

Landscape degradation affects red fox (*Vulpes vulpes*) diet and its ecosystem services in the threatened *Ziziphus lotus* scrubland habitats of semiarid Spain



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ABSTRACT

Habitat loss and landscape degradation affect carnivorous mammal populations and the ecosystem services they provide, but these services are poorly assessed in semi-arid ecosystems. In the *Ziziphus* semiarid scrublands, a priority habitat for conservation in Europe, we investigated how red fox diet relates to habitat loss and landscape alteration. We further evaluated potential top-down effects of foxes on vegetation through seed dispersal and the control of rabbit herbivory (fruit depulption interfering seed dispersal). By sampling fox scats, we evaluated the variation in fox diet and its relationship to landscape features and rabbit abundance and activity in 17 habitat remnants distributed throughout the *Ziziphus* habitat range. Fox diet varied, with diet diversity peaking at intermediate land-use diversity, likely as a consequence of fox's ability to use natural foods and human-derived resources. We confirmed that red fox acts as seed disperser for many species and that it might contribute to control rabbit population and its impact on *Ziziphus lotus* regeneration by interference on seed dispersal, though this needs experimental corroboration. However, these services were affected by landscape degradation. Our results show that red fox is fundamental for *Ziziphus* semiarid ecosystem providing key ecosystem services which are presently jeopardized by strong landscape degradation.

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1. Introduction

Habitat loss and alteration of natural landscapes through farming, urbanization or infrastructures among others, are major drivers of Global Change and the Biodiversity Crisis (Sala et al., 2000; Foley et al., 2005). Large and medium-sized mammals are among the most susceptible animals to land use change (Luck, 2007). In particular, carnivorous mammals are commonly considered to be sensitive to habitat loss, fragmentation and landscape degradation because of their large spatial requirements, low reproduction rate, hunting and/or human persecution (Woodroffe, 2000; Virgós et al., 2002). They are further facing declines in their prey populations in many areas caused by human land use. Knowledge on abundance, activity and diet of carnivores in human-modified landscapes is important because they provide key ecosystem services such as herbivore prey population regulation

(Ripple and Beschta, 2012), long distance seed dispersal (Jordano et al., 2007; Suárez-Esteban et al., 2013), landscape connectivity and plant recovery after land abandonment (Escribano-Ávila et al., 2014).

Although carnivores are sensible to landscape degradation, some, like the red fox (*Vulpes vulpes*), can adapt to human-modified and fragmented habitats (Contesse et al., 2004; Salek et al., 2015), being able to live in deforested agricultural environments with small remnants of forests, woodlands or scrublands (Fedriani et al., 2001; Virgós et al., 2002). The adaptability of red fox to anthropogenic landscapes relies on its high diet plasticity and opportunistic behavior (Díaz-Ruiz et al., 2013). These characteristics are important because agricultural and urban habitats often provide high quantity of food resources and favorable cost-benefit ratio of searching for food (Contesse et al., 2004).

Mediterranean ecosystems have a long history of human disturbance which has resulted in very diverse degrees of landscape and habitat degradation. The effects of anthropogenic landscape disturbance and habitat fragmentation on carnivores have

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been studied in mesic Mediterranean climate (Virgós et al., 2002; Delibes-Mateos et al., 2008). However, information on carnivore abundance and diet in semiarid habitats of the Mediterranean Basin is scarce (but see Rodríguez and Delibes, 1992; Dell'Arte and Leonardi, 2005; Lara-Romero et al., 2012) even though drylands are among the habitats most threatened by Global Change (Foley et al., 2005) and that many semiarid areas have been heavily impacted by changes in human land-use in the last decades (e.g., greenhouse agriculture intensification and urbanization, see Mendoza-Fernández et al., 2015). Moreover, knowledge on the role of carnivores on key ecosystem services as seed dispersal and herbivore pressure regulation in Mediterranean semiarid habitats is virtually lacking (but see Meserve et al., 2016, for north central Chile), especially in which concerns to how these services are affected by habitat loss and landscape degradation.

The “Mediterranean arborescent matorral with *Ziziphus lotus*” (*Ziziphus* habitat hereafter), is a singular semiarid habitat from southeastern Iberian Peninsula, declared a priority habitat for conservation by the European Directive 92/43/EEC (Tirado, 2009; Mendoza-Fernández et al., 2015). This habitat has a high ecological and biogeographical value due to its rich endemic xerophyte flora and its links with North African ecosystems. Red fox (*Vulpes vulpes*) is the most abundant carnivore in this habitat and plays a disproportionate role as seed disperser of the keystone species *Z. lotus* in the remnants of this habitat in Europe (Cancio et al., 2016). It has been shown that severe habitat loss is provoking the collapse of the seed dispersal service for this keystone species (Cancio et al., 2016), although no information is available on its effects on seed dispersal at community level or on herbivory pressure control. Here we analyze how red fox's diet in *Ziziphus* habitat remnants relates to habitat loss and landscape alteration throughout the habitat distribution range in the southeastern semiarid part of Iberian Peninsula. We further investigate the potential regulation of rabbit herbivory (by fruit depulping interfering seed dispersal and recruitment) by this carnivore as well as its role as seed disperser at the community level in this habitat. Our working hypothesis states that provided the red fox opportunism, habitat loss and landscape alteration should affect fox diet, which should tailor the availability of food resources. We further predict that seed dispersal and rabbit herbivory control should be seriously affected by landscape degradation and habitat loss because landscape features affect fox activity and diet.

2. Methods

2.1. Study sites

This study was conducted in 17 *Ziziphus* habitat remnants covering much of the original range of the habitat in the Iberian Peninsula. These remnants are found within landscapes with different land-use intensity and most of them were more than 1 km apart from each other, spanning a total of 140 km (see details in Table 1; see Fig. 1 in Cancio et al., 2016, for a map of localization of study sites in southern Iberian Peninsula). The Mediterranean arborescent matorral with *Ziziphus lotus*” (habitat 5220 in Annex 1 of the European Union's Habitats Directive 92/43/EEC) is an habitat 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 basically 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. This original area of distribution has been reduced and fragmented by intensive greenhouse-based agriculture and urban expansion in the last 55 years (Tirado, 2009; Mendoza-Fernández

et al., 2015). In many localities, less than 5% of the original area occupied in the 1950s remains whereas habitat loss is still ongoing (authors personal observation), which has led to a dramatic situation for conservation of this habitat.

2.2. Collection and analyses of feces and the Standardized Index of red fox activity

During three consecutive years (2012–2014) we surveyed transects in the 17 study habitat remnants for red fox scats collection. Transects were centered approximately in the remnant and surveyed monthly along August–March when most fruit species in the habitat bear ripen fruit and when *Z. lotus* fruits are available on the ground for rabbits, red fox and other vertebrates. 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 wide band. The species that defecated each scat was identified according to the size, shape and smell combination (López-Bao and González-Varo, 2011; González-Varo et al., 2015). We cannot rule out the possibility of some miss-classification of faeces since some bias in adjudication of species's scat is commonly reported (Harrington et al., 2010). From these data we obtained an index of red fox activity in each population (Table 1). Specifically, we calculated the number of red fox feces collected in each population each year per km of transect (IKA hereafter) and averaged it across years. 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). Along these transects we also counted the number of rabbit (*Oryctolagus cuniculus*) latrines as an indicator of relative abundance of this prey (Palomares, 2001), which is considered the red fox's preferred prey in the Iberian Peninsula (Díaz-Ruiz et al., 2013).

For analyses of scats content, samples were broken up in the lab to disaggregate all components and remove all seeds. Contents were classified in 6 major fractions: *Z. lotus* fruits, other fruits, other plant material, invertebrates, vertebrates (including rabbit, rodents and other vertebrates) and human-generated garbage material. We counted all seeds found in feces. Percentage volume of each fraction was then estimated visually. We estimated an index of diet diversity (Shannon's H') at habitat-remnant level, based on mean relative abundance of each fraction. Likewise, we separately obtained a fruit diet diversity index for each remnant. Most studies on diet variation of red fox aim to distinguish between vertebrate preys, with especial attention to lagomorphs and rodents (Delibes-Mateos et al., 2008; Díaz-Ruiz et al., 2013). Thus, to analyze red fox diet variation among populations and to relate diet diversity to landscape features and rabbit abundance we first pooled all vertebrates into a single fraction, and additionally explored such relationships for rabbit and rodent volume separately.

2.3. The role of red fox as seed disperser in *Ziziphus* habitat remnants

We evaluated the role of red fox as seed disperser through the product of the red fox IKA and frequency of occurrence (OF), averaged across months and years, of different seed species at each habitat remnant studied (see Cancio et al., 2016, for a similar approach). Such product represents an estimation of the quantitative component of the dispersal service by red fox for each plant species (dispersal service hereafter) in each remnant. We further obtained a community-level seed dispersal service for each

Table 1
Study populations and landscape and remnant size characterization. Sampling effort in each population is also given. Natural habitat cover and land-use diversity are measured from the relative cover of the different land uses in 1.5 km circle around the centroid of the habitat remnant. Habitat remnant area is measured as the area of the convex hull encapsulating all *Ziziphus* adults in the remnant. Details for these estimations are provided in methods along with the characterization of landscape types, that follows McIntire and Hobbs (1999).

Population	Coordinates UTM (X)	Coordinates UTM (Y)	Annual rainfall (mm)	Mean T ^a (° C)	Aridity (GA index)	Landscape type	% of natural habitat	Land-use diversity (Shannon H')	Habitat remnant area (ha)	Track length (km)	N. of years of sampling
Béjar	608753	4162689	320	16.4	0.272	Relict	5.72	0.548	1084.5	1.479	3
Campohermoso	573207	4089516	255	17.4	0.2372	Fragmented	25.69	0.813	7.2	0.694	2
Ctro. de Visitantes ^a	566902	4074470	223	18.1	0.2131	Variegated	92.57	0.716	569.1	1.600	3
Dalías ^a	516503	4068393	253	17.9	0.2344	Relict	7.29	0.541	2.2	0.664	3
El Ejido ^a	517838	4068287	253	17.9	0.2351	Relict	8.74	0.712	37.6	1.185	3
Fernán-Pérez	584412	4086871	265	17.2	0.2448	Fragmented	15.90	0.723	246.9	2.473	1
Guazamara ^a	608941	4134043	268	17.7	0.2323	Fragmented	31.89	0.800	50.4	1.999	3
Níjar ^a	570227	4088796	275	16.9	0.2543	Fragmented	40.37	0.822	354.9	2.728	3
Playazo ^a	587885	4079328	235	18.1	0.2225	Fragmented	10.93	0.625	187.0	4.248	3
Puerto Lumberas	605781	4154249	326	16.2	0.2783	Fragmented	27.10	0.633	2498.8	0.838	3
Rambla Retamar	562378	4077811	224	18	0.2139	Fragmented	56.91	0.990	165.5	3.829	1
Retamar	564303	4079496	233	17.7	0.2214	Variegated	83.36	0.631	188.1	1.272	2
S. Alhamilla	552531	4089557	288	16.5	0.2734	Variegated	80.62	0.741	109.7	1.817	3
Sta. María Águila	520643	4071120	260	17.7	0.237	Relict	6.42	0.523	80.2	1.212	1
Torre García	563288	4075416	221	18.1	0.2114	Variegated	64.76	0.760	710.9	2.132	3
Toyo-Alquián ^a	558505	4078249	219	18.1	0.2114	Fragmented	41.71	0.898	1377.3	1.183	3
Vega Cañada	557620	4082307	246	17.4	0.2322	Fragmented	22.06	1.018	6.5	0.645	2

^a Habitat remnants used in sampling of seed depulping by rabbits.

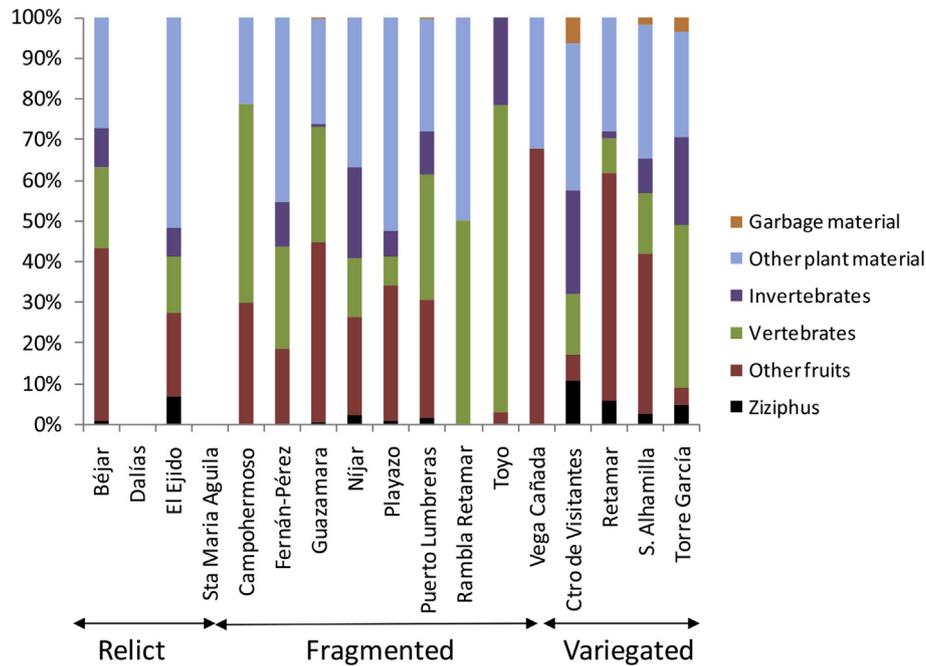


Fig. 1. Red fox diet composition (relative volume of different diet fractions in percentage) in the study populations based on fecal samples. Only major fractions of diet are represented. Note there was no scat in Dalías and Sta. María Águila. The landscape type surrounding each population is also indicated.

remnant as the across-species averaged value of the dispersal service in each remnant. We additionally obtained an average value of dispersal service for each plant species across all study remnants, that we will call the species-specific regional disperser service by red fox. To achieve regional values of red fox dispersal service comparable between seed species, we normalized species-specific values to the highest value obtained for all plant species (that is, the species with maximum dispersal service equals 1 and the other

species are referred to that one). Finally, we compared the list of species being dispersed by red fox with the list of fleshy-fruited plant species registered in remnants of the region (data from Rey et al., 2016).

2.4. Rabbit depulping of *Z. lotus* fruits

Depulping (i.e., in situ consumption of fruit pulp without

apparent seed damage) of *Z. lotus* fruits by rabbits was noticeable in all studied habitat remnants. Provided that depulped seeds remain undispersed and no *Z. lotus* recruit was ever observed under conspecifics (see results), we used such rabbit activity as an indicator of broad-sense rabbit herbivory, which potentially decreases regeneration of the keystone species of this habitat. *Z. lotus* fruit depulping was evaluated during a single year in a subset of 7 habitat remnants (Table 1). During all the fruit fall season (fruits are not bird-dispersed and they simply fall to the ground where they become available for mammals) we estimated the amount of fruit depulped by rabbits under 10 adult fruiting trees haphazardly chosen to cover the whole area of these 7 habitat remnants. We used permanent 50 × 50 cm quadrats to this end and counted monthly from October to March all the depulped and non-depulped fruits present. Then we derived a cumulative percentage of the fruits depulped for the whole season at each remnant and investigated its relationship to rabbit abundance across habitat remnants. We inferred depulping by rabbit based on two evidences. First, while rabbits latrines were abundant near fruit sources, other vertebrates potentially responsible for depulping, mainly rodents, were either scarce (*Elyomys quercinus*, *Rattus norvegicus*, *Mus musculus* and *Mus spretus*; Rey et al., unpublished) or mainly granivorous (*Apodemus sylvaticus*) as to generate the high percentage of depulped fruits detected in all populations (see results); second, photo-traps detected rabbits visiting *Z. lotus* fruit offerings in trays.

We further looked for some indirect evidence to show that fruit depulping by rabbits could be affecting *Z. lotus* population regeneration. First, we used information on *Z. lotus* germination (Cancio et al., 2016, and unpublished) to show decreased seed germination from whole fruits and rabbit-depulped fruits compared seeds defecated by red fox. Second, we surveyed recently emerged seedlings in the same 50 × 50 cm quadrats of fruit depulping estimation (70 quadrats in total) and followed their survivorship. Third, we related rabbit abundance to the total juvenile number and the ratio juvenile/adult in the remnants as indicators of long-term plant population regeneration. For this, we surveyed *Z. lotus* juveniles and adults at each habitat remnant through an exhaustive monitoring of the whole remnant area by 6 observers who walked at regular pace covering each 20 m-width bands between observers.

2.5. Habitat remnant and landscape features characterization

To characterize remnant features (*Z. lotus* habitat remnant area) we (geo)located with GPS all *Z. lotus* adult individuals present in each remnant and then defined the remnant area as the convex hull encapsulating all the *Z. lotus* individuals of each remnant. To characterize landscape features (natural habitat cover and land use diversity), 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. We used for such evaluation data from 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 habitat remnants 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 m resolution) for 2 Murcia habitat remnants. Details on the procedure followed to such characterization may be found in Cancio et al. (2016). We obtained a diversity index of cover use (Shannon index) as a measure of landscape complexity or compositional heterogeneity (Fahrig et al., 2011) based on the proportion cover of each use. We further 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%). The ascription of each remnant 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 it.

We further characterized climate at each habitat remnant in terms of annual rainfall, mean temperature and aridity (GAI) from CGIAR-CSI (<http://www.cgiar-csi.org>) to the resolution of 30 arc seconds (approximately 1 km at the equator).

2.6. Statistical analyses

Variation in red fox diet was tested by compositional analyses using PERMANOVAs conducted on Bray-Curtis pair-wise dissimilarity matrices (Clarke and Gorley, 2006) between fecal samples. We conducted the analysis with the six diet fractions described above. Factors in this analysis were landscape type (relict, fragmented and variegated), considered as a fixed effect, and site-remnant, as random effect nested within the landscape type. Pair-wise comparisons were conducted to identify differences between landscape types. The diet fractions most responsible for significant differences in diet between landscape types were determined by a similarity percentage analysis (SIMPER). To prevent analyses from being influenced by the most abundant diet fractions, the relative percent (volumes) of fractions were fourth-root transformed (Clarke and Warwick, 2001). PERMANOVAs and SIMPER were implemented in PRIMER 6.1.15 with 10000 permutations.

Variation in rabbit abundance between landscape types was examined by fitting General Linear Models (GLM) and using log-transformed data. We further examined with GLM linear and quadratic relationships of red fox and rabbit abundance to remnant area (log-transformed) and landscape features (percentage cover of natural habitat and land-use diversity) and to climate.

Likewise, we used GLM to investigate the relationships of diet diversity (and diet fractions) with landscape features and rabbit abundance. Visual inspection of these relationships by scatterplots showed that some relationships could be non-linear. Therefore, we first conducted quadratic polynomial regression to test the assumption of linearity for each predictor separately. Then, if the quadratic term was significant, such term was kept in a multiple regression that incorporated all simple terms of the predictors plus the quadratic ones probed to indicate non-linearity. The multiple regression for each response variable was fitted with best-model solution procedure and model choice based on Akaike Information Criteria corrected for small sample sizes (AICc). We further used Δ_i AIC (with $\Delta_i = AIC_i - AIC_{min}$) to choice among models that cannot be considered invalid using the cut-off point of $\Delta_i < 2$ (Burnham and Anderson, 2002). Among them, we eventually choose that model with less number of predictors (the most parsimonious one) since the number of cases available strongly recommend caution with the number of predictors incorporated in the model.

To relate community-level dispersal service by red fox with each landscape and remnant features we used also GLM.

Multiple regression was used to evaluate red fox predation pressure on rabbit abundance. In this case, rabbit abundance was the dependent variable while red fox abundance and percentage volume of rabbit in red fox diet were the predictors representing two different components of the predation pressure. Collinearity of these two predictors was tested using variance inflation factor (VIF), and assuming VIF > 2.50 as cutoff point for denoting

collinearity problem. Finally, we examined how rabbit abundance relates to its herbivory pressure through a Spearman correlation between mean number of depulped seeds in the whole season and the rabbit abundance in 7 studied habitat remnants. Spearman rank correlations were also used to relate population regeneration (abundance of juveniles and juvenile/adult ratio) with rabbit abundance.

Previous to these analyses we conducted multiple regression of each major response variable of this study (fox and rabbit abundance and fox's diet and ecosystem services) on geographic (x, y) coordinates (Legendre, 1993). Except for fox abundance, which resulted positively related to longitude, none other significant relationships with geographic coordinates emerged (Table A1.A), so that most patterns described in results are not due to underlying spatial structures.

Because our emphasis here is not on intra-site variability over time but on the variation across sites, we collapsed for all these relationships the intra and inter-annual variability within site into a single average per site in order to scaling up to regional level.

3. Results

We collected a total of 590 excrements of red fox during 3 study years. Seven fecal samples were too deteriorated to make any reliable estimate of diet composition and were not included in the analyses. Red fox activity, as estimated by IKA, considerably varied between populations (range 0–46.5) and increased linearly with the remnant area ($b = 0.27 \pm 0.12$, $t = 2.32$, $P = 0.035$, $R^2 = 0.26$) while decreased with mean temperature ($b = -0.86 \pm 0.22$, $P = 0.028$; $R^2 = 0.23$; see also Table A1.B).

3.1. Variation in diet composition as indicated by fecal samples

PERMANOVA analysis verified that red fox diet varied between landscape types ($Pseudo-F_{2,559} = 2.99$, $P = 0.037$) and sites ($Pseudo-F_{15,559} = 5.03$, $P < 0.001$). In particular, diet composition significantly varied between fragmented and variegated landscapes (pairwise comparison $t = 2.38$, $df = 46.16$, $P = 0.018$, average dissimilarity = 62.8; with other plant material, other fruits and vertebrates contributing more to such dissimilarity, 26.9%, 26.0% and 23.6% of the dissimilarity, respectively) but not between relict and fragmented landscapes ($t = 0.28$, $df = 64.74$, $P = 0.92$, average dissimilarity = 58.9) or between relict and variegated landscapes ($t = 1.14$, $df = 19.53$, $P = 0.31$; average dissimilarity = 61.9). In any case, within-landscape type dissimilarity in red fox diet was rather comparable to between-sites (within landscape) dissimilarity, what is likely a consequence of large between-site variation in diet composition (Fig. 1). Thus, mean dissimilarity among diet samples was 57.7 within relict landscapes, 59.8 within fragmented landscapes, and 65.2 within variegated landscapes.

3.2. Diet diversity in relation to rabbit abundance and landscape features

Diet diversity of red fox in *Ziziphus* scrublands was unrelated to rabbit relative abundance, natural habitat cover in the landscape or habitat remnant area (Table 2). In contrast, the diversity of fractions in the diet was significantly and non-linearly associated to land-use diversity (peaking at intermediate values; Fig. 2a, Table 2). Noticeably, rabbit volume in red fox diet did not show any positive significant relationship with the relative abundance of this prey (Table 2), but it was related non-linearly to land-use diversity, peaking at intermediate values (Fig. 2b). Rodent volume was not significantly predicted by any landscape feature or by rabbit abundance. Finally, fruit diversity in diet was non-linearly related

to habitat remnant area, with consumed fruit diversity peaking at intermediate habitat remnant sizes (Fig. 2c).

3.3. Community and regional-level seed dispersal service by red fox

From our surveys of scats within *Ziziphus* habitat remnants we detected that red fox dispersed seeds of 11 wild fleshy fruit species, an undefined number of grasses, 1 naturalized fruit species and 4 cultivated species (Table 3). Other 4 fleshy-fruited species, characteristic of the flora of this habitat, and commonly present in the remnants (*Lycium intricatum*, *Whitania frutescens*, *Maytenus senegalensis* and *Rhamnus lyciodes*), never appeared in the scats and apparently were not dispersed by red fox in the region. Fruits occurred in 355 out of 583 red fox scats. Fruit occurrence in red fox diet samples did not vary among landscape types ($F_{2,12} = 0.38$, $P = 0.69$, least-square means = 0.557 ± 0.114 in variegated; 0.533 ± 0.085 in fragmented; 0.695 ± 0.153 in relict landscapes). When present, fruits represented a large amount in the diet sample (mean = 54.03%, range: 5–100% of the fecal remains).

The regional dispersal service by red fox for each species was largely variable, as estimated by the normalized index (Table 3). *Ficus carica* and *Z. lotus* achieved the highest dispersal service by red fox, followed by the cultivated palm *Phoenix dactylifera* and the wild palm *Chamaerops humilis*. Many other species were infrequently dispersed, attaining a dispersal service by red fox 2-orders of magnitude lower than that of *F. carica* or *Z. lotus*, being dispersed frequently just in one remnant (Table 3).

Community-level dispersal service by red fox (both for the total fruit species and for native fruit species) considerably varied throughout the region (Table 3) but did not depend of landscape type ($F_{2,14} = 1.28$, $P = 0.31$). This was corroborated by lack of relationships (both linear and quadratic) of seed dispersal service with the percentage of natural habitat cover in the landscape (either based on number of fruit species dispersed or in the community-level dispersal service; $P > 0.05$ in all these models). In contrast, land-use diversity was associated non-linearly to the seed dispersal service by red fox, with peaks at intermediate values of diversity of uses. This is shown by the significant quadratic relationship for the total number of fruits species dispersed (Fig. 3a) and by the marginal quadratic relationship for the community-level dispersal service (Fig. 3b). Finally, habitat remnant area was linked positively to dispersal service, since both the total number of fruit species and the community-level dispersal service for native fruits increased linearly with the increase in the habitat remnant (Fig. 3 c and d, respectively).

3.4. Rabbit population regulation and herbivory pressure control by red fox

Rabbits considerably impacted on the amount of seeds of *Z. lotus* depulped, with means ranging between $37.6 \pm 6.9\%$ of total fruits fallen to the ground in Playazo and $95.2 \pm 2.3\%$ in Dalías, with an average across all remnants of $73.4 \pm 3.3\%$ of the available fruits. Hence, it clearly affected the amount of fruits available for consumption by seed dispersers on the ground. Rabbit abundance, estimated by number of latrines per km and month, considerably varied among habitat remnants (range between 1.37 in Fernán Pérez and 34.59 in Ejido remnants), although such variation was not affected by landscape type ($F_{2,14} = 0.55$, $P = 0.59$; least-square means: Relict = 17.81 ± 5.06 ; Fragmented = 11.89 ± 5.06 ; Variegated = 11.4 ± 5.06). Moreover, variation in rabbit abundance was not related to any landscape feature (natural habitat cover and land use diversity; $P > 0.05$ in linear and quadratic regression models, data not shown), remnant area ($P > 0.05$ in linear and quadratic models) or climate variable ($P > 0.05$ for annual rainfall,

Table 2

Abiotic and biotic effects on red fox's diet diversity and vertebrate prey components of diet (rabbits and rodents). Non-linearity was first tested for each predictor separately using polynomial quadratic regression. Afterwards, quadratic significant terms were incorporated into a multiple regression together with the linear terms of the four predictors. Multiple regressions were solved by best-model selection with model choice based on AICc. Regressions are shown for four response variables: a) diet diversity, b) fruit diversity, c) rabbit volume and d) rodent volume in diet (first row). Predictors were landscape features (NHC = percentage of natural habitat cover; LUD = land-use diversity; Remnant area) and prey abundance (rabbit abundance as latrines/km). Significant effects at $P < 0.05$ are in bold type.

	a) Diet diversity			b) Fruit diversity			c) Rabbit volume			e) Rodent volume		
Quadratic regression testing linearity assumption	b ± 1 S.E	t	P	b ± 1 S.E	t	P	b ± 1 S.E	t	P	b ± 1 S.E	t	P
NHC	−0.007 ± 0.005	−1.50	0.16	−0.005 ± 0.009	−0.49	0.63	0.0043 ± 0.011	0.34	0.74	0.01 ± 0.01	0.93	0.37
NHC ²	0.000 ± 0.000	1.75	0.11	0.000 ± 0.000	0.60	0.57	−0.000 ± 0.000	−0.18	0.86	−0.000 ± 0.000	−1.11	0.29
LUD	3.91 ± 1.73	2.25	0.04	4.10 ± 3.57	1.15	0.28	8.47 ± 4.25	1.99	0.07	7.39 ± 5.17	1.43	0.18
LUD ²	−2.90 ± 1.09	−2.66	0.02	−3.33 ± 2.29	−1.46	0.17	−5.93 ± 2.66	−2.21	0.047	−4.61 ± 3.26	1.42	0.18
Remnant area	0.29 ± 0.28	1.01	0.33	1.24 ± 0.25	4.88	0.0005	−0.10 ± 0.55	−0.18	0.86	−0.12 ± 0.54	−0.22	0.86
Remnant area ²	−0.01 ± 0.01	−0.91	0.38	−0.04 ± 0.01	−4.65	0.0007	0.006 ± 0.020	0.29	0.78	0.01 ± 0.02	0.31	0.76
Rabbit abundance	−0.01 ± 0.01	−1.17	0.27	−0.02 ± 0.02	−1.11	0.29	−0.003 ± 0.022	0.17	0.86	−0.02 ± 0.02	−0.69	0.50
Rabbit ab ²	0.000 ± 0.000	1.24	0.24	0.001 ± 0.001	1.03	0.33	−0.000 ± 0.001	−0.75	0.47	0.000 ± 0.001	0.61	0.56
Best model coefficients	b ± 1 S.E	t	P	b ± 1 S.E	t	P	b ± 1 S.E	t	P	b ± 1 S.E	t	P
NHC	−	−	−	−	−	−	−	−	−	−	−	−
LUD	3.91 ± 1.73	2.25	0.04	−	−	−	8.43 ± 3.71	2.27	0.04	−	−	−
LUD ²	−2.90 ± 1.09	−2.66	0.02	−	−	−	−5.86 ± 2.34	−2.51	0.03	−	−	−
Remnant area	−	−	−	1.24 ± 0.25	4.88	0.0005	−	−	−	0.05 ± 0.04	1.34	0.20
Remnant area ²	−	−	−	−0.04 ± 0.01	−4.65	0.0007	−	−	−	−	−	−
Rabbit abundance	−	−	−	−	−	−	−0.01 ± 0.0049	−2.17	0.052	−	−	−
Best-model fit	Likelihood ratio $\chi^2 = 16.97$, df = 2, P = 0.0002			Likelihood ratio $\chi^2 = 19.98$, df = 2, P = 0.00005			Likelihood ratio $\chi^2 = 14.58$, df = 3, P = 0.002			Likelihood ratio $\chi^2 = 1.94$, df = 1, P = 0.16		
	AICc = −14.42			AICc = −3.59			AICc = 9.14			AICc = 11.25		

mean temperature and aridity, Table A1.B). However, red fox predation pressure seems to affect rabbit abundance as shown by the significant multiple regression of rabbit abundance on fox abundance and volume of rabbit in its diet ($F_{2,12} = 4.57$, $P = 0.03$, $R^2 = 0.43$). This regression reflected that rabbit abundance was strongly negatively influenced by rabbit volume in diet while fox abundance affected it less and positively (standardized partial regression coefficients, $\beta = -1.02 \pm 0.34$, $t = -3.02$, $P = 0.01$, in case of rabbit volume in diet; and 0.74 ± 0.34 , $t = 2.18$, $P = 0.0499$, in case of red fox IKA; collinearity of these predictors was not problematic since the VIF for both was 2.42). This suggests that a negative effect of red fox in rabbit abundance was mediated by the amount of rabbit in fox's diet rather than by fox abundance.

Noticeably, rabbit abundance was positively related with the number of *Z. lotus* diaspores that remain depulped by rabbits under the maternal plants (Spearman $r_s = 0.82$, $N = 7$ habitat remnants, $P = 0.023$), indicating that the more rabbits in the population the more seeds remaining undispersed on the ground. Furthermore, the proportion of depulped fruits tends to be negatively related to the amount of *Z. lotus* seeds dispersed by red fox at each remnant ($r_s = -0.595$, $N = 7$, $P = 0.159$), which suggests that some interference of seed dispersal by rabbits may occur. Natural seedling emergence in the quadrats used for fruit depulping estimation was rather scarce compared to fruit abundance, occurring only in 18 of 70 quadrats and summing up 35 seedlings in total (mean density \pm SE = 0.50 ± 0.12 seedlings/quadrat, range 0.20–1.50, $N = 7$ remnants). No seedling survived at the end of the rainfall season in these quadrats. Long-term *Z. lotus* population regeneration, as estimated by abundance of juveniles and the juvenile/adult ratio, largely varied between remnants (range 0–809 juveniles, 0–17.6 juveniles per 100 adults, respectively) and no juvenile was detected under conspecific. Five out of seventeen remnants have no *Z. lotus* juveniles, meaning regeneration collapse, and four of these remnants have no *Z. lotus* seed dispersal by red fox either, suggesting that collapse of seed dispersal by red fox may be causing collapse of regeneration. Finally, we corroborated a negative relationship between rabbit abundance in the remnants and both the number of juveniles and the juvenile/adult ratio ($r_s = -0.579$,

$P = 0.015$; $r_s = -0.575$, $P = 0.016$, $N = 17$, respectively), which may be indicative on negative effects of rabbits on *Z. lotus* population regeneration.

4. Discussion

4.1. Effects of habitat loss and landscape features on red fox diet

Red fox is a generalist predator that uses food resources according to their availability, having an opportunistic feeding behavior (Dell'Arte et al., 2007; Delibes-Mateos et al., 2008; Díaz-Ruiz et al., 2013). Thus, we hypothesized that fox diet in *Ziziphus* scrublands would be variable and tailored to the particular food availability on each locality. Our data confirmed that red fox diet is variable and diverse through the region, yet no clear pattern for food resource exploitation emerged according to the landscape type gradient. The diversity of the diet in red fox has been shown to vary according to abundance of preferred prey (e.g., Dell'Arte et al., 2007). In particular, in the Iberian Peninsula diet diversity increases if the abundance of its preferred rabbit prey decreases (Delibes-Mateos et al., 2008). In *Ziziphus* scrublands, fox diet (both volume of major fractions as diet diversity) seems however to be more directly influenced by landscape features than by the availability of preferred food. Thus, all the significant relationships found here were with landscape or remnant features (land-use diversity or habitat remnant area). We did not detect any relationship of diet diversity with rabbit abundance in such remnants, but diet diversity was related to landscape complexity, peaking at intermediate values of land-use diversity. This result is congruent with the idea that habitat heterogeneity may be the main factor underlying a wide trophic niche for opportunistic carnivores in rural areas (Lucherini et al., 1995). A recent biogeographic review highlighted that Iberian red foxes modify their feeding habits according to environmental variables, which are in turn associated with the availability of their main prey (Díaz-Ruiz et al., 2013). Within the semiarid distribution range of the *Ziziphus* scrublands in Spain, the most patent environmental gradient that red fox faces currently is the gradient of landscape transformation and habitat loss. Thus, it is

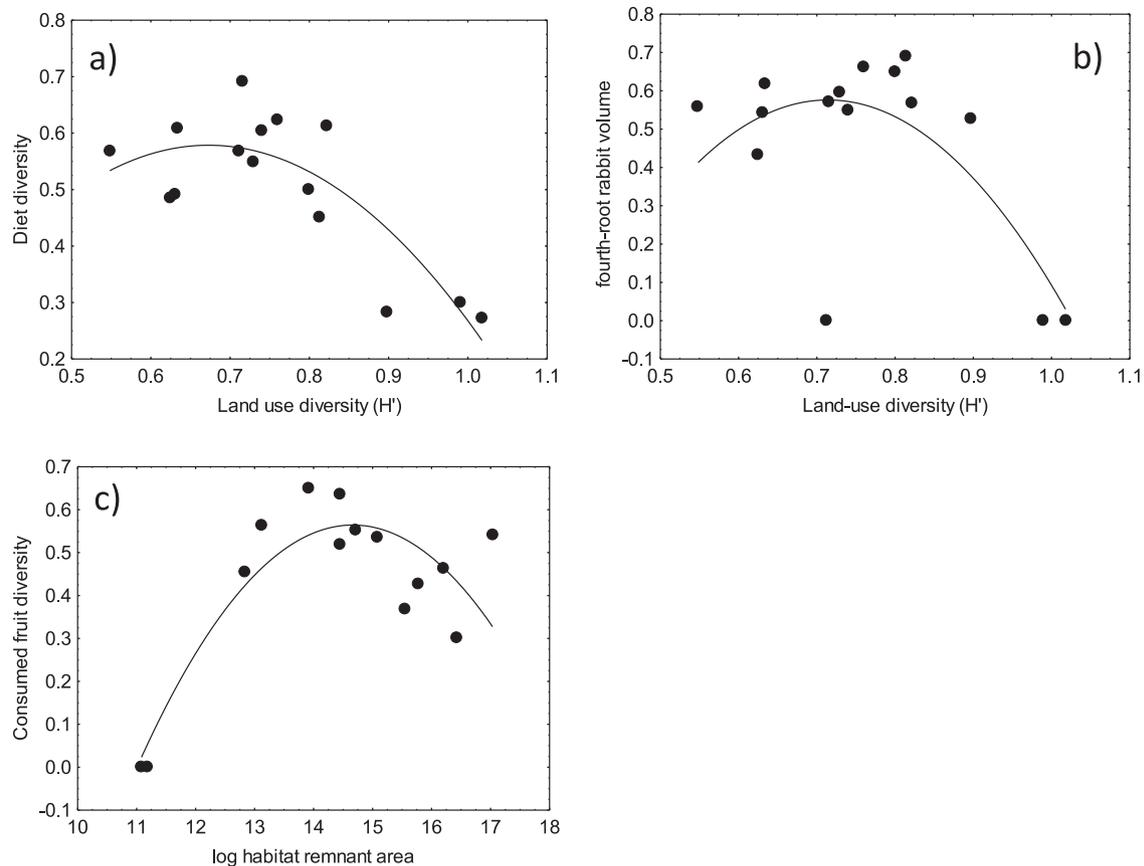


Fig. 2. Significant relationships of red fox diet diversity, consumed fruit diversity and rabbit volume in diet to landscape (land-use diversity) and remnant (remnant area) features. Diet diversity is measured as Shannon index of whole diet based on the percentage volume of each major fraction; consumed fruit diversity is measured as Shannon index for consumed fruits based on their percentages in diet; rabbit volume is estimated as percentage relative to the volume summed by all fractions of diet. See Table 1 for definitions of landscape and remnant features. We did not collect any scats in tracks from 2 populations, which were removed from analyses.

likely that intermediate land-use diversity (and/or intermediate remnant sizes) in our study reflects a favorable heterogeneity of food resources for foxes. Intermediate complexity is shaped by a notable presence of both natural habitat – providing wild vertebrate preys as rabbits and rodents, as well as some native fruits like *Ziziphus*, dwarf palm, wild olives, etc – and rural and urban habitats – providing cultivated fruits and vegetables, garbage and rats. In fact, the most preferred prey in southern Iberia (rabbit) was not included in the diet according to its relative availability. Likewise, rodent trapping during *Ziziphus* fruit availability period in 7 of the studied remnants (Rey et al., unpublished) further shows that rodent abundance did not correlate with rodent volume in diet (Spearman $r_s = 0.43$, $P = 0.40$). Intricate relationships among habitat remnant features (size, shape, isolation), abundance of food resources, and landscape features are likely shaping the generalist diet of this carnivore species in semiarid *Ziziphus* scrublands but they are beyond the scope of this paper.

4.2. The role of red fox as seed disperser in *Ziziphus* scrubland habitats

Carnivores from temperate latitudes often consume cultivated and wild fruits and are seed dispersers of many fruit species (for example, Koike et al., 2008; López-Bao and González-Varo, 2011). In particular, red fox is widely recognized as seed disperser of many fruit species in the Mediterranean region (Herrera, 1989; Rosalino and Santos-Reis, 2009). We detected seeds of 11 wild fruit species in red fox scats collected in remnants of *Ziziphus* scrublands

through its range in southern Spain, that represent ca. 75% of the list of fruit species that are commonly found in this habitat. They also contributed significantly to disperse naturalized and cultivated fleshy-fruited plant species (see López-Bao and González-Varo, 2011). There is scarce information on vertebrate seed dispersal in Mediterranean arid ecosystems (but see Rodríguez and Delibes, 1992, with European badger). Arid scrublands are prone to a paucity of avian seed dispersers, since Mediterranean avian frugivores are normally associated to forest and dense arborescent scrublands (for example, Herrera, 1985). Carnivores may provide essential seed dispersal service in Mediterranean arid ecosystems, as is the case of *Ziziphus* habitat. We have shown elsewhere (Cancio et al., 2016) that red fox is much more abundant in *Ziziphus* habitat remnants than other non-avian vertebrates seed dispersers (other carnivores and wild boar) with the exception of lizards. It is also the main seed disperser of *Z. lotus* (Cancio et al., 2016), a keystone species on this habitat. Thus it is likely to play a fundamental seed dispersal service at the community level in this habitat. Moreover, as typically found for carnivores, red fox dispersal service at regional level substantially differed between plant species (Table 3), which is much probably related to marked preferences by some fruit species (González-Varo et al., 2015). Consequently, its activity as seed disperser can potentially influence the future community composition of this habitat.

Dispersal service and the number of fruit species dispersed by red fox considerably varied through the whole range of the habitat in semiarid Spain. Noticeably, both the number of fruit species dispersed and the community-level dispersal service were related

Table 3

Occurrence frequency (OF) of seeds of different fruit species in scats of red fox in the studied *Ziziphus* habitat remnants. This information is used to obtain red fox dispersal service both at the level of each plant species (two last columns) and to the community level (two last rows). **Regional dispersal service** for each fruit species is the product of its OF averaged across remnants and the mean red fox IKA through the region, and it measures the mean number of scats of red fox containing seeds of that species per km of track conducted throughout the whole region. **Normalized regional dispersal service** is the regional dispersal service of the species divided by that of the species with maximum seed dispersal throughout the region. **Community-level dispersal service** is the dispersal service averaged across species in a given habitat remnant site considering the regional species pool (that is, the whole list of species dispersed by red fox in the region). **Community-level dispersal service for natives** is the same value but calculated only for the pool of native fruit species. **Kilometer index of abundance (IKA)** measures the number of red fox scats per km and year and it is also a measure of relative fox abundance.

	Habitat remnant site*														Regional values			
	Bj	Ch	Cv	Ej	Fp	Gz	Nj	Py	Pl	Rr	Rt	Sa	Tg	Ta	Vc	O.F. regional mean (%) ± SE	Regional Dispersal Service	Normalized Regional Dispersal Service
Native fruits OF (%)																		
<i>Asparagus</i> sp.**	0	0	0	0	0	0	0	0	0	0	0	2.0	0	0	0	0.13 ± 0.13	0.013	0.007
<i>Ceratonia siliqua</i>	0	0	0	0	8.3	0	11.7	4.6	1.7	0	0	4.0	0	0	0	2.02 ± 0.94	0.204	0.105
<i>Chamaerops humilis</i>	0	0	0	0	0	2.5	0	24.1	0	0	10.0	5.0	0	0	0	2.77 ± 1.69	0.280	0.144
<i>Citrullus colocynthis</i>	0	0	3.2	0	0	0	0	0	0	0	0	0	0	0	0	0.22 ± 0.22	0.022	0.011
<i>Ephedra fragilis</i>	0	0	0	0	0	0	0	0	0	0	0	6.9	0	0	0	0.46 ± 0.46	0.047	0.024
<i>Phillyrea angustifolia</i>	0	0	0	0	0	7.5	0	0	3.4	0	0	0	0	0	0	0.73 ± 0.53	0.074	0.038
<i>Pistacia lentiscus</i>	0	0	0	0	0	0	0	1.2	0	0	0	2.2	0	0	0	0.23 ± 0.16	0.023	0.012
<i>Olea europaea oleaster</i>	3.5	0	3.2	0	0	5	3.3	0	12.0	0	0	0	0	0	0	1.80 ± 0.85	0.182	0.094
<i>Rubia peregrina</i>	0	0	0	11.1	0	0	0	0	1.7	0	0	1.0	0	0	0	0.92 ± 0.74	0.093	0.048
<i>Ziziphus lotus</i>	6.9	0	29.0	33.3	0	4.9	13.3	4.6	6.8	0	25.0	8.9	15.6	0	0	9.89 ± 2.89	0.999	0.515
Grasses	0	0	0	0	0	0	0	0	0	0	0	1.0	0	0	0	0.07 ± 0.07	0.007	0.003
Naturalized fruits OF (%)																		
<i>Ficus carica</i>	17.2	33.3	0	11.1	16.7	35.0	15.0	32.2	14.5	0	30.0	20.8	4.4	7.7	50.0	19.20 ± 3.71	1.939	1.000
Cultivated fruits OF (%)																		
<i>Cucumis melo</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	7.7	0	0.51 ± 0.51	0.052	0.027
<i>Olea europea</i>	0	0	0	0	0	5.0	0	0	0	0	0	1.0	0	0	0	0.40 ± 0.34	0.040	0.021
<i>Phoenix dactylifera</i>	37.9	0	0	0	12.5	10.0	0	9.2	0.9	0	0	25.7	0	0	0	6.42 ± 2.95	0.648	0.334
<i>Prunus armeniaca</i>	0	0	0	0	0	0	0	2.3	0	0	0	1.0	0	0	0	0.22 ± 0.16	0.022	0.011
Unidentified	0	22.2	0	0	0	0	1.7	8.1	3.4	0	5.0	3.0	0	7.7	0	3.40 ± 0.18	0.343	0.177
Number of dispersed fruit species	4	2	3	3	3	7	5	8	8	0	4	11	3	3	1			
Total number of scats	29	9	31	9	24	40	60	87	117	2	20	101	45	13	2			
Kilometer index of abundance (IKA)	6.5	13.0	13.2	2.5	9.7	6.7	7.3	6.8	46.5	0.5	7.9	18.5	7.0	3.7	1.6			
Community-level dispersal service	0.27	0.45	0.293	0.09	0.23	0.29	0.21	0.37	1.29	0	0.34	0.92	0.10	0.05	0.05			
Community-level dispersal service for natives	0.07	0	0.43	0.11	0.08	0.08	0.21	0.24	1.03	0	0.28	0.53	0.13	0	0			

*Béjar (Bj), Campohermoso (Ch), Centro de Visitantes (Cv), El Ejido (Ej), Fernán-Pérez (Fp), Guazamara (Gz), Níjar (Nj), Playazo (Py), Puerto Lumbreras (Pl), Rambla Retamar (Rr), Retamar (Rt), Sierra Alhambilla (Sa), TorreGarcía (Tg), Toyo-Alquíán (Ta), Vega Cañada (Vc).

***Asparagus* sp. includes *A. albus* and *A. horridus* whose seeds are rather difficult to distinguish.

to some landscape and remnant features indicative of habitat loss and human landscape alteration. A combination of heterogeneous landscape, composed by a mosaic of natural and cultivated habitats, and the occurrence of large habitat remnants seems to promote both the number of fleshy-fruited plants dispersed and the community-level seed dispersal service by red fox (Fig. 3). This means that if the loss of this habitat continues, most of the dispersal service provided by this major seed disperser may collapse. In fact, collapse of seed dispersal by habitat loss and degradation has been already certified for *Z. lotus* in the region (Cancio et al., 2016).

At least as important as the number of species dispersed, it is the ability of red fox to promote functional connectivity of the landscape since its home range is normally large. We suggest that the ability of red fox to move through degraded landscapes, from urban to cultivated and natural habitats during the diurnal-nocturnal daily cycle (Lucherini et al., 1995; Fedriani et al., 1999), should promote functional connectivity of the *Ziziphus* habitat remnants by its seed dispersal service. The median of distances from a *Ziziphus* habitat remnant to the nearest remnant in the whole region is 2388 m (range 311–7342 m; 25 remnants identified, Rey et al., unpublished), that hardly falls within the home ranges described by Barrul and Mate (2015) for red fox in semi-desert habitats in the Iberian Peninsula (220–650 ha). Assuming that the vertebrate disperser home range determines the range of seed dispersal

distance (Spiegel and Nathan, 2007), this means that such promotion of connectivity is still working in some parts of the region. In other parts, however, it would be already short-circuited (1-km radius home range accounts for 314 ha assuming circular home range) or at least seriously compromised. Moreover, increased loss and fragmentation of the habitat, which is still observed in the region, may cause in the future the overall loss of the functional connectivity provided by red fox. Future studies should go in depth on the ability of red fox to promote functional connectivity of this habitat and the risk connectivity short-circuits if habitat loss continues.

4.3. The role of red fox controlling seed depulping of keystone plant species by rabbit and its cascading effects on plant regeneration

Carnivores may regulate herbivore populations and their impact in plant communities and ecosystems through top-down effects (Terborgh et al., 1999; Ford and Goheen, 2015). We approached this ecosystem service using depulping of *Z. lotus* seeds as broad-sense herbivory activity potentially limiting the population regeneration of this keystone species. Fruit depulping is an antagonistic activity that becomes a problem for plant regeneration if depulped or partially depulped seeds remain undispersed, suffer higher risk

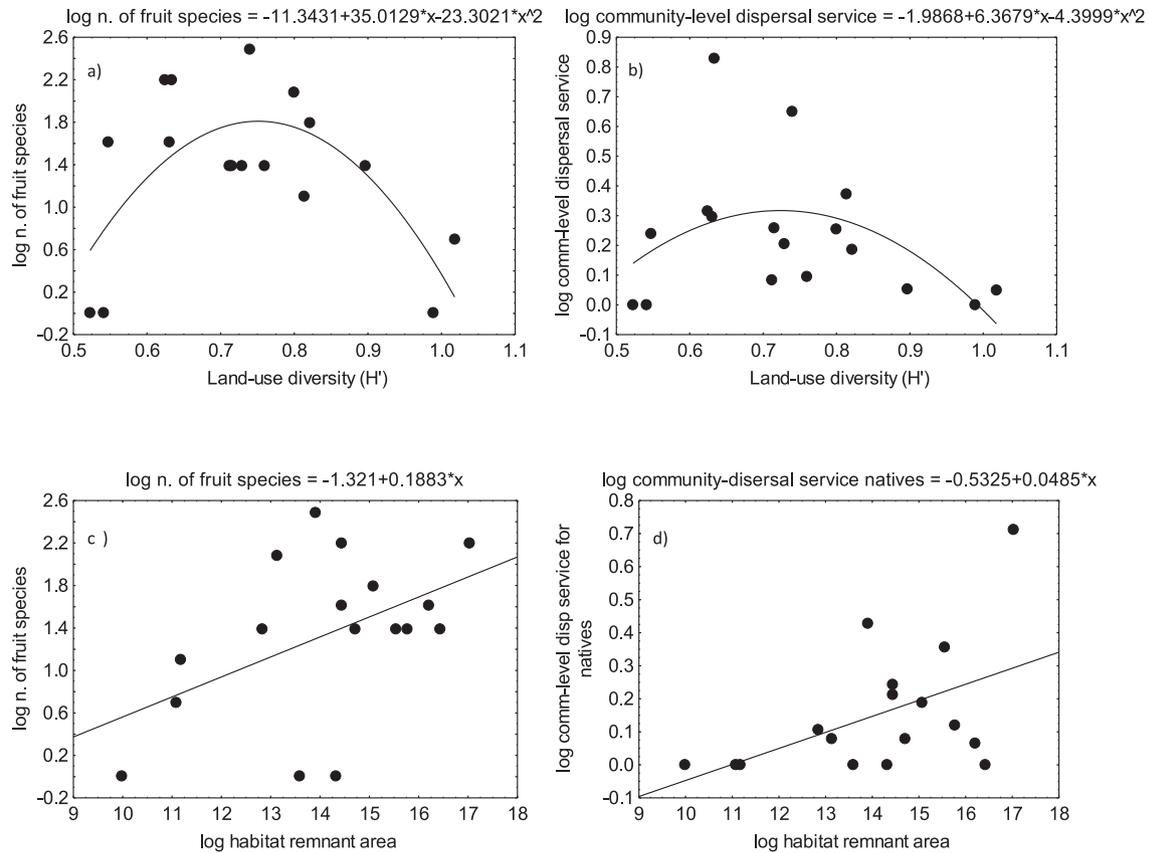


Fig. 3. Significant relationships found between the variation in seed dispersal by red fox at the community level (number of fruit species dispersed and community-level dispersal service; see Table 3 and text for definitions) and landscape and habitat remnant features (Table 1), across the whole distribution of the *Ziziphus* habitat.

of pathogen infection and/or decreased rate of seed germination, or if seedlings emerging from undispersed seeds have no opportunities to recruit (Traveset et al., 2007), though there is no much empirical evidence corroborating such extreme. Although some studies suggest that pulp feeders may in fact enhance endozoochore plant recruitment (Loayza and Knight, 2010; Fedriani et al., 2012), most of the mentioned constrains for plant regeneration associated to fruit depulping are clearly acting in our study system: (1) *Z. lotus* seeds depulped by rabbits remained undispersed under the maternal plants and the magnitude of seed depulping depended on rabbit abundance in the remnants, affecting in some cases to almost all fruit crop and interfering potentially with seed dispersal by red fox. (2) Experimental trials of seed germination conducted with *Z. lotus* in common garden conditions (Cancio et al., 2016, and unpublished data) suggest that seeds from rabbit-depulped fruits germinate in a significant lower proportion than seeds processed by red fox gut. In particular, rabbit depulping accounts for a loss of 40 percent points of germination rate compared seeds defecated by fox ($25.7 \pm 1.8\%$ germination rate, $N = 572$, for rabbit-depulped seeds; $66.6 \pm 0.5\%$, $N = 21$, for seeds defecated by fox), although rabbit-depulped seeds still germinate better than seeds within intact fruits ($13.2 \pm 2.0\%$, $N = 296$). (3) Our surveys of seedlings and juveniles of *Z. lotus* indicate that short- and long-term recruitment of this species is null under conspecifics (this study; Rey et al., 2016), and that the collapse of seed dispersal service by red fox is apparently related to the collapse in *Z. lotus* population regeneration. (4) Rabbit abundance is negatively correlated with the abundance of *Z. lotus* juveniles and the ratio juvenile/adult across habitat remnants. All this evidence supports that rabbit depulping of seeds, which depends on the rabbit

abundance, may considerably impact on the natural regeneration of *Z. lotus* populations. Nonetheless, provided that seeds from rabbit-depulped fruits germinate somewhat better than intact fruits, we cannot rule out the possibility that some seeds from rabbit-depulped fruits become established seedlings after the infrequent water runoff in some seasonal streams occupied by the species. Other factors that limit juvenile regeneration, as habitat fragmentation and degradation, are probably acting and their relative importance as determinants of population regeneration collapse merit further research.

Many different factors may affect populations of keystone preys as rabbits, among them food resources, diseases, climate, and predators (Virgós et al., 2003). Neither landscape transformation nor climate variation related to rabbit abundance in this study, although the possibility exists that our sampling design and analyses (that collapsed intra-annual and inter-annual variability) failed to detect the inherent complexity of the predator/prey dynamics. Widespread generalist predators, like red fox, may regulate rabbit populations, however, this phenomenon is not well understood, and some authors have shown that this is more likely to occur under low rabbit abundance (Trout and Tittensor, 1989; Saunders et al., 2010). A combination of fox abundance and volume in diet has been recently shown to contribute to regulate rabbits in some localities of Spain (Fernández de Simón et al., 2015). Interestingly, we found that fox abundance and rabbit volume in fox diet both had combined effects on rabbit abundance. In fact volume in diet, rather than fox abundance, negatively impacted on rabbit population in *Ziziphus* habitat remnants. Since the more rabbits in the habitat remnant the more seeds remaining undispersed on the ground, factors increasing volume of rabbits in red

fox diet would be promoting its role as regulator of herbivory pressure. The most patent trend in this sense was that rabbit volume in diet was non-linearly related with land use diversity, peaking at intermediate landscape complexity level (Table 2 and Fig. 2b).

In short, these results suggest that red fox regulates to some extent rabbit herbivore population and that this might have top-down effects on *Z. lotus* natural regeneration. Further studies on recruitment with experimental exclusions of red fox and rabbits will be needed for definitive conclusions on this regard (Ford and Goheen, 2015).

4.4. Conclusions

Our results suggest that red fox provides two fundamental ecosystem services in threatened semiarid *Ziziphus* scrublands. First, red fox provides fundamental seed dispersal at the community level as well as functional connectivity in the landscape that may enhance natural regeneration and recovery of the habitat. Second, it might be playing a role regulating rabbit and controlling its impact on *Z. lotus* population regeneration, though this still needs experimental corroboration. Since *Z. lotus* is keystone for the establishment of other plant species, and provide resources for other many animals in this habitat (Tirado, 2009), the effects on its population regeneration may cascade to others in the habitat. These two ecosystem services may however be presently compromised by strong landscape degradation.

Author contribution

PJR and IC conceived and designed the work; IC, PJR, AGR, JMB, AJM, and JI conducted the field work; IC, AGR and JMB analyzed scat samples; TS processed habitat and landscape data and conducted GIS analyses; PJR and IC conducted the statistical analyses; IC and PJR led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2017.05.004>.

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