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8 **Naturalization of almond trees (*Prunus dulcis*) in semi-arid**  
9 **regions of the Western Mediterranean.**  
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## Abstract

1 Agricultural land abandonment is rampant in present day Europe. A major consequence of this  
2 phenomenon is the re-colonization of these areas by the original vegetation. However, some  
3 **agricultural**, exotic species are able to naturalize and colonize these abandoned lands. In this  
4 study we explore the ability of almonds (*Prunus dulcis* D.A. Webb.) to establish in abandoned  
5 croplands in semi-arid areas of SE Iberian Peninsula. Domesticated during the early Holocene  
6 in SW Asia and the Eastern Mediterranean, the almond has spread as a crop all over the world.  
7 We established three plots adjacent to almond orchards on land that was abandoned and  
8 reforested with Aleppo pine (*Pinus halepensis* Mill.) and Holm oak (*Quercus ilex* L.) about 20  
9 years ago. We recorded the abundance of almond seeds, seedlings, juveniles, pre-  
10 reproductives and adults in these plots, and determined their recruitment microhabitat. We  
11 found natural regeneration in all three plots, with almond density higher than 150 individuals/ha  
12 in each plot. About half of the almonds in the plots were juveniles, although 7% were one-year  
13 seedlings and 3% were adult trees. This suggests that colonization of abandoned lands is an  
14 ongoing gradual process. Most naturally established almonds were under tree cover, although  
15 this was not the most abundant microhabitat, avoiding the negative impact of browsing by Red  
16 Deer (*Cervus elaphus*) and domestic sheep and goats. In addition, the mean distance from the  
17 nearest seed source was 77 m. These findings suggest the action of mobile almond dispersers.  
18 Several Corvid species including the Carrion Crow (*Corvus corone*) and the Magpie (*Pica pica*)  
19 have been observed consuming and moving almonds in the study area. Our study has  
20 demonstrated that almonds are colonizing abandoned lands mostly **as a consequence of**  
21 effective seed dispersal by some animals. We **show** that almonds have the **potential** to become  
22 fully naturalized in the near future in many semi-arid areas of the Western Mediterranean.  
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## Keywords

38 **Rosaceae, seed dispersal, dyplochory, diszoochory, crop, land abandonment.**  
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## Introduction

Abandonment of agricultural activities, mostly in marginal and less productive lands, is a widespread phenomenon in Europe (Verburg and Overmars, 2009; Renwick et al., 2013). Dramatic changes in plant communities and land cover happen after land abandonment (Poyatos et al., 2003; Gehrig-Fasel et al., 2007; Cramer et al., 2008; Stoate et al. 2009). Abandoned croplands are often recolonized by native species that were removed from those areas when humans started to cultivate them. Nevertheless, many crops become naturalized themselves. This naturalization process has happened since the beginning of agriculture, leading to the origin of many invasive species (Reichard and White, 2001). Arid environments can be especially sensitive to invasion by domestic species (Loope et al., 1988; Rejmanek and Randall, 1994). Although we generally think of herbaceous species, trees have also naturalized in exotic places after being introduced for horticulture or forestry (Richardson and Rejmánek, 2011). For example, the sweet chestnut *Castanea sativa* now occupies many areas in the Mediterranean Basin after being disseminated by Greek and Roman civilizations (Conedera et al., 2004). Similarly, most invasive *Pinus* species were introduced in novel areas for their use in commercial forestry and agroforestry (Richardson, 1998).

The almond, *Prunus dulcis* (Mill.) D.A. Webb (syn. *Amygdalus communis* L. and *Prunus communis* Archang) (Rosaceae), is an economically important nut tree crop. With an apparent origin as an edible crop in southwest Asia and the eastern Mediterranean (Browicz and Zohary, 1996; Delplancke et al., 2013; Ladizinsky, 1999; Roher, 2012) it has been spread all over the arid and semi-arid world by the actions of man. The almond tree is probably one of the earliest domesticated trees in the Old World, with archaeological evidence suggesting domestication about 6,300-5,300 yr. BP (Zohary et al., 2012). The annual world production of almonds exceeds 2 million tons (FAO, 2013). Spain is the second largest producer of almonds in the world with a production of approximately 69,636 tons (USDA, 2013). Presently, approximately 571,183 ha are under cultivation in Spain (Ministerio de Agricultura, Alimentacion y Medio Ambiente, 2012), although this area is continuing to decrease due to abandonment of groves.

The almond tree is a small deciduous tree reaching 5-8 m in height. The 25–40 mm fruit is ovoid-oblong and flattened. The pulp (mesocarp) is dry and leathery, splitting on maturity to reveal the stone (Rohrer, 2012). Although there are some anecdotal reports (Blanca and Díaz de la Guardia, 1998; Rohrer, 2012) no quantitative studies have been performed on the process of naturalization of almond populations. The main goal of our study is to demonstrate that almond trees can effectively colonize semi-arid regions of the Western Mediterranean. In this study, in three areas from SE Spain where almonds seem to be naturalized, we characterized 1) the density and life stage structure of naturalized almonds, 2) the microhabitat distribution of established almonds, and 3) the frequency and intensity of browsing by mammals.

## Methods

### Study site

1 Our study site is located in the Hoya de Guadix-Baza in the north of the Province of Granada  
2 (37° 19' 42" N, 3° 2' 27" W). This is a zone that was intensively cultivated in the past but  
3 presently is a mosaic of oak dehesas intermixed with aforestation patches and dryland  
4 agriculture, especially almonds.  
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6 The study site has a continental Mediterranean climate with strong fluctuations in  
7 temperature (mean = 14.4° C with maximum and minimum reaching 40° C and -14° C,  
8 respectively). Summers are hot and dry while winters are cold. Precipitation is low (250-300  
9 mm/yr) and concentrated in fall and winter.  
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11 In this zone we selected three aforestation plots that had been planted with Aleppo pine  
12 (*Pinus halepensis* Mill.) and Holm oak (*Quercus ilex* L.) in approximately 1995 (Figure 1).  
13 Although there has been recruitment of additional species, the vegetative cover of woody plants  
14 is still almost exclusively of these two species; in addition, all three plots have extensive areas  
15 of bare ground and herbaceous vegetation. Pines mostly range from about 2 – 6 and up to 8 m  
16 in height with branches all the way to the ground creating protected shaded understories. Oak  
17 trees vary mostly from approximately 0.5 to 3 m in height; they also have branches all the way  
18 to the ground but the canopies are less dense and therefore provide less shade.  
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47 Figure 1. Spatial distribution of the three study plots. Red lines indicate the transects and green dots show the locations of the tagged almond trees  
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50 Plots 1 (≈3.2 ha) and 2 (≈2.75 ha) are about 150 m apart and separated by a cultivated  
51 grain field. This set of plots and the connecting agricultural field are nearly completely  
52 surrounded with almond groves. Pines and oaks in these plots were skewed to the taller end of  
53 the range of heights and there was minimal evidence of mortality of planted trees. Plot 3,  
54 approximately 3.5 km away, forms part of a much more extensive aforestation plot (≈45.5 ha)  
55 that connects upslope to the adjacent Sierra de Baza. Because of the extensive size we  
56 selected four subplots (total ≈3.9 ha) to subsample. Almond cultivation, at least presently, is  
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1 much less extensive in the vicinity of this plot, although there are reproductive almonds along  
2 the roadside running past the plot. Pines and oaks in this plot were skewed to the lower end of  
3 the range of heights and there was greater mortality of planted trees.  
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## 5 6 **Study design**

### 7 *Vegetative cover and almond tree density*

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9 We surveyed 6 arbitrarily located transects in both Plot 1 and Plot 2 and 8 transects in Plot 3 (2  
10 in each subplot). Transects were 50 m long x 2 m wide for a total area of 100 m<sup>2</sup>. A 50-m tape  
11 was stretched out and a 2-m long metal rod centered on the tape was used to delineate the  
12 width of the transect. At each 1 m along the transect from 0 to 50 m we recorded the vegetative  
13 cover at the tape and at 1 m to each side of the tape (ends of pole) for a total of 153 points per  
14 transect. Of a total of 3060 microhabitat points, 10 were recorded as almond tree and 8 as  
15 broom. Because of these very small sample sizes and the fact that no almond trees were found  
16 beneath almonds and only one beneath broom, these two categories were excluded from  
17 analyses.  
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19 We also counted the number of almond trees encountered in each transect,  
20 independent of life stage. In addition, for each 2 m length of transect (2 x 2 m quadrat) we  
21 recorded the presence/absence of ungulate and lagomorph feces as well as the number of  
22 almond seeds, distinguishing undamaged from opened and consumed. Almonds are consumed  
23 in the study site by corvids and rodents. Consumed almonds can be attributed to functional  
24 group of predator based on the way the stone is opened: corvids open the stone along the  
25 seam leaving it in two equal halves (clean cut), while rodents nibble the stone from the apex  
26 leaving a hole.  
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### 28 *Microhabitat, plant size and life stage, and browsing*

29 We systematically searched each plot, intending to tag and georeference the first 100 individual  
30 trees that we found in each plot. However, we went over the target sample size in Plots 1 (103  
31 trees) and 2 (116 trees). Only a small portion of these individuals were in the aforementioned  
32 transects, and consequently, we did not include transect as an identification variable for the  
33 tagged trees. We took the following data for each individual almond tree: (1) Microhabitat: pine,  
34 oak, or open interspace (bare ground and herbaceous cover combined). One almond tree found  
35 beneath a broom (*Retama sphaerocarpa*) was excluded from subsequent analyses. (2) Height.  
36 (3) Basal stem diameter (BSD): measured at 5 cm above the soil surface. (4) Reproductive  
37 status: presence/absence of fruits. (5) Browsing: intensity of herbivory was measured as the %  
38 of branch tips that had been browsed. We distinguished between browsing by lagomorphs  
39 (Iberian hares, *Lepus granatensis*, and rabbits, *Oryctolagus cuniculus*) and ungulates (domestic  
40 sheep and goats and red deer, *Cervus elaphus*). Whereas lagomorphs cut the stems by means  
41 of clean and diagonal incisions, the ungulates rip them off.  
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43 Based on the height, BSD, presence of fruits, stem lignification, and presence of  
44 cotyledons, we categorized the plants into one of four life stage classes: (1) Seedling: ≤ 0.25 cm  
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1 BSD with green stems. Seedlings were recognized because they always had the almond  
2 attached. (2) Juvenile: 0.25 – 0.6 cm BSD and more extensive lignification of the stem. (3) Pre-  
3 reproductive:  $\geq 0.6$  cm BSD with stems extensively lignified. (4) Reproductive: distinguished by  
4 the presence of fruit. There was substantial overlap in the BSDs of pre-reproductive and  
5 reproductive individuals.  
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#### 7 8 9 *Distance to nearest reproductive tree*

10 Because individual trees were georeferenced, we calculated their distance to the nearest  
11 reproductive adult outside the plot using the geographic information system software QGIS  
12 1.8.0 (QGIS Development Team). For Plots 1 and 2 and some subplots in Plot 3 this was the  
13 distance to the edge of the nearest almond grove, but for some subplots of Plot 3 this was the  
14 distance to the row of almonds along the roadside.  
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#### 19 **Data Analysis**

20 Between-plot differences in almond tree density were analyzed using a General Linear Model  
21 (GLM), including transects as the independent variable and fitting the dependent variable  
22 (number of almond trees per transect) to a Poisson distribution. Between-plot differences in  
23 microhabitat structure and life stage classes were assessed by Contingency Analysis and  
24 Likelihood Ratio Tests, including transect as an independent variable. The proportion of trees  
25 browsed was compared among plots and among microhabitats by GLMs, fitting the dependent  
26 variable (browsed trees vs. unbrowsed trees) to a binomial distribution. Browsing intensity was  
27 compared among microhabitats with a GLM by fitting the dependent variable (percent of  
28 consumed branches) to a normal distribution. All analyses were performed using R 3.0.0 (R  
29 Development Core Team 2013).  
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#### 37 **RESULTS**

##### 38 **Density and relationship to seed sources**

39 The density of established almond trees (almond trees/100 m<sup>2</sup>  $\pm$  1 SD [Range]) was 1.50  $\pm$  0.84  
40 [0-2] in plot 1, 1.83  $\pm$  0.98 [1-3] in plot 2, and 1.62  $\pm$  1.41 [0-4] in plot 3. Plots did not differ in the  
41 densities of almond trees ( $z = 1.22$ ,  $df = 2$ ,  $p = 0.225$ , GLM poisson). The mean distance to the  
42 nearest reproductive tree was 76.8  $\pm$  2.9 m, ranging from 4.8 up to 207.7 m. Furthermore, 90%  
43 of the almond trees were farther than 20 m from the closest seed source.  
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48 Overall, 12% of the 2 x 2 m quadrats had almond seeds. However, plots differed in  
49 almond seed abundance ( $\chi^2 = 20.8$ ,  $df = 2$ ,  $p < 0.0001$ ), with 20% of the quadrats in plot 2  
50 having almond seeds, 13% in plot 1 and only 4% in plot 3. The presence of almond seeds  
51 increased significantly with the cover of trees in the quadrats (slope= 0.03  $\pm$  0.005,  $\chi^2 = 32.8$ ,  $df$   
52 = 1,  $p < 0.0001$ , logistic regression). This relationship was significant for Plots 1 and 2, but not  
53 for Plot 3. In total, only 27% of the almond seeds were undamaged, the remaining being  
54 consumed by animals (mostly corvids and rodents).  
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### Life stage structure of almond trees

Most of the censused almond trees were juveniles (53.6%; N=319 trees) and pre-reproductives (37.3%) (Table 1). Nevertheless, 6.6% of the established almond trees were one-year seedlings and 2.5% were reproductive trees (Table 1). There were significant among-plot differences in life stage structure (Table 1; Likelihood Ratio = 136.27, df = 6, p < 0.0001, N = 319 trees). Most trees in plot 1 were juveniles (89%). In plot 2, juveniles and pre-reproductive individuals were similarly abundant and together comprised 89% of the established almond trees. Finally, in plot 3 over half of the individuals were juveniles, although there were also large numbers of pre-reproductives. In addition, plot 3 was the only plot that had reproductive trees and the only plot without seedlings.

### Vegetative cover and microhabitat occupancy of almond trees

Most of the surface of all three plots was open ground, ranging from 83% in plot 1 to 90% in plot 3 (Table 1). Nonetheless, plots differed significantly in microhabitat structure ( $\chi^2 = 188.15$ , df = 10, p < 0.0001); based on cover, oak was the predominant woody plant microhabitat in plot 1, pine was the predominant woody plant microhabitat in plot 2, and oak and pine were similarly important in plot 3.

There were differences between the observed and expected microhabitat distribution of almond trees in all plots (**Plot 1:**  $\chi^2 = 304.545$ , df = 2, p < 0.0001, N = 1021. **Plot 2:**  $\chi^2 = 113.789$ , df = 2, p < 0.0001, N = 1034. **Plot 3:**  $\chi^2 = 35.502$ , df = 4, p < 0.0001, N = 1324). In all plots the number of trees in open was lower than expected based on the cover of the open microhabitat, although the difference was smallest in plot 3 and largest in plot 1 (Table 1). Despite this similarity, plots differed in their patterns of microhabitat occupation across plots. In plot 3 most of the trees were in open ground, even though it was fewer than expected. In contrast, most trees in plot 1 were under oak and nearly half of the trees in plot 2 were under pine while a similar but lower number were in open ground. In plot 3 there were more trees under pines than expected, whereas in plots 1 and 2 there were more than expected underneath both pines and oaks.

	Plot 1				Plot 2				Plot 3				Total			
	Total	Open	Oak	Pine	Total	Open	Oak	Pine	Total	Open	Oak	Pine	Total	Open	Oak	Pine
Seedling	8	-	8	-	13	-	2	11	0	-	-	-	21	0	10	11
Juvenile	89	-	79	10	58	4	11	43	24	2	2	20	171	6	92	73
Pre-reproductive	6	2	3	1	45	43	-	2	67	63	1	3	118	108	4	6
Reproductive	0	-	-	-	0	-	-	-	8	8	-	-	8	8	-	-
Total Trees	103	2	90	11	116	47	13	56	99	73	3	23	318	122	106	90
Microhabitat points	918	759	114	45	918	795	16	107	1206	1103	36	67				
Expected Trees		85	13	5		100	2	14		90	3	6				

Table 2. Abundance of almond trees per microhabitat and life stage in each plot. Also shown are the expected number of almond trees per microhabitat according to a random distribution.

When pooling the three plots to reduce small cell values, there was a significant difference among stages in the pattern of microhabitat recruitment ( $\chi^2 = 306.300$ ,  $df = 9$ ,  $p < 0.0001$ ,  $N=319$ ). Whereas most seedlings and juveniles were found under the canopies of oaks or pines), most pre-reproductive and all reproductive trees were in open ground (Table 1).

### Browsing damage

The abundance of herbivorous mammals, estimated as the proportion of quadrats with excrements, varied among plots both for ungulates ( $\chi^2 = 42.77$ ,  $df = 2$ ,  $p < 0.0001$ , binomial GLM) and lagomorphs ( $\chi^2 = 8.84$ ,  $df = 2$ ,  $p < 0.01$ ). Whereas 38% of the quadrats in plot 2 had ungulate excrements, only 12% in each of the other two plots did. For lagomorphs we observed a similar pattern, with 5% of the quadrats in plot 2 but only 1% in the other two plots having excrements.

About 53% of the studied trees were browsed by mammals when pooling the three plots. However, the proportion of trees browsed differed among plots ( $\chi^2 = 77.9$ ,  $df = 2$ ,  $p = 0.0001$ ), with 26% of the trees being browsed in plot 1, 54% in plot 2 and 86% in plot 3 (Table 2). Most herbivory was caused by **ungulates**, although damage by lagomorphs was also important, especially in plot 3 (Table 2). When a plant was browsed, mammals damaged on average 83.4% of the branches (pooling the three plots). However, there were among-plot differences in this measure of browsing intensity ( $\chi^2 = 17.56$ ,  $df = 2,165$ ,  $p < 0.0001$ , GLM). In plot 1, 65% of the branches on browsed trees were damaged, and this proportion increased to 82% in plot 3 and 94% in plot 2 (Table 2).

Plots	Almond trees	Browsed trees				Browsing Intensity $\pm$ SD
		Total	By ungulates	By lagomorphs	By both	
1	103	27	11	16	0	65.3 $\pm$ 32,0
2	116	54	42	11	2	94.5 $\pm$ 14,3
3	100	86	56	12	18	82.1 $\pm$ 20,6

Table 3. Browsing frequency (number of trees damaged) and intensity (proportion of stems damage per tree) in each studied plot. Ungulates are red deer, domestic sheep and goats, whereas lagomorphs are Iberian hare.

**The proportion of trees browsed differed among** microhabitats for the two demographic stages with sufficient individuals to analyze (juveniles:  $\chi^2 = 17.6$ ,  $df = 2$ ,  $p < 0.0001$ ; pre-reproductive:  $\chi^2 = 30.9$ ,  $df = 2$ ,  $p < 0.0001$ ). Whereas 96% of pre-reproductive and 100% of juveniles were browsed in open sites, only 0% and 25% were browsed under oaks and 3.6% and 21.9% under pines, respectively. Furthermore, 100% of the reproductive trees located in



1 open sites were also browsed, and 20% of the seedlings under oaks and 18% under pines were  
2 browsed.

3 Browsing intensity also differed among microhabitats ( $\chi^2 = 7.39$ ,  $df = 2, 154$ ,  $p < 0.0009$ ,  
4 only considering browsed juveniles and pre-reproductives pooled). Whereas  $88.4 \pm 2.0$  % of the  
5 branches in trees located in open sites and  $82.3 \pm 4.8$  of the branches from trees under pines  
6 were browsed, only  $69.6 \pm 4.5$ % of the branches were browsed when under oaks.  
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## 10 DISCUSSION

11 Our study has shown that almonds are actively colonizing abandoned lands **that were**  
12 **subsequently afforested in semi-arid areas of SE Spain. This finding adds an additional *Prunus***  
13 **species to the seven species already included in the updated global list of invasive alien trees**  
14 **(Rejmanek and Richardson, 2013).** The density of almonds was high in all three study plots,  
15 with more than 150 individuals/ha. These values appear high when compared with other  
16 **anecdotal** studies. For example, natural establishment of almonds is apparently only sporadic in  
17 abandoned orchards from Southeastern France, where most colonization is by fleshy-fruited  
18 bird-dispersed species (Debussche and Isenmann, 1994; Debussche et al., 1982). In addition,  
19 all anecdotal observations on feral populations of almonds suggest that they colonize roadsides,  
20 with little indication that they escape from this highly disturbed microhabitat (Blanca and Díaz de  
21 la Guardia, 1998; Guix et al., 2001; Rohrer, 2012). Our study indicates that in semi-arid  
22 environments of the **southeastern** Iberian Peninsula, almonds are able to establish not only in  
23 highly disturbed areas but also in more natural settings. Although the three plots were actively  
24 afforested, pine-oak woodlands are native and abundant in the study area. In fact, we have  
25 found almond seedling and saplings in natural oak-pine woodlands adjacent to almond  
26 orchards. **Furthermore, these seedlings and saplings were far enough from any seed source to**  
27 **suggest the action of active mobile dispersers.**  
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38 Our data indicate that the colonization of abandoned lands by almonds has occurred  
39 gradually but consistently through time since afforestation was established twenty years ago.  
40 About half of the almonds in the plots were juveniles, although 7% were one-year seedlings and  
41 3% were adult trees. That is, almond incursion was not a single, event occurring shortly after  
42 the planting of oaks and pines, when the plots were largely empty and disturbed. **We are also**  
43 **confident that the reproductive trees colonized the plot after the afforestation was made, based**  
44 **on their relatively small size and their apparent absence from the area in previous high**  
45 **resolution aerial photographs (available in Rediam webpage at**  
46 **[www.juntadeandalucia.es/medioambiente/ site/rediam](http://www.juntadeandalucia.es/medioambiente/site/rediam)).**  
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52 In order to naturalize, seeds must be dispersed out of cultivated areas to sites suitable  
53 for germination, growth, and survival. Effective propagule dispersal is essential for the  
54 naturalization and regeneration of plant populations (Blackburn et al., 2011, Schupp et al.,  
55 2010). In particular, seed dispersal by vertebrates is often implicated in the spread of alien plant  
56 species (Rejmanek and Richardson, 1996; Richardson et al., 2000). Dispersal distances, timing  
57 of the colonization process, and microhabitat distribution of recruits all suggest that biotic agents  
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1 mediated the movement of almonds into the study plots. The dry seed without a fleshy pulp  
2 combined with the relatively hard endocarp of almonds likely limits the potential disperser  
3 assemblage to large seed-eating birds and rodents. In fact, sweet almonds are consumed and  
4 dispersed by rodents, woodpeckers and corvids in Asia (Kester et al., 1991), North America  
5 (Gebhardt et al., 2011; Hasey and Salmon, 1993; Robert, 1979) and Israel (Moran and Keidar,  
6 1993), likely contributing to the establishment of feral populations. In our plots we have  
7 observed almonds broken open by birds. At least four corvid species (raven, *Corvus corax*,  
8 carrion crow, *Corvus corone*, magpie, *Pica pica*, and to a lesser extent chough, *Pyrrhocorax*  
9 *pyrrhocorax*) consume almonds in the study area (Soler and Soler, 1991). In addition, green  
10 woodpeckers (*Picus viridus*) have been observed consuming almonds in semi-arid habitats of  
11 southeastern Spain (J.M. Avilés, pers. com.). Finally, we have also observed almonds  
12 consumed by dormice (*Eliomys quercinus*).  
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18 We believe that in our study site birds are the agents moving almonds out of orchards  
19 into afforestations to consume them. There is abundant evidence showing that corvids prefer to  
20 hoard seeds in afforestations (Purves et al., 2007; Gómez, 2003). In contrast to acorns and  
21 some other nuts, sweet almonds are too big and hard to be easily eaten. Birds first must break  
22 the stone in order to access the edible kernel. We observed many broken almonds on top of  
23 small rocks usually located in open sites. We presume that corvids use those rocks as anvils,  
24 since we have observed some carrion crows behaving in this way. However, many sweet  
25 almonds are apparently too hard and remain unbroken, as indicated by the frequent presence of  
26 almonds laying on the ground in the afforestations. Some of these almonds may be subsequently  
27 found by rodents, which could secondarily disperse them to safe microsites, such as under pine  
28 and oak canopies (Beck and Vander Wall, 2011; Gomez et al., 2008; Puerta-Piñero et al., 2010;  
29 Vander Wall, 2001, 2002). In fact, we found most of the almonds that had been apparently  
30 consumed by dormice in these covered microhabitats. It is important to note that, because oaks  
31 and pines were planted twenty years ago, they still have a shrubby shape, with lower branches  
32 lying on the ground. This overall shape likely provides rodents with good shelter from predation.  
33 In addition, burial in the soil or beneath litter, either by birds as primary dispersers or by rodents  
34 as secondary dispersers of seeds dropped or discarded by birds, likely benefits these large nuts  
35 by reducing desiccation and increasing the ability to hydrate and germinate (Vander Wall,  
36 2001).  
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47 Such diplochory would explain why most naturally established almonds were under tree  
48 cover, despite this not being the most abundant microhabitat. In fact, there is a relationship  
49 between the presence of almond seeds and the tree cover in plots 1 and 2. An indirect positive  
50 effect of dispersing almonds beneath pines and oaks is that emerging plants are protected from  
51 mammalian herbivores (García et al., 2000; Gómez and Hódar 2008). Thus, whereas almost all  
52 almond trees located in open sites were heavily browsed by ungulates and hares, less than  
53 25% of them were browsed, and only relatively mildly, when located in covered microhabitats.  
54 Facilitation of tree seedlings and saplings by nurse plants has been repeatedly demonstrated in  
55 semi-arid environments (Flores and Jurado, 2003). In most occasions, facilitation apparently  
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1 occurs because nurse plants protect seedlings and saplings from stressful environments  
2 (Pugnaire and Luque, 2001; Lortie and Callaway, 2006). Nevertheless, protection against  
3 herbivores is also an important benefit provided by nurses (García and Obeso, 2003; Gómez,  
4 2005; Gomez-Aparicio et al., 2008). We believe that this is the main reason recruiting almond  
5 trees are more abundant under oaks and pines. Ungulates have been demonstrated to shape  
6 the spatial structure of recruitment in other Mediterranean trees (Gómez et al., 2001; Gómez-  
7 Aparicio et al., 2005; Gómez and Hódar, 2008). In fact, the few individuals located in open sites  
8 were completely browsed. However, our preliminary evidence is that more open conditions are  
9 apparently necessary for reaching reproductive maturity; all 8 reproductive adults were found in  
10 open interspaces. This suggests a potential life-stage conflict (Schupp, 2007). Summing up, as  
11 occurs in many other plant species (Vander Wall and Longland, 2004), diplochory appears to be  
12 advantageous for initial establishment of almond trees in our study site, though the longterm  
13 consequences are less clear.

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15 In summary, this study has demonstrated that *Prunus dulcis* is actively naturalizing in  
16 semi-arid afforestations in the southeastern Iberian Peninsula. The process of naturalizing in  
17 relatively natural environments, not just along roadsides, is likely more widespread than  
18 previously appreciated. We suggest that this process is more evident and faster in abandoned  
19 lands that have been subsequently afforested than in simply abandoned lands, because  
20 corvids tend to move most seeds into forested areas (Gómez 2003). However, there is no  
21 reason to believe this process only occurs in afforestations.

## 22 23 24 25 26 27 28 29 30 31 32 33 **Acknowledgments**

34 Dr. Puerta-Piñero reviewed a preliminary version of this manuscript.  
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## References

- 1 Beck, M.J. & Vander Wall, S.B., 2011. Diplochory in western chokecherry: you can't judge a  
2 fruit by its mesocarp. *Oecologia* 165, 131-141.  
3
- 4 Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U.,  
5 Richardson, D.M., 2011. A proposed unified framework for biological invasions. *Trends Ecol.*  
6 *Evol.* 26, 333–339  
7
- 8 Blanca, G. & Díaz de la Guardia, C., 1998. *Prunus* L. In: Castroviejo, S., C. Aedo, M. Laínz, F.  
9 Muñoz Garmendia, G. Nieto Feliner, J. Paiva & C. Benedí (eds.), *Flora iberica* 6, 444-466.  
10 Real Jardín Botánico, CSIC, Madrid. In: [http:// www. Floraiberica.org/](http://www.Floraiberica.org/) [03-09-2013].  
11  
12
- 13 Browicz, K. & Zohary, D., 1996. The genus *Amygdalus* L. (*Rosaceae*): Species relationships,  
14 distribution and evolution under domestication. *Genetic Resources and Crop Evolution* 43,  
15 229-547.  
16
- 17 Conedera, M., Krebs, P., Tinner, W., Pradella, M., Torriani D., 2004. The cultivation of  
18 *Castanea sativa* (Mill.) in Europe, from its origin to its diffusion on a continental scale.  
19 *Vegetation History and Archaeobotany* 13, 161-179.  
20  
21
- 22 Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land  
23 abandonment and ecosystem assembly. *Trends in Ecology and Evolution* 23, 104-112.  
24
- 25 Debussche, M. & Isenmann, P., 1994. Bird-dispersed seed rain and seedling establishment in  
26 patchy Mediterranean vegetation. *Oikos* 69, 414-426.  
27
- 28 Debussche, M., Escarré, J., Lepart, J., 1982. Ornithochory and plant succession in  
29 Mediterranean abandoned orchard. *Vegetatio* 48, 255-266.  
30
- 31 Delplancke, M., Alvarez, N., Benoit, L., Espindola, A., Joly, H.I., Neuenschwander, S., Arrigo  
32 N., 2013. Evolutionary history of almond tree domestication in the Mediterranean basin.  
33 *Molecular Ecology* 22, 1092-1104.  
34  
35
- 36 Food and Agriculture Organization (FAO), 2013. *FAO Statistical Databases: Agriculture*. FAO,  
37 Rome.  
38
- 39 Flores, J. & Jurado, E., 2003. Are nurse-protégé interactions more common among plants from  
40 arid environments? *Journal of Vegetation Science* 14, 911-916.  
41
- 42 García, D. & Obeso, J.R., 2003. Facilitation by herbivore-mediated nurse plants in a threatened  
43 tree *Taxus baccata*: local effects and landscape level consistency. *Ecography* 26, 739-750  
44
- 45 García, D., Zamora, R., Hódar, J.A., Gómez, J.M., Castro, J., 2000. Yew (*Taxus baccata* L.)  
46 regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. *Biological*  
47 *Conservation* 95, 31-38.  
48  
49
- 50 Gebhardt, K., Anderson, A.M., Kirkpatrick, K.N., Shwiff, S.A., 2011. A review and synthesis of  
51 bird and rodent damage estimates to select California crops. *Crop Protection* 30, 1109-1116.  
52
- 53 Gehrig-Fasel, J., Guisan, A., Zimmermann, N.E., 2007. Tree line shifts in the Swiss Alps:  
54 climate change or land abandonment? *Journal of Vegetation Science* 18, 571-582.  
55
- 56 Gómez, J.M., 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in  
57 a heterogenous landscape. *Ecography* 26, 573-584.  
58  
59  
60  
61  
62  
63  
64  
65

- 1 Gómez, J.M, 2005. Ungulate effect on the performance, abundance and spatial structure of two  
2 montane herbs: A 7-yr experimental study. *Ecological Monographs* 75, 231-258.
- 3 Gómez, J.M & Hódar, J.A., 2008. Wild boars (*Sus scrofa*) affect the recruitment rate and spatial  
4 distribution of holm oak (*Quercus ilex*). *Forest Ecology and Management* 256, 1384-1389.
- 5  
6 Gómez, J.M., Hódar, J.A., Zamora, R., Castro, J., García, D., 2001. Ungulate damage on  
7 Scots pines in Mediterranean environments. Effects of association with shrubs. *Canadian*  
8 *Journal of Botany* 79, 739-746.
- 9  
10 Gómez, J.M., Puerta-Piñero, C., Schupp, E.W., 2008. Effectiveness of rodents as local  
11 dispersers of Holm oaks. *Oecologia* 155, 529-537.
- 12  
13 Gómez-Aparicio, L., Zamora, R., Gómez, J.M., 2005. The regeneration status of the  
14 endangered *Acer opalus* subsp. *granatense* throughout its geographical distribution in the  
15 Iberian peninsula. *Biological Conservation* 21, 195-206.
- 16  
17 Gómez-Aparicio, L., Zamora, R., Castro, J., Hódar, J.A., 2008. Facilitation of tree samplings by  
18 nurse plants: microhabitat amelioration or protection against herbivores? *Journal of*  
19 *Vegetation Science* 19, 161–172.
- 20  
21 Guix, J.C., Soler, M., Martin, M., Fosalba, M., Mauri, A., 2001. Introducción y colonización de  
22 plantas alóctonas en un área mediterránea: evidencias históricas y análisis cuantitativo.  
23 *Orsis* 16, 145-185.
- 24  
25 Hasey J. & Salmon, T.P., 1993. Crow damage to almonds increasing; no foolproof solution in  
26 sight. *California Agriculture* Sept-Oct 1993, 21-23.
- 27  
28 Kester, D.E., Gradiziel, T.M., Grasselly, C., 1991. Almonds (*Prunus*). *Acta Horticulturae* 290,  
29 701-758.
- 30  
31 Ladizinsky, G., 1999. On the origin of almond. *Genetic Resources and Crop Evolution* 46, 143-  
32 147.
- 33  
34 Loope, L.L., Sanchez, P.G., Tarr, P.W., Loope, W.L., Anderson, R.L., 1988. Biological invasions  
35 of arid land nature reserves. *Biological Conservation, Biological Invasions of Nature*  
36 *Reserves* 44, 95–118.
- 37  
38 Lortie, C.J. & Callaway, R.M., 2006. Re-analysis of meta-analysis: support for the stress-  
39 gradient hypothesis. *Journal of Ecology* 94, 7-16.
- 40  
41 Ministerio de Agricultura, Alimentacion y Medio Ambiente, 2012. Encuesta sobre superficies y  
42 rendimientos de cultivos de España. NIPO: 280-13-016-9.
- 43  
44 Moran, S. & Keidar, H., 1993. Checklist of vertebrate damage to agriculture in Israel. *Crop*  
45 *Protection* 12, 173-182.
- 46  
47 Poyatos, R., Latron, J., Llorens, P., 2003. Land use and land cover change after agricultural  
48 abandonment. *Mountain Research and Development* 23, 362-368.
- 49  
50 Puerta-Piñero, C., Gómez, J.M., Schup, E.W., 2010. Spatial patterns of acorn dispersal by  
51 rodents: do crop size and ungulate presence matter? *Oikos* 119, 179-187.
- 52  
53 Pugnaire, F.I. & Luque, M.T., 2001. Changes in plant interactions along a gradient of  
54 environmental stress. *Oikos* 93, 42-49.
- 55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1 Purves, D.W., Zavala, M.A., Ogle, K., Prieto, F., Rey Benayas, J.M., 2007. Environmental  
2 heterogeneity, bird-mediated directed dispersal, and oak woodland dynamics in  
3 Mediterranean Spain. *Ecological Monographs* 77, 77-97.
- 4 REDIAM (Red de Información Ambiental de Andalucía).Consejería de Medio Ambiente y  
5 Ordenación del Territorio.Descarga de ortofotografías y datos del territorio.  
6 <http://www.juntadeandalucia.es/medioambiente/site/rediam> [Consulta: 11/09/2014 ]  
7
- 8 Reichard, S.H. & White, P., 2001. Horticulture as a pathway of invasive plant introductions in  
9 the United States. *Bioscience* 51, 103-113.
- 10
- 11
- 12 Rejmanek, M. & Randall, J.M., 1994. Invasive alien plants in California: 1993 summary and  
13 comparison with other areas in North America. *Madroño* 41, 161-177.
- 14
- 15 Rejmanek, M. & Richardson, D.M., 1996. What attributes make some plant species more  
16 invasive? *Ecology* 77, 1655-1661.
- 17
- 18 Rejmánek, M. & Richardson, D.M., 2013. Trees and shrubs as invasive alien species - 2013  
19 update of the global database. *Diversity and Distributions* 19,1093-1094.
- 20
- 21 Renwick, A., Jansson, T., Verburg, P.H., Revoredo-Giha, C., Britz, W., Gocht, A., McCracken,  
22 D., 2013. Policy reform and agricultural land abandonment in the EU. *Land Use Policy* 30,  
23 446-457.
- 24
- 25 Richardson D.M. 1998. Forestry trees as invasive aliens. *Conservation Biology* 12, 18-26.
- 26
- 27 Richardson, D.M. & Rejmanek, M., 2011. Trees and shrubs as invasive alien species –a global  
28 review. *Diversity and Distributions* 17, 788-809.
- 29
- 30
- 31 Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J., Rejmánek, M., 2000. Plant  
32 invasions: The role of mutualisms. *Biological Reviews* 75, 65-93.
- 33
- 34 Robert R.C., 1979. The evolution of avian food-storing behaviour. *The American Naturalist* 114,  
35 418-438.
- 36
- 37 Rohrer, J.R., 2012. *Prunus dulcis*, in Jepson Flora Project (eds.) Jepson eFlora,  
38 [http://ucjeps.berkeley.edu/cgi-bin/get\\_IJM.pl?tid=39976](http://ucjeps.berkeley.edu/cgi-bin/get_IJM.pl?tid=39976), accessed on Nov 20 2013.
- 39
- 40
- 41 Schupp, E.W., 2007. Suitable sites for dispersal are context dependent. In: Dennis, A.J., E.W.  
42 Schupp, R.J. Green, and D.A. Westcott, eds., *Seed Dispersal: Theory and Its Application in*  
43 *a Changing World*. CAB International, Wallingford, UK, pp. 445-462.
- 44
- 45 Schupp, E. W., Jordano, P., Gómez, J. M., 2010. Seed dispersal effectiveness revisited: a  
46 conceptual review. *New Phytologist* 188, 333–353
- 47
- 48 Soler, J. J., Soler, M., 1991. Análisis comparado del régimen alimenticio durante el período  
49 otoño-invierno de tres especies de córvidos en un área de simpatria. *Ardeola* 38, 69-89.
- 50
- 51 Stoate, C., Baldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R.,  
52 Rakosy, L., Ramwell, C., 2009. Ecological impact of early 21st century agricultural change  
53 in Europe- A review. *Journal of Environment Management* 91, 22-46.
- 54
- 55
- 56 USDA, 2013. California Almond Forecast. United States Department of Agriculture. National  
57 Agricultural Statistics Service, California Field Office (Mayo 2013)
- 58
- 59 Vander Wall, S.B., 2001. The evolutionary ecology of nut dispersal. *The Botanical Review* 67,  
60 74-117.
- 61
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62  
63  
64  
65

Vander Wall, S.B., 2002. Masting in animal-dispersed pines facilitates seed dispersal. *Ecology* 83(12), 3508-3516.

Vander Wall, S.B. & Longland, W.S., 2004. Diplochory: are two seed dispersers better than one? *Trends in Ecology and Evolution* 19: 155-161.

Verburg, P.H. & Overmars, K.P., 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.

Zohary, D., Hopf, M., Weiss, E., 2012. *Domestication of plants in the Old World*, 4<sup>th</sup> edition. Oxford University Press.

**\*Highlights (for review)**

- *Prunus dulcis* is colonizing abandoned agricultural lands in some semi-arid areas of SE Iberian Peninsula
- Differences in the distribution among life stages were found between the microhabitats and the plots studied.
- Minimal measured dispersal distances suggest the actions of highly mobile almond dispersers (zoochory)
- Tree cover reduced the impact of browsing mammals during the process of naturalization.
- However, the most suitable microhabitat changes through the lifecycle of almond trees.