The potential role of synzoochory in the naturalization of almond tree

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Abstract

Domesticated plants can occasionally naturalize, becoming feral elements of natural communities. This is only possible if crops overcome the abiotic and biotic barriers that restrict their dispersal and recruitment. The naturalization of almond trees (*Prunus dulcis, (Mill.) D.A. Webb*) was recently reported in SE Spain, but the mechanisms driving it remain to be established. In this study, we begin to elucidate how almonds overcome dispersal and initial establishment limitations, the first steps in feralization. We characterized seed removal and demographic structure in feral *Prunus dulcis* populations. Additionally, we investigated whether seed burial facilitated germination of almonds under greenhouse conditions. Our results indicate that dispersal by rodents (*Apodemus* and *Rattus*) might be an important mechanism favouring almond naturalization in SE Spain. Germination experiments showed that seed burial promotes germination and seedling emergence, suggesting that seed caching might play a beneficial role in recruitment. Lastly, our demographic surveys revealed that recruitment does not seem to be influenced by proximity to the maternal plant. We propose that rodents have a synzoochorous relationship with almonds, promoting their feralization and facilitating their establishment in natural communities.

Introduction

Crop domestication is not a linear, unidirectional process. Sometimes, cultivated species escape cultivation and naturalize into wild communities through a process known as feralization. This process is conditioned on overcoming biological and environmental factors that limit the establishment and reproduction of cultivated species (Richardson et al., 2000). These factors act as bottlenecks of seed dispersal and recruitment of new individuals.

The first key step in the feralization of domesticated plants is seed dispersal, which determines where seeds arrive and potentially recruit (Schupp & Fuentes, 1995). Many species of plants are dispersed by *synzoochory*, defined as the transport of seeds by granivorous animals that cache food in nests, burrows or directly in the ground, often in sites suitable for establishment

(Gómez et al., 2019). In some cases, cached seeds are not consumed because the animal does not recover them (Vander Wall, 2001). Synzoochory represents a unique evolutionary tension since the animals that act as vectors are simultaneously seed predators. Synzoochorous interactions can be placed along a continuum between mutualism and antagonism depending on the overall balance between its positive and negative outcomes. In other words, these plant-animal interactions are defined by the relationship between the benefits of dispersal and the costs of depredation (Gómez et al., 2019).

Synzoochory appears to be particularly relevant for nut-producing trees (Vander Wall, 2001). The almond, *Prunus dulcis,* is an emblematic nut tree and the most economically important nut crop at a global scale (FAOSTAT 2019). It is presently cultivated in dry environments around the world, with most of the production located in the Western US (80% of world total), Australia (6%) and Spain (5%; FAOSTAT 2019). In Spain it is a major crop and landscape feature, covering 657.771 hectares of agricultural land in 2018 (MAPAMA 2018). Feral forms of the crop also occur and Homet-Gutiérrez et al. (2015) showed that the spontaneous recruitment of almonds, particularly close to cultivated areas, is a frequently occurring phenomenon, at least in SE Spain.

Given that the cultivated area containing almond orchards has increased significantly in the past few years (11% increase between 2016 and 2018, MAPAMA) expansion of feral almond populations can be expected in the coming decades. These feral populations constitute a valuable agronomic resource as well as an interesting case of tree naturalization. However, they remain largely unexplored and the drivers of almond feralization are yet to be established.

Considering the absence of wild almond relatives in the western Mediterranean basin (Delplancke et al., 2013), the naturalization of almonds can be regarded as a process of endoferalization, where recruited individuals come directly from domesticated populations without having undergone hybridization with any wild taxa (Gressel, 2005). The natural expansion of any plant from an introduced population depends on successful establishment, which requires: 1) the dispersal of almonds from cultivated areas; 2) the survival and germination of these seeds; and 3) the establishment, survival and growth of seedlings (Richardson et al., 2000). In the present work we begin to address this three-step process to better understand the ecological dynamics underlying almond naturalization.

Given the distribution patterns and microhabitats where feral almonds occur, Homet-Gutiérrez et al., (2015) posited that the process of almond (endo)feralization must have been mediated by active dispersal by biological vectors. The morphological characteristics of almonds i.e. nuts without pulp and with a relatively hard endocarp, limit potential dispersers to two groups: corvids and rodents (Vander Wall & Beck, 2012).

Both corvids and rodents store food to varying degrees in caches in the soil or on the soil beneath litter or moss, a behaviour that can benefit seeds by increasing soil moisture and ultimately the rate of germination (Vander Wall, 2001; Gómez et al., 2008; Vander Wall & Beck, 2012; Pesendorfer et al., 2016).

The behaviour of the two groups of vertebrate vectors leads to distinct dispersal patterns, which might ultimately affect the spatial structure of plant populations. Rodents have relatively small home ranges and thus disperse seeds short distances (< 100 m) and they often cache seeds beneath shrubs, resulting in a short and approximately uniform dispersal kernel centred around the seed source and in many cases disproportionately concentrated beneath shrubs (Gómez et al., 2008; Wang & Chen, 2009). On the other hand, corvids disperse seeds up to several hundred meters from the source trees, creating a more diffuse, long-tailed dispersal kernel that may or may not be biased towards certain habitats (Gómez, 2003; Pesendorfer et al., 2016; Castro et al., 2017; Martínez-Baroja et al., 2019).

In this study, we aimed to throw light on whether seed dispersal by vertebrates might indeed facilitate the feralization of almonds in SE Spain. If synzoochory is promoting recruitment, it can lead to reproductive and self-sustaining populations that span all age classes and become a landscape and agronomic feature. We addressed this hypothesis with four different studies geared toward characterizing the phases of dispersal and recruitment. First, to determine whether dispersal by barochory alone might be a successful dispersal mechanism, we established transects with stores of almonds to estimate the likelihood of almonds to survive and germinate on the soil surface. Second, we approximated the probability of seed dispersal by different vectors through removal experiments that we maintained and tracked over seven months. Note that following Gómez et al., (2008) and Schupp et al., (2010) we consider the process of seed dispersal to be the horizontal movement of a seed away from where it is encountered, independent of the fate of the seed. Third, to evaluate potential facilitative effects of seed-caching behaviour, we conducted germination experiments to determine whether almonds were more likely to germinate when superficially buried (as per synzoochory) or when left on the soil surface. Fourth, we identified natural recruitment patterns by surveying the spatial and demographic structure of feral almond populations. If natural seed dispersal results in successful establishment, then naturalized populations should be self-sustaining and span multiple demographic stages.

If almond dispersal and establishment are driven by synzoochory, we would expect to find that almonds will not remain on the ground long enough to germinate because they are removed by biological vectors. Additionally, we would expect seeds in feeders to be removed regularly, and the removal rate would be higher in the feeders accessed by the most quantitatively effective vectors (sensu Schupp et al., 2010). If these tend to store seeds in caches, we should find that seed burial favours germination. A combination of seed removal by either rodents or corvids and a tendency to germinate when buried in cache-like conditions can be taken

as an indirect, first stage indication that synzoochory is relevant for the naturalization of almonds.

Materials and methods

Study site

We conducted this study in Granada province (SE Spain), a region with hot and dry summers and cold winters with scattered precipitation distributed mostly through spring and autumn. We set up four study sites (see Appendix A: Fig. 1), each in a feral population for which we could establish the approximate age of naturalization: 1) Alhama (37° 01′27.0"N, 3°57′45.2"W), established between 2004−2010; 2) San Miguel (37°11′38.3"N, 3°34′56.4"W), established between 1973-1986; 3) Víznar (37°13′07.5"N, 3° 33′44.4"W), established between 1973−1986; and 4) Hernán Valle-Guadíx (37°19′50.5"N, 3°03′12.4"W), established between 1980−1986. Population age was established based on aerial photographs, comparing the temporal sequence of pictures obtained from periodic photogrammetric flights between the years 1945 and 2017 (accessible through http://fototeca.cnig.es/). We established population age as the time window between the last picture where we could determine with certainty that no feral almond trees were visible and the first picture in which trees were present.

Experimental design

Seed removal experiments

We carried out field experiments to identify and characterize the vectors involved in almond removal and to indirectly quantify the relative role of passive and active secondary dispersal.

Transects

The purpose of this experiment was to quantify the rates of removal of almonds from the ground by animals independent of the microhabitat, basically, to determine whether almonds on the ground (e.g., dispersed by barochory) persist untouched and are thus potentially able to germinate and establish without the intervention of animal dispersers/seed predators. In the population "Hernán Valle-Guadix", we established four 50 m transects. They were located across areas that differed in vegetation type and cover, (i.e., spanning multiple microhabitats) and both with and without feral almond trees. Along each transect, we laid out ten piles of ten ink-marked almonds, one every five meters. In total we laid out 400 ink-marked almonds, 100 in each transect. We did not replace these almonds and noted every week the number of almonds that remained in each pile to quantify the removal rate. We defined an almond as dispersed if it

had been displaced 0.5 m or more in order to conservatively exclude seeds potentially moved by natural processes other than intentional dispersal (as in Gómez et al., 2008).

Feeders

The purpose of this experiment was to identify the animal seed dispersers and their relative quantitative importance to the dispersal of almonds. On 6 and 7 October 2018 we set up a feeder experiment to differentiate the contributions of distinct disperser groups to the removal of almonds. A replicate consisted of one feeder each of three distinct types, and there were three replicates at each of the four populations. The three feeder types in a replicate were: (1) a wooden tray 0.3 m × 0.2 m placed on a 1.5 m wooden stake and uncovered, (2) 0.3 m × 0.2 m frame placed on the ground and uncovered, and (3) same as (2) but covered by a steel mesh enclosure (1 × 1 cm mesh) open on two sides (10 cm × 10 cm opening; see Appendix A: Fig. 2). These feeders were designed assuming that only birds would take almonds from the elevated feeder, only rodents would remove almonds from beneath the mesh barrier, and both groups could access the uncovered almonds on the ground. We placed a total of 36 traps divided in three replicate groups of the three feeder types in each of the four feral populations (total 12 replicates of the three trap types). Replicates were placed under fruit-bearing feral almond trees, with the bird feeder directly beneath the tree canopy and with the other two feeders 1 m to the E and W. We placed nine almonds in each feeder; almonds were counted and replenished every week for 27 weeks. In total we placed 8748 ink-marked almonds. Finally, three motion active cameras with day and night vision (Moultrie S-50i Game Camera, EBSCO Industries, Inc., Birmingham, AL) were placed at approximately 1.5 m facing the feeders and rotated weekly between locations and feeders. All removal experiments were conducted using cultivated almonds of the "Comuna" commercial type, which spans a wide diversity of morphotypes and genotypes (Socias & Gradziel, 2017).

Germination

We conducted a greenhouse germination experiment to determine whether seed burial facilitates almond germination and establishment. In late September 2018, we visited nine populations, four feral and five cultivated (i.e., almond orchards; see Appendix A: Table 1) and selected 12 random individuals in each separated by at least 10 m, resulting in a total of 48 feral and 60 cultivated almond trees. We then randomly chose two almonds from each tree, (N = 216 almonds). In December 2018 we cracked the shells of the almonds to facilitate imbibition and kept them for two weeks in wet vermiculite at 4°C in darkness to ensure cold stratification (García-Gusano et al., 2004). We then put half of the almonds on the surface of 5 cm x 5 cm x 6 cm pots filled with vermiculite and buried the other half at a depth of

3 cm, mimicking the activities of a seed-caching disperser. This experiment took place over eight weeks, during which we measured radicle protrusion on a weekly basis, gently removing the vermiculite when needed to check germination status of buried almonds.

Spatial structure of feral populations

In April 2019 we set up a survey of each of the four study populations to determine the demographic structure of feral almond populations and to characterize the micro-habitats in which natural recruitment is most likely. In each population we established five 50 m x 2 m transects, set at a minimum of 30 m intervals (see Appendix A: Fig. 3), covering a total area of 500 m^2. We started each transect close to either the oldest (largest) trees in the population or the adjacent orchard, considering these as the most likely original seed sources. We conducted two censuses of each transect over a fortnight, recording every almond tree within the transect, classifying them based on Homet-Gutiérrez et al., (2015) but with slight modifications to make it more comprehensive and representative of the population structure we observed across sites. The final classification is based on the tree's reproductive state, height, and diameter at breast height (DBH) in five life-stage categories: (1) seedling (Non-reproductive; Height <50 cm), (2) sapling (Non-reproductive; Height > 50 cm), (3) juvenile (Reproductive; Height < 250 cm, <30 cm DBH), (4) adult (Reproductive; Height > 250 cm; <30 cm DBH), and (5) source plant (Reproductive; Height > 250 cm, >30 cm DBH). For each tree we encountered, we also noted its GPS position, basal diameter, distance to the nearest source plant, and cover type (classified as open, herbaceous, or woody).

Data analyses

We performed all analyses and plotted graphs using RStudio 3.5, and we used the Geographic Information System QGis2.18 to create our maps.

Seed removal

We calculated seed removal rate in transects with a Survival Analysis using the
Kaplan-Meier estimator. We create a *Surv* object with 'survfit' function of the "survival" r package (Therneau, 2020), which takes as arguments "Time" as time of observation (in our case measured in weeks), and "Event" as an indicator of the almond removal where it is 1 if the event was observed and 0 if not.
To calculate removal rate from the feeders, we calculated the percentage of almonds removed from each type of feeder every week. Then we estimated whether this removal rate varied among feeder types, feeder groups and populations and through time using general mixed models with a quasi-binomial link function in order to avoid overdispersion. In these models population (four levels: Alhama, Hernán Valle-Guadix, SanMiguel, Víznar), replicate (nested within population, three levels) and feeder type (nested within replicate, three levels: Bird, Rodent, All) were treated as factors and 'week' was used as a covariate.

Germination

We compared germination rates using a Logistic Regression model, in which the response variable was either germinated (1) or not (0) and the factors were treatment (surface *vs*. buried), population (nine levels, nested within degree of cultivation; see Appendix A: Table 1) and degree of cultivation (feral *vs*. cultivated).

Spatial structure

To analyse the spatial structure, we first calculated the distance between observed individuals and the source plant considering the aforementioned distance as the hypotenuse of a triangle with two known sides: the position on the transect (x) and the distance to the transect (y). Afterwards, we grouped individuals in distance classes of 5 m, and we calculated the average age of each class.

Results

Seed removal

Transects
The survival probability of almonds on transects fell from a rate of 50% at Week 6 to 7.5% at Week 19 (Fig. 1). At this point, only two piles had seeds left (9 and 8 almonds, respectively) both in the same transect (Tr. 1). We only detected one germinating seed (out of 400) in the course of the survey, and it was nevertheless removed by the following survey date.

Feeders
Removal of seeds from both types of ground feeders was nearly always >50% in all populations and replicates, often reaching 100%. By contrast, almonds were removed only occasionally from the elevated feeders (often ~ 0%; Fig. 2). These removal rates differed not only among feeder types, but also exhibited spatial variation (significant differences among populations and replicates) and fluctuated through time (significant differences across weeks; Table 1, Fig. 2). Moreover, temporal variation in removal rates differed among populations, likely reflecting changes in vector activity and/or presence through time among populations (Table 1).
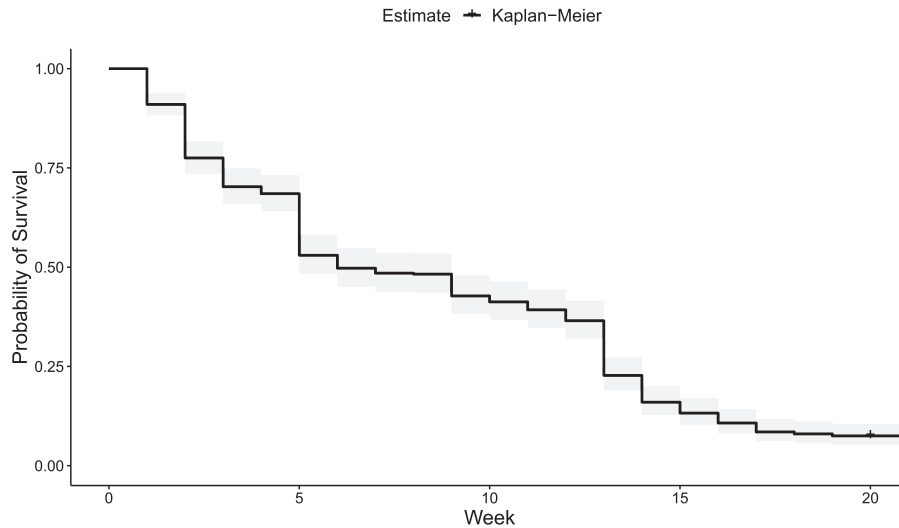
Fig. 1. Probability of seed survival on the ground over the duration of the experiment. The plot represents the Kaplan-Meier estimator computed from 40 stores of 10 almond kernels distributed along four different transects (see text for details). Survival probability of seeds after 20 weeks was negligible. During the 20 weeks of observation, only one seed (0.25%) germinated, and was nevertheless removed, presumably by a rodent.
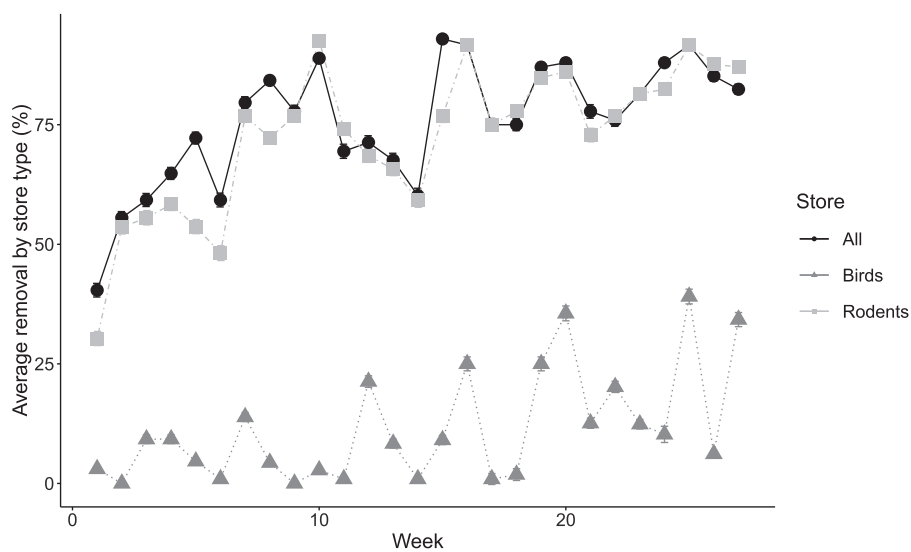

Fig. 2. Proportion of seeds removed from the three types of feeders. Each feeder was designed to ensure that access was more likely by a given vector or combination of vectors: open ("All", black circles), on a stand ("Birds", dark grey triangles), with a metal mesh cover ("Rodents", grey squares). Each point represents the mean ($\pm$ SE) of 12 stores of each type spread across the four study populations (three stores of each type/population) over the central 27 weeks. Significantly more seeds were removed from the two feeder types on the ground ("Rodents"; "All") than from "Bird" feeders ($p < 0.0001$; Table 1).

Three potential disperser species were recorded, two rodents (wood mouse, *Apodemus sylvaticus* and black rat, *Rattus rattus;* see Appendix A: Fig. 4) and a bird (magpie, *Pica pica*), although the total activity of the latter was hard to determine as it was not recorded actively removing almonds; it just perched on the feeder and occasionally opened kernels by pounding on them. Of the two rodents, *A. sylvaticus* seems to be more abundant and was recorded in all four populations, while rats were only recorded in one population (Alhama).

Germination experiments

The proportion of almonds that germinated was significantly higher when they were buried under the soil surface. Our analyses also showed that the percentage of germination of almonds was significantly greater for cultivated than feral almonds and differed significantly among populations for both types of almonds (Fig. 3, see Appendix A: Table 2).

Table 1. Differences in almond removal rates among populations, replicates and feeder types over nine months. The table represents the results of a general linear mixed model where removal rate (in %) was the response variable and population, replicate (i.e., the groups of feeders of the three types) and feeder type were treated as discrete factors and time (expressed in weeks, n = 27) as a co-variate. 1 0.61 0.608 4.866 0.0276*

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Week	1	4.59	4.59	36.69	$p < 0.0001$
Pop	3	22.44	7.48	59.84	$p < 0.0001$
Replicate	1	0.61	0.61	4.87	0.0276
Feeder:Replicate	3	53.17	17.72	141.78	$p < 0.0001$
Replicate:Pop	3	10.05	3.35	26.80	$p < 0.0001$
Week:Pop	3	2.68	0.89	7.16	$p < 0.0001$
Feeder:Replicate:Week	3	7.60	2.53	20.26	$p < 0.0001$
Residuals	1028	128.51	0.12		

Spatial structure

Population demographic structure (Fig. 4) was clearly different among populations. The population with the oldest average and median life stages was Alhama, while Víznar had the largest number of seedlings and saplings. Alhama was the densest (0.17 individuals/m^2), while the other three populations had similar, lower densities (0.03 individuals/m^2 San Miguel, 0.02 individuals/m^2 Hernán Valle-Guadix, 0.08 individuals/m^2 Víznar). We did not observe any clear aggregation pattern in feral almond populations, regardless of age, except in San Miguel, where density and age decrease uphill away from the putative source (see Appendix A: Fig. 3 and Table 3). Recruitment seemed to take place preferentially under plant cover (50% of seedlings and 55% of saplings were found under either herbaceous or woody plant cover).

Discussion

Our results provide preliminary evidence that almond feralization in SE Spain is likely facilitated by synzoochory. Our field experiments indicated that rodents are the quantitatively most important vectors, and their seed-caching behaviour could facilitate seed germination and the development of seedlings.

Most almonds left on the soil surface disappeared before germinating, therefore, passive dispersal processes are likely to play only a minor role in natural recruitment. Moreover, our feeder experiments showed that the disappearance of seeds was due to removal by biotic vectors, mostly rodents.

Almonds were consistently removed from the ground while few were taken from the elevated feeders. It would thus appear that rodents are the primary vector responsible for the dispersal of almonds. Images obtained from our camera traps showed
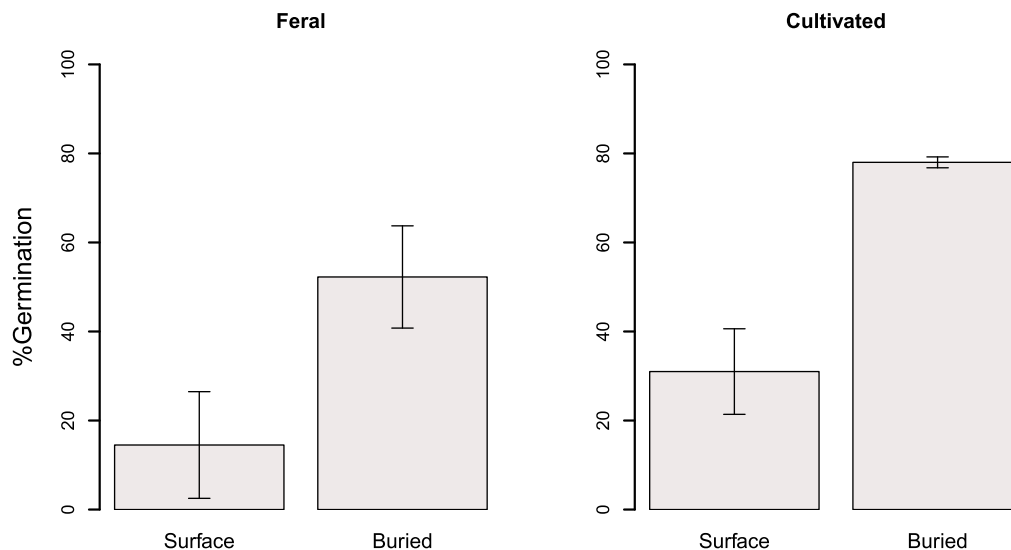

Fig. 3. Germination Results. The bars represent % Germination with the standard errors of in-shell cracked kernels either buried 3 cm deep or placed on the soil surface. Almonds were collected from feral and cultivated individuals, cracked open and stratified for two weeks in the dark at 4 °C. Both population of origin and treatment were significant ($p \sim 0.001$; $p < 0.0001$ respectively). See text and see Appendix A: Tables 1 & 2 for details.
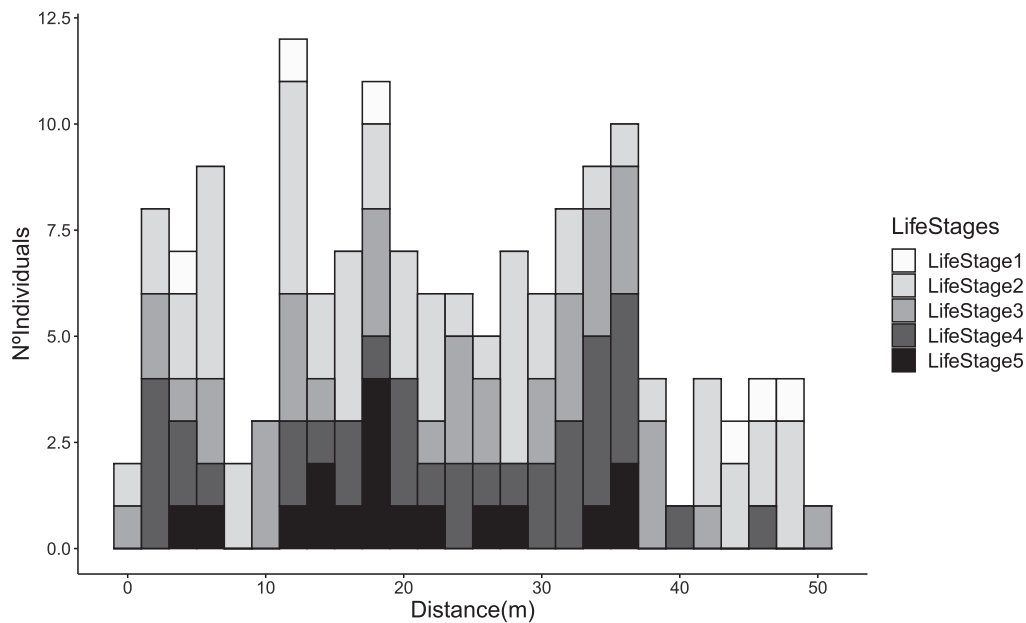
Fig. 4. Demographic structure of feral almond populations. The figure shows the number of recorded individuals, their life stage classes, and the distance to the nearest source tree. The bars represent the aggregated data for the four populations (obtained from five 50 m x 2 m transects, set at a minimum of 30 m intervals in each population). No clear spatial pattern was detectable, except in the case of San Miguel, where life stage and frequency of plants decreased with distance from the source. See main text for details and see Appendix A: Table 3 for population-specific data.

that wood mice (*Apodemus sylvaticus*) and rats (*Rattus rattus*) were the most frequent visitors to our feeders and the only ones that were recorded actively taking almonds. Furthermore, we observed in our camera trap images that rats can climb up to the standing feeders and might have been responsible for the removal of seeds that could have otherwise been attributed to birds. Magpies (*Pica pica*) were captured by cameras on several occasions and exhibited some interest in the almonds, but we obtained no clear evidence of a removal event. Anecdotal evidence from other research projects and personal observations by some of the authors corroborate that corvids, mostly magpies and carrion crows (*Corvus corone*) can on occasions pick almonds from trees or the soil and open and eat them, but this seems to be a rather sporadic event and it is unclear how often kernels are actually cached. In conclusion, although corvids cannot be ruled out as dispersal vectors, especially given the documented importance of corvids as nut dispersers in other systems (Gómez, 2003; Pesendorfer et al., 2016, 2017; Castro et al., 2017; Martínez-Baroja et al., 2019) our data indicate that in the case of the almond in SE Spain, rodents of the genera *Apodemus* and *Rattus* appear to be much more relevant.

Our germination experiments also support a potential role for scatter-hoarders in the naturalization of almond. Seeds of feral and cultivated almonds germinated at significantly higher rates (2x) when buried 3 cm below the soil surface than when left on the soil surface. This can easily correlate with a higher propensity for germination in seed caches of wood mice (Gómez et al., 2008).

It is important to remember that at this point we have no information on the qualitative component of seed dispersal (sensu Schupp et al., 2010) by any of the vectors, that is, on the fate of dispersed seeds. Our support of the hypothesis that synzoochory is the mechanism driving almond feralization is based on indirect evidences. Given the very high removal rates and the low densities of recruits, it appears that the probability of any harvested seed successfully recruiting is very low. Further, broken almond shells are frequently observed in our study sites, often in sheltered areas, suggesting that dispersers, especially rodents, may lie more on the antagonistic end of the mutualism−antagonism continuum (Gómez et al., 2019) with more seeds consumed than cached − likely many more. This might be particularly true when kernels are removed by black rats, as these tend to behave generally as seed predators (Vander Wall, 2001; Vander Wall & Beck, 2012), although they may also act as dispersers on occasion, leaving intact partially consumed seeds in protected sites (husking stations; (McConkey et al., 2003; Shiels & Drake, 2011). In our case, wood mice are qualitatively the most important vector and are expected to be also rather relevant in qualitative terms. *Apodemus* are known to disperse and scatterhoard numerous large-seed nut species in many habitats (Iida, 2006; Takahashi et al., 2006; Pons & Pausas, 2007; Gómez et al., 2008; Merceron et al., 2017). Some of the removed almonds are surely cached, as is typical for interactions of mice with large seeds (e.g. Vander Wall, 2001; Gómez et al., 2008; Vander Wall & Beck, 2012; Gómez et al., 2019; Martínez-

Baroja et al., 2019). Moreover, recruitment patterns also support that rodents, especially *Apodemus* mice, might be qualitatively important. According to our data, almond seedlings and saplings are found mostly under dense vegetation, a pattern that is congruent with scatter-hoarding by wood mice, which tend to place their caches preferentially under shrub or grass cover (José M. Gómez et al., 2008; Perea et al., 2011; Wang & Corlett, 2017). Seeds placed beneath cover might not only increase the probability of germination, but also facilitate the growth and survival of seedlings once germinated by protecting against extreme insolation and herbivory (Bertness & Callaway, 1994; Maestre et al., 2001; Garcia, 2007; Brooker et al., 2008; Perea et al., 2014).

Our analyses of the demographic patterns of feral almond populations showed that recruitment is particularly active in Alhama, while it was minimal in Hernán Valle-Guadix (see Appendix A: Table 3). Interestingly, the latter population was also where the feeders had the lowest overall removal rate which might indicate that recruitment is limited by dispersal in this population. Spatial demographic patterns did not exhibit any clear structure and did not match those expected under pure barochory, where we would expect recruitment to be clustered beneath and immediately adjacent to maternal plants with the possibility of recruitment at somewhat greater distances down slope from fruiting plants (Traveset & Rodríguez, 2008; Nield et al., 2019). For example, in San Miguel, recruitment was documented at substantial distances from the putative source tree even though transects were oriented uphill from them on a steep slope (20 m vertical drop). Up-slope distribution of recruited plants makes dispersal by gravity unlikely, but it has been correlated to rodent activity (Perea et al., 2011).

Our results show that animal vectors actively remove and disperse almonds and that they might also be instrumental to their consequent germination and establishment and, ultimately, feralization. Quantitatively, the primary vectors involved in this process appear to be rodents, especially *Apodemus*, although we cannot fully rule out the occasional participation of corvids. However, much remains to be learned about the quality of dispersal provided by each vector (e.g., the total ratio between cached seeds and consumed seeds; Gómez et al., 2019). More direct data are needed on the fates of almond dispersed by different vectors, including explicit quantification of dispersal, storage and predation, to ascertain the relevance of synzoochory for almond feralization.

Of course, these results do not preclude barochory as an important mechanism of almond dispersal, especially on steep slopes and/or associated to anthropogenic dispersal. Indeed, it is not uncommon to see recruitment occurring along roadsides immediately adjacent to almond orchards, and in other locations that can be most parsimoniously explained considering post-harvest handling and transportation. However, our results suggest that this may be the exception rather than the norm, especially considering that many feral almond stands cannot be explained without taking into account longer-distance movements of almonds away from orchards and transportation corridors.

The range of feral almond trees coincides with that of Mediterranean ecosystems in which rodents play a fundamental role in maintaining forest dynamics (Gómez et al., 2008; Muñoz et al., 2009; Zhang et al., 2017). However, almond trees present a striking case. Even though they have been cultivated in this area for thousands of years, according to our data and personal observations, mature feral populations are rare. The feralization of almonds may be an emerging phenomenon favoured by the simultaneous abandonment of farming land in marginal areas over the past few decades, much of which was cultivated with almonds, and the increase in the surface devoted to almond orchards in irrigated, industrial farms (MAPAMA, 2018). As a result, more almonds are available to seed predators and dispersers, which in turn can be dispersed into more fallow land.

In conclusion, our findings suggest the idea that the naturalization of almond trees might be facilitated by a synzoochorous interaction with vertebrates (rodents) whose seed-caching behaviour could favour the dispersal and recruitment of the tree. Further research is required to quantify the different potential outcomes of the interaction we have recorded and to understand the ecological and agronomic dynamics associated to these novel feral almond populations.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2020.11.004.

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