

The colonization of abandoned land by Spanish juniper: Linking biotic and abiotic factors at different spatial scales



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ABSTRACT

Colonization of abandoned lands by woody vegetation may be a great opportunity for ecosystem recovery given the current and future trend of land abandonment. This may help to reverse the generalized condition of ecosystem degradation of developed countries which is an urgent need. However, ecosystem recovery in abandoned lands can be seriously limited by biotic and abiotic factors. Identify such factors and determine the relevant spatial scales at which they operate will help to understand natural patterns of colonization of abandoned lands and may be useful to guide restoration activities. We used Spanish juniper remnant woodlands and old fields recently colonized by the species to assess the variation in post-dispersal seed predation and environmental suitability to plant recruitment. These biotic and abiotic factors are two of the most limiting for vegetation recovery in abandoned lands, at the regional and local spatial scale. We found that recruitment was controlled by factors operating at different spatial scales in a hierarchical manner along different stages of the process. The regional scale was determinant for post-dispersal seed predation and seedling abundance which was, in turn, controlled by environmental suitability at the local spatial scale. Post-dispersal seed removal was higher in old fields than in mature woodlands, hence increasing seed limitation, a pervasive constraint for plant recruitment in abandoned lands. Environmental suitability for plant recruitment did not decrease as a result of previous farming uses at the regional scale, a common pattern in areas not subjected to intensive farming practices. Abandoned lands in Mediterranean areas seem to have a strong potential for ecosystem recovery being the biotic factors (e.g. seed availability) more limiting than the abiotic ones when non-intensive farming practices have been performed. This together with predictions of increase in land abandonment in low productive areas makes old fields especially relevant from an ecosystem recovery perspective.

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1. Introduction

The detrimental effects of global change drivers on species conservation and ecosystem functioning are quite well established (Millennium Ecosystem Assessment, 2005). However, certain drivers such as the abandonment of land use could lead to the regeneration of forest species and the colonization of old fields (Schröter et al., 2005). The abandonment of agricultural land became widespread in many developed regions during the second half of the last century (Mottet et al., 2006; Rey Benayas et al., 2007), and

land-use change models predict an increase in this trend in coming decades (Rousenvell et al., 2006). As a result, ecological recovery of abandoned lands may be an opportunity for reversing the current trend of habitat degradation (MEA, 2005). However, biotic and abiotic factors operating at several spatial scales can seriously constrain plant recruitment and thereby ecosystem recovery in these abandoned lands (Cramer et al., 2008).

Plant recruitment is a multi-stage process connected by transitional processes such as seed dispersal, post-dispersal predation, seedling emergence and survival. For many woody species some of those transitional processes involve biotic interactions between plants and animals (e.g. seed dispersal, post-dispersal predation) which are controlled at large spatial scales (Puerta-Piñero et al., 2012). By contrast, processes such as germination or seedling survival seem to be more affected by abiotic factors (e.g. soil

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moisture and nutrient content and light availability) that mainly vary at fine spatial scales (García and Houle, 2005, and references therein).

Post-dispersal seed predation is known to be especially limiting in the recovery of degraded lands such as fragmented (Santos and Telleria, 1994; González-Varo et al., 2012), burned (Torre and Díaz, 2004) or formerly cultivated areas (Wijdeven and Kuzee, 2000). The abundance of seed predators such as small mammals is often higher in these early successional stages. This is due to the low structure complexity of the vegetation in degraded lands, usually dominated by shrubs and herbaceous vegetation forming an abundant understory at the ground level that reduces the predation risk of small mammals (Ostfeld et al., 1997). At fine spatial scales higher seed predation rates are expected in more covered microhabitats (Díaz, 1992; Manson and Stiles, 1998) with larger seed clumps or greater seed density (Hulme, 1994, see Janzen, 1970; Connell, 1971 for details on predictions of changes in seed predation with parent plant distance).

Once dispersed seeds escape predation, the fate of surviving seeds and seedlings is mainly modulated by abiotic factors which affect seeds germination and seedling survival (e.g. moisture, light and nutrients). These abiotic factors, in turn, determine the suitability of the different microhabitats present in an ecosystem (Gómez-Aparicio et al., 2005 and references therein). In the case of abandoned fields, the availability of suitable microhabitats could be especially limiting due to former farming activities (Dupouey et al., 2002; Flinn and Marks, 2007). Thereby to understand how colonization proceeds in abandoned lands driving ecosystem recovery, is necessary to identify which are the main biotic and abiotic constraints for this process and the spatial scales at which they operate.

Ecosystems in the Mediterranean Basin have a long, intense history of land use which has been abandoned in certain areas (i.e. northern fringe) since the mid-twentieth century coinciding with industrialization and rural exodus. This has led to the gradual re-forestation of these areas (Barbero et al., 1990; Debussche et al., 1999; Chauchard et al., 2007). Spanish juniper (*Juniperus thurifera* L.) woodlands have been particularly affected by this process (Olano et al., 2008). During the past century, its populations experienced a sharp decline due to the intense use of the species for wood and derived forest products and habitat destruction (Gauquelin et al., 1999). Land abandonment has allowed the densification of its woodlands and the colonization of former agricultural lands and livestock pastures (Gimeno et al., 2012a). Therefore, it is a good study system for widen the knowledge regarding how ecosystem recovery, driven by plant recruitment, proceed in abandoned lands. Spanish juniper woodlands are priority habitats for conservation in the 2000 Natura Network, act as refuge for endemic species and form part of the cultural and historical heritage (Olano et al., 2008). This makes the study of Spanish juniper colonization of abandoned lands particularly interesting not only from an ecological point of view, but also from a conservation and sustainable management perspective.

In a previous study, we determined the dispersal patterns of Spanish juniper at different spatial scales after land abandonment. We found that seed arrival to old fields was not limited due to the dispersal activity of a rich dispersal community, although the quantity of seeds dispersed in old fields was lower than in woodland remnants (Escribano-Avila et al., 2012). In previous studies we also found spatial concordance between microhabitats in which more seeds are dispersed and the suitability of such microhabitats for germination and seedling survival (Escribano-Avila et al., 2012, 2013). However, we do not know if the seed dispersal pattern is consistent with the recruitment pattern or how post-dispersal seed predation and microhabitat environmental conditions could be affecting seedling establishment in relation to land use. Thus, we

have combined experimental and observational data on post-dispersal seed removal, natural recruitment and abiotic conditions considering several spatial scales to evaluate the following hypotheses: (i) post-dispersal seed removal is controlled at the regional and local scale with greater seed removal in recently colonized old fields and in more covered microhabitats with greater seed density (Manson and Stiles, 1998; Hulme, 1994). (ii) Early recruitment is controlled at the local scale by environmental variables (i.e. water, soil nutrient content and light availability), which are known to be more favorable beneath canopies (Gauquelin et al., 1992; Montesinos et al., 2007; Escribano-Avila et al., 2013). However, such environmental conditions could change according to previous land use (Gimeno et al., 2012a). In this case, an indirect effect of regional scale on seedling establishment could be expected being the final outcome of which hardly foreseeable.

2. Methods

2.1. Study area and species

The Spanish juniper (*J. thurifera* L.) is a dioecious tertiary-relict tree endemic to continental areas of the western Mediterranean Basin. It forms low density pure or mixed-species woodlands in poor, shallow, rocky soils. The most extensive woodlands of Spanish juniper are found in Spain, particularly in the central high plateaus that range between 800 and 1200 m a.s.l., and are subjected to a continental Mediterranean climate (Gauquelin et al., 1999). Males and females flower at the end of winter, and fertilized female cones take 22 months to develop and ripen (Adams, 2004; Montesinos et al., 2006). Mature cones are then dispersed by birds and mammals in low and high density seed clumps, respectively (Santos et al., 1999; Escribano-Avila et al., 2012). Rodents and granivore birds consume both fruits and seeds (Santos and Telleria, 1994 and references therein). Non-predated seeds germinate approximately 15 months after dispersal usually from April to September with the highest peak between May and June (Escribano-Avila et al., 2013). The study was conducted at two sites belonging to the Natura 2000 network in Guadalajara province, central Spain, *Torremocha* and *Maranchón* located in *Alto Tajo* Natural Park and *Parameras de Maranchón, Hoz de Mesa y Arangoncillo* (SCI), respectively (Fig. 1A). The two sites are 1250 m (Maranchón) and 1278 m (Torremocha) m.a.s.l., and are separated by a distance of c. 20 km. The climate is Mediterranean continental with an annual rainfall of about 500 mm and a pronounced summer drought. Mean annual temperature is 10.2 °C, with January being the coldest month (mean temperature: 2.4 °C) and July the warmest (mean temperature: 19.5 °C) (data provided by the Spanish Meteorology Agency, www.aemet.com). Snowfalls occur from November to April at both sites.

2.2. Study system and sampling design

The territory was classified into three habitat types: mature woodland remnants, recently colonized old fields and active agricultural lands (Fig. 1B), the latter of which was beyond the scope of this study. Spanish juniper cover in mature woodland remnants is over 30% with a high abundance of reproductive adult trees, while it is less than 15% in recently colonized old fields. Most trees in this habitat type are Spanish juniper newcomers, and there are rarely more than 4 adult reproductive trees per hectare. Traditional management in woodland remnants has been logging and extensive grazing (see Gimeno et al., 2012a; Escribano-Avila et al., 2012), and these practices are still actively carried out at our study sites by local people in a traditional and extensive fashion. Old fields were devoted to crops or livestock pastures.

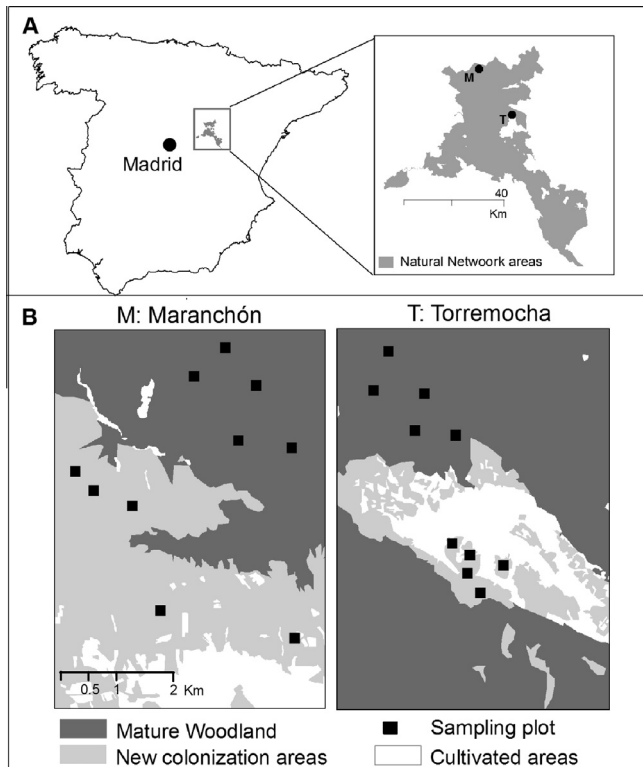


Fig. 1. (A) Study area within the Iberian Peninsula. On the top right, a close-up of the protected areas, Alto Tajo and Parameras de Maranchón, Hoz de Meas y Aragoncillo (Natura 2000 Network) where the study sites are located. (B) The different study sites and the distribution of the habitats describing the ongoing process of *J. thurifera* expansion. In each sampling plot ($N = 20$), 4 sampling stations were established in the microhabitats: female and male Spanish juniper canopies, shrubs and open gaps for a total of 80 sampling stations in which post-dispersal seed removal, recruitment and environmental variables were studied.

To account for the most relevant spatial scales in the colonization process, we performed a nested design including the regional and local spatial scales. The regional spatial scale included different habitats occurring at the landscape level and extended over several hectares (site and habitat). The local spatial scale represented environmental heterogeneity varying at a fine-grained spatial scale and extending over less than a few square meters, referred as microhabitat. In this study, the local spatial scale was characterized by four main microhabitats: Spanish juniper female and male canopy cover (sex-ratio was balanced in the study area, personal observation), shrubs and open gaps. This last category, open gap, was characterized by the lack of canopy cover with bare soil or soil covered by biological crust, or creeping vegetation. An intermediate spatial scale (plot) including several microhabitats within a habitat type was used to characterize the heterogeneity between the regional and the local scale. We established a total of 20 plots ($100\text{ m} \times 50\text{ m}$) in the two studied habitats, mature woodland remnants and old fields at two different sites located at a distance of c. 20 km. In each plot one sampling station was established in each of the 4 microhabitats for a total of 80 sampling stations (see Fig. 1).

2.3. Abundance of predators

Censuses were performed at each sampling station using standard Sherman live traps to identify and determine the abundance (frequency of capture) of small rodents. (*Apodemus sylvaticus* and *Mus spretus* are the targeted species in this territory.) These censuses were carried out before the seed monitoring periods in the

experimental seed removal experiment to avoid interference. Two-night trapping sessions were conducted in February and March 2009 and one in February 2011 during new moon to avoid low capture rate mediated by a moon effect on the risk perceived by small mammals (Vickery and Bider, 1981; Kotler et al., 1991). We placed a total of 3 traps in each sampling station covering a total surface of 3 square meters. The traps were baited with apple and a paste made of tuna fish in oil and flour, and the doors were oriented in opposite directions. A piece of waterproof cotton was added to protect captured rodents from the cold. The traps were activated at dusk and checked at dawn. Trapped rodents were released immediately following identification. The abundance index of rodents was estimated as the number of captures per 100 traps/night.

We sampled granivore bird density in March 2009 and 2011. The sites and habitat types were censused once each year. In mature woodland remnants, we established a 2 km length transect with a 50 m wide main belt which included the studied plots (Santos et al., 1999). In recently colonized old fields, bird censuses were taken from a watching point from where the whole plot was visible. All potential granivores walking along the transects or seen or heard from the watching points were recorded. The total sampling effort was 400 min. Density was estimated as the mean number of birds seen or heard by site and habitat divided by the sampled surface in each habitat type. All necessary permits were obtained from the corresponding authorities, and all animal manipulation was performed following national and international recommendations.

2.4. Post-dispersal seed removal experiment

To evaluate post-dispersal seed removal, we carried out field experiments after the seed dispersal season in April 2009 and April 2011. Seed depots (Petri dishes) were placed at each sampling station ($N = 80$) mimicking clump size and number of seeds in clumps deposited by the species' main dispersers, carnivores and thrushes. The seed clumping pattern of a carnivores was simulated with 2 groups of 18 seeds (two seed depots), whereas we used 6 groups of two seeds (three seed depots) for thrushes, this variable is hereafter referred as seed clumping type. The whole surface of the sampling station was covered with seed depots placed 50 cm from one another and nailed to the ground with a wooden stick. Small holes were made in the bottom of each depot for water drainage, and gloves were used to prevent human scent from interfering with the experiment. The experiments were carried out during new moon nights in both years. Removal rates were estimated by counting the number of remaining seeds in each depot after 3, 5, 7 and 15 days in relation to the amount of seeds offered. We assume seed removal was proportional to seed predation as it has been proved by other fleshy fruited plants (see e.g. Hulme, 1994). Birds and rodents were excluded from seed depots in ten randomly chosen sampling stations using a wire mesh (1.2 cm). These were used as a control to assess background seed loss due to rain, runoff or wind (Kelrick et al., 1986; Hulme, 1994). Although previous works have shown that Spanish juniper seeds can be removed by ants (Montesinos et al., 2007), they were inactive in our study area at the time the experiments were carried out.

2.5. Seedling abundance

Seedling abundance was sampled in June 2009 and 2011 in all sampling stations ($N = 80$) in which the seed removal experiment was performed. All seedlings up to two years old were counted in 4 quadrats ($30 \times 30\text{ cm}$) in 2009 and in 6 quadrats in 2011. Two additional quadrats were evaluated in 2011 due to the low seedling density found in 2009. Seedling density (seedlings/m²)

was calculated for each year, and their sum was used in statistical analyses.

2.6. Soil properties and canopy openness

A core from the upper 5–15 cm of soil was randomly obtained in each sampling station (80 soil cores) in May to evaluate soil conditions at the peak of germination (Escribano-Avila et al., 2013). Water content and nutrient supply greatly influence seedling establishment and could change as a result of previous farming activities (Dupouey et al., 2002; Flinn and Marks, 2007). Thus, gravimetric soil moisture content was measured as the difference between wet soil and dry soil until constant weight, expressed as water weight/dry soil weight (hereafter referred as moisture content). Dry soil was sieved to 2 mm grains for chemical analyses. We performed soil digestion following the Kjeldahl method (Radojevic and Bashkin, 1999). The supernatant was then analyzed with an automatic chemistry analyzer to obtain total nitrogen content on each soil sample (mg/g of dry soil) (Skalar 4000 SAN System, Segmented Flow Analyzer; Skalar, Breda, The Netherlands; Equipment located in Nutri-Lab www.nutrilab-urjc.es).

Radiation for each microhabitat was estimated with hemispherical photographs taken in each sampling station with a digital camera (Cool Pix 995, Nikon, Tokyo, Japan), coupled to a fish-eye lens, of 180° field of view (FCE8, Nikon) set horizontally on a tripod. Photographs were taken at a height of 15 cm, which is the maximum height reached by seedlings up to two years old (authors' personal observation). All photographs were taken on the same day in March with cloudy conditions to ensure homogeneous illumination of the overstory canopy and a correct contrast between the canopy and the sky. The resulting images were analyzed for canopy openness using Hemiview canopy analysis software version 2.1 (1999, Delta-T Devices Ltd., UK). We estimated the global site factor (GSF) which is the proportion of direct and indirect radiation reaching under each canopy where seedlings were located. The resulting measure varied from 0 to 1 with 0 corresponding to a totally closed canopy (minimal radiation) and 1 to an open gap with no canopy at all (maximal radiation). Hereafter, this variable is referred to as canopy openness.

2.7. Understory cover at the microhabitat and plot level

Since vegetation cover at ground level could influence the anti-predatory behavior of seed consumers (Manson and Stiles, 1998; Hulme, 1994), we estimated the percentage of understory covering the ground (e.g. branches of the same canopy) under the canopies of female and male juniper trees and in shrub microhabitats at all sampling stations, hereafter referred to as understory cover. Understory cover was zero in open microhabitats, according to the criteria established for this microhabitat. We also estimated percentage understory and tree cover at the plot level.

2.8. Statistical analyses

We performed General Linear Models to evaluate the scale of variation and the possible effects of previous land use (i.e. farming activities) on the abiotic filters which may affect recruitment. Thus, we performed a GLM for each of the three response variables: soil moisture content, total nitrogen soil content and canopy openness. (Gaussian error distributions and identity as link function) using site, habitat and microhabitat as fixed effects plus the interaction terms habitat × site and habitat × microhabitat.

In order to evaluate our hypotheses, we performed three Generalized Linear Mixed Models (GLMM) with the response variables seed removal, seedling presence/absence and seedling density. For the seed removal experiment, we used the percentage of seeds

removed from the depots as the dependent variable and site, habitat, microhabitat, seed clumping type, year and the covariable understory cover as fixed factors. The error distribution considered was binomial and the link function used was logit. In the case of seedlings we used a sequential approach as a large number of sampling stations had no seedlings. Thus, we performed a GLMM to model seedling presence/absence (binomial error distribution and link function logit) and a second GLMM for sampling stations where seedlings were present and the response variable was seedling density (Poisson error distribution link function log). Both models included the fixed factors: site, habitat, microhabitat and the environmental covariables canopy openness, soil moisture content and total nitrogen. Collinearity between these environmental variables was previously evaluated, and non-significant correlations were found. Plot was included as a random factor in all analyses.

Model selection on GLMM was performed according to Bolker et al. (2009), Zuur et al. (2009) which is briefly described. We constructed “the beyond the optimal model” including all possible interactions between fixed factors (site, habitat and microhabitat) plus the effect of seed clumping type and understory cover at the microhabitat level in the case of the seed removal experiment. For the GLMM on seedling presence/absence, only site and habitat were full crossed, and the covariables moisture content, total nitrogen and light availability were included. No interactions were included in the beyond the optimal model for seedling density due to scarcity of sampling stations with seedling presence and the lack of certain levels on the superior ones (e.g. no seedlings in the open microhabitat in old fields habitat). The covariables moisture content, total Nitrogen and canopy openness were also included. With this structure of fixed effects, we then optimized the structure of the random effects (effect of plot on the estimate of the intercept of the model and effect of plot on the estimate of the intercept add up to the parameter estimates of microhabitat) for the seed removal experiment and seedling presence/absence. In the case of seedling abundance, only the random effect of plot on the intercept of the model was considered, as there were not enough data to evaluate the random effect of plot on each level of microhabitat. The models were fitted by Restricted Maximum Likelihood criteria (REML), and the random structure to be retained for further analyses was selected by the lowest Akaike information criteria (AIC). Once random effects were optimized, we performed model selection for fixed effects fitted by Maximum likelihood (ML). Among all the possible combinations of independent variables given the beyond the optimal model for each dependent variable, we selected the best-fitting model that minimized the second-order Akaike information criterion (AICc). If only one model had an AICc > 2 with respect to the rest of the models, it was considered the best model. When differences between several models had an AICc < 2.0, they were considered approximately equivalent in explanatory power (Burnham and Anderson, 2002). In this case, we quantified the relative importance of the predictor variables included in the subset of best-fitting models with AICc < 2.0 and calculated the full-average model (Burnham and Anderson, 2002). All statistical analyses were conducted in R environment (R Development Core Team, 2012) using the additional packages “lme4” (Bates et al., 2012) and “MuMIn” (Barton, 2012).

3. Results

3.1. Abundance of seed predators

Two mice species were detected in the census: *A. sylvaticus* and *M. spretus*. The frequency of mice capture per site was higher in Maranchón than in Torremocha especially in 2009. The lowest

frequency was found in the mature woodland remnant of Torremocha in both years and the highest in the mature woodland remnant of Maranchón in 2009 (Table A1 in appendix A). The granivore birds detected in the census were *Fringilla coelebs*, *Lullula arborea*, *Serinus serinus*, *Emberiza* sp., *Carduelis cannabina*, *Carduelis carduelis* and *Alauda arvensis*. Granivore bird density varied between each year-site-habitat combination, and the highest density was found in the old fields of Maranchón in 2011 (Table A1).

3.2. Water, nitrogen soil content and canopy openness models

The abiotic variables studied varied mainly at the local scale. Thus, among the factors analyzed in the GLMs microhabitat was the most relevant, as shown in Table 1. The variation of the abiotic variables at the regional scale was rather reduced and no consistent patterns of variation between habitats were found. Soil moisture content did not vary at the regional scale and the significant effects found for nitrogen content and light availability were context-dependent (site × habitat) as shown in Tables 1 and 2. The tree studied abiotic variables, moisture content, total nitrogen and canopy openness significantly varied among microhabitats. Male and female juniper canopies were the microhabitats with greatest soil moisture and nitrogen content followed by shrubs and open gaps. Maximum values of canopy openness were reached in open gaps. However a significance interaction effect between microhabitat and habitat was found for canopy openness due to a more open canopy of the junipers in woodland remnants than in old fields (Tables 1 and 2).

3.3. Understory and tree cover

Understory cover was greater at Maranchón than at Torremocha at the microhabitat and at the plot level (Fig. 2B, Table A.2). Understory cover was also greater in recently colonized old fields than in mature woodlands especially beneath the canopy of junipers, which was consistent at the two study sites. The Torremocha woodland was the habitat with the lowest understory cover, and recently colonized old fields in Maranchón had the highest understory cover (Fig. 2B). At the plot level the greatest understory was found in the old fields located at Maranchón whereas the greatest tree cover was found in Torremocha woodland (Table A.2).

3.4. Post-dispersal seed removal percentages and seed removal modeling

We detected no seed removal in the excluded seed depots. Thereby our results on seed removal can we be attributed to seed predators present in the study area. The total percentage of seed removal was $23 \pm 0.03\%$ (Mean ± S.E.). Seed removal was higher in Maranchón than in Torremocha (Mean ± SE: $29.40 \pm 1.09\%$ and $17.28 \pm 1.36\%$, respectively) and in recently colonized old fields than in remnant woodlands (27.0 ± 2.29 and 20.06 ± 1.95

respectively) at both sites. However, differences between habitats were greater at Maranchón than at Torremocha. The woodland of this locality had the lowest seed removal ($16.71 \pm 1.64\%$) as shown in Fig. 2A. Seed removal percentages were generally higher under male and female Spanish juniper canopies, than under shrubs or in open gaps (Fig. 2A). Seed removal percentage was similar for the seed clumping type of carnivore and thrushes ($23.52 \pm 1.6\%$ and $22.94 \pm 1.53\%$, respectively). Total seed removal percentage was similar in the two studied years (2009: $23.40 \pm 1.73\%$ and 2011: $23.16 \pm 1.48\%$).

The optimum structure for random effects included plot with an effect on the intercept of the model and an effect on the slope of microhabitat. This means that the percentage of predation occurring in each microhabitat changed between plots. For the fixed effects structure, we obtained three models with $AICc < 2$. The three models included the variables site and habitat full crossed with their interaction, while the variables seed clumping type and understory cover at the microhabitat level were only included in one model each (Table 3A). As all three models had equivalent explanatory power; we performed a model averaging procedure to determine the importance of each predictor variable. The variables site, habitat and the interaction among them had a relative importance of 1, while the variables seed clumping type and understory cover had a relative importance of 0.29 and 0.19, respectively. Thus, the most relevant effect was the interaction between site and habitat, according to which post-dispersal seed predation was greatest in the old fields located in Maranchón (Table 4). The random effect of plot introduced a standard deviation of 0.7 on the parameter estimate of the intercept of the model (Table 4). The microhabitat which presented the strongest random effect due to plot was the female canopy followed shrubs and finally open gaps.

3.5. Recruitment patterns. Seedling presence probability and seedling abundance models

A total of 66 seedlings was recorded in the study area (42 in 2009 and 24 in 2011). Most seedlings were found under female and male juniper canopies (62% and 21% respectively), followed by the shrub microhabitat (17%), and no seedlings were found in open gaps (Fig. 2C and E).

Model selection for seedling presence obtained one model with $AICc < 2$. This included the fixed variables site, habitat and canopy openness (Table 3B). The random effect of plot only affecting the intercept of the model was the best fit to the data, and the variance introduced by each plot on the intercept of the model was very low (Table 5). Torremocha and woodland remnants presented the highest probability of seedling occurrence. The probability of seedling occurrence was negatively correlated to canopy openness (no seedlings were recorded in open gaps where canopy openness is maximum c. 1) as shown in Fig. 2C and E.

Table 1
General linear model on abiotic environmental variables.

	DF	Water			Nitrogen			Canp.Op		
		Resi. Dev.	% Dev.	P-val	Resi. Dev.	% Dev.	P-val	Resi. Dev.	% Dev.	P-val
Null		45.514			954.43			5.91		
Site	1	45.41	0.10	0.657	826.17	13.44	<0.001*	5.87	0.68	0.092
Hab.	1	44.567	0.84	0.206	783.6	5.15	0.0083	5.85	0.34	0.238
Microhab.	3	37.273	7.30	0.003*	501.08	36.05	<0.001*	1.25	78.63	<0.001*
Site x Hab	1	36.935	0.34	0.422	468.27	6.55	0.02*	1.18	5.60	0.0355*
Hab x Microhab	3	36.445	0.49	0.818	428.34	8.53	0.09	1.03	12.71	0.012*

Significance effects of factors are denoted with stars (*). DF: Degrees of Freedom. Resi. Dev.: Residual Deviance. % Dev: Percentage of deviance explained. P-val: P-value. Canp. Op: Canopy openness.

Table 2
Parameter estimates of the GLMs for the abiotic environmental variables.

	Water			Nitrogen			Canp.Op		
	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value
Intercept	0.86	0.25	0.001*	4.78	0.87	<0.001*	0.97	0.04	<0.001*
Torreño	-0.07	0.23	0.764	-1.25	0.78	0.114	-0.01	0.04	0.768
Old fields	-0.25	0.37	0.496	1.37	1.24	0.271	-0.03	0.06	0.614
Female	0.62	0.32	0.060	4.83	1.11	<0.001*	-0.47	0.05	<0.001*
Male	0.83	0.33	0.016*	6.49	1.11	<0.001*	-0.58	0.05	<0.001*
Shrub	0.60	0.32	0.070	1.65	1.11	0.140	-0.47	0.05	<0.001*
Torreño × Old fields	0.26	0.33	0.430	-2.56	1.56	0.023*	0.11	0.05	0.039*
Old fields × Female	-0.02	0.46	0.970	-1.85	1.56	0.240	-0.21	0.08	0.007*
Old fields × Male	0.00	0.46	0.100	-3.71	1.56	0.02*	-0.03	0.08	0.704
Old fields × Shrub	-0.37	0.46	0.425	-0.64	1.56	0.700	0.01	0.08	0.918

Missing levels “Maranchón”, “Woodland remnant”, “open” and their interactions are included in the intercept. Canp.Op: Canopy openness.

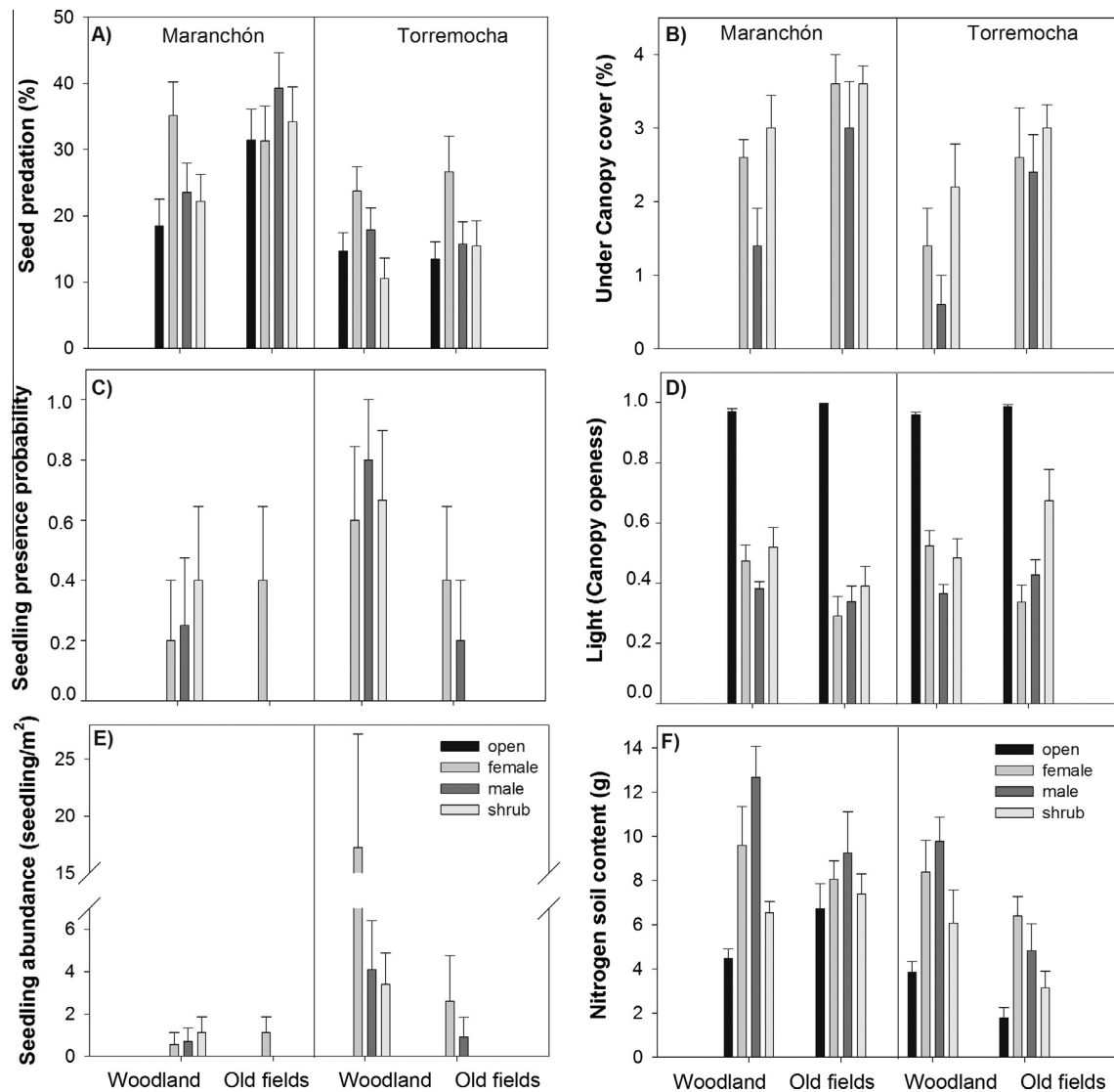


Fig. 2. Response variables post dispersal seed predation, probability of seedling presence and seedling abundance are represented on the left-hand side of the panel (A, C, E, respectively). The covariables undercanopy cover, Canopy openness, and nitrogen content are represented on the right-hand side of the panel (B,D,F).

Model selection for seedling abundance obtained two models with AICc < 2. The first model included the variables site, canopy openness and nitrogen soil content, while the second model added the effect of microhabitat (Table 3C). According to the averaged estimates of the two models, Spanish juniper seedlings were more abundant in microhabitats with greater nitrogen content and with

greater canopy openness. It is worth to be noted that, in this case, the maximum value of canopy openness was lower than in the model performed to explain seedling presence probability. This was due to the lack of seedlings in the sampling stations located in open microhabitats which had the maximum canopy openness (only sampling stations with at least one seedling were considered

Table 3
Model selection for seed predation, and seedling presence and abundance.

(A) Sd. Remv	Mods	S	H	SxH	MH	UCC	SCT			K	Loglik	AICc	Delta	W*
	1	×	×	×						14	−1529.75	3088.05	0.00	0.52
	3	×	×	×		×				15	−1529.29	3089.20	1.15	0.29
	2	×	×	×			×			15	−1529.70	3090.03	1.98	0.19
	W _i	1	1	1		0.29	0.19							
(B) Sdl pres	Mods	S	H	SxH	MH	UCC	Water	N	Canp.Open	K	Loglik	AICc	Delta	W*
	1	×	×						×	5	−32.09	75	0	1
(C) Sdl Abun	Mods	S	H	SxH	MH	UCC	Water	N	Canp.Open	K	Loglik	AICc	Delta	W*
	1	×						×	×	5	−16.01	46.30	0.00	0.71
	2	×			×			×	×	7	−12.39	48.11	1.81	0.29
	W _i	1			0.29			1	1					

(A) Post-dispersal seed removal; (B) probability of seedling presence; (C) seedling abundance. Each column represents a different predictor variable (S, site; H, habitat; SxH, site x habitat interaction; UCC, Under canopy cover; SCT, Seed Clumping Type; Y, year). K: number of parameters. W_i: Akaike Weight of the model. W*: Relative importance of variables. The cross indicates the variable was present in the model.

Table 4
Averaged estimates and standard errors for the seed removal experiment.

Fixed effects	Estimate	SE
Intercept	−1.76	0.17
Maranchon	0.25	0.24
Old fields	−0.17	0.24
Maranchón × Old fields	1.03	0.33
Under canopy cover	−0.08	0.07
Clumping type carnivore	−0.02	0.07
Random effects		
		SD
Intercept		0.70
Female tree		1.53
Male tree		1.17
Shrub		1.34

Missing estimates for the levels “Torremocha”, “Woodland remnants” and their corresponding interaction terms are comprised in the intercept.

Table 5
Estimates and standard errors seedling presence and seedling abundance.

	Estimate	SE
Seedling presence		
Fixed effects		
Intercept	1.48	0.94
Torremocha	1.54	0.66
Old fields	−2.08	0.70
Canopy openness	−5.09	1.70
Random effects		
		SD
Intercept	3.12 e−06	
Seedling abundance		
Fixed effects		
Intercept	−2.03	0.62
Canopy openness	4.13	0.89
N	0.15	0.03
Torremocha	1.27	0.33
Male	−0.78	0.24
Shrub	−0.46	0.27
Random effects		
		SD
Intercept	0.31	

Missing estimates for the levels “Maranchón”, “Woodland remnants” and “Female” are comprised in the intercept.

to model seedling abundance, see Section 2.8). *Torremocha* site presented higher seedling abundance than Maranchón, and the most favorable microhabitat was the under female Spanish juniper canopy, followed by shrubs and the male juniper canopy (Table 5), (Fig. 2).

4. Discussion

Variation at the regional scale played an important role in the post-dispersal seed removal pattern as we hypothesized. Seed removal was greater in old fields than in mature woodland remnants, which agrees with other studies (Chapman and Chapman, 1999; Nepstad et al., 1996; Matías et al., 2009). However, we found an interaction effect between site and habitat type that may be due to differential management and landscape structure. Contrary to our hypothesis and previous works (Dupouey et al., 2002), former farming activities performed in old fields did not affect seedling abundance, which was higher in microhabitats with intermediate levels of nutrient and canopy openness. Thus, seedling abundance was mainly controlled by factors operating at the local spatial scale as also predicted. However, a relevant effect of regional scale (site) was also found, suggesting that other factors than those measured in this study varying at the landscape scale (e.g. plant fecundity) could still be relevant in determining seedling establishment patterns (Clark et al., 1998). Overall our results suggest that biotic factors rather than abiotic ones control ecosystem recovery in non intensive old fields.

4.1. Post-dispersal seed removal increases seed limitation in abandoned fields

Post-dispersal seed predation is a major constraint in the recovery of degraded lands (Santos and Telleria, 1994; Torre and Diaz, 2004), and our study system is not an exception (Ostfeld et al., 1997; Wijdeven and Kuzee, 2000). Thus, a higher percentage of seed removal was found in recently colonized old fields than in mature woodland remnants coinciding with the results obtained for seed predators abundance. Contrary to our expectations seed clumping type and variation at the local spatial scale (i.e. microhabitat) did not play an important role in the seed removal pattern found. According to Hulme (1993,1994), negative density dependence processes are rarely found for seeds larger than 10 mg. Spanish juniper seeds are c. 3 times heavier than this threshold which could explain the reduced importance of seed clumping in explaining the seed removal pattern observed. Thus, Spanish juniper seeds may not suffer negative density dependence on greater seed clumps due to their seed size.

Microhabitats with greater seed availability and canopy cover are expected to suffer higher seed predation (Manson and Stiles, 1998; Hulme, 1993). Our results match these expectations, as seed predation under female juniper canopies and in open gaps tended to be the greatest and the lowest, respectively. However, this variable was not relevant in explaining the post-dispersal seed removal pattern. We argue that the effect of microhabitat on the removal pattern was reduced due to the random variability occurring at

each plot, a mesoscale between the regional and local spatial scale, which modulated seed removal occurring in each microhabitat. Understory cover at the plot level could be part of that variability, as this variable greatly influences the predation risk perceived by small mammals and their movement pattern between individual microhabitat features (Kotler and Brown, 1988; Kotler et al., 1991; Vásquez et al., 2002). According to the so-called optimal foraging theory, rodents are expected to preferentially select female juniper canopies for feeding, as this microhabitat has a higher seed density than others (Hulme, 1994). However, if rodents have to travel through an open plot to reach the female canopy, the predation risk could be too high, and suboptimal microhabitats from a food abundance perspective would be preferred for being safer (Lima and Dill, 1990; Verdolin, 2006). This is supported by the interaction effect between site and habitat found at the regional scale which seems to be related to understory cover at the plot level and at the local scale (Manson and Stiles, Hulme, 1993). Old fields in Maranchón and the woodland remnant in Torremocha were the habitat-site combinations with the greatest and lowest seed predation, respectively matching the understory pattern found. Additionally it has been argued that the vicinity of cereal crops could reduce seed predation on adjacent patches, as rodents could prefer to use crops for foraging (Todd et al., 2000; González-Varo et al., 2012). This is concordant with the observed pattern in which seed predation was lower at the site where old fields and active croplands formed a mosaic structure (i.e. old fields in Torremocha).

4.2. Former agricultural land use did not modify soil suitability for recruitment

Biotic and abiotic process operating at different spatial scales determine plant recruitment (Gómez-Aparicio, 2008). We predicted the local scale would be relevant in determining seedling establishment patterns and additionally the regional scale, i.e. habitat type, may had an indirect effect due to modifications in soil conditions as a result of former farming activities (Flinn and Marks, 2007). Although these predictions were confirmed, the effect of regional scale did not seem to be due to the impact of former agricultural activities on soil suitability, as only the probability of seedling presence and not seedling density was affected by habitat type. Thus, we found no variation in seedling abundance at the regional scale between old fields and mature woodlands. This result is in agreement with our previous findings on Spanish juniper seed germination and seedling survival (Escribano-Avila et al., 2013) and with the lack of differences found in soil nitrogen, moisture soil content and canopy openness at the regional (habitat) scale in this study. Consequently, soil properties relevant for seed germination and seedling survival did not seem to have been modified by former farming activities and did not limit plant recruitment.

Despite that seedling abundance was controlled by microhabitat suitability, specifically nitrogen content and canopy openness which were optimal beneath female juniper canopies (Montesinos et al., 2007; Gimeno et al., 2012b; Cambecèdes et al., 2013), the variable site also played a relevant role in the recruitment process. According to Clark et al. (1998), some variables varying at the landscape scale are critical for plant recruitment, i.e. reproductive tree density, fecundity and seed dispersal. In this study such variables were higher at the site where more abundant seedlings were found (Escribano-Avila et al., 2012) which has also the lower predator abundance and post-dispersal seed removal.

4.3. Biotic rather than abiotic factors controls plant recruitment in old fields offering opportunities for ecosystem recovery

In our study site biotic factors, seed dispersal and post-dispersal seed removal, seem to be more important than abiotic factors in

controlling ecosystem recovery in old fields. According to previous works (Cramer et al., 2008), biotic factors control ecosystem recovery in old fields when the abiotic threshold of degradation related to land use intensity is not passed. Old fields that were abandoned during the mid-twentieth century in developed countries were never subjected to intensive agriculture practices, due to their low productivity (Pinto-Correia and Mascarenhas, 1999), thereby being their recovery likely controlled by biotic factors rather than abiotic ones. Restoration practices necessary to amend biotic factors, such as seed limitation, are less costly in time and money than abiotic ones (e.g. soil nutrients content or structure). This fact, together with predictions of increase in land abandonment in low productive areas (Rousenvell et al., 2006) makes old fields especially relevant from an ecosystem recovery perspective.

5. Conclusions

Spanish juniper recruitment was controlled by factors operating at the studied hierarchical spatial scales. The regional spatial scale was relevant for biotic interactions i.e. seed dispersal and post-dispersal seed predation, which controlled seed availability in a defined spatial pattern, whereas seedling abundance was mainly controlled by environmental suitability varying at the local spatial scale. Our results also show that post-dispersal seed removal increased seed limitation, a pervasive constraint for plant recruitment in old fields, with more intense seed removal in old fields with greater shrub cover, which seems to be a generalized pattern. Soil environmental variables did not vary at the regional scale due to previous farming activities, and consequently, did not constrain seedling establishment. This may be a general pattern for old fields not previously subjected to intensive farming activities and made such old fields interesting targets for ecosystem recovery.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.06.021>.

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