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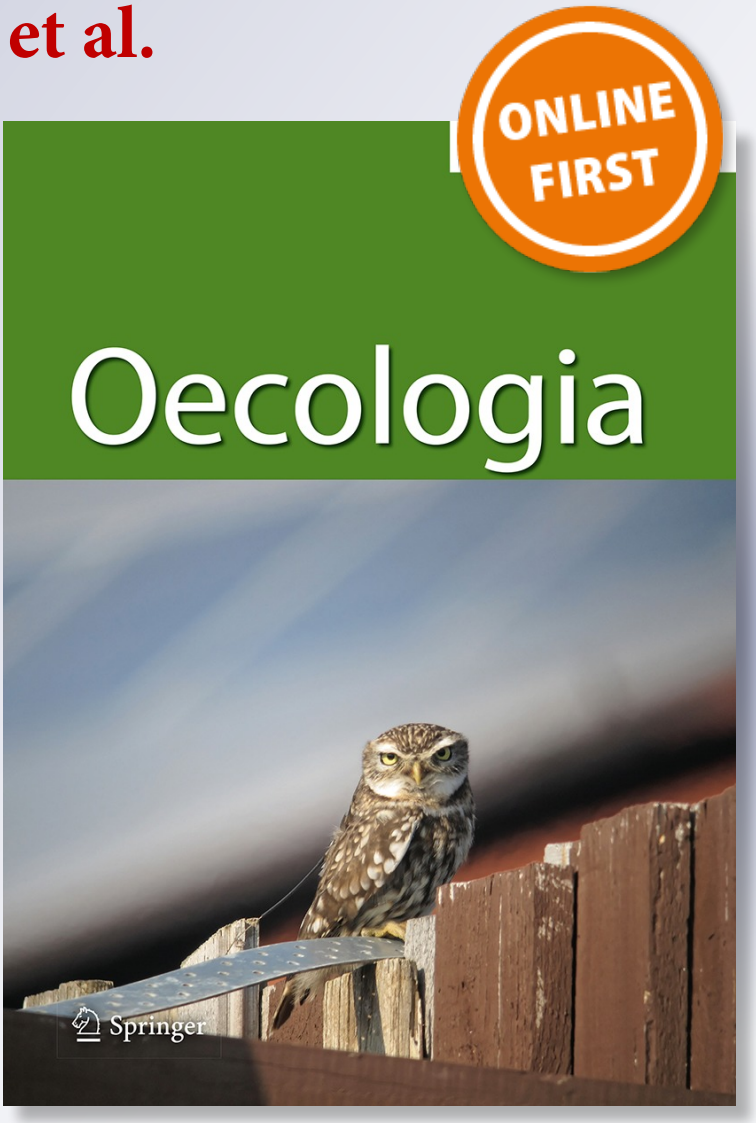
Oecologia

ISSN 0029-8549

Oecologia
DOI 10.1007/s00442-017-3848-x



Springer

Oecologia
DOI 10.1007/s00442-017-3848-x

PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Effective nut dispersal by magpies (*Pica pica* L.) in a Mediterranean agroecosystem

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Received: 19 September 2016 / Accepted: 27 February 2017

Abstract Scatter-hoarding animals such as corvids play a crucial role in the dispersal of nut-producing tree species. This interaction is well known for some corvids, but remains elusive for other species such as the magpie (*Pica pica*), an abundant corvid in agroecosystems and open landscapes of the Palearctic region. In addition, the establishment of the individual dispersed seeds—a prerequisite for determining seed-dispersal effectiveness—has never before been documented for the interaction between corvids and nut-producing trees. We analyzed walnut dispersal by magpies in an agroecosystem in southern Spain. We used several complementary approaches, including video recording nut removal from feeders, measuring dispersal distance using radio tracking (with radio transmitters placed inside nuts), and monitoring the fate of dispersed nuts to the time of seedling emergence. Magpies were shown to be highly active nut dispersers. The dispersal distance averaged 39.6 ± 4.5 m and ranged from 4.1 to 158.5 m. Some 90% of the removed walnuts were cached later, and most of these (98%) were buried in the soil or hidden under plant material. By the time of seedling emergence, ca. 33% of nuts remained at the caching location. Finally, 12% of the cached nuts germinated and 4% yielded an emerged seedling, facilitating the transition to the next regeneration stage. The results demonstrate for the first time that magpies can be an effective scatter-hoarding disperser of a nut-producing tree species, suggesting that this bird species may play a key role in the regeneration and expansion of broadleaf forests in Eurasia.

Keywords *Corvidae* · Forest regeneration · *Juglans* · Radio tracking · Scatter-hoarding · Seed caching · Seed dispersal effectiveness

Communicated by Carlos L. Ballare.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-017-3848-x) contains supplementary material, which is available to authorized users.

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Introduction

Seed dispersal of large-seeded species of paramount relevance in the context of temperate forests is largely ascribed to a plant–animal interaction in which a vertebrate vector is responsible for direct seed transport (Vander Wall 1990; Johnson et al. 1997; Pesendorfer et al. 2016). Several bird species from the *Corvidae* family are among the most active dispersers for these trees, acting as scatter-hoarding animals that cache seeds in a large number of locations across the landscape for later consumption, disperse a very large number of seeds, and usually cover distances exceeding hundreds or even thousands of meters (Bossema 1979; Darley-Hill and Johnson 1981; Lenda et al. 2012; Pesendorfer et al. 2016). A fraction of the seeds may remain unrecovered, providing the opportunity for seed germination and tree recruitment (Vander Wall 1990; Pesendorfer et al. 2016). In fact, the interaction between corvids and many tree species from the *Fagaceae* or *Juglandaceae*

Published online: 16 March 2017

plant families is considered a key mutualistic relationship for the regeneration, colonization, and expansion of forests in the Northern Hemisphere, helping to explain the postglacial migration and current distribution of temperate forests (Johnson and Webb 1989; Johnson et al. 1997; Vander Wall 1990; Mosandl and Kleinert 1998; Pesendorfer et al. 2016).

The role of corvids in the transport of nuts has been noted since ancient times (e.g., Aristotle and Theophrastus; Thanos 1994), and has been intensively studied in several species throughout the Holarctic region for decades (e.g., Grinnell 1936; Richards 1958; Bossema 1979; Cristol 2005; Pesendorfer et al. 2016 and references therein). In North America, at least seven species are described as being dispersers of nuts from *Fagaceae* or *Juglandaceae* species (Cristol 2005; Pesendorfer et al. 2016). However, the dispersal of large nuts such as acorns and walnuts by corvids in Eurasia is ascribed mostly to a single species, the European jay (*Garrulus glandarius* L.) (Bossema 1979; Pesendorfer et al. 2016), and—to a much lesser extent—to the rook (*Corvus frugilegus* L.) (Waite 1985; Källander 2007; Lenda et al. 2012). Knowledge of the roles of other corvids in the regeneration of these tree species in the Palearctic is almost negligible. In particular, the black-billed magpie (*Pica pica* L., hereafter referred to as "magpie"), a common corvid in Eurasia, is considered to have little relevance to tree dispersal, as it is assumed to preferentially cache perishable food while caching few nuts within short distances and to have a recovery time of only a few days (Henty 1975; Waite 1985; Birkhead 1991).

Several pieces of evidence, however, suggest that magpies might be noteworthy vectors in nut dispersal. It is well established that magpies cache food items (Henty 1975; Clarkson et al. 1986; Birkhead 1991), have the capacity to recall cache locations (Zinkivskay et al. 2009; Feenders and Smulders 2011), and have a well-developed hippocampus (Healy and Krebs 1992; Brodin and Lundborg 2003)—a brain region linked to spatial memory and food-storing behavior. Magpies are also suggested to be the most likely dispersers of almond trees in agroforestry systems (Homet-Gutiérrez et al. 2015), and reports on acorn dispersal—although very scant—are available (Birkhead 1991). In short, several clues support the idea that magpies may play an influential role in nut dispersal for Eurasian tree species. However, to date, the magnitude of nut dispersal and the recovery rate for this bird have never been documented.

Although many studies have addressed the dispersal of nut-producing trees by corvids (e.g., review by Pesendorfer et al. 2016), there is still a gap in our knowledge concerning the implications of this mutualistic interaction for forest regeneration. Studies reporting a link between the vector and the plant are based mostly on evidence arising from synchronous observations of dispersal and seedling-recruitment patterns (e.g., Mosandl and Kleinert 1998; Gómez 2003; Hougner et al. 2006; Castro et al. 2012; Lenda et al. 2012; Puerta-Piñero et al. 2012). This procedure has demonstrated beyond a doubt that corvids are major vectors for nut dispersal. However, a fine-grained quantification of the effect of animal seed-dispersal vectors requires precise knowledge concerning the fate of the dispersed seed—an aspect seldom addressed in studies of seed dispersal (Schupp and Fuentes 1995; Schupp et al. 2010), and (as far as we know) never addressed for the interaction between corvids and nut-producing tree species. Radio tracking with small transmitters embedded in the seed is a method that has recently been used to study nut dispersal (e.g., Pons and Pausas 2007; Tamura and Hayashi 2008; Morán-López et al. 2015). By replacing the transmitter-containing nut after dispersal with another unmanipulated nut that is able to germinate and continue the recruitment process, we may be able to monitor the magnitude of effective seed dispersal. Although this method could still underestimate the probability of recruitment if the dispersed nuts are re-cached, it has the potential to provide a more accurate measure of the qualitative component of seed-dispersal effectiveness (sensu Schupp et al. 2010) and a more comprehensive picture of the role of corvids in the recruitment of nut-producing tree species.

In this study, we analyze the activity of magpies, a common corvid in open landscapes and agroforestry systems throughout Eurasia, in relation to the dispersal of the common walnut (*Juglans regia* L.). Nut removal, dispersal distance, cache location, and seedling emergence were precisely monitored, providing the necessary framework to analyze the seed-dispersal effectiveness mediated by a vertebrate vector. Given the already known scatter-hoarding behavior of magpies and their capacity to remember caching sites, together with observations made under field conditions supporting magpie nut dispersal (Birkhead 1991; Homet-Gutiérrez et al. 2015; author's pers. obs.), we hypothesize that magpies are effective nut dispersers. Four specific questions were posed. (1) Do magpies disperse walnuts in the study area? (2) What are the characteristics of dispersal events in terms of habitat selection, caching type, and dispersal distance? (3) What is the recovery rate of cached nuts? (4) What are the germination and emergence rates of unrecovered nuts? The answers to these questions will allow us to determine an accurate value of the qualitative component of seed-dispersal effectiveness and the role of magpies as dispersers for a nut-producing tree.

Materials and methods

Study site and natural history of the system

The study was conducted in an agroforestry system located in the Vega de Granada (SE Spain, 37° 10′ 03.43″N, 3° 36′

57.80″W), a flat and irrigated agricultural area of small-sized farms located at ca. 650 m a.s.l. This area is used mainly for crop production: mostly vegetables, maize, tree plantations, and pasture. The soil is deep and loamy, and the climate is Mediterranean, with hot, dry summers and mild winters. The mean annual rainfall is 394 ± 71 L m^2 y^{-1} and the mean temperature 15.3 ± 0.1 °C (period 2006–2015, based upon climatic data from a meteorological station located at IFAPA Research Field Station, 1.5 km from the study site). Common walnut (*Juglans regia*; the target plant species of this study) is traditionally grown in the farms of the area (presumably since Roman times; Buxó 1997), usually as scattered trees close to houses.

The study site was a 1.8-ha farm (hereafter referred to as "core site") plus surrounding fields where nut dispersal could be registered with radio tracking. The core site, which is used mostly for research purposes, is divided into three main areas (habitats, hereafter), namely (1) a broadleaf stand, (2) a pine stand, and (3) cropland (Fig. 1). The broadleaf habitat is a 7000-m^2 mixed tree plantation of poplar (*Populus* × *euroamericana* (Dode) Guinier, clone I-214) and hybrid walnut (*Juglans major* × *Juglans regia* MJ 209xRa) with an even number of individuals and with all trees being evenly spaced at a planting density of 400 individuals ha^{-1}. Tree diameter at breast height in October 2015 was 27.6 ± 0.3 cm for poplar and 9.6 ± 0.2 cm for hybrid walnut. The pine habitat consisted of 2000 m^2 of Aleppo pine saplings (*Pinus halepensis* Mill.), evenly spaced at a density of 1200 individuals ha^{-1}. Saplings had a height of 1.95 ± 0.04 m by October 2015, with lower branches touching the ground. The cropland habitat covers the rest of the core site area and is used for vegetable production (Fig. 1). It also contains some scattered fruit trees (3–6 m tall) such as plums, apples, pears, persimmons, fig trees, and peaches, for a total of 34 individuals. The three habitat types were plowed in late August 2015, one week before the start of this study.

The black-billed magpie is a corvid that is widely distributed across the Palearctic, and is the most abundant corvid in southern Europe (Cramp and Perrins 1994; Martí and Del Moral 2003). It is particularly abundant in agroecosystems and open landscapes where other nut-dispersing corvids such as the European jay are usually absent (Martí and Del Moral 2003; Martínez 2011). The magpie is a common

Fig. 1 Orthorectified aerial photograph of the study area, taken with a drone. The area surrounded by a *dashed red line* is the core site. The *dashed yellow line* delimits the broadleaf habitat, the *green dashed line* the pine habitat, and the rest of the area within the core site corresponds to the cropland habitat. *Yellow dots* indicate the positions of cached nuts dispersed from feeder 1 and *green dots* those of cached nuts dispersed from feeder 2. The *orange triangles* show the positions of the feeders. One nut with a radio transmitter was dispersed towards the east outside the area of the picture and is not shown here. The image was taken with a GoPro 4 Black Edition camera attached to a drone (Phantom 2 UAV) during a photogrammetric flight at a height of 50 m on 23rd January 2016. The photos were processed with the Agisoft PhotoScan 1.2.0 software, which was also used for the final image with a pixel resolution of 10 cm

species in the Iberian Peninsula, but was absent in the study area until some years ago despite being common in nearby areas at distances of ca. 20 km. Regular bird sampling in the study area since 1985 (J.C., unpublished data) showed that it appeared in low numbers (occasional individuals) in 2002 and started nesting in 2008. The magpie population has steadily increased since then, and it is currently a common breeding bird in the area. Coinciding with its arrival at the study site, the emergence of walnut seedlings in the fields became evident. We made preliminary observations in 2012 and confirmed that magpies were dispersing nuts picked directly from *J. regia* trees of the area. These observations were not methodical, but they led us to formulate the hypotheses and sampling design for this study.

Sampling the magpie–walnut interaction

We studied the magpie–walnut interaction using three complementary approaches: (1) monitoring the removal of non-radio-tagged nuts offered in feeders; (2) monitoring the removal and dispersal distances of radio-tagged nuts offered in feeders; and (3) monitoring the post-dispersal recovery rate and seedling recruitment for nuts that replaced the radio-tagged nuts. Nut dispersal was sampled in all cases within the period of natural nut ripening and dispersal in the study area. The coordinates of all dispersed nuts and feeders were marked with a GPS, which allowed dispersal distances to be calculated using Quantum GIS. For the core site, we also constructed an orthophoto from photos with a pixel resolution of 5 cm (Fig. 1).

The removal of non-radio-tagged nuts placed in feeders was monitored from September 5 to October 26, 2015 (see Fig. S1 in the Electronic supplementary material, ESM, for feeder details). A total of 165 nuts were offered in bunches of 20 (occasionally 10 or 5; Table 1), and a video camera with a continuous recording system and day and night vision was placed ca. 1.5 m from the nuts (model SSC-758HQ DVR and SSC-56C36 camera; Advance Security, Belleville, IL, USA). Also, we conducted nonsystematic direct observations from a hide. A fraction of the nuts (120) were weighed before placing them in the feeders, and they were labeled with a number on the shell using waterproof permanent ink. This procedure was chosen as an initial method to test nut removal by magpies (i.e., before using radio transmitters) in order to reduce nut manipulation and potential distrust by magpies. It also allowed us to ascertain the disperser's identity and activity.

The dispersal of radio-tagged nuts placed in feeders was monitored from October 25 to December 12, 2015. To do this, a radio transmitter (PIP2 Tag Ag392; Biotrack, Wareham, UK; weight: 2.2 g; mean life span: 3 months) was placed inside the nut, which allowed us to relocate dispersed nuts and to measure exact dispersal distances. Nut removal was also video recorded with a movement-sensitive system (Moultrie M-990i; Moultrie Products, Birmingham, AL, USA), as well as with day and night vision. For each sample, the walnut shell was split open along the suture, a portion of the kernel of similar weight to the transmitter was excised, the transmitter with its antenna rolled up was placed inside the nut, and then the two halves of the nut were glued together with Loctite® (Fig. S2 in the ESM). Five transmitter-containing nuts were used, either in a single feeder or divided into groups of two and three nuts in the two feeders simultaneously. Eventually, we noted that magpies refused to pick some radio-tagged nuts from the feeders, which might have been due to desiccation or to some other cue that we could not identify. In those cases, we changed the transmitter to another nut. Once removed from the feeders, the nuts with the radio transmitter were located (usually within a few hours after dispersal) with the help of a radio-tracking receiver with a unidirectional Yagi antenna (Biotrack) plus a hand-held metal detector (White's Auto-Scan Personal Search Detector, Tulsa, OK, USA) for exact location of the nut/transmitter, which was particularly necessary for buried nuts. The caching characteristics were categorized as: (1) superficial, nuts left visible on the soil surface; (2) buried, nuts buried in bare soil; and (3) under plant material, nuts hidden below leaf litter or below leaves of live vegetation (the latter including forbs, grasses, vegetables, or the pine branches that were touching the ground in the pine habitat).

For the study of post-dispersal recovery rate and seedling recruitment, once a nut with a transmitter was located, the nut was placed back in the feeders, and an unmanipulated nut of similar weight was placed in the same location. The point where the nut was found was marked with a wooden stake (12 cm × 9 mm × 9 mm) 50 cm away from the nut, and a small metal rod was placed under the nut to facilitate later relocation with the metal detector. Approximately 6 months later (from 5 to 24 May 2016), coinciding with the period of seedling emergence in the study area, we sampled the statuses of all those nuts, categorizing them as absent (assigned as recovered), nongerminated, germinated, and emerged seedling. For emerged seedlings, we also noted seedling height.

Data analyses

We analyzed differences in weight between removed and nonremoved nuts from the feeders with a one-way ANOVA. The effect of nut weight on dispersal distance was assessed with a linear mixed model in the nlme R package (Pinheiro et al. 2016), using nut as a random effect because the same transmitter-containing nuts were placed in the feeders several times. Differences in caching types were analyzed with contingency tests, and the effect of caching

Table 1 Summary of the number of nuts offered and removed from feeders during the study period

	Date	Feeder	Number of nuts offered	Number of nuts dispersed
Non-radio-tagged nuts	05/09/15	1	20	18
	06/09/15	1	20	19
	08/09/15	1	20	20
	09/09/15	1	20	15
	11/09/15	1	20	14
	13/09/15	1	20	6
	18/09/15	1	20	15
	21/10/15	1	10	9
	21/10/15	2	10	4
	26/10/15	1	5	5
			$\Sigma = 165$	$\Sigma = 125$
Radio-tagged nuts	25/10/15	1	5	4
			5	5
	26/10/15	1	5	1
	27/10/15	1	5	4
	28/10/15	1	5	5
	29/10/15	1	5	2
			5	2
	1/11/15	1	5	4
	2/11/15	1	5	3
	3/11/15	1	5	4
	5/11/15	1	5	2
	7/11/15	2	5	3
	9/11/15	2	5	3
	10/11/15	2	3	1
	10/11/15	1	2	2
	15/11/15	1	3	1
	17/11/15	1	5	5
	25/11/15	1	5	3
	01/12/15	1	5	5
	04/12/15	1	5	2
	10/12/15	1	5	3
	12/12/15	1	4	4
			$\Sigma = 102$	$\Sigma = 68$

type on recovery rates using a glm with a binomial distribution. The effects of habitat type and distance from the feeder on nut dispersal were analyzed with spatial statistics. This analysis was restricted to the core site given that the habitats persisted through the study period in this area, whereas the crops changed from September to December outside the core site, precluding the definition of permanent habitats. For this, we fitted point process models with the R package spatstat (Baddeley and Turner 2005). The models considered a nonhomogeneous Poisson process, with the density of dispersed nuts within the core site depending on two spatial covariates: habitat type (broadleaf, pine, or farmland) and a map of the distance of each 1 × 1 m pixel to the feeder. The performance of this model was assessed through likelihood ratio tests during model simplification. This procedure was performed for the nuts dispersed from feeder 1, as the number of nuts from feeder 2 was insufficient to perform this analysis. Analyses were performed with R version 3.1.1 in all cases (R Core Team 2014).

Results

Nut removal from feeders

A total of 193 nuts were removed from feeders, including nuts with and without transmitters (68 and 125, respectively; Table 1). In 98% of the cases, the disperser was

video recorded or directly observed from the hide, and it was a magpie in all cases. No magpies consumed nuts in the feeders, and the number of nuts removed was 1 in all dispersal events. The number of magpies observed simultaneously in the feeders ranged from 1 to 5. Removed nuts were heavier (9.44 ± 0.17 g) than nonremoved nuts (8.67 ± 0.32 g; $F = 4.47$, $df = 1, 118$, $p = 0.037$). Overall, the magpies showed high activity and were able to remove all or most of the nuts within a few hours (Table 1).

Dispersal distance and caching characteristics

Dispersal distance was measured for 66 radio-tagged nuts. Mean dispersal distance was 39.6 ± 4.5 m, with a range of 4.1–158.5 m (Fig. 2a). Two nuts containing transmitters were not found despite thorough searching up to a distance of at least 300 m from the core site (not considered for analyses), and they were likely carried long distances based on video camera recordings of these nuts (see the ESM for a video of one of the cases). Nut weight did not affect dispersal distance (L. ratio = 0.58, $p = 0.45$).

Of the dispersed nuts, 10.6% were not cached but rather consumed immediately after removal from the feeder (the nut was found open, with the transmitter partially or entirely outside), whereas the remaining 89.4% (59 nuts) were cached. Of those, 55.9% were buried in the soil (at a depth of 1–3 cm in all cases), 42.4% were cached under plant material, and only one (1.7%) was left on the ground surface ($\chi^2 = 25.36$, $df = 2$, $p < 0.001$). In all cases the nuts were cached individually. Two of the nuts cached under plant material were located on a roof, although they were still hidden below litter.

The point process models did not show a significant effect of habitat type on the density of dispersed nuts (Δ dev = 0.94, $df = 2$, $p = 0.63$), but they did show a significant negative effect of distance from the feeder (Δ dev = 114.62, $df = 1$, $p < 0.001$; Fig. 2b).

Nut recovery and seedling recruitment

By May 2016, we were able to determine the fate of 49 of the 59 cached radio-tracked nuts; the remaining 10 nuts were either lost (four sampling points within the core site could not be relocated) or dispersed outside the core site, where the ground was tilled before the sampling time (thus provoking the loss of the sampling point). Of these 49 nuts, 67.3% were recovered, 20.4% did not germinate, 12.2% germinated (including emerged ones), and 4.1% produced an emerged seedling (Fig. 3).

Nut recovery was 73.5% in the cropland habitat, 57.1% in the broadleaf habitat, and 33.3% in the pine habitat, although there were no significant differences among habitat types ($\chi^2 = 3.79$, $df = 2$, $p = 0.15$). Non-recovered nuts were an average distance of 37.2 ± 6.2 m from the feeder vs 27.5 ± 4.3 m for the recovered nuts. Nonetheless, these means were not significantly different (logistic regression, $\chi^2 = 1.61$, $df = 1$, $p = 0.20$).

We could not unequivocally determine the animal that removed the cached nuts, but we often observed magpies recovering nuts in the study area, and found a large number of nuts consumed and opened in two halves, as is characteristic of magpies (Homet-Gutiérrez et al. 2015; author's pers. obs.). No other animal was directly observed removing the nuts dispersed by the magpies. Recovery activity spanned the entire study period, and we observed magpies consuming recovered nuts until early May 2016.

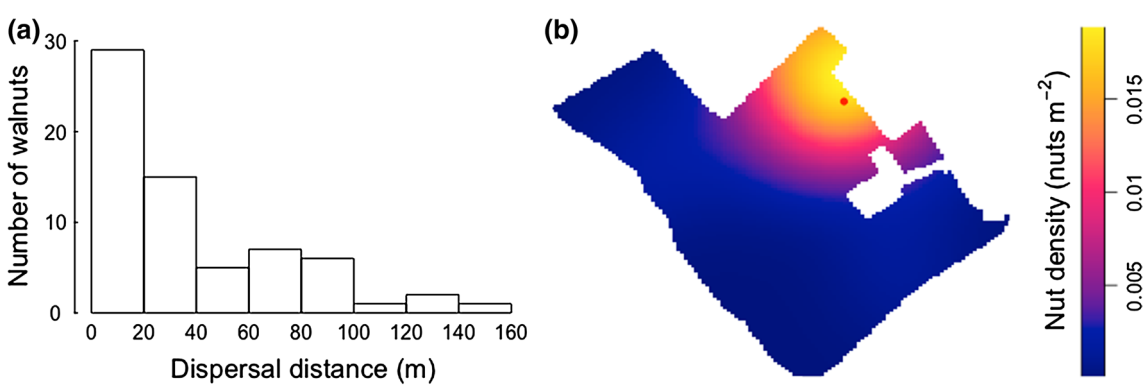

Fig. 2 Distribution of radio-tagged nuts dispersed by magpies. **a** Histogram showing the frequency of dispersal distances. **b** Kernel-smoothed density of cached nuts encountered in the core site for radiolabeled nuts dispersed from feeder 1 (marked as a *red dot*). The map shows the intensities of the point pattern generated by caching points within the plot. The density of caching points drops with increasing distance from the feeder. The space occupied by gravel roads and buildings was eliminated for the analysis

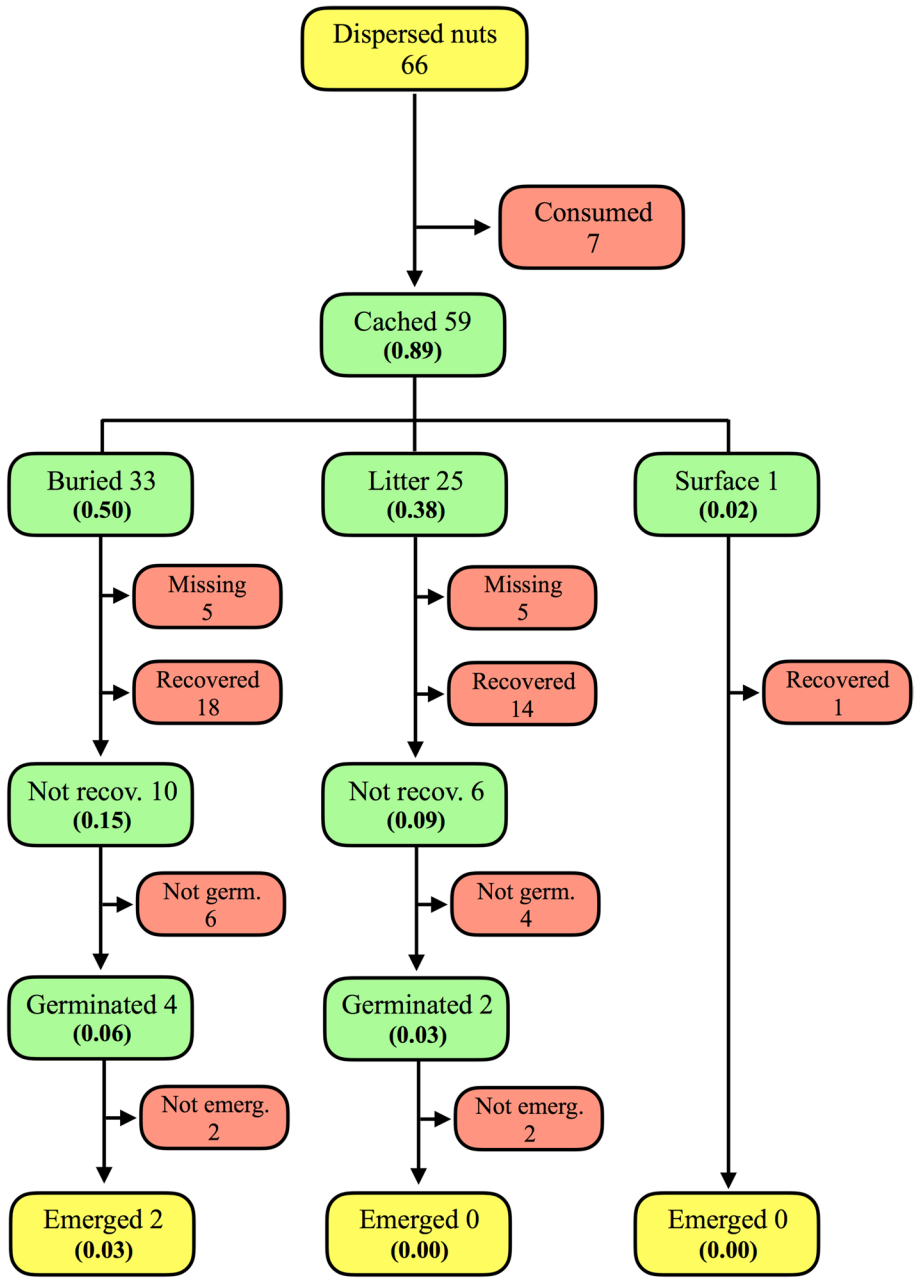

Fig. 3 Path diagram indicating the stages in the qualitative component of seed-dispersal effectiveness (SDE) for the magpie–walnut interaction. The *numbers in the boxes* indicate the numbers of nuts available for the next demographic transition (*green boxes*) and those that were lost for recruitment (*red boxes*). The *yellow boxes* indicate the starting (total number of monitored nuts) and the ending (number of emerged seedlings) points. *Numbers in parentheses* show the transition probability for each stage from the number of dispersed seeds. The heights of the seedlings were 12.0 and 14.8 cm, respectively. Data for the three habitat types have been pooled for simplicity. *Not-recov*. not recovered

Discussion

In this study, the magpie, an abundant corvid in Eurasian agroecosystems and open landscapes, proved to be an effective disperser of a large-seeded species, moving a large number of walnuts over dispersal distances that reached 158 m. Furthermore, a fraction of the nuts were not recovered after caching and they resulted in effective early seedling recruitment. Magpies had previously been suggested as dispersers for nut-producing tree species such as oaks (Birkhead 1991) or almond trees (Homet-Gutiérrez et al. 2015), but this interaction had never been demonstrated or measured in the context of plant recruitment. Our study contributes to the understanding of the role of scatter-hoarding corvids in the regeneration of Eurasian forests, and for the first time provides precise information on the qualitative component of seed-dispersal effectiveness for the interaction between birds and nut-producing trees.

Nut dispersal

Most of the nuts that were offered in the feeders were quickly dispersed and cached, and only a small fraction (ca. 10%) were consumed just after removal. This behavior is typical in scatter-hoarding animals, which display

vigorous dispersal activity when the resource is abundant, presumably in order to accumulate as much of it as possible during the short period of availability (Clarkson et al. 1986; Vander Wall 2001). After nut removal from feeders or trees, magpies also displayed a behavior similar to that of other corvids (Bossema 1979; Cristol 2005). On arriving at a place to hide the nut, they wandered for a few seconds as if selecting their preferred site, presumably checking for potential competitors that could steal the cached nut. In fact, in some cases they flew away with the nut and searched for another site. To cache the nut, they pushed it with the beak, sometimes hammering on it to bury it in the soil, and then they covered the site with soil or litter in such a way that the exact caching point became undetectable to the human eye (see Birkhead 1991 for a description of similar behavior). In addition, the majority of the cached nuts were buried in the soil or hidden under plant material, both of which are microhabitats that may favor seed germination and seedling recruitment by reducing the risk of predation and desiccation (Bossema 1979; Vander Wall 1990, 2001; Gómez 2004). Furthermore, magpies preferred heavier nuts, therefore favoring a trait (large seed mass) that may enhance seedling establishment (Castro et al. 2006).

The observed dispersal distances lie within the lower range described for the rook, a corvid with a documented role in walnut dispersal (Lenda et al. 2012). Nonetheless, the body mass of the rook (around 500 g) is much larger than the mass of the magpie (around 200 g). In addition, two of the transmitters were lost, perhaps as a consequence of long-distance dispersal. In fact, we observed several events in which a magpie flying from a feeder with a nut was lost in the distance, likely far beyond the maximum dispersal distance recorded (see the ESM). In any case, 7.3% of the nuts were dispersed beyond 100 m, a distance and proportion great enough to support the contention that magpies can act as long-distance seed dispersers (Cain et al. 2000). Thus, magpies can play a relevant role in the expansion of nut-producing trees into new areas, a key step in the regeneration of the temperate forest (Pesendorfer et al. 2016).

The seed rain generated also supports the idea that magpies are effective dispersers in agroecosystems and agroforestry mosaics, since nuts were invariably cached alone, one by one, and were widely distributed throughout different habitats of the landscape. Some consequences of the spatial structuring of the seed rain for plant recruitment also seem plausible, as shown by the facts that caching density decreased with distance from the source (as would ultimately be expected for a cost–benefit trade-off; Clarkson et al. 1986) and that there were significant differences in caching characteristics. Nonetheless, our results are based on a single study site, which precludes the generalization of patterns. Further studies including more study areas and a larger sample size would be necessary to ascertain the relationship between habitat characteristics, dispersal distance, and its potential implications for effective long-distance dispersal. Radio tracking, combined with the monitoring of the fate of seeds that replace the dispersed, radio-tagged seeds, has proven to be an appropriate method for answering these questions.

Post-dispersal nut recovery and seed dispersal effectiveness

Radio tracking also allowed us to obtain accurate estimates of nut recovery, which reached 67% ca. 8 months after dispersal. Magpies were the only animals observed recovering the nuts. We cannot rule out the pilfering of some of the nuts by rodents, but these animals appear to play a minor role in this system, as throughout the study period we found only three nuts exhibiting rodent chewing marks vs. a high number (not recorded) of nuts opened in two halves as magpies do. We cannot discount pilfering by other magpies, either, or re-caching by the original magpie. In any case, the consequence for plant recruitment is that, after nut dispersal by magpies, a large fraction (at least 32.6%) of the seeds remained on site until the following spring, ready to start the next regeneration stage.

As a final result, 4% of the cached nuts rendered an emerged seedling, thus providing a net value of seed dispersal effectiveness up to the seedling stage that could generate recruitment. In addition, the number of emerged seedlings might have been higher if the final sampling had been conducted a few weeks later, as all the germinated (but not emerged) seedlings showed a healthy radicle protruding into the soil. In fact, since the arrival of magpies in the study area ca. 15 years ago, there has been abundant walnut seedling emergence around the farms at distances of dozens to hundreds of meters from adult trees (authors' pers. obs.). Although this rarely translates into adult walnut recruitment due to yearly ploughing, it is very likely that walnut expansion would occur if ploughing were discontinued, as documented for example by Lenda et al. (2012) for walnuts dispersed by rooks in abandoned farms in Poland.

In summary, this study demonstrates the relevance of magpies as scatter-hoarding dispersers of nut-producing trees, and for the first time provides an accurate estimate of seed-dispersal effectiveness for a bird–plant interaction that is crucial to the regeneration and expansion of temperate, large-seeded trees (Pesendorfer et al. 2016). Magpies are abundant in open landscapes such as agricultural land and successional shrublands—habitat types that are usually avoided by Eurasian jays for their nut-dispersal activity (Gómez 2003; Pons and Pausas 2007; Leverkus et al. 2016), and where jays are often rare or absent (Andrén 1990; Pons and Pausas 2008;

Cramp and Perrins 1994). This may increase the relevance of the magpie as a key species for the demography of nut-producing trees in anthropogenic landscapes where habitat fragmentation and reduced forest cover are common. In short, our results support the hypothesis that magpies act in the regeneration and expansion of Eurasian temperate forest, thus increasing the number of corvid species with known key mutualistic roles in forest regeneration.

Acknowledgements This study was supported by the projects CGL2014-53308-P of the Spanish Government and Remedinal 3 (S2013/MAE-2719) of the Madrid Government. The Consejería de Medio Ambiente (Junta de Andalucía) provided fieldwork permission. LMB was supported by a FPI scholarship (BES-2015-075276) from the Spanish Government. AL acknowledges support from the University of Granada and Project GEI Spain (CGL2014-52838-C2-1-R) funded by the Spanish Ministerio de Economía y Competitividad, including European Union ERDF funds. We thank Dr. E.W. Schupp and two anonymous reviewers for providing suggestions that enhanced the manuscript.

Author contribution statement JC, LPC, PVS, SR, and JMRB conceived and designed the experiments. JC, MMM, AL, and LMB performed the field work. JC, MMM, and AL performed statistical analyses. JC wrote the first draft of the manuscript; all authors provided editorial advice.

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