RESEARCH PAPER

Regeneration of a keystone semiarid shrub over its range in Spain: habitat degradation overrides the positive effects of plant–animal mutualisms

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ABSTRACT

- Global change drivers are currently affecting semiarid ecosystems. Because these ecosystems differ from others in biotic and abiotic filters, cues for plant regeneration and management derived from elsewhere may not be applicable to semiarid ecosystems. We sought to determine the extent to which regional variation in regeneration prospects of a long-lived semiarid keystone shrub depends on anthropogenic habitat degradation, plant–animal interactions and climate determinants.

- We investigated the regeneration ability (*via* population size structure, juvenile density and juvenile/adult ratio), fruit set and seed dispersal of *Ziziphus lotus* in 25 localities spanning the range of its threatened habitats in Spain. We dissected the relative contribution of different regeneration determinants using multiple regression and structural equation modelling.

- Population regeneration was extremely poor, and size structures were biased towards large classes and low juvenile densities and juvenile/adult ratios. Poor regeneration was often coincident with seed dispersal collapse. However, the positive effect of seed dispersal on population regeneration disappeared after considering its relationship with habitat degradation. Protected areas did have juveniles. Together, these data suggest that habitat degradation directly impacts juvenile establishment.

- Our results provide insights into habitat and species management at the regional level. *Z. lotus* populations are currently driven by persistence-based dynamics through the longevity of the species. Nonetheless, collapsed seed dispersal, poor regeneration and the removal of adults from their habitats forecast extinction of *Z. lotus* in many remnants. The extreme longevity of *Z. lotus* provides opportunities for recovery of its populations and habitats through effective enforcement of regulations.

INTRODUCTION

Global change drivers, such as habitat degradation, loss and fragmentation, interact with climate to affect the regeneration ability of populations of threatened plant species (Bruna *et al.* 2009; Cordeiro *et al.* 2009; Tang *et al.* 2011; González-Varo *et al.* 2012). Plant–animal mutualisms, especially pollination and seed dispersal, are crucial for the regeneration of populations of many plant species and are susceptible to disruption by the global change drivers mentioned above (see meta-analytical reviews by Markl *et al.* 2012; González-Varo *et al.* 2013; Magrach *et al.* 2014; Fontúrbel *et al.* 2015; Neuschulz *et al.* 2016). The loss of biological interactions due to anthropogenic disturbances may result in the extinction of species (Caughlin *et al.* 2015; Valiente-Banuet *et al.* 2015; McConkey & O'Farrill 2016). However, studies on threatened plant species have rarely dissected the relative impact of habitat degradation, plant–animal interactions and/or climate on variation in the regeneration ability of populations at the regional scale, even though

such assessment may help elucidate the mechanisms involved in species' extinction due to human land use in relict landscapes (González-Varo *et al.* 2015).

The management of threatened woody plant species and their habitats is typically based on local determinants of population regeneration, although factors responsible for variation in population regeneration at the regional scale are frequently neglected (but see García *et al.* 1999; Lázaro *et al.* 2006; Traveset *et al.* 2012). This clearly reflects the tendency to investigate the regeneration of plant populations, focusing fundamentally on small-scale processes and/or on few populations (García 2001; Traveset *et al.* 2003; García & Houle 2005; González-Varo *et al.* 2012; Escribano-Ávila *et al.* 2014; Rey & Alcántara 2014). Although this approach allows the identification of critical demographic stages and processes (bottlenecks) for population regeneration dynamics, it hinders the integration of such knowledge in habitat and species management at the regional level because small-scale effects may not necessarily translate into regional-scale

variation in population regeneration (Herrera *et al.* 2011; McConkey *et al.* 2012; Hayes 2013; Lavabre & García 2015). Therefore, analysing the variation in species regeneration and the determinants of such variation at large scales is essential for more adequate management of species and habitats (García *et al.* 1999; Lázaro *et al.* 2006; Tang *et al.* 2011; Traveset *et al.* 2012; Linares 2013). Knowledge of factors affecting the regeneration of populations of keystone species is particularly important (Power *et al.* 1996; but see Mills *et al.* 1993). Specifically, regeneration prospects of keystone plant species and factors affecting them may be used as tools for evaluating the health of natural habitats, as they have a disproportionate influence on the persistence of many other plant and animal species (Mills *et al.* 1993; Power *et al.* 1996; García & Zamora 2003).

Impacts of anthropogenic disturbances on plant–animal interactions and plant population regeneration have been widely studied in temperate and tropical forests and woodlands (Markl *et al.* 2012; Magrach *et al.* 2014; Fontúrbel *et al.* 2015) but not as frequently in other ecosystems, such as arid and semiarid lands. Environmental filters, particularly abiotic filters, acting on plant community regeneration in semiarid ecosystems are distinct from those acting in other regions (Kéfi *et al.* 2007; Maestre *et al.* 2012). Therefore, cues for plant community regeneration and management obtained from other ecosystems may not be applicable to semiarid ecosystems. Here, we investigated the effect of habitat degradation on regional variation in regeneration prospects of *Ziziphus lotus*, a keystone shrub inhabiting threatened semiarid habitats in southern Spain. Previous studies on this species report seed dispersal collapse (Cancio *et al.* 2016) or disruption due to depulpation of fruits by rabbits (*Oryctolagus cuniculus*; Cancio *et al.* 2017) and that both local- and landscape-scale remnant degradation and disturbances affect the seed dispersal of *Z. lotus* (Rey *et al.* 2017). Semiarid Mediterranean ecosystems of south-eastern Spain are among the most singular and threatened habitats in Europe (Mota *et al.* 2004; Kéfi *et al.* 2007; Tirado 2009) that have witnessed one of the highest rates of long-term land degradation (Puigdefábregas & Mendizábal 1998). The ongoing anthropogenic impact on these ecosystems has occurred not only locally but also on a regional level, enhancing the extinction risks of endangered plant species (Benito *et al.* 2009). Thus, implementing regulations based on the current state of these habitats is urgently needed at the regional scale.

Here, we specifically aimed to: (i) evaluate the prospects of regeneration of populations of *Z. lotus* across its entire habitat range in the Iberian Peninsula; (ii) comparatively weigh the effects of habitat degradation and climate and the outcomes of plant–animal mutualisms and antagonisms (seed dispersal, pollination and herbivory) on regional-scale variation in regeneration prospects (estimated based on juvenile density and juvenile/adult ratio); and (iii) provide insights on habitat and species management for the conservation of woody plants. Based on previously reported impacts of large- and local-scale habitat degradation and that of rabbits on the seed dispersal of *Z. lotus*, we hypothesised that the relative effect of biotic interactions can be as important on the regeneration of *Z. lotus* as the effect of habitat degradation or regional climate variation.

MATERIAL AND METHODS

Study system and area

The study system used here was the 'Mediterranean arborescent matorral with *Ziziphus lotus*' (European Habitat Directive, habitat 5220, Annex 1 of Directive 92/43/EEC), hereafter referred to as the *Ziziphus* habitat, with a focus on its keystone plant species, *Z. lotus*. This habitat has singular ecological and biogeographic values because of its rich endemic xerophytic flora and its link with North African ecosystems (Tirado 2009). It is restricted to semiarid areas in the southeast of the Iberian Peninsula, where it previously occupied large extensions in seasonal streams ('ramblas') and coastal plains. During the last 60 years, however, the original area of distribution of this habitat has been reduced and fragmented by intensive greenhouse-based agriculture and urban expansion. At many sites, less than 5% of the area that was occupied in the 1950s is left, indicating extreme habitat loss (Mota *et al.* 1996; Mendoza-Fernández *et al.* 2015).

Ziziphus lotus (hereafter referred to as *Ziziphus*; Rhamnaceae) is distributed across North Africa, the Sahara Desert and the Arabian Peninsula. In Europe, *Ziziphus* grows in south-eastern Spain and Sicily. It is considered as an ecosystem engineer, as it is a keystone species that shelters vertebrates, facilitates the growth of many plant species and creates islands of fertile soil (Tirado 2009). It is pollinated in the region mainly by flies, solitary and social bees (especially honeybees, *Apis mellifera*) and wasps (González-Robles *et al.* unpublished), and produces globular reddish-brown fruits of 10–15-mm diameter with two seeds enclosed within a hard endocarp (referred to as the seed hereafter). Fruiting occurs between July and early August. Ripe fruits remain on the plant until December, which is when they fall to the ground and remain available until February or March. Red fox (*Vulpes vulpes*) is the major seed disperser of *Ziziphus* in the region, although other carnivorous mammals and wild boar (*Sus scrofa*) also contribute to its dispersal locally (Cancio *et al.* 2016). The contribution of medium-sized birds (thrushes, pigeons, partridges and starlings) and lizards to *Ziziphus* seed dispersal is negligible (Cancio *et al.* 2016, 2017; Rey *et al.* 2017). Rabbits depulpate (*i.e.* consume the fruit pulp without leaving any apparent seed damage) 38–95% of the fruits fallen to the ground (Cancio *et al.* 2017). Thus, rabbits interfere with the seed dispersal of *Ziziphus* by other seed dispersers. As a result, many seeds remain beneath the maternal plants where no seedling recruitment occurs.

Study sites and surveys

This study was conducted in 25 *Ziziphus* habitat remnants spread throughout the entire range of the species in the Iberian Peninsula (Fig. 1). This area spans more than 260 km in the SE Iberian Peninsula. Of the 25 habitat remnants, seven were located within protected areas. To evaluate population regeneration prospects in each habitat remnant, we surveyed and geolocated all adult and juvenile *Ziziphus* present in each remnant. Juvenile (non-flowering/non-fruiting individuals with < 1 m crown diameter and 0.5 m height) and adult surveys in each habitat remnant were conducted between 2014 and 2015. An exhaustive monitoring of the whole remnant area was conducted using six observers, each covering a 20-m wide band adjacent to that of neighbouring observers. In cases of small individuals growing close to adults, soil was excavated to a

depth of 10–15 cm to search for evidence of re-sprouting (tap-roots, burls or thick roots coming from nearby adults), as *Ziziphus* is capable of sprouting repeatedly after cutting. Juvenile density (number of juveniles ha^{-1}) and juvenile to adult ratio in the remnants were used as indicators of long-term population regeneration. These two parameters are useful indicators of the regeneration potential because juvenile banks of woody vegetation are formed over multiple years, and thus capture the supra-annual variation in processes affecting population regeneration. They are particularly suitable for describing plant regeneration niches and population and community dynamics (*e.g.* Alcántara *et al.* 2015; Rey *et al.* 2016). For juvenile density, the area occupied by the population was estimated in a GIS platform using the convex hull encapsulating all geolocated adults in the population.

Size structure has also been repeatedly used as a rapid assessment tool for determining the natural regeneration prospects and conservation status of plant populations (García *et al.* 1999; Lázaro *et al.* 2006; González-Varo *et al.* 2012; Traveset *et al.* 2012). The size structure of *Ziziphus* populations was evaluated in a subset of 19 out of 25 remnants. In each of these 19 remnants, several groups of neighbouring individuals (three to ten groups, depending on the spatial aggregation of individuals) were randomly selected, and the perpendicular diameter and height of each individual measured. Subsequently, size was estimated as the volume of a hemi-ellipsoid, and the individuals sampled were then classified into six size classes: <0.1, 0.1–1, 1–10, 10–100, 100–

1000 and >1000 m^3. The number of individuals sampled per remnant ranged from nine to 88, depending on the population size.

In 18 of the 25 habitat remnants, habitat degradation, climate, average fruit set of reproductive *Ziziphus* (which was considered as an indicator of the pollination success), seed dispersal and rabbit abundance (as a surrogate for herbivore pressure; Cancio *et al.* 2017) were also characterised. Note however that other factors apart from differences in pollination could account for variation in fruit set (*e.g.* nutrient availability, regional variation in climate). Remnant degradation in the study area was due to abandoned agricultural crops (*e.g.* old *Agave* plantations), livestock grazing, quarries and illegal rubble and dumps, which reduced the population size, adult density and spatial aggregation of *Ziziphus*, thus inducing structural changes in the *Ziziphus* population within the remnant. Thus, habitat degradation was estimated from variables associated with population fragmentation within each remnant. To characterise remnant features, discrete *Ziziphus* patches were defined within each remnant using a 15-m radius adult aggregation circular buffer (Figure S1). This buffer was based on the median distance between individuals in the two largest and most well-preserved remnants of the region (see Rey *et al.* 2017). Nine metrics of remnant quality were measured: area, total number of adult *Ziziphus*, proportion of the remnant area covered by *Ziziphus* patches, mean patch area, proportion of the total area of patches represented by the largest patch and by patches of isolated adult *Ziziphus*, mean perimeter/area of the patches, mean distance to the nearest neighbouring
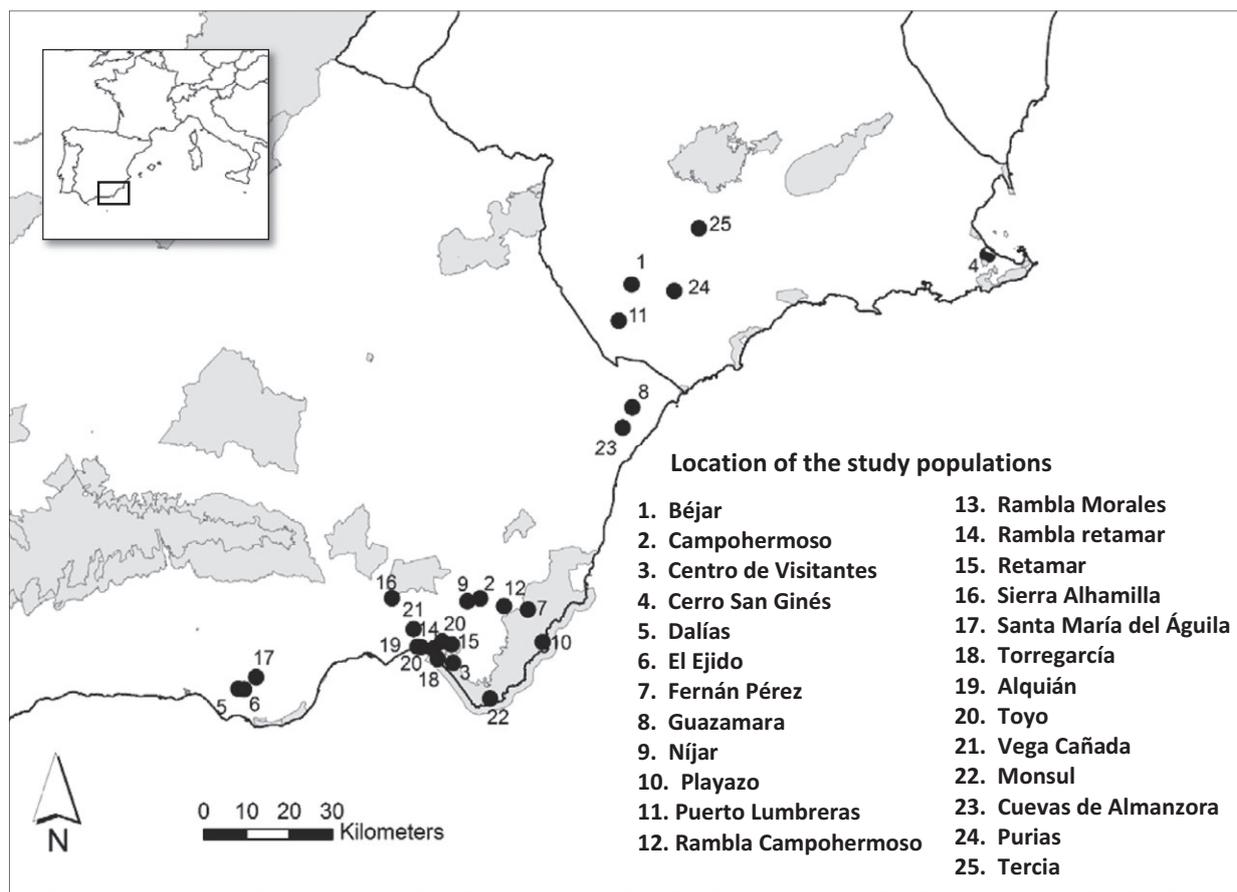

Location of the study populations

1. **Béjar**
2. **Campohermoso**
3. **Centro de Visitantes**
4. **Cerro San Ginés**
5. **Dalías**
6. **El Ejido**
7. **Fernán Pérez**
8. **Guazamara**
9. **Níjar**
10. **Playazo**
11. **Puerto Lumbreras**
12. **Rambla Campohermoso**

13. **Rambla Morales**
14. **Rambla retamar**
15. **Retamar**
16. **Sierra Alhamilla**
17. **Santa María del Águila**
18. **Torregarcía**
19. **Alquián**
20. **Toyo**
21. **Vega Cañada**
22. **Monsul**
23. **Cuevas de Almanzora**
24. **Purias**
25. **Tercia**

Fig. 1. Location of the study populations of *Ziziphus lotus* in southeastern Iberian Peninsula. Protected areas are illustrated in grey.

patch and aggregation index based on the distance to nearest neighbouring patch. For the set of habitat remnants studied, we showed previously that these metrics of remnant quality/degradation may be summarised using principal components analysis (PCA) in two major factors: F1 (41.2% of variance) and F2 (35.5%; Rey *et al.* 2017). F1 defined a gradient of the size and shape of characteristic *Ziziphus* patches with positive loadings of mean *Ziziphus* patch area, and negative loadings of mean perimeter/area and the proportion of area of *Ziziphus* patches represented by isolated adults (Table A.2 in Rey *et al.* 2017). F2 defined a gradient of *Ziziphus* aggregation and population area, with positive loading of the aggregation index, the proportion of *Ziziphus* patch area represented by the largest patch, and negative loading of the remnant area.

Climate for each remnant was characterised using the Global Aridity Index (GAI) from CGIAR-CSI (http://www.cgiar-csi.org) with a resolution of 30 arc sec (approximately 1 km at the equator). GAI combines precipitation and potential evapotranspiration throughout the whole year, with lower values indicating higher aridity.

Mean *Ziziphus* fruit set was measured as the ratio of the number of mature fruits produced to the number of flowers produced in eight to 25 individuals (most commonly 25, depending on the population size) haphazardly chosen to ensure an even spread throughout the population. Flower and fruit densities were measured using four 15×15 cm quadrats placed on the canopy of each shrub according to the cardinal points. The number of flowers and ripe fruits were estimated three and two times per plant, respectively, during the peak periods, *i.e.* May–June and September, and the ratio between the maximum fruit and flower densities in such surveys was used as our estimate of annual fruit set. For each individual plant we obtained the average fruit set corresponding to the years 2014 and 2015.

Ziziphus seed dispersal in each remnant was estimated by sampling the scat of potential seed dispersers, including mammalian carnivores and wild boars. A seed mobility index (SMI) was calculated as the product of scat abundance per km and year (IKA) and the frequency of occurrence of seeds in the scat (OF), therefore reflecting the number of scats per km and year that contain seeds of *Ziziphus* (Cancio *et al.* 2016). Scat sampling was conducted monthly from August to March over four consecutive years (2011–2015) in permanent transects centred in the remnant. In each transect, two observers collected the scat found within two 6-m wide bands. Transect length (ranging from 0.66–4.25 km) differed among remnants according to their area (see Rey *et al.* 2017). Scat of mammalian species were identified based on their size, shape, colour and smell (see Fedriani *et al.* 2010; López-Bao & González-Varo 2011). Scat were examined in the laboratory to check for *Ziziphus* seeds. SMI was averaged across all 4 years, thus capturing the supra-annual variation in seed dispersal. In the same transects, the number of fresh rabbit latrines per km and year in each remnant were also recorded, as an indicator of rabbit abundance (Palomares 2001). Data sheet used in most analyses of this study is shown in Table S1.

Statistical analyses

Generalised linear models (GLMs) were used to analyse the variation in population regeneration parameters, habitat degradation, fruit set and seed dispersal between remnants located in protected and unprotected areas. Normal error structure and log link function were used in these analyses since this link function better controlled for departure from normality. Generalised linear ordinal-multinomial models with logit link function were used to analyse the variation in size structure among *Ziziphus* populations and provided the categorical and ordinal nature of the dependent variable.

To explore the effect of climate and habitat degradation (predictors) on fruit set, SMI and rabbit abundance (response variables), best subset multiple regression analyses were conducted; in the case of SMI, fruit set was also considered a predictor. Separate simple regression analyses were also conducted to examine the direct relationships between population regeneration parameters (juvenile density and juvenile/adult ratio, as response variables) and predictors indicative of habitat degradation (F1 and F2), climate (GAI), reproductive success (fruit set) and seed dispersal (SMI). Subsequently, predictors with $P < 0.1$ were incorporated in a best subset multiple regression of regeneration parameters. Best subset multiple regression is a procedure that explores all possible competing nested models against each other, from the full model containing all the predictors (*i.e.* the most parameterised one) to the less parameterised ones, containing just single predictors. The best model was chosen based on Akaike Information Criteria corrected for small sample sizes (AICc). All these regressions were conducted using GLM with normal error distribution and a log link function.

Prior to these analyses, a multiple regression of each response variable (population regeneration parameters, SMI, fruit set and rabbit abundance) on geographic (latitude, longitude) coordinates was conducted (Legendre 1993; see Rey *et al.* 2016; Cancio *et al.* 2017 for similar procedure). No significant relationships emerged (Table S2); therefore, patterns described in the results were not due to underlying large-scale spatial gradients.

All the analyses were conducted in STATISTICA 8.0 (StatSoft, Tulsa, OK, USA).

Structural equation modelling (SEM)

A causal model explaining regional variation in *Ziziphus* population regeneration was built using the information on habitat remnant features, fruit set, SMI and climate in 18 study sites (Fig. 2A). This model was tested using SEM (Pugesek *et al.* 2003); however, given the limited number of cases for conducting a complex SEM, a model simplification strategy was necessary. Therefore, only those variables of Fig. 2A (SMI and F1) that entered into the best subset multiple regression for each response variable of that model were eventually incorporated into SEM. The hypothesis of causal relationships of the simplified model was tested with a chi-square goodness of fit test, which compares the observed covariance matrix with that expected from the relationships shown in the model (Shipley 1997). Since small sample sizes provide limited statistical power, the null hypothesis of a good model fit was less likely to be rejected. Therefore, comparative fit index (CFI; cut-off value for good model fit > 0.9) and Steinger's root mean square error of approximation (RMSEA) were further used as indices of model fit (Tomer & Pugesek 2003). The latter provides evidence that the model is not a poor approximation, but a good

one; RMSEA <0.1 indicates that the model does not fit poorly, and RMSEA <0.05 indicates a very good fit (Tomer & Pugesek 2003, pp 131 and 133). Furthermore, because the small sample size may compromise the reliability of parameter estimates, Monte Carlo simulations were conducted for these estimates with 1,000 bootstrap samples of 18 habitat remnants. The final parameter estimate was the mean of those produced in the 1,000 re-samplings, and a given parameter estimate was considered significant if the 95% confidence interval (CI) did not include zero. SEM and Monte Carlo simulations were conducted with SEPATH module of STATISTICA 8.0 (StatSoft).

RESULTS

We detected significant differences between protected and unprotected areas for the first component of habitat remnant quality (F1) but not F2. Mean F1 scores for remnants in protected areas were positive, whereas those for remnants in unprotected areas were negative (Table 1). This suggests that habitat remnants within protected areas contain large patches of aggregated *Ziziphus* individuals, whereas those in unprotected areas frequently comprise isolated individuals or long patches, indicating more internal degradation and fragmentation of the population.

Regional variation in fruiting success, seed dispersal service and rabbit abundance

Fruiting success (estimated as mean individual fruit set) varied among populations by more than one order of magnitude (range: 0.018–0.256 fruits flower^{-1}; coefficient of variation CV = 71.3, median = 0.07, N = 18 populations). This variation was not directly related to habitat remnant degradation or climate (see best subset multiple regression, Table S3). Seed dispersal (SMI) also varied substantially among populations, ranging from 0–6.87 scat with *Ziziphus* seeds per km and year (CV = 175.59, median = 0.40). Best subset multiple regression showed that this variation was mainly associated with F1 (Table S3). However, SMI was not affected by fruit set, rabbit abundance or F2. Additionally, herbivore pressure (*i.e.* rabbit abundance) ranged from 1.15–27.7 latrines per km and year (CV = 77.54, median = 9.89), and rabbit abundance across habitat remnants was not associated with habitat degradation or climate (Table S3). Neither fruit set nor SMI varied significantly between *Ziziphus* remnants located in protected and unprotected areas (Table 1). However, rabbit abundance in unprotected areas was ca. three-fold higher than that in protected areas (Table 1).

Regional variation in population regeneration prospects

Our surveys of the 25 habitat remnants identified 10,446 *Ziziphus* individuals, of which 991 were juveniles. *Ziziphus* population size (sum of juveniles and adults) was highly variable among habitat remnants (range = 5–5405 individuals; CV = 262.40; median = 85). Population regeneration parameters varied accordingly; the density of juveniles was much lower than that of reproductive adults and variable among remnants (juveniles: range = 0–1.14 juveniles ha^{-1}, CV = 261.25, median = 0.012; adults: range = 0.005–6.87 adults ha^{-1},

CV = 121.14, median = 0.92). In particular, no juvenile was detected in eight of the 25 habitat remnants, clearly indicating population regeneration collapse. The juvenile/adult ratio was very low and highly variable among habitat remnants (range = 0–0.18, CV = 137.18, median = 0.019). Moreover, juvenile density and juvenile/adult ratio varied significantly between protected and unprotected areas (Table 1). Juvenile density was correlated with both adult density (r = 0.67, $P < 0.001$) as well as juvenile/adult ratio (r = 0.70, $P < 0.001$). Juvenile/adult ratio and juvenile density were also correlated with population size (r = 0.68, $P < 0.001$; r = 0.92, $P < 0.001$, respectively) but not with the area occupied by the population (r = −0.02, $P = 0.93$; r = 0.09, $P = 0.68$, respectively).

Size structure varied among populations (ordinal-multinomial test; $\chi^2 = 157.07$, $P = 0.001$) and was biased towards large or extremely large size classes in most populations (Figure S2). The number of individuals in the smallest size classes was higher in the five populations located in protected areas than in populations in unprotected areas, where the smallest size classes were frequently absent (Figure S2).

Significant abiotic and biotic predictors of *Ziziphus* population regeneration

Simple regression analyses showed that both juvenile density and juvenile/adult ratio were positively correlated with SMI (Table 2A); four of the six remnants with zero SMI also showed zero juvenile density. This suggests that the disruption and collapse of seed dispersal determines, at least to some extent, the long-term collapse of population regeneration. Importantly, seed dispersal by red fox, the major *Ziziphus* seed disperser, was not correlated with any population regeneration parameter (juvenile density: b = 0.30 ± 0.43, $P = 0.49$; juvenile/adult ratio: b = 0.22 ± 0.25, $P = 0.40$), highlighting the relevance of other seed dispersers for effective population regeneration. Population regeneration parameters were positively correlated with F1. However, regional-scale variation in population regeneration showed no correlation with fruit set and only a marginal correlation with climate (GAI) and rabbit abundance (Table 2A). The combination of significant predictors of population regeneration parameters in multiple regression showed that juvenile density was mainly associated with F1, whereas juvenile/adult ratio was positively affected by F1 and negatively by rabbit abundance (Table 2B).

Dissecting the relative importance of habitat quality, climate and plant–animal interactions in regional variation of *Ziziphus* population regeneration

After model simplification (see Methods), SEM analysis of the simplified conceptual scheme produced the model solution reflected in Fig. 2B. Because model fit indices were satisfactory (Maximum likelihood Chi-square = 8.33, df = 8, $P = 0.40$, CFI = 0.99, RMSEA = 0), the effects of habitat remnant degradation, seed dispersal and herbivore abundance on population regeneration parameters are adequately depicted under the hypothesis of causal relationships (Fig. 2B). They explained 68% and 78% of the variation in juvenile/adult ratio and juvenile density, respectively, in the region. The model corroborated the strong effects of remnant quality/degradation on population regeneration. These effects were direct, rather than
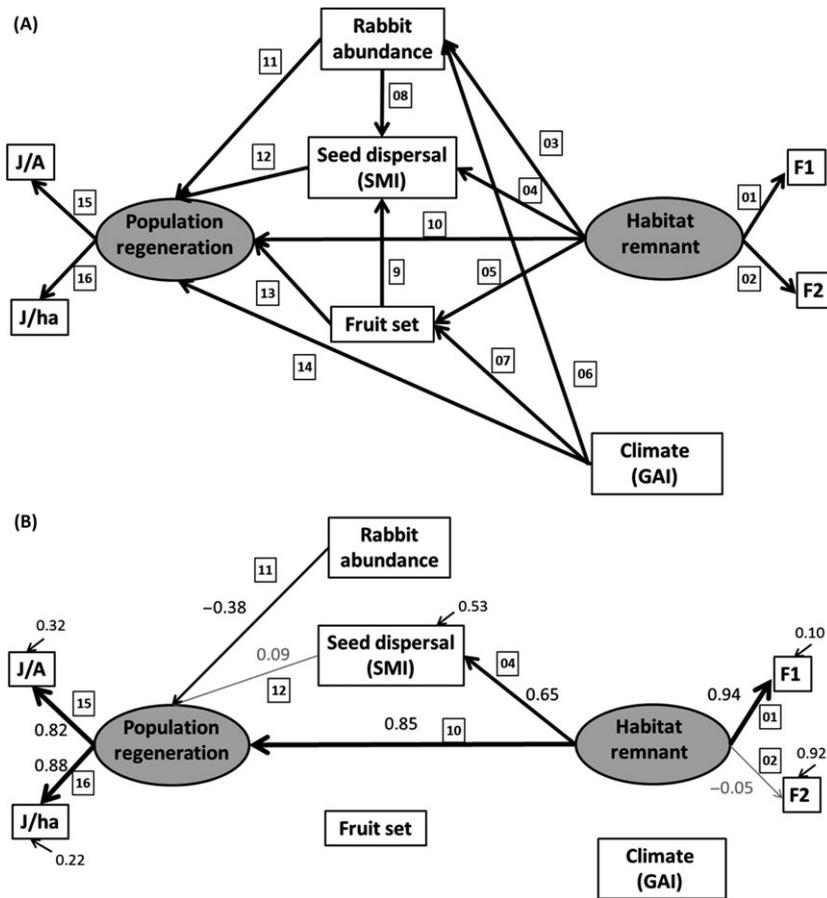
Fig. 2. (A) Conceptual model of the effects of climate, habitat remnant quality and *Ziziphus* interactions with animals (rabbit abundance as surrogate for herbivore pressure, mammalian seed dispersal and pollination/fruiting success) on *Ziziphus* population regeneration (J/A = juvenile/adult ratio; J/ha = juvenile density). Habitat remnant quality (combination of F1 and F2 principal components of habitat degradation as described in Methods) and climate (measured as Global Aridity Index, GAI) are proposed to potentially affect population regeneration directly and indirectly. The indirect effects of abiotic determinants on population regeneration would occur *via* pollination service (fruit set), rabbit abundance and seed dispersal (Seed Mobility Index, SMI). Seed dispersal is further proposed to be potentially affected by fruit set and by rabbit abundance, the latter due to its effects on fruit depulpation cascading in plant regeneration (Cancio *et al.* 2017). Variables within boxes are measured (manifest) variables, while variables within grey ellipses are latent constructs formed from measured manifest variables. Path coefficients are identified with numbers within boxes on each arrow in the model. (B) Model solution for the simplified SEM applied to the conceptual model depicted in (A). Full model in Fig. 2A was first simplified using best subset multiple regression for each response variable of that model (see also Tables S3, 2) and the numbered paths were those eventually entering into the SEM. Even though GAI pertained to the best subset for juvenile/adult regression (Table 2B), its incorporation in the final model gave very poor fit and volatility of parameter estimates. In contrast, the model fit and parameter estimates considerably improved after its removal. Significant causal relationships (paths) are illustrated with black arrows while non-significant ones appear as grey arrows. Standardised path coefficients appear in black on the arrows. Small arrows pointing to manifest variables are errors for each variable.

being mediated by seed dispersal, and were determined exclusively by F1. The positive effects of seed dispersal (SMI) on population regeneration parameters, previously shown with a simple regression, were cancelled out by the strong and positive effect of remnant quality on SMI. Herbivore abundance also had a negative influence on population regeneration prospects. Taken together, these results suggest that regional variation in the probabilities of population regeneration is driven primarily by habitat remnant quality descriptors and secondarily by the negative influence of rabbits (standardised path coefficients of 0.85 and −0.38, respectively). Less degraded remnants with larger *Ziziphus* patches, low proportion of isolated adults, large population size and lower perimeter/area ratio are more favourable for long-term population regeneration, independent of climate variation.

DISCUSSION

Management of threatened plant species and habitats requires a thorough knowledge of the regeneration prospects of populations at the local and regional levels (*e.g.* García *et al.* 1999; Traveset *et al.* 2012; Linares 2013) as well as the effect of interactions among different global change drivers, such as climate change and habitat loss, fragmentation and degradation, on such prospects (González-Varo *et al.* 2013). Here, we showed that the prospects of natural regeneration of *Ziziphus* populations throughout its range in Spain are rather poor. An average of one juvenile was observed per ten adults across 25 habitat remnants; however, eight out of those 25 remnants showed a complete lack of juveniles. The best-preserved remnants had two juveniles per ten adults, accounting for a density slightly

Table 1. Variation between *Ziziphus* habitat remnants located in protected and unprotected areas in habitat quality, biotic interaction outcomes (fruit set, seed dispersal (SMI), rabbit abundance) and *Ziziphus* population regeneration parameters. Tests were conducted with GLM considering normal error structure and log link function. Sample sizes were seven and 18 populations for protected and unprotected areas, respectively, in the case of juvenile ha^{-1} and juvenile/adult ratio, while for fruit set, SMI, rabbit abundance and habitat quality (F1 and F2) they were five and 13 populations, respectively. F1 captures the size and shape of the *Ziziphus* characteristic patches; F2 describes a gradient of *Ziziphus* aggregation and population area. Significant differences are highlighted in bold.

response variables	Wald χ²	P	protected mean ± SE	unprotected mean ± SE
F1	**4.09**	**0.043**	**0.67 ± 0.39**	**−0.26 ± 0.24**
F2	0.58	0.45	−0.28 ± 0.42	0.11 ± 0.27
Fruit set	0.14	0.70	0.078 ± 0.344	0.090 ± 0. 0.184
Seed dispersal (SMI)	0.55	0.46	1.69 ± 0.52	0.96 ± 0.57
Rabbit abundance	**4.18**	**0.04**	**4.64 ± 0.67**	**12.60 ± 0.15**
Juvenile ha^{-1}	**5.59**	**0.02**	**0.278 ± 0.305**	**0.028 ± 1.88**
Juvenile/adult ratio	3.47	0.06	0.058 ± 0.267	0.023 ± 0.423

superior to one juvenile ha^{-1}. These densities and juvenile/adult ratios are lower than those typically found on trees and shrubs with low regeneration capacity (*e.g.* García *et al.* 1999; Hampe & Arroyo 2002; Lázaro *et al.* 2006; Katsavou & Ganatsas 2012; Traveset *et al.* 2012; Linares 2013). Accordingly, the size structure of *Ziziphus* populations was biased towards large-sized classes in most remnants, which is associated with the high longevity of this species. Low regeneration in shrub and forest species is common in unfavourable conditions (*e.g.* in peripheral populations) and in nutrient-poor and

climatically stressful environments (García & Zamora 2003; and references therein). Low regeneration has been reported in mountain ranges and semiarid climate in the Mediterranean area (García *et al.* 1999, 2002; Castro *et al.* 2004; Lázaro *et al.* 2006; Linares 2013), where many long-lived plants are currently present as relict and endemic stress-tolerant species (Médail & Verlaque 1997; García & Zamora 2003). *Ziziphus* habitats under study are at the extreme of the aridity gradient in the Iberian Peninsula as well as at the border of its distribution, and *Ziziphus* is considered a stress-tolerant species (Tirado 2009). Therefore, low regeneration of this woody species is expected to occur naturally. Additionally, we showed that the regeneration prospects of this species and its future persistence are being severely compromised by the recent and rapid habitat destruction and degradation of the habitat remnants.

Effect of plant–animal interactions on the regional-scale variation of *Ziziphus* population regeneration

Weak regeneration of long-lived relict species in peripheral populations and under unfavourable conditions has been attributed to recruitment failure due to insufficient viable seed production and dispersal (*e.g.* Hulme 1996; Hampe & Arroyo 2002; Traveset *et al.* 2012) and/or to safe-site or establishment limitation (García *et al.* 1999; Hampe & Arroyo 2002; Lázaro *et al.* 2006; Mendoza *et al.* 2009; Linares 2013). In the case of *Ziziphus* populations under study, viable seed production was high in the remnants, ranging from 410–50.14 × 10⁶ fruits, depending on the population size. Cancio *et al.* (2016) showed that seed viability and germination rates are also high in these *Ziziphus* populations. Furthermore, we showed that fruit set was not directly related to population regeneration parameters. On the contrary, several facts suggest that limited dispersal and antagonistic interaction with rabbits affect recruitment and

Table 2. Regressions explaining the variation across habitat remnants of two plant regeneration estimators (density of juveniles and juvenile/adult ratio). (A) Simple regressions in relation to: (1) climate variable (global aridity index: GAI); (2) habitat remnant parameters (F1 and F2); (3) seed dispersal parameters (seed mobility index SMI: mean number of scat containing seeds per km and year = IKA x OF); (4) reproductive success parameter (fruit set: number mature fruits to flower production); and (5) herbivory and fruit depulpation (rabbit abundance as surrogate for this antagonistic pressure). (B) Significant simple predictors at $P < 0.1$ were later incorporated into a best subset multiple regression of regeneration. Model choice was based on AIC corrected for small sample sizes (AICc).

predictors	density of juveniles (ha^{-1})			juvenile/adult ratio		
	b ± SE	Wald χ²	P	b ± SE	Wald χ²	P
(A) Simple regressions						
Climate variable						
Aridity (GAI)	−5.06 ± 2.98	2.88	0.09	−0.52 ± 0.53	0.97	0.33
Habitat remnant parameters						
F1	**0.24 ± 0.04**	**33.02**	**0.000**	**0.034 ± 0.09**	**16.24**	**0.000**
F2	−0.05 ± 0.07	0.53	0.47	−0.007 ± 0.012	0.38	0.54
Seed dispersal						
SMI by mammal disperser guild	**0.08 ± 0.03**	**7.38**	**0.006**	**0.013 ± 0.005**	**6.57**	**0.01**
Reproductive success						
Mean fruit set	−1.19 ± 1.10	1.16	0.28	−0.10 ± 0.19	0.29	0.59
Herbivory and fruit depulpation						
Rabbit abundance	−0.011 ± 0.008	1.85	0.17	−0.002 ± 0.001	3.45	0.06
(B) Best model multiple regression on significant (*P* < 0.1) regressors						
F1	**0.23 ± 0.039**	**34.83**	**0.000**	**0.023 ± 0.009**	**6.17**	**0.012**
GAI	−3.35 ± 1.76	3.63	0.06	–	–	–
SMI	out	out	out	0.007 ± 0.005	2.51	0.11
Rabbit abundance	–	–	–	**−0.003 ± 0.0001**	**7.54**	**0.006**
Model solution fit	Likelihood ratio χ² = 22.05, *P* = 0.0002, AICc = −9.62			Likelihood ratio χ² = 18.33, *P* = 0.0003, AICc = −67.99		

regeneration of *Ziziphus* populations. First, both seed dispersal and fruit depulpation by rabbits were directly associated with variation in regeneration parameters among populations (Table 2). It is possible that the negative correlation between rabbit abundance and population regeneration is partly caused by fruit depulpation (ranging from 35 to 95% of fruits), since the depulped seeds remain under maternal plants where seedling recruitment does not occur (Cancio *et al.* 2017). Second, regeneration collapse, indicated by the absence of juveniles, was observed in six out of 18 remnants. Moreover, four of these six remnants also showed seed dispersal collapse (see also Rey *et al.* 2017). Third, the higher the seed dispersal was in a remnant, the higher the juvenile/adult ratio and juvenile density (Table 2).

Poor seedling establishment probably also limits the regeneration of *Ziziphus* populations. Seeds sown and 1-year-old seedlings planted over 2 years in three contrasting microhabitats and seven habitat remnants resulted in zero recruitment without watering and protection against herbivores (González-Robles *et al.* unpublished). In contrast, seeds sown in common garden conditions with watering resulted in relatively high germination rates (Cancio *et al.* 2016; González-Robles *et al.* unpublished). Nonetheless, establishment limitation, which is probably associated with climate factors and soil fertility stress (see *e.g.* Tirado *et al.* 2015), is consistent regionally, as variation in aridity across the region does not have a substantial influence on population regeneration.

Habitat remnant degradation effects on population regeneration of *Ziziphus*

Anthropogenic effects also influence population regeneration, both directly and indirectly. On one hand, our results showed that population regeneration parameters and size structure were directly affected by habitat degradation, independently of its effects on seed dispersal. Habitat fragmentation and degradation, including fragmentation within each population, affect seedling establishment of Mediterranean shrubs and trees by reducing the appropriate sites for recruitment, as shown in the case of *Myrtus communis* (González-Varo *et al.* 2012) and *Olea europaea* (Rey & Alcántara 2014). It is also plausible that human activities within remnants (livestock grazing, quarries, illegal rubble and dumps, *etc.*) directly hampered the establishment and survival of juveniles (see González-Varo *et al.* 2012).

On the other hand, the effect of seed dispersal on population regeneration prospects appeared to be associated with habitat remnant degradation across the region, which was a strong predictor of variation in *Ziziphus* seed dispersal (Table S3). Moreover, when relationships between population regeneration and SMI or habitat degradation were considered together in the SEM analysis, the positive relationships between seed dispersal and population regeneration parameters were cancelled out, suggesting that the effect of seed dispersal on population regeneration was mainly due to habitat degradation. Effects of habitat loss, fragmentation and degradation on seed disperser abundance and dispersal levels are widely recognised (reviewed in Markl *et al.* 2012; Magrach *et al.* 2014; Fontúrbel *et al.* 2015), but infrequently and inexplicitly linked with population regeneration. Such effects have also been recorded extensively for *Ziziphus* (Cancio *et al.* 2016; Rey *et al.* 2017). The cascading effects of disturbances on natural regeneration and habitat conservation *via* seed dispersal operate not only locally (within

remnants), but also at the regional and landscape levels (Herrera *et al.* 2011). Landscape degradation may decrease the connectivity among remnants by hindering long-distance dispersal, for which carnivores and other mammals act as adequate mobile links (Kremen *et al.* 2007; Escribano-Ávila *et al.* 2014). We have shown elsewhere that landscape disturbance is as important as within-habitat remnant degradation for seed dispersal in *Ziziphus* (Rey *et al.* 2017).

Regeneration prospects, persistence and implications for conservation

Our study demonstrated overall poor regeneration prospects of *Ziziphus* populations in south-eastern Spain. The size structure of the populations and the collapse of seed dispersal and regeneration anticipate an extinction of the species in many remnants. This seems a general problem among threatened species due to intensive land use, climate change and other drivers of global change (Traveset *et al.* 2012; González-Varo *et al.* 2015).

Ziziphus is a long-lived shrub reaching up to 35 m in diameter and 4 m in height (see also Tirado 2009). García & Zamora (2003) proposed that the persistence of species through longevity, rather than regeneration from seeds, is a valuable demographic strategy against species extinction in the Mediterranean region. Evidence in favour of this proposal is found in relict populations of species of many different biogeographic and historical origins (*e.g.* Zamora *et al.* 1998; García *et al.* 1999, 2002; Hampe & Arroyo 2002; Médail *et al.* 2002; Picó & Riba 2002; Lázaro *et al.* 2006). Therefore, it is possible that the persistence of *Ziziphus* populations in south-eastern Spain relies on adult survival and longevity as well as on vegetative regeneration rather than on regeneration from seeds. This implies that *Ziziphus* populations in the region are ascribed to remnant population dynamics with adults surviving for long periods, which partially offsets the lack of recruitment caused by environmental stress and anthropogenic degradation (García *et al.* 1999; García & Zamora 2003). Although longevity can delay local extinctions of long-lived species (Kuussaari *et al.* 2009; Krauss *et al.* 2010), our data suggest that *Ziziphus* extinction in some remnants is a matter of time because of the elevated susceptibility of its small and disturbed populations to environmental stochasticity. Extinction debt, *i.e.* the number of populations expected to be extinct because of habitat loss, fragmentation or degradation (Kuussaari *et al.* 2009), is likely for long-lived species under recent large-scale habitat destruction (Cousins 2009), and was recently described in relict Mediterranean fragmented habitats where collapse of regeneration has been documented (González-Varo *et al.* 2015).

Once the major determinants of regeneration of a species have been identified at regional levels, the persistence strategy based on longevity provides opportunities for the recovery of its populations and habitats (García *et al.* 1999; González-Varo *et al.* 2015). In this study, we showed that habitat degradation and rabbit activity were the two major factors affecting *Ziziphus* regeneration (Fig. 2B). Moreover, the degradation of remnants was less in protected areas, and Cancio *et al.* (2017) showed that rabbit populations were naturally better controlled in protected than in unprotected areas. Therefore, habitat degradation and rabbit abundance should be controlled in unprotected areas to improve the prospects for *Ziziphus* regeneration.

Demographic studies generally agree that population dynamics are minimally sensitive to changes in recruitment among

long-lived plants (Álvarez-Buylla *et al.* 1996; Franco & Silvertown 2004; Bruna *et al.* 2009). For managing long-lived species, greater attention is now given to the survival and growth of adult stages than to fecundity, seed dispersal and recruitment (Bruna *et al.* 2009; but see Caughlin *et al.* 2015). Our results suggest that under scenarios of intense and accelerated habitat loss, fragmentation and degradation, such as those experienced by the *Ziziphus* habitat over its entire range, a multi-purpose management strategy is necessary for keystone plant species (see also Cancio *et al.* 2017; Rey *et al.* 2017). First, this strategy should preserve adults as warranty for the persistence of populations in the long term. This would require strict regulations against the removal of adults from their habitats. Second, the strategy should encourage population regeneration by attracting seed dispersers, controlling herbivores and improving the habitat for recruitment (González-Varo *et al.* 2015). This would entail further protection against recurrent disturbances of severely degraded, unprotected remnants. Lastly, this strategy should enhance the connectivity among habitat remnants, especially the unprotected remnants, by facilitating long-distance movement of seed dispersers. This would enable population restoration at the landscape level (Rey *et al.* 2017). Remarkably, effective application of the already existing regulations would essentially fulfil the measures outlined above. Notably, adequate management of *Ziziphus* will probably result in the conservation of many other species, as 25 of the 37 woody plants species present in this habitat are recruited beneath the *Ziziphus* canopy (data from Rey *et al.* 2016), and 82 insect species utilise *Ziziphus* floral resources in the region (González-Robles *et al.* unpublished).

Drylands, including arid, semiarid and dry areas, are among the most susceptible ecosystems to common drivers of global change (Foley *et al.* 2005; Kéfi *et al.* 2007). To manage these ecosystems, it is imperative to understand how global change drivers interact with each other to disrupt ecological interactions and reduce the regeneration prospects and biodiversity of communities (*e.g.* Maestre *et al.* 2012). Results of this study may be extrapolated to drylands currently exposed to the accelerated impact of intensive land use and climate change.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Details of 15-m radius circular *Ziziphus* aggregation buffers for habitat quality metrics.

Figure S2. Size structure of 19 study populations.

Table S1. Data sheet used in this study.

Table S2. Multiple regression of each response variable of this study on geographic coordinates.

Table S3. Best subset multiple regression models.

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