasian Jays *Garrulus glandarius* in European temperate forests. Acta Ornithologica 53:155.

Leverkus, A. B., J. M. Rey Benayas, and J. Castro. 2016. Shifting demographic conflicts across recruitment cohorts in a dynamic post-disturbance landscape. Ecology 97:2628–2639.

Madden, C. F., B. Arroyo, and A. Amar. 2015. A review of the impacts of corvids on bird productivity and abundance. Ibis 157:1–16.

Molina-Morales, M., J. G. Martínez, and J. M. Avilés. 2012. Factors affecting natal and breeding magpie dispersal in a population parasitized by the great spotted cuckoo. Animal Behaviour 83:671–680.

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

Morán-López, T., F. Valladares, F. Tiribelli, J. E. Pérez-Sepúlveda, A. Traveset, and M. Díaz. 2018. Fragmentation modifies seed trait effects on scatter-hoarders' foraging decisions. Plant Ecology 219:325–342.

Nabuurs, G. J., et al. 2007. Forestry. Pages 541–584 *in* B. Metz, O. R. Davidson, P. R. Bosch, R. Dave, and L. A. Meyer, editors. Climate Change 2007: mitigation. Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, New York, USA.

Pesendorfer, M. B., T. S. Sillett, W. D. Koenig, and S. A. Morrison. 2016a. Scatter-hoarding corvids as seed dispersers for oaks and pines: a review of a widely distributed mutualism and its utility to habitat restoration. Condor 118:215–237.

Pesendorfer, M. B., T. S. Sillett, and S. A. Morrison. 2016b. 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.

Pesendorfer, M. B., T. S. Sillett, S. A. Morrison, and A. C. Kamil. 2016c. Context-dependent seed dispersal by a scatter-hoarding corvid. Journal of Animal Ecology 85:798–805.

Pons, J., and J. G. Pausas. 2007a. Rodent acorn selection in a Mediterranean oak landscape. Ecological Research 22:535–541.

Pons, J., and J. G. Pausas. 2007b. Acorn dispersal estimated by radio-tracking. Oecologia 153:903–911.

Pons, J., and J. G. Pausas. 2008. Modelling jay (*Garrulus glandarius*) abundance and distribution for oak regeneration assessment in Mediterranean landscapes. Forest Ecology and Management 256:578–584.

Pulido, F. J., and M. Díaz. 2005. Regeneration of a Mediterranean oak: a whole-cycle approach. Ecoscience 12:92–102.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rey Benayas, J. M., J. M. Bullock, and A. C. Newton. 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Frontiers in Ecology and the Environment 6:329–336.

Rey Benayas, J. M., L. Martínez-Baroja, L. Pérez-Camacho, P. Villar-Salvador, and K. D. Holl. 2015. Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland. New Forests 46:841–853.

Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review: Tansley review. New Phytologist 188:333–353.

U.N. 2017. Transforming our world: The 2030 agenda for sustainable development. United Nations, New York, New York, USA.

Vander Wall, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, Illinois, USA.

Verburg, P. H., and K. P. Overmars. 2009. Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. Landscape Ecology 24:1167–1181.

Villar-Salvador, P., J. L. Nicolás, N. Heredia, and M. Uscola. 2013. *Quercus ilex* L. Pages 226–250 *in* J. Pemán, R. M. Navarro-Cerrillo, M. A. Prada, and R. Serrada, editors. Producción y manejo de semillas y plantas forestales. Tomo II. Organismo Autónomo Parques Nacionales, Madrid, Spain.

Waite, R. K. 1985. Food caching and recovery by farmland corvids. Bird Study 32:45–49.

Whelan, C. J., D. G. Wenny, and R. J. Marquis. 2008. Ecosystem services provided by birds. Annals of the New York Academy of Sciences 1134:25–60.

Wootton, J. T., and M. Emmerson. 2005. Measurement of interaction strength in nature. Annual Review of Ecology, Evolution, and Systematics 36:419–444.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2989/full