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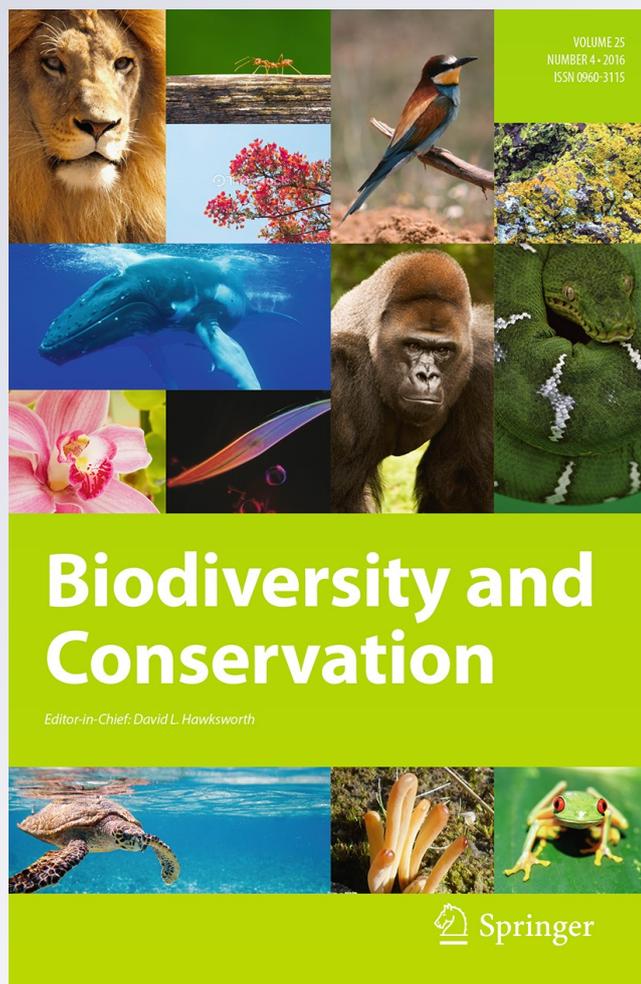
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Habitat loss exacerbates regional extinction risk of the keystone semiarid shrub *Ziziphus lotus* through collapsing the seed dispersal service by foxes (*Vulpes vulpes*)

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Abstract Habitat loss and landscape degradation affect animal-mediated seed dispersal, often collapsing the regeneration of endangered plant species and habitats in anthropogenic landscapes. We first compared the role of red fox and other vertebrates as seed disperser for the keystone scrub *Ziziphus lotus*. Because it turned out that foxes are the major *Z. lotus* dispersers, we investigated how fox activity and dispersal service relate to habitat loss and landscape alteration in the threatened *Ziziphus* semiarid scrublands, a priority habitat for conservation in Europe. Considering its opportunistic behavior, we hypothesized that landscape features should affect moderately fox abundance, while influence in a large extent its dispersal service. Accordingly, we predicted that a substantial decline in *Ziziphus* fruit consumption rather than in disperser activity would be responsible for seed dispersal collapse under severe habitat loss. We evaluated fox activity and dispersal service in 17 populations of *Z. lotus* spread through the range of its habitat in Spain and found within landscapes with different land-use intensity. We certified the collapse of the dispersal service by fox under severe habitat loss and confirmed that fox activity was less affected by habitat loss or landscape alteration than consumption of *Ziziphus* fruits. Consequently, the decline of consumption of *Ziziphus* fruits under severe habitat loss triggers the collapse of its seed dispersal. Results suggest that without increase of the remnant areas other managements may not suffice to achieve seed dispersal and habitat restoring. Dispersal service and natural regeneration in many *Ziziphus* habitat remnants will possibly cease in the future if habitat loss continues.

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Introduction

Alteration of natural landscapes by human land use and concomitant loss of natural habitats (e.g., through farming, urbanization and infrastructures) are among the main drivers of Global Change and the biodiversity crisis (Sala et al. 2000; Fahrig 2003; Lindenmayer and Fischer 2006). Beyond producing direct loss of species, alteration of landscapes and habitat fragmentation also affect critically important ecosystem services (Bianchi et al. 2006; Kremen et al. 2007). One of the typically affected ecosystem services is seed dispersal through mobile organisms (Magrath et al. 2014; Fontúrbel et al. 2015). Many vertebrates act as vehicles for seed dispersal of many plants species through natural and anthropogenic landscapes, but they are sensitive in a variable level to landscape alteration and habitat fragmentation (Cordeiro and Howe 2003; Rodríguez-Cabal et al. 2007; García et al. 2010; Rey and Alcántara 2014). There is growing evidence that present-day landscape features determine not only animal diversity (Fahrig et al. 2011), but also the extent and efficiency of ecological services provided by mobile organisms, such as seed dispersal and pollination (Kremen et al. 2007; Fontúrbel et al. 2015). Moreover, animal-seed dispersal is fundamental for the natural regeneration of plant populations because it often has cascading effects along the regeneration cycle (Jordano and Herrera 1995; Rey and Alcántara 2000). Thus, to assess the potential for natural regeneration and habitat recovery in anthropogenic landscapes it is crucial to evaluate whether landscape transformation might limit or even collapse the seed dispersal service provided by vertebrates (Traveset et al. 2012; Rey and Alcántara 2014), and the extent to which vertebrate seed-dispersers play a role as ‘restorers’ in anthropogenic landscapes (Swift et al. 2004; Matías et al. 2010; Suárez-Esteban et al. 2013; Escribano-Ávila et al. 2014).

Mediterranean ecosystems have a long history of human disturbance which has resulted in very diverse stages of landscape and habitat degradation (Valladares et al. 2004). The effects of anthropogenic landscape disturbance and habitat fragmentation on seed dispersal have been studied in mesic Mediterranean woodlands (for example, Santos et al. 1999) and termo-mediterranean scrublands (Traveset et al. 2012; González-Varo et al. 2012; Rey and Alcántara 2014). However, there is no information on the disruption by human alteration of the vertebrate-seed dispersal service in Mediterranean semiarid habitats, despite many semiarid areas have been heavily impacted by changes in human land-use in the last decades (green-house agriculture intensification and urbanization, e.g., Mota et al. 1996). This is the case of the “Mediterranean arborescent matorral with *Ziziphus lotus*” (*Ziziphus* habitat hereafter), a singular habitat type from southeastern Iberian Peninsula, which is a priority habitat protected under European Directive 92/43/EEC (Benito et al. 2009; Mendoza-Fernández et al. 2015). This habitat has a high ecological and biogeographical value due to its rich endemic flora and its links with North African ecosystems. *Ziziphus lotus* (Rhamnaceae) is the keystone species in this habitat where it facilitates the growth of many other plant species and serves as refuge for many birds and mammals (Tirado 2009). Seed dispersal under field conditions has not been previously quantified in *Z. lotus* although its seeds are easily visible in scats of some carnivores (authors, personal observation), especially in Red fox’s (*Vulpes vulpes*), but also in European badger’s (*Meles*

meles), Stone marten's (*Martes foina*), and some ungulates (Wild boar, *Sus scrofa*). Other carnivores, primates and cattle are known to disperse other *Ziziphus* species (Zhang and Wang 1995; Grice 1996; Varela and Bucher 2006).

Large-sized carnivores are top predators commonly considered to be sensitive to habitat loss and fragmentation because of their large spatial requirements, low reproductive rate, and human persecution (Woodroffe 2000; Gittleman et al. 2001). However, there is ample evidence that some small and medium-sized carnivores (for example, many canid and mustelids), like the red fox, are able to adapt to human-modified and fragmented habitats (Contesse et al. 2004; Baker and Harris 2007; Salek et al. 2014), being able to live in deforested agricultural environments with small remnants of natural habitats (Fedriani et al. 2001; Virgós et al. 2002). In particular, the adaptability of red fox to anthropogenic landscapes is based on its high plasticity and opportunistic behavior (Lovari et al. 1996; Contesse et al. 2004). Red fox frequently feeds also on cultivated and wild fruits and has been described as seed disperser of many fruit species in the Mediterranean region (Rosalino and Santos-Reis 2009; Fedriani and Wiegand 2014).

As part of ongoing research on the potential for natural regeneration and recovery of the *Ziziphus* habitat, we show that red fox is the major seed disperser for *Z. louts* and investigate how red fox's activity and dispersal service to *Z. lotus* relate to habitat loss and landscape alteration throughout the plant's distribution range in the Iberian Peninsula. Our working hypothesis is that provided the red fox opportunism, landscape alteration and habitat loss (that is, present-day landscape features) should affect only moderately its abundance and activity, whereas its seed dispersal service for *Z. lotus* should be affected in a higher extent by landscape features. Under such hypothesis we predict that the role of red fox as *Z. lotus* seed-disperser would be proportional to the *Ziziphus* natural habitat cover remaining in the landscape, collapsing where natural habitat became relict. Accordingly, a substantial decline in *Ziziphus* fruit consumption by red fox rather than in disperser abundance would be triggering *Z. lotus* seed dispersal collapse under severe habitat loss conditions.

Materials and methods

Species and study system

The focus of our study is the "Mediterranean arborescent matorral with *Z. lotus*" (habitat 5220 in Annex 1 of the European Union's Habitats Directive 92/43/EEC). This habitat is dominated by *Z. lotus*, accompanied by open pre-desertic scrubs like *Periploca laevigata*, *Lycium intricatum*, *Asparagus stipularis*, *A. albus*, *Maytenus senegalensis* and *Whitania frutescens*. In Europe, this habitat is restricted to semiarid areas in the southeast of the Iberian Peninsula, where it should occupy most of the plains and seasonal streams (namely 'ramblas') in the coastal belt of the region. However, this original area of distribution has been reduced and fragmented by intensive greenhouse-based agriculture and urban expansion in the last 55 years (Mota et al. 1996). In many sites less than 5 % of the area occupied in the 50 s is left, which has led to a dramatic situation for conservation of this type of habitat.

Ziziphus lotus is a North African taxon distributed across Northern Africa, Sahara desert and Arabian Peninsula. In Europe, it only occurs in Spain and Sicily. *Ziziphus lotus* is a keystone and ecosystem engineering species because provides shelter for vertebrates,

facilitates the growth of many plant species, and its potent radicular system creates islands of soil fertility and influences the hydraulic properties of the habitat (Tirado 2009). Currently *Z. lotus* populations suffer a collapse in natural regeneration, with low density and establishment of seedlings (PJ Rey et al. unpublished), persisting mainly thanks to its sprouting ability. *Ziziphus lotus* produces globular brown-reddish drupes of 9–12 mm diameter, each containing two seeds enclosed within a hard endocarp (stone). Hereafter we will use the term seed in reference to the whole dispersal unit formed by the two seeds and the stone. Fructification occurs between July and early August when fruits are ripe and available for consuming. To our knowledge there is no previous published information on seed dispersal of *Z. lotus*, but based on our surveys of vertebrate scats (carnivores, wild ungulates and lizards) in *Ziziphus* habitat remnants, red fox acts as major seed disperser in the region (see “Results”). Furthermore, although we cannot rule out a role of medium-sized birds (thrushes, pigeons or starlings) in seed dispersal of *Z. lotus*, we have not detected seeds offside cover of conspecifics that could be attributable to birds (PJ Rey et al. unpublished).

Study area

This study was conducted in 17 *Z. lotus* populations localized in *Ziziphus* habitat remnants covering much of the original range of the habitat in the Iberian Peninsula. Most populations were more than 1 km apart from each other, spanning a total of 140 km (Fig. 1). Further details of each population are shown in Table 1.

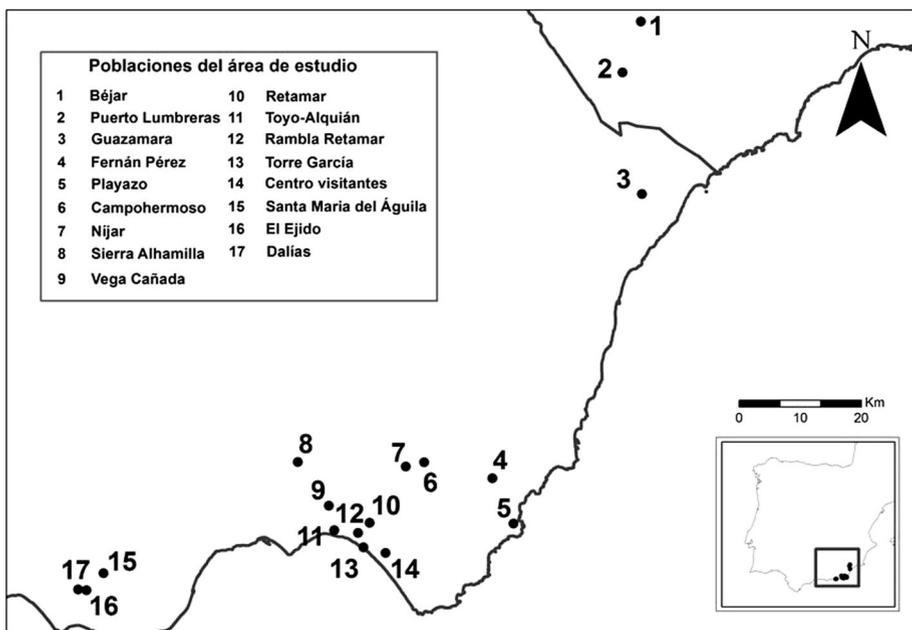


Fig. 1 Study populations in southeastern Spain

Table 1 Study populations and landscape characterization

Population	Coordinates UTM (X)	Coordinates UTM (Y)	Landscape type	Population size (No. of adults)	% of natural or seminatural habitat	Total number of red fox scats collected	Track length (km)	No. of years of sampling
Béjar	608753	4162689	Relict	89	5.72	29	1.479	3
Campohermoso	573207	4089516	Fragmented	20	25.69	9	0.694	2
Ctro. de Visitantes	566902	4074470	Variegated	1367	92.57	31	1.600	3
Dalías	516503	4068393	Relict	15	7.29	0	0.664	3
El Ejido	517838	4068287	Relict	64	8.74	9	1.185	3
Fernán-Pérez	584412	4086871	Fragmented	80	15.90	24	2.473	1
Guazamara	608941	4134043	Fragmented	81	31.89	40	1.999	3
Níjar	570227	4088796	Fragmented	255	40.37	60	2.728	3
Playazo	587885	4079328	Fragmented	101	10.93	87	4.248	3
Puerto Lumbresas	605781	4154249	Fragmented	102	27.10	117	0.838	3
Rambla Retamar	562378	4077811	Fragmented	68	56.91	2	3.829	1
Retamar	564303	4079496	Variegated	80	83.36	20	1.272	2
S. Alhambilla	552531	4089557	Variegated	133	80.62	101	1.817	3
Sta. María Aguila	520643	4071120	Relict	109	6.42	0	1.212	1
Torre García	563288	4075416	Variegated	4598	64.76	45	2.132	3
Toyo-Alquián	558505	4078249	Fragmented	1015	41.71	13	1.183	3
Vega Cañada	557620	4082307	Fragmented	9	22.06	2	0.645	2

Sampling effort in each population and percentage cover of natural or seminatural habitat is also given. See methods for details on landscape characterization (following McIntire and Hobbs 1999) and quantification of percentage cover of natural and seminatural habitat

Collection and analyses of feces and the standardized index of red fox activity

During three consecutive years (2012–2014) we surveyed transects in 17 populations of *Z. lotus* for red fox and other vertebrates scats collection. Transects were surveyed monthly along the period of *Ziziphus* ripe fruit availability on the ground (August–March). The transect at each population was conducted by two observers, its length in each population varied according to the area occupied by the population (Table 1) and the scats were recorded in a 6 m-width band. Each scat was identified according to size, shape, color and smell combination (see Fedriani et al. 2010; López-Bao and González-Varo 2011). From these data we obtained an index of red fox and other vertebrates activity in each population. Specifically, we calculated the number feces collected in each population each year per km of transect (IKA hereafter) and averaged it across years. In the particular case of red fox, this value is finally used here as a Standardized Index of red fox activity in each population (e.g. Cavallini 1994). Although not free of problems, scats density or abundance have been reputedly considered as an efficient and inexpensive method to evaluate the relative abundance and activity of canids, and is commonly used with red fox (for example, Cavallini 1994; Webbon et al. 2004).

For analyses of scats content, samples were broken up in the lab to disaggregate all components and remove all seeds. We counted all seeds found in feces. Because our focus here is on how landscape transformation and habitat loss affect the seed dispersal service for *Ziziphus* we paid attention to *Z. lotus* seeds occurrence and number of seeds in each scat. Variation in the whole diet and its relationship to landscape features will be considered elsewhere.

Frequency of *Ziziphus* seed occurrence and seed mobility index (SMI)

We obtained for each population the frequency of *Z. lotus* seeds occurrence in red fox scats (OF) and the average number of *Z. lotus* seeds in feces with seeds (NS). The first was used as an estimator of the relative frequency of red fox fruit consumption in the population. NS assesses both intensity of consumption and seed clumping. An especially important composite variable that integrates the contribution of red fox to *Z. lotus* seed dispersal is the seed mobility index (SMI): $SMI = IKA \times OF \times NS$.

SMI evaluates the amount of *Ziziphus* seeds mobilized from the source plants by red fox in a population as a consequence of fox abundance or activity (IKA), and frequency and intensity of *Ziziphus* fruit consumption. We should note that the soundness of using this approach relies in the assumption that fox scat detectability is similar across study sites.

To weight the role of red fox as seed disperser for *Z. lotus* in relation to other vertebrates, we also estimated the product of $IKA \times OF$ for other vertebrate scats (Stone marten, European badger, Common genet, Wild boars and *Lacerta lepida*) collected in our surveys. The product of these two components of the dispersal service comparatively assesses the mobilization of *Z. lotus* seeds by different vertebrates to different points within the habitat remnants.

Seed viability and germination tests

We assessed the viability of seeds defecated by red fox through flotation. We collected 356 ripe *Z. lotus* fruits from at least five different adults in 9 populations and 95 seeds from red fox feces. Floating seeds were assumed to be non-viable. To corroborate the reliability of

the floating test we also tested 10 non-floating and 10 floating seeds for viability using tetrazolium chloride (ISTA 1999), which is considered a more reliable viability test. Seeds were cut in half along the longitudinal axis to expose the embryo, and then submerged during 4 h in a 0.5 % tetrazolium chloride solution in a 0.1 M phosphate buffer. We also subjected soy and pea seeds to the staining solution as a positive control. The embryo was classified as either viable (pink/red) or dead (white embryo). All non-floating seeds became stained, denoting viability, while no floating seed yielded positive results in this test. All remaining undispersed *Z. lotus* seeds (322 seeds; range 18–65 depending on population) and 21 defecated seeds were sown in pots under common garden conditions and checked for germination during one year.

Landscape type characterization

We characterized landscape type following the classification of McIntire and Hobbs (1999) for fragmented landscapes. This classification is based on the representation of natural or seminatural habitats in the landscape and defines 4 types of landscapes according to their continuity and level of alteration: (1) relict (natural or seminatural habitat represents <10 % in the landscape), (2) fragmented (10–60 %), (3) variegated (60–90 %) and (4) continuous or intact (>90 %). Our ascription of each population to a particular landscape type was based on the cover currently represented by natural or seminatural states of this habitat relative to other land uses surrounding the focal population. More specifically, we (geo)located with GPS all adult individuals in each population and then defined the population area as the convex hull encapsulating all the individuals of each population. We used a 1.5 km radius circle centered on the centroid of this hull as the unit to evaluate habitat and land use cover in the landscape. For this evaluation we used the land-use and vegetation cover cartography 2006 (1:10.000) of Junta de Andalucía (<http://www.juntadeandalucia.es/medioambiente/site/rediam>) for 15 Andalusian populations and CORINE Land Cover 2006 (<http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster#tab-additional-information>) (1:100.000, 100 meters resolution) for 2 Murcian populations. In order to classify land-use cover within our 1.5 km radius circles, we considered natural or seminatural states of the habitat those land-uses corresponding to “ramblas” and natural scrublands (dense or disperse) in relatively flat areas or smooth hillsides, which are typical habitat requirements for *Z. lotus*. Land-use cartography was cross-checked based on our field knowledge of each population and its surroundings as well as on a close examination of land-use polygons using orto-photographs from year 2013. The percentage cover of the natural and seminatural habitat together with its corresponding habitat use is given in Table 1. Land-use may be found in Online Resource 1, Table A1. We further obtained an index of diversity of cover use (Shannon index) as a measure of landscape complexity or compositional heterogeneity (Fahrig et al. 2011) based on proportion cover of each use. Finally, we also considered the population size (total number of adults *Z. lotus* in the area covered by the population).

Statistical analyses

Variation in SMI and its components between landscape types was analyzed using General Linear Models. Prior to analyses, we log transformed SMI, IKA, and mean NS, and applied angular transformation to OF. Likewise, we analyzed the relationships between SMI components and landscape and population features (population size log transformed for accounting for large between population differences). Separate linear and quadratic

Table 2 Abundance of scats (number of scats per km and study year) of red fox and other vertebrates detected in our surveys averaged across *Z. lotus* habitat remnants (range between populations is shown within parentheses)

	<i>Vulpes vulpes</i>	<i>Canis foena</i>	<i>Meles meles</i>	<i>Genetta genetta</i>	<i>Sus scrofa</i>	<i>Lacerta lepida</i>
Abundance of scats per km of track (IKA)	8.91 (0.00–46.54)	0.25 (0.00–1.48)	0.03 (0.00–0.21)	0.0035 (0.00–0.06)	0.86 (0.00–5.07)	0.87 (0.00–7.59)
<i>Z. lotus</i> seed occurrence in scats (OF)	57/583	2/26	2/4	0/1	9/83	1/70
IKA x OF	0.871	0.023	0.015	0.000	0.093	0.012

It is also shown *Z. lotus* seed occurrence (referred to all scats found across populations) in scats of each vertebrate species and the product of these two components of the dispersal service. Such a product comparatively represents the weight of each disperser in the mobilization of *Z. lotus* seeds to distinct points in the habitat remnants. Normalized to sum 1 across vertebrate species, such product shows that a single species (*V. vulpes*) was responsible for the mobilization of 87 % of seeds to distinct points in the remnants

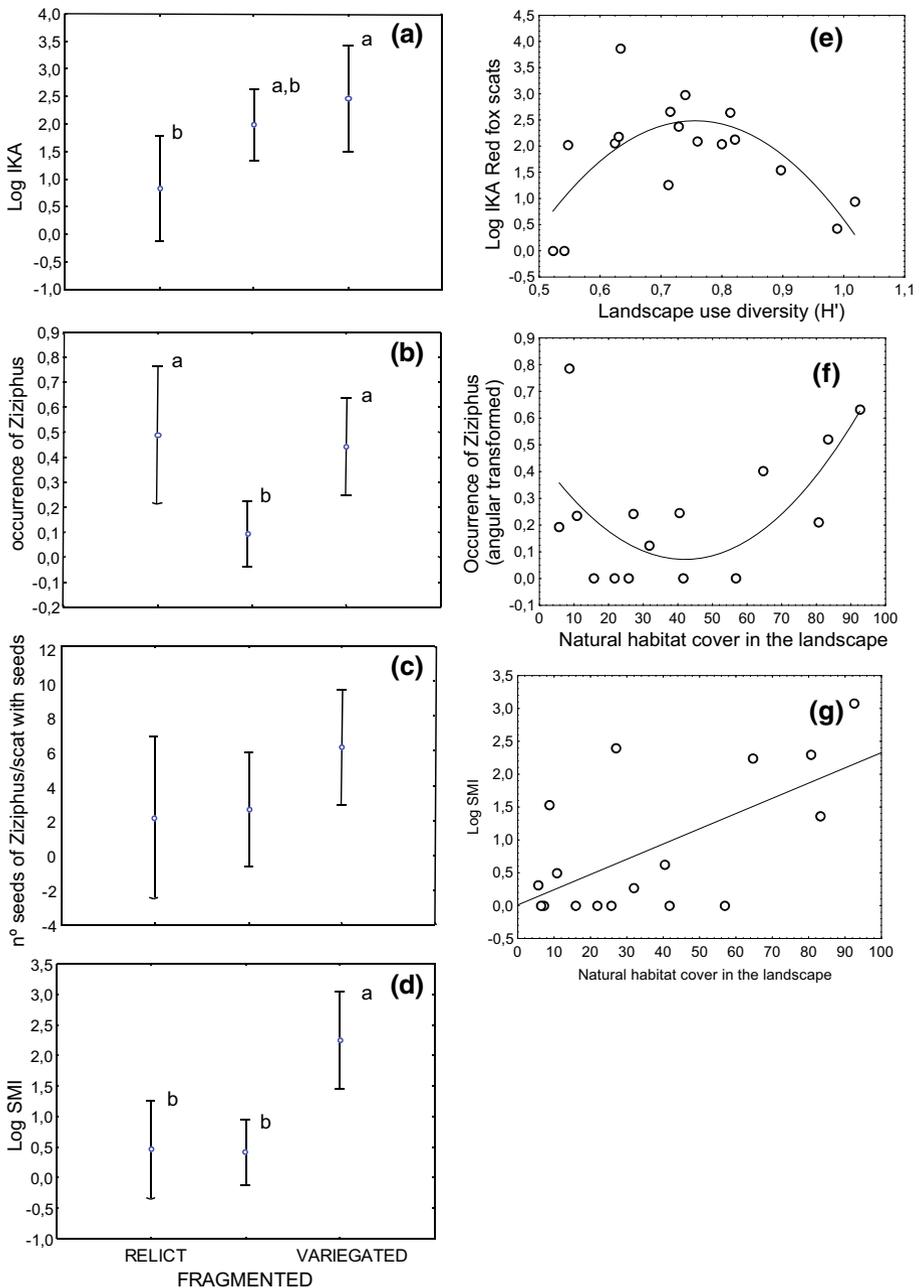


Fig. 2 Left panels: variation in SMI by red fox (d) and its components IKA (a), frequency of occurrence of *Ziziphus* seeds in feces (b), and number of *Ziziphus* seeds in samples with *Ziziphus* (c), according to landscape types. Predicted least-squares means \pm 95 % confidence intervals are shown, identifying Tukey's post hoc differences with different letters. Right-hand panels (e–g) shows the detected significant relationships of SMI and its components to landscape features and rabbit abundance

regression models were conducted for each predictor and dependent variable. We did not try fitting multiple regressions due to sample size limitations.

We compared the viability and germination rates of defecated and intact seeds between populations. We included a factor identifying defecated/intact seeds nested within population and used contrast tests to explore whether germination rates were higher for defecated compared to intact seeds. Generalized Linear Models with binomial error and logit link function were considered for these analyses. Otherwise stated, least-square adjusted means ± 1 SE are shown in results.

Results

We collected a total of 590 scats of red fox during 3 study years. In two populations, Dalías and Sta. María del Águila, no sample was ever collected in the surveys, thereby these populations were only used for estimation of IKA and SMI (i.e., 0 in both cases). *Ziziphus* fruit remains and seeds occurred in 57 out of 583 scats (range among populations 0–34.8 % of scats), lacking in scats from 5 populations.

We further collected scats of other vertebrates in the same surveys, but they were at least tenfold less abundant than red fox's scats (Table 2) in the habitats remnants through the whole study region. In particular, European badger and Common genet were extremely rare in the habitat remnants, while *Z. lotus* seed dispersal by *Lacerta lepida* was very infrequent (Table 2). The product of IKA \times OF for each vertebrate indicates that red fox accounts for 87 % of *Z. lotus* seed dispersal to distinct points within the habitat remnants (Table 2).

Variation in seed dispersal service by red fox and its components

Red fox activity in *Ziziphus* habitats estimated as standardized feces abundance (IKA), varied significantly according to landscape type ($F_{2,14} = 3.69$, $P = 0.05$) with mean IKA tending to be lower in relict than in variegated landscapes (Fig. 2a). In particular, we did not find any red fox fecal samples in tracks conducted in two relict populations located on relict landscapes (Dalías and Sta. María del Águila). However, red fox IKA did not relate significantly to *Ziziphus* habitat cover in the landscape ($F_{1,15} = 2.30$, $P = 0.15$ in linear regression; $F_{2,14} = 1.20$, $P = 0.33$, in the test of the whole quadratic model). In contrast, red fox IKA was related to land-use diversity, describing a non-linear relationship (quadratic regression: $F_{2,14} = 7.15$, $P = 0.007$, $R^2 = 0.51$, Fig. 2e), peaking at landscapes with intermediate values of land-use diversity. Red fox IKA did not relate significantly to *Z. lotus* population size ($F_{1,15} = 1.44$, $P = 0.25$, in linear regression; $F_{2,14} = 1.17$, $P = 0.34$, in the test of the whole quadratic model).

Occurrence of *Ziziphus* (OF) in excrements varied significantly among landscape types ($F_{2,12} = 7.50$, $P = 0.008$), with fragmented landscape showing significantly lower OF in the diet than both variegated and relict landscapes, which did not differ from each other (Fig. 2b). Accordingly, OF did not relate linearly ($F_{1,13} = 1.31$, $P = 0.27$) but kept an U-shaped relationship with natural habitat cover (Fig. 2f) in the landscape (whole model test of the quadratic regression: $F_{2,12} = 4.39$, $P = 0.037$, $R^2 = 0.42$), showing a minimum at intermediate values. It tended also to decrease linearly with landscape land-use diversity ($b = -0.93 \pm 0.45$, $t = -2.41$, $P = 0.06$). OF did not relate to *Z. lotus* population size ($F_{1,13} = 0.78$, $P = 0.20$, in linear regression; $F_{2,12} = 0.93$, $P = 0.42$, in the whole quadratic model).

NS, the last component of the SMI, did not vary among landscape types ($F_{2,7} = 2.19$, $P = 0.18$, seven populations lacking fecal samples with *Ziziphus* were excluded from these analyses) because there was a notable variation within each landscape type (Fig. 2c). No significant linear ($F_{1,8} = 3.17$, $P = 0.11$) or quadratic relationship ($F_{2,7} = 1.60$, $P = 0.27$) was detected between NS and the percentage cover of natural habitat in the landscape, the land-use diversity (linear: $F_{1,8} = 1.26$, $P = 0.29$; quadratic: $F_{2,7} = 1.42$, $P = 0.30$), or the population size of *Z. lotus* (linear: $F_{1,8} = 1.98$, $P = 0.20$; quadratic: $F_{2,7} = 0.87$, $P = 0.46$).

Finally, SMI varied largely between landscape types ($F_{2,14} = 8.91$, $P = 0.003$). We did not detect seed dispersal service for *Z. lotus* ($SMI = 0$) in 7 populations, due to either lack of red fox activity (2 populations) or to absence of *Z. lotus* seeds in the fecal samples (5 populations). Post-hoc tests clearly showed that SMI was higher in variegated than both in fragmented and relict landscapes, which did not differ from each other. In fact, predicted mean SMI was four to five-fold higher in variegated than in fragmented or relict landscapes (Fig. 2d). While SMI was null in 5 out of 9 populations from fragmented landscapes (in all cases by lack of *Z. lotus* in the fecal samples) and 2 out of 4 populations of relict landscapes (both lacking red fox fecal samples in the tracks), all 4 populations from variegated landscapes have some dispersal service by red fox. This trend was confirmed by the highly significant linear positive relationship of SMI to percentage cover of natural or seminatural habitat ($F_{1,15} = 7.27$, $P = 0.006$, $R^2 = 0.41$, Fig. 2g). However, land-use diversity did not affect dispersal service for *Z. lotus* (linear relationship: $F_{1,15} = 0.52$, $P = 0.58$; quadratic: $F_{2,14} = 3.02$, $P = 0.08$). In contrast to previously found for its components, SMI did relate significantly to *Z. lotus* population size, increasing linearly ($F_{1,15} = 6.38$; $P = 0.023$, $R^2 = 0.25$; $b = 0.37 \pm 0.14$, in linear regression; no significant pattern found in quadratic models, $F_{2,14} = 2.98$, $P = 0.08$), although such a relationship was weak compared to other predictors of SMI (see above).

Viability and germination rates of seeds dispersed by red fox

Seed viability was clearly affected by seed source (tree collected vs. fecal samples; Wald Chi square = 21.12, $df = 1$, $P < 0.0001$). Almost all seeds dispersed by red fox were viable (LS-mean viability = 0.98, $N = 95$), whereas 20 % of seeds from the trees were non-viable (LS-mean viability = 0.82, $N = 356$). Germination rate was variable among populations (Wald Chi square = 50.1, $df = 9$, $P < 0.0001$). Mean seed germination for undispersed seeds ranged between $68.0 \% \pm 0.44$ in Puerto Lumberas and $12.9 \% \pm 0.38$ in Toyo, whereas it was $66.6 \% \pm 0.47$ for dispersed seeds. A contrast test between dispersed and undispersed seeds shows significant difference in seed germination rate (Likelihood ratio Chi square = 4.23, $df = 1$, $P = 0.0396$), indicating that seed pass through the red fox gut affected positively germination.

Discussion

Landscape effects on the red fox seed dispersal service for *Ziziphus lotus*

Studies on the effects of landscape degradation and habitat fragmentation on animal-mediated seed dispersal have rendered disparate results. While many case studies and a meta-analytical review (Magrath et al. 2014) showed negative effects on animal-mediated

seed dispersal (Santos and Tellería 1994; Rodríguez-Cabal et al. 2007, Cordeiro et al. 2009) other meta-analytical approaches (Markl et al. 2012) did not show effect of fragmentation but effects of other disturbances as logging and hunting. Other recent meta-analytical review by Fontúrbel et al. (2015) found that habitat degradation has overall a negative effect on seed-disperser animal diversity, whereas habitat fragmentation negatively affects interaction rates. They specifically conclude that while mammal diversity does not seem to be affected by landscape degradation, seed dispersal rates were negatively affected. We do not explore here how the diversity of vertebrate seed dispersers was affected by landscape degradation and habitat loss, though our data on activity of other vertebrates and *Z. lotus* seeds OF in their scats clearly reflect the over-dominance of red fox in *Z. lotus* seed dispersal. In fact, comparison of the product of IKA \times OF for each vertebrate (Table 2) renders that red fox is responsible for the mobilization of ca. 90 % of seeds that are dispersed to distinct points in the *Z. lotus* habitat remnants. Thus *Z. lotus* seed dispersal would be clearly compromised by those factors affecting the interaction rate with red fox.

We asked how landscape degradation and habitat loss could affect *Ziziphus* seed dispersal service by red fox, and predicted that dispersal service would be proportional to *Ziziphus* habitat cover remaining in the landscape, collapsing where this habitat became relict. We confirmed this prediction since we detected a highly significant and positive linear relationship between the *Ziziphus* seed mobility index (SMI) and natural habitat cover in the landscape, and a collapse of seed dispersal by red fox in some relict landscapes, achieving its regional maximum in quasi-continuous *Ziziphus* habitat landscapes (over 90 % cover). Collapse of seed dispersal has been found under strong habitat loss and fragmentation in other species both for seeds dispersed by mammals and by birds (Santos et al. 1999; Cordeiro and Howe 2003; Rodríguez-Cabal et al. 2007). In fact, only this variable explained more than 40 % of variation in SMI in our study. This, along with the finding that SMI did not relate to landscape heterogeneity (i.e. to land-use diversity) and only related weakly to *Z. lotus* population size, suggests that habitat loss and fragmentation, rather than changes in other attributes of the landscape associated to degradation, affect *Ziziphus* seed dispersal by red fox. In any case, the complex relationships between landscape features, habitat fragmentation, fruit production and abundance of alternative food resources on the dispersal service of red fox and other vertebrate merit further research.

Studies on seed dispersal effectiveness and dispersal service by frugivores should examine quantitative and qualitative components of dispersal (Schupp et al. 2010), however these components have rarely been examined under scopes of landscape and habitat degradation and/or fragmentation (but see Santos et al. 1999; Rey and Alcántara 2014). Even more scarce are studies examining dispersal effectiveness with carnivore seed dispersal under habitat degradation and loss (Santos et al. 1999; López-Bao and González-Varo 2011). Because of the opportunism and dietary plasticity of red fox (Dell'Arte et al. 2007; Delibes-Mateos et al. 2008; Hartová-Nentvichová et al. 2010; Díaz-Ruiz et al. 2013) and its adaptation to rural and urban habitats (Lovari et al. 1996; Goldyn et al., 2003; Contesse et al. 2004), we expected that the component of the *Z. lotus* dispersal service related to activity (i.e., abundance) of red fox were less affected by severe habitat loss and anthropogenic landscape alteration than components related to the use of *Ziziphus* as food (*Ziziphus* OF in de diet and the NS in feces with seeds). Our results confirm such expectation substantially.

On the one hand, *Ziziphus* habitat cover in the landscape (an inverse measure of habitat loss) did not relate significantly to activity of red fox, while landscape use

diversity did it in a non-linear way, i.e., activity peaking at intermediate values but steadily decreasing in continuous or in very heterogeneous landscapes. Several studies have found that the activities of red fox and other wild canids are affected by landscape diversity, increasing linearly (Oehler and Litvaitis 1996) or peaking at intermediate levels of agricultural land occurrence (Kurki et al. 1998; Fedriani et al. 1999). The multifunctionality for red fox of intermediate levels of land use diversity probably underlies such a relationship but the exploration of the exact causes shaping the observed activity pattern is beyond the scope of this paper and is dealt elsewhere (I. Cancio et al. unpublished). On the other hand, *Ziziphus* OF in red fox scats varied significantly among landscape types showing a minimum sited through the range of the natural habitat cover at intermediate to low values (significant U-shaped relationship), with red fox consuming frequently *Ziziphus* in more continuous natural landscapes, especially from 60 % cover onwards (Fig. 2f.). Congruently, OF further tended to decrease linearly with land use diversity, since very high diversity emerges from fragmentation and degradation of continuous natural landscapes.

Finally, the last component of the dispersal service here considered, number of seeds deposited in the same scat (NS) is indicative of seed clumping and may be interpreted as inversely related with seed dispersal quality, since just one seedling could eventually become a reproductive adult from such scat. This was the least predictable component of the SMI. Such unpredictability may be caused by the scarce power of our tests since only 10 populations had feces with *Ziziphus* seeds. In any case it may be concluded that this component of the seed dispersal service did not shape the detected relationship of SMI to habitat cover since it neither varied among landscape types nor was related to habitat cover or land-use diversity.

Our results suggest thus that the decline in the frequency of use of *Ziziphus* fruits rather than the abundance and activity of the red fox in remnants of this habitat is responsible of a marked decline in dispersal service of *Ziziphus* associated to habitat loss.

Viability and germination rates of *Z. lotus* seeds processed in red fox gut

A better understanding of the quality of seed dispersal service by vertebrates requires knowledge on the effects of seed processing in vertebrate gut. The benefits of seed processing in the guts of foxes have been investigated in terms of viability and germination of seeds and subsequent seedling survival. Results were inconsistent among seed species (Varela and Bucher 2006; Silva et al. 2005; Fedriani and Delibes 2009; Rosalino et al. 2010) with some species enhancing their germination and/or survival of seedlings while other experiencing neutral or prejudicial effects. We found that *Ziziphus* seeds processed in the red fox gut had enhanced viability and germination compared to seeds taken directly from trees, something also found for other Mediterranean species like *Celtis australis* (Traba et al. 2006) or *Pyrus bourgaena* (Rosalino et al. 2010). Likewise, enhanced germination after processing in the gut of carnivores has been reported in other species of *Ziziphus* (Varela and Bucher 2006; Maraghini et al. 2010), which is probably related to the need of scarification of their thick stony endocarp. The majority of red fox scats with *Ziziphus* seeds were found in open interspaces (81.6 %). Since *Ziziphus* species need direct solar exposition for seedling establishment (Varela 2004), red fox acts as an efficient disperser for this species because it moves seeds away from parent plants to potentially safe microsites favorable for establishment, although further seedling recruitment studies are needed to confirm this suggestion.

Implications for regeneration and conservation of *Ziziphus* scrubland habitats

Knowledge about seed dispersal service is important for evaluating the state of the plant regeneration and has potential for management, conservation and restoration (Matías et al. 2010; Rey and Alcántara 2014; Escribano-Ávila et al. 2014). In the case of *Z. lotus* there was virtually no information about seed dispersal. We have shown in this paper that red fox is the major fruit consumer and seed disperser of this species. Much of the *Ziziphus* seed dispersal in the semiarid *Ziziphus* scrublands habitats of southeastern Iberian Peninsula seems to depend on red fox, because it is largely the most abundant of its dispersers, consume its fruits frequently and is an efficient seed disperser that enhances germination of the seeds.

Some findings of this study provide insights on how habitat loss and landscape alteration are heavily affecting the potential as 'restorer' of red fox through disruption of its seed dispersal service. We have shown that drastic habitat alteration, fragmentation and loss of the *Ziziphus* scrubland habitats dramatically diminish the seed dispersal service (estimated as SMI) and some of its components, frequently causing collapse. Our results suggest that the decay of the use of *Ziziphus* as food under severe habitat loss (a measure of interaction rate) rather than abundance of red fox would be triggering the collapse of seed dispersal service in this species under severe habitat loss. These results have important implications for understanding the potential for natural regeneration and recovery of *Ziziphus* scrubland habitat. Despite red fox is considered a generalist and opportunistic species able to inhabit anthropogenic landscapes, we found that in 7 out of the 17 studied *Ziziphus* populations the dispersal service collapse (i.e. it was null or undetectable through three study years), either by no activity of red fox in the habitat remnants (2 populations in relict landscapes) or by lack of *Ziziphus* fruit consumption (5 populations in fragmented landscapes). Moreover, the fact that a single variable, *Ziziphus* habitat cover in the landscape, explained more than 40 % of the dispersal service should alert us on the exacerbated risk of collapse of the dispersal service and natural regeneration of the species in other remnants in the future, provided that the loss of this habitat is still ongoing in the region. The risk of extinction of the seed dispersal interaction, and of its ecological function, clearly exists and could be preceding the regional species loss (Valiente-Banuet et al. 2015). Our results further warn about the difficulty of natural recovery of this habitat, even when active management is dedicated to improve the state of the habitat remnants, if we do not increase the cover of the habitat in the landscape to attract dispersers and increase its interaction with *Ziziphus*. *Z. lotus* is considered a keystone species in this ecosystem, providing food and shelter for many animals, constituting fertility islands for the establishment of many other species and regulating its hydraulic function (Tirado 2009). Consequently, the collapse of its seed dispersal and recruitment may have disproportionate cascading effects on species diversity maintenance and community dynamics, as well as in the function and services (Maestre et al. 2012) of this singular semiarid ecosystem.

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