

# Diverse guilds provide complementary dispersal services in a woodland expansion process after land abandonment

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## Summary

1. Land abandonment due to increasing depopulation of rural areas is an ongoing trend in developed countries worldwide. Abandoned lands represent an opportunity for ecosystem recovery, an urgent need for biodiversity conservation. Seed dispersal services provided by animals are a key feature for this process. Different dispersers may differentially contribute to plant recruitment under different ecological conditions, leading to complementary dispersal services.

2. We studied the dispersal services, quantified as the contribution to plant recruitment, provided by the main dispersal guilds of Spanish juniper *Juniperus thurifera* L.: small-to-medium-sized strongly frugivorous birds (thrushes) and medium-to-large-sized carnivorous mammals (red fox and stone marten). To do this, we studied seed fate from seed dispersal to seedling survival during 2 years and estimated seed dispersal effectiveness (seedlings recruited per m<sup>2</sup>) in two ecological contexts derived from ecosystem recovery after a historical period of degradation: remnant woodlands and old fields.

3. Results showed a clear shift in the contribution to plant recruitment between these guilds, resulting in complementary and non-redundant dispersal services. Thrushes were the main contributors to plant recruitment in woodlands (73%), leading to population growth but with a reduced impact on the colonization of old fields where carnivores contributed to 80% of recruitment (42% red fox, 38% stone marten). The dispersal complementarity observed for thrushes and carnivores is a consequence of their functional diversity, mainly driven by their differences in feeding and movement behaviour.

4. *Synthesis and applications.* The combination of short-distance, strongly frugivorous dispersers (e.g. passerine birds) together with big generalist frugivores with long-distance movements (e.g. carnivorous mammals) maintained (i) effective seed dispersal services in remnant woodlands and (ii) the connectivity between patches promoting old fields colonization and woodland expansion. Thus, it is in heterogeneous landscape mosaics ecosystems (e.g. agro-environments) where functionally diverse disperser communities play a key role in ecosystem recovery. By performing effective dispersal services across an array of habitat types, functionally diverse disperser communities assist natural restoration of human-impacted ecosystems all over the world. Thus, dispersal communities provide an important ecosystem service that may replace costly human-mediated restoration projects.

**Key-words:** carnivores, context dependence, dispersal community, ecosystem recovery, forest expansion, functional redundancy, *Juniperus thurifera*, old fields colonization, seed dispersal effectiveness, thrushes

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## Introduction

Habitat degradation is occurring at an unprecedented rate, which makes ecosystem recovery an urgent need to sustain biodiversity and assure the provision of goods and services (MEA 2005). Land abandonment is an ongoing trend in developed countries, due to increasing depopulation of rural areas, and abandoned lands represent an opportunity for ecosystem recovery (Lamb, Erskine & Parrota 2005). One of the most limiting constraints in the restitution of ecosystems in abandoned lands is the recovery of forest structure and complexity (Cramer, Hobbs & Standish 2008). Restoration projects involving plantation of dominant tree species have been carried out in many areas with good results (see Brunet 2007). However, these projects are costly, especially when large areas are to be recovered. Animal seed dispersers can provide a valuable ecosystem service in facilitating ecosystem recovery after land abandonment, especially when fleshy fruited plants are the dominant species. In this regard, the arrival of pioneer trees to newly abandoned land is often the most critical phase (Debussche & Lepart 1992; Duncan & Chapman 1999), since specialized frugivores often avoid open areas with no fruit availability. Moreover, the arrival of these pioneer trees plays a critical role in ecosystem recovery, since they serve as perches for frugivorous birds and act as recruitment foci favouring colonization and spontaneous succession (Chazdon 2003; Lamb, Erskine & Parrota 2005).

Seed dispersal of many tree and shrub species is performed by a diverse array of animals that feed on fruits and regurgitate or defecate intact seeds (Howe & Smallwood 1982). Different species or guilds forming a dispersal community have different morphological and behavioural traits that influence the quantity of seeds dispersed and the probability of recruitment of those seeds (Schupp, Jordano & Gomez 2010). For instance, body size is positively related to the amount of seeds dispersed per visit, gut passage time, home range size and dispersal distance (Jordano *et al.* 2007; Nathan *et al.* 2008). The particular use of specific microhabitats and landscape elements, such as sleeping or reproduction sites, determines seed deposition patterns (Russo, Portnoy & Augspurger 2006), which greatly affects the probability of recruitment of dispersed seeds (Wenny & Levey 1998). Thus, morphological and behavioural traits determine both quantity (number of seeds dispersed) and quality (probability of recruitment of dispersed seeds) of seed dispersal, and with it the seed dispersal effectiveness (quantity  $\times$  quality), defined as the contribution of dispersal agents to plant recruitment (Schupp, Jordano & Gomez 2010).

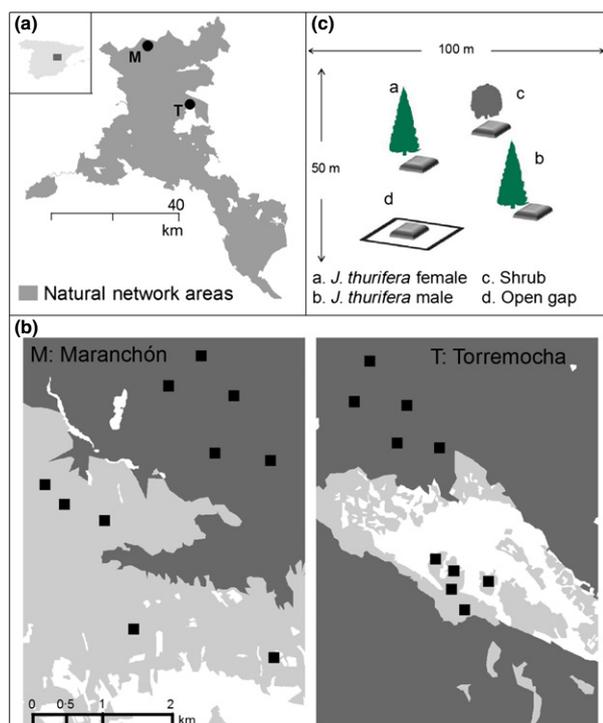
The effectiveness of the different members of a dispersal community provides important information for plant population ecology and evolutionary biology. However, despite its importance, the estimation of seed dispersal effectiveness has been tackled only in a modest number of

studies and remains an elusive goal (Howe & Miriti 2004). The evidence available shows that dispersal communities are usually composed of dispersers that contribute differentially to plant recruitment, with dispersal services often relying on few key dispersers, which suggests that dispersal communities may be complementary rather than redundant (Brodie *et al.* 2009; Calviño-Cancela & Martín-Herrero 2009; McConkey & Brockelman 2011). Moreover, it has been suggested that the relative contribution of a particular disperser to plant recruitment may change depending on the environmental context (Calviño-Cancela & Martín-Herrero 2009; Schupp, Jordano & Gomez 2010). However, empirical evidence regarding the context dependence of dispersal effectiveness is rather limited, and it has rarely been tackled explicitly with adequate replication, in spite of its ecological and evolutionary importance (Schupp, Jordano & Gomez 2010). Certainly, more information regarding the differential contribution to plant recruitment of different dispersers and how such contribution may change under different ecological contexts is needed to better understand the consequences of seed dispersal (Agrawal *et al.* 2007). From an applied perspective, two specific tasks are especially urgent to guide conservation priorities and promote ecosystem recovery, namely: (i) to decipher whether the contribution of different dispersers to plant recruitment is redundant or complementary under different ecological contexts and (ii) to identify key dispersers, that is those contributing disproportionately to plant recruitment, in the different stages of ecosystem recovery (Mills, Soulé & Doak 1993; Schupp, Jordano & Gomez 2010).

The aim of this study was (i) to determine the contribution of a varied dispersal community, (ii) to evaluate how such contribution may shift under different ecological scenarios derived from land-use abandonment and (iii) to provide useful information to guide ecosystem recovery. For such purpose, we used Spanish juniper *Juniperus thurifera* L. remnant woodlands and old fields recently colonized by the species as a result of land abandonment (Olano *et al.* 2008). The recovery of Spanish juniper woodlands and the colonization of old fields is being mediated by two main dispersal guilds: thrushes (*Turdus viscivorus*, *T. philomelos*, *T. merula*, *T. iliacus*, *T. pilaris*) and carnivores (*Vulpes vulpes* and *Martes foina*) (Santos, Tellería & Virgós 1999; Escribano-Avila *et al.* 2012). These guilds differ in morphology and behaviour, which may result in different contributions to Spanish juniper recruitment. Thrushes are small-sized (65–130 g) strongly frugivorous birds. They track the landscape and select patches with high abundance of fruits, avoiding open areas where fruiting trees are scarce (Jordano 1993; Santos, Tellería & Virgós 1999; García, Zamora & Amico 2011), and dispersing seeds over short distances (0–500 m) (Jordano *et al.* 2007; Breitbach *et al.* 2012). On the other hand, carnivores are medium-to-large-sized mammals (1–6 kg) and generalist feeders that consume fruits opportunistically (Genovesi, Secchi & Boitani 1996;

Díaz-Ruiz *et al.* 2013). They occupy large home ranges that include different habitat types, such as forests, open areas and farmlands (Genovesi, Sinibaldi & Boitani 1997; Goldyn *et al.* 2003), and have the ability to disperse seeds over long distances (1–2 km) (Rodel & Stubbe 2006; Jordano *et al.* 2007; González-Varo, López-Bao & Guitián 2013).

Hence, according to their contrasting body size, feeding behaviour and habitat use, we predict that (i) thrushes would be the main contributors to plant recruitment in woodland remnants, whereas (ii) carnivores would be the main contributors in old fields. Thus, overall we predict that (iii) the contribution of thrushes and carnivores to plant recruitment would shift in woodlands and old fields, resulting in complementary and thereby non-redundant, dispersal services. In order to evaluate our predictions, we estimated seed dispersal effectiveness (quantity  $\times$  quality) of thrushes and carnivores using a spatially and temporally replicated design. Specifically, seed dispersal quantity and quality data were used to build a stochastic model that returns the amount of seedlings per square metre contributed by dispersers in each microhabitat within each habitat studied.



**Fig. 1.** (a) Location of the study areas. (b) Spatial arrangement in the landscape of mature remnant woodlands (dark grey), recently colonized old fields (light grey) and cultivated areas (white). Black squares represent the 100  $\times$  50 m plots where the sampling stations used in the experiments were located. (c) Simplified representation of the arrangement of the four sampling stations established in each type of microhabitats in a sampling plot.

## Materials and methods

### STUDY AREA AND STUDY SPECIES

This study was conducted in the surroundings of two protected areas of the Natura network, Alto Tajo and Parameras de Maranchón, Hoz de Mesa y Aragoncillo (centroid 40°58'N, 2°7'W Guadalajara province, central Spain) where we selected two study areas, Maranchón and Torremocha del Pinar (Fig. 1a). The two study areas are separated by 20 km and have similar climatic conditions and a mean elevation of 1278 m a.s.l. The climate is continental Mediterranean with an annual rainfall of *c.* 500 mm, a pronounced summer drought and extreme cold winters. 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). Snowfalls occur from November to April (data from the nearest meteorological station in Molina de Aragón located 20 and 40 km from Maranchón and Torremocha del Pinar respectively, www.aemet.es).

Spanish juniper is a tertiary relict dioecious tree with a distribution confined to the western Mediterranean Basin (Terras *et al.* 2008). It is the dominant species in low-density woodlands (Gauquelin *et al.* 1999) with trees ranging from 3 to 10 m in height and 1 to 10 m in canopy width. Flowering occurs at the end of winter, and wind-pollinated female cones take 20 months to mature, becoming fleshy blue arceutids with mean weight and size of  $0.55 \pm 0.19$  g and  $10.02 \pm 1.18$  mm, respectively, and mean number of seeds per arceutid of  $3.31 \pm 1.18$  (mean values  $\pm$  SD,  $N = 900$ ), with average seed weight of  $4 \pm 2$  mg ( $N = 2980$ ). Dispersed seeds take *c.* 16 months to emerge, reaching maximum emergence rates in the second spring after dispersal (Escribano-Avila *et al.* 2013).

The two main habitats studied were woodland remnants and old fields recently colonized by Spanish juniper. In mature woodland remnants (hereafter referred as woodlands), the relative cover of Spanish juniper canopy was *c.* 37% (ranging between 30% and 45%) with a high abundance of adult trees, and shrub cover varied between 5% and 30%. In the past, woodlands were devoted to logging and extensive grazing, and some woodland patches were destroyed due to agriculture and their conversion into pasturelands. This exploitation was drastically reduced or even abandoned by the second half of the 20th century as a result of human exodus (Olano *et al.* 2008). These old fields are currently being colonized by Spanish junipers that reach *c.* 9% canopy cover (ranging between 5% and 15%), with a low density of adult trees (0–4 individuals  $\text{ha}^{-1}$ ), and most individuals are newcomers. Active agricultural land devoted to crops is widespread in the landscape (Fig. 1b).

### SAMPLING DESIGN

Sampling areas and procedures varied for observational data (seed dispersal quantity, specified below) and experimental data. To experimentally assess seed predation, seedling emergence and survival of Spanish juniper, we established five plots (100  $\times$  50 m) in each habitat type per study site. The distance between old fields and woodlands was  $520.61 \pm 87.6$  m in Maranchón and  $472 \pm 58.23$  m in Torremocha, being such differences non-significant (Wilcoxon test,  $W = 13$ ,  $P$ -value = 1), and the distance between plots was *c.* 400 m. Within each plot, one sampling station was established in each of the four dominant microhabitats identified

(Spanish juniper female and male trees, shrubs and open gaps) for a total of 80 sampling stations (two sites  $\times$  two habitats  $\times$  five plots  $\times$  four microhabitats, see Fig. 1b,c).

#### SEED DISPERSAL QUANTITY

Thrush droppings and carnivore scats were considered as individual and comparable faecal deposits (hereafter faeces). In order to account for differences in faeces density (and thus detectability) between guilds and habitats and obtain reliable estimates of the quantitative component of seed dispersal, sampling effort and schemes varied between habitats and dispersers according to their abundance, habitat use and behaviour. In old fields, where faecal density was low for all dispersers, we sampled the whole area of the study plots for both mammal and thrush faeces (a total of five ha in 2 years). The sampling was performed along parallel transects within the plots, where the relative cover of each microhabitat was also recorded. In woodlands, the sampling effort was lower than in old fields due to higher faecal density of both guilds, especially for thrushes; accordingly, we surveyed 1.2 ha for carnivores vs. 0.43 for thrushes. In 2009, to sample seed dispersal by thrushes, we established three subplots (20  $\times$  50 m in size separated by 20 m) in each of the five experimental plots established in woodlands (a total of 15 subplots per study site; Maranchón and Torremocha) and we sampled ten 10  $\times$  1 m transects in each subplot in a random compass direction from Spanish junipers and from shrubs. In 2011, we surveyed two of the three subplots per plot with four 10  $\times$  1 m transects (one for each microhabitat: *J. thurifera* females and males, shrubs and open gaps). Transects were surveyed for thrushes faeces twice per each study year (during the dispersal season, November–December and February–March). The radius of the canopy of each tree and shrub was measured to estimate the surface beneath the canopy, assuming a circular shape. To quantify seed dispersal by carnivores in woodlands, we established one 2000  $\times$  3 m transect in each study site (Torremocha and Maranchón) running between the experimental plots (see Fig. 1). These two transects were surveyed fortnightly during the dispersal season (November–March in both study years), collecting all fresh faeces and recording the microhabitat where they occurred.

#### SEED PREDATION

Seed removal experiments were performed after the seed dispersal season in April 2009 and 2011. Two seed depots (Petri dishes with small holes for water drainage) with one clump of 18 seeds each and three depots with two clumps of two seeds each were placed at each sampling station ( $N = 80$ , see Fig. 1) mimicking the seed deposition patterns of carnivores and thrushes, respectively. Seed depots were placed 50 cm from one another and nailed to the ground with a wooden stick. Removal levels were estimated by counting the seeds remaining in each depot after 3, 5, 7 and 15 days, and calculating the predation rate as the percentage of seeds removed. Background seed loss due to rain, runoff, wind or invertebrates was evaluated with depots placed inside a wire-netting cage, to exclude vertebrate predators. No background seed losses (neither seed removal nor seed damage) were detected.

#### SEEDLING EMERGENCE AND SURVIVAL

Seeds were collected from carnivore ( $N = 1440$ ), and thrush ( $N = 480$ ) faeces were carried to the laboratory where pellet

material was removed and non-viable seeds discarded (seeds floating in water were considered unviable). Seeds were air-dried and stored at 4 °C until they were sown in the field. Seeds were sown at the Torremocha experimental stations ( $N = 40$ ) in April 2009 under the ground surface (30 mm depth) simulating the clumping patterns of dispersers (2 and 18 seeds per clump for thrushes and carnivores, respectively) and covered with a wire-netting cage. No seed removal or damage was observed for seeds protected with these cages in the seed predation experiment (see above); thus, we are confident that invertebrates did not affect the final rates of emergence and seedling survival. The cages were monitored periodically for 3 years, and seedling emergence and survival were recorded. For additional details, see Escribano-Avila *et al.* (2013).

#### ESTIMATION OF DISPERSERS CONTRIBUTION TO PLANT RECRUITMENT USING STOCHASTIC SIMULATION

The contribution of each disperser species or guild to recruitment in each studied microhabitat, habitat and site was estimated by means of stochastic simulations. In contrast to deterministic models, stochastic simulation allows us to take into account the stochastic nature of environmental conditions, thus better reflecting the nature and complexity of the recruitment process (Calviño-Cancela & Martín-Herrero 2009). Our model is an adaptation of the model used in Calviño-Cancela & Martín-Herrero (2009) and consisted of a series of life stages (dispersed seeds, surviving seeds, emergent seedlings and surviving seedlings) connected by a series of processes (seed dispersal, post-dispersal seed predation, seedling emergence and seedling survival), each with its own set of empirical transition probabilities measured in the field for each dispersal species/guild (see Fig. 2). The original set of transition probabilities for each process obtained in the field during the 2 years of study was resampled 500 times by random selection with replacement (Efron 1982; Manly 1998), and the final output of each simulation iteration was the result of the product of the randomly selected transition probabilities at each stage (number of seeds dispersed in each habitat and microhabitat by each disperser  $\times$  the probability of surviving predation  $\times$  the probability of seedling emergence  $\times$  the probability of seedling survival). Thus, we obtained the average number of 2-year-old seedlings per square metre (SDE) generated by each disperser in each microhabitat, habitat and site. The contribution to plant recruitment of each disperser in each habitat was the sum of the SDE values for each disperser in each microhabitat weighted by the relative cover of each microhabitat in the corresponding habitat. We also obtained the seed quantity (number of seeds dispersed per square metre) and seed quality (calculated, for simplicity, as SDE/quantity).

Goodness of fit of the model was assessed by comparing the seedling density predicted by the simulation model and that observed in the field using independent sampling. Natural seedling density in the study area was measured in June 2009 and 2011, when natural emergence peaks. Seedlings (from recently emerged up to 2 years old) were counted in sampling quadrats of 30  $\times$  30 cm in the four studied microhabitats with 15 and 10 replicates per microhabitat in 2009 and 2011, respectively. Seedling density was resampled 250 times per year, thus obtaining 500 values, and compared to the seedling density predicted by the model (500 iterations). We evaluated whether model predictions fell within the confidence limits of the empirical data (Loehle 1997).

## DATA ANALYSES

We used a generalized linear model with Gaussian error distribution to test whether overall SDE varied between sites, habitats and dispersers (including interaction terms). We plotted SDE landscape graphs to visualize the contribution to plant recruitment of each disperser and its relationship with the quantity and the quality components (Schupp, Jordano & Gomez 2010): a group of SDE landscape graphs for each microhabitat within each habitat and another for each habitat (pooling the contribution to recruitment in all microhabitats weighted by their relative cover). Statistical analyses and SDE landscape graphs were performed in R Environment (R Development Core Team 2012).

## Results

## STOCHASTIC MODEL INPUT DATA AND VALIDATION

Average seed dispersal, percentage of predation, seedling emergence and survival in each microhabitat within each habitat obtained by stochastic modelling for each dispersal agent are shown in Table 1. Seedling densities predicted by the stochastic model were similar to those observed in the independent sampling, except in the microhabitat underneath female trees where the model underestimated seedling density (see Supporting Information Fig. S1 for more details).

## SEED DISPERSAL EFFECTIVENESS PATTERNS

Seedling recruitment generated by the dispersal community did not vary significantly between the two study sites (Maranchón:  $110 \pm 65.4$  seedlings  $\text{ha}^{-1}$ ; Torremocha:  $150 \pm 118.9$  seedlings  $\text{ha}^{-1}$ ;  $F_{1,10} = 0.39$   $P > 0.05$ , Table 2). However, recruitment was *c.* 150 times greater in mature woodland remnants than in recently colonized old fields ( $258 \pm 109.5$  vs.  $1.8 \pm 0.8$  seedlings  $\text{ha}^{-1}$ , respectively;  $F_{1,9} = 15.98$   $P < 0.05$ , Table 2). This was mainly due to differences in dispersal quantity, which was much lower in old fields (Fig. 3). Dispersal quality was also greater in woodlands, although differences between the two habitats were not so great (Fig. 3). Suitability for recruitment in

woodlands was similar in all canopied microhabitats, but was significantly lower in open gaps. In old fields, shrubs had a higher suitability for recruitment than juniper canopies. All dispersers showed higher effectiveness in woodlands than in old fields, although there was a significant interaction effect between the most effective disperser and habitat type that was consistent at both study sites ( $F_{2,5} = 5.98$   $P = 0.047$ , Table 2).

The differential contribution to plant recruitment found in woodlands and old fields was related to differences in the dispersal quantity of the different dispersers in each habitat, their deposition pattern in each microhabitat and the relative cover of each microhabitat within each habitat. In woodlands, thrushes dispersed *c.* 3 and 6 times more seeds than red foxes and stone martens, respectively (Fig. 3), and deposited them mostly beneath female and male juniper canopies (Fig. 3), where suitability for recruitment was relatively high (Fig. 3). Thus, the greater dispersal quantity of thrushes together with their pattern of seed deposition beneath junipers made thrushes the most effective in woodlands, generating 565 seedlings  $\text{ha}^{-1}$  (Fig. 4). Red foxes and stone martens preferentially dispersed seeds beneath shrubs, which presented a similar suitability for recruitment to juniper canopies in woodlands (Table 1). However, both carnivore species dispersed fewer seeds than thrushes, making their contribution to plant recruitment lower than that of thrushes (159 and 50.5 seedlings  $\text{ha}^{-1}$  for red fox and stone martens, respectively, Figs 3 and 4). Both guilds dispersed fewer seeds in old fields, although carnivores dispersed a slightly higher quantity of seeds than thrushes. The deposition patterns among microhabitats were similar to those previously described for mature woodlands. However, the relative cover of microhabitats varied greatly between mature woodlands and old fields, with a much lower canopy cover of Spanish juniper in the latter (Fig. 3). The higher number of seeds dispersed by carnivores in shrubs, together with the greater suitability of this microhabitat for recruitment, made the red fox and stone marten the most important contributors to recruitment in old fields. These species generated 2.25 and

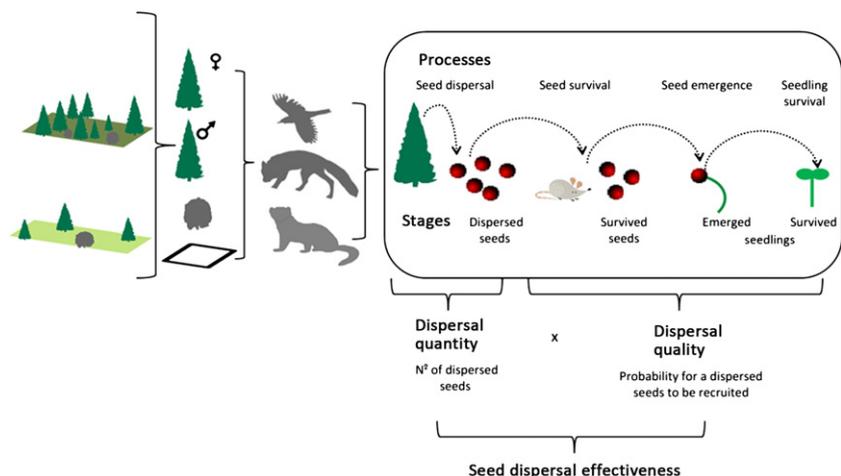


Fig. 2. Chart showing the stages and processes from the seed dispersal effectiveness framework studied in this work. Each stage is connected to the subsequent one by a transition probability determined by the corresponding process that was empirically studied for seeds dispersed by each dispersal species in each microhabitat and habitat.

**Table 1.** Mean  $\pm$  SE parameters used in the stochastic modelling

	Dispersal (seeds m <sup>-2</sup> )		% Predation		% Emergence		% Survival	
	Mean	$\pm$ SE	Mean	$\pm$ SE	Mean	$\pm$ SE	Mean	$\pm$ SE
W								
Open								
T	0.27	0.09	0.15	0.04	0.02	0.00	0.00	0.00
RF	0.31	0.18	0.18	0.02	0.02	0.00	0.30	0.02
ST	0.23	0.08	0.18	0.01	0.02	0.00	0.40	0.01
Female								
T	4.55	0.51	0.25	0.01	0.18	0.00	0.44	0.02
RF	0.28	0.30	0.34	0.19	0.26	0.01	0.53	0.00
ST	0.02	0.02	0.42	0.18	0.25	0.02	0.54	0.01
Male								
T	1.75	0.20	0.20	0.06	0.13	0.00	0.38	0.02
RF	0.21	0.15	0.21	0.01	0.11	0.00	0.75	0.04
ST	0.11	0.12	0.25	0.06	0.11	0.00	0.73	0.01
Shrub								
T	1.11	0.65	0.16	0.06	0.06	0.00	0.00	0.00
RF	1.14	0.46	0.18	0.09	0.16	0.00	0.77	0.01
ST	0.51	0.03	0.19	0.07	0.16	0.00	0.76	0.00
OF								
Open								
T	<0.001	<0.001	0.19	0.04	0.000	0.000	0.000	0.000
RF	<0.001	<0.001	0.10	0.14	0.000	0.000	0.000	0.000
ST	<0.001	0.001	0.06	0.08	0.01	0.02	0.25	0.35
Female								
T	0.14	0.16	0.36	0.06	0.13	0.00	0.10	0.00
RF	0.002	0.002	0.18	0.26	0.04	0.06	0.12	0.17
ST	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Male								
T	0.06	0.07	0.32	0.16	0.10	0.01	0.18	0.01
RF	0.001	0.001	0.15	0.21	0.05	0.07	0.29	0.41
ST	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Shrub								
T	0.03	0.05	0.31	0.12	0.09	0.01	0.43	0.004
RF	0.10	0.13	0.24	0.19	0.17	0.02	0.65	<0.001
ST	0.13	0.17	0.20	0.15	0.18	0.01	0.62	0.02

W, woodland; OF, old fields; T, thrushes, RF, red fox; ST, stone marten.

**Table 2.** Results of the generalized linear model with Gaussian error distribution to test the effect of site, habitat and disperser on seed dispersal effectiveness. Non-significant interactions between factors were excluded from the model

	d.f.	d.f. resid	F	P
Null		11		
Site	1	10	0.39	0.557
Habitat	1	9	15.98	0.01
Disperser	2	7	5.93	0.047
Habitat x Disperser	2	5	5.98	0.047

2 seedlings ha<sup>-1</sup>, compared to 1.1 seedlings ha<sup>-1</sup> derived from thrush dispersal activities (Fig. 4).

## Discussion

The dispersal services provided by the dispersal community of Spanish juniper were complementary rather than

redundant, owing to differences in feeding behaviour and movement ranges between dispersal guilds. Thrushes were by far the most effective dispersers in woodlands, leading to population growth, whereas carnivores were the most effective dispersers outside woodlands, promoting the colonization of nearby abandoned lands and leading to Spanish juniper expansion, as we predicted. The combination of both guilds led to the maintenance of dispersal services throughout the landscape, promoting ecosystem recovery, with no active restoration action being needed. The dispersal complementarity found in this and previous studies (Brodie *et al.* 2009; Calviño-Cancela & Martín-Herrero 2009; McConkey & Brockelman 2011) seems a general pattern and points out the importance of preserving the whole diversity of dispersal communities in order to assure dispersal functionality, resilience and recovery of ecosystems, especially in landscape mosaics resulting from human exploitation.

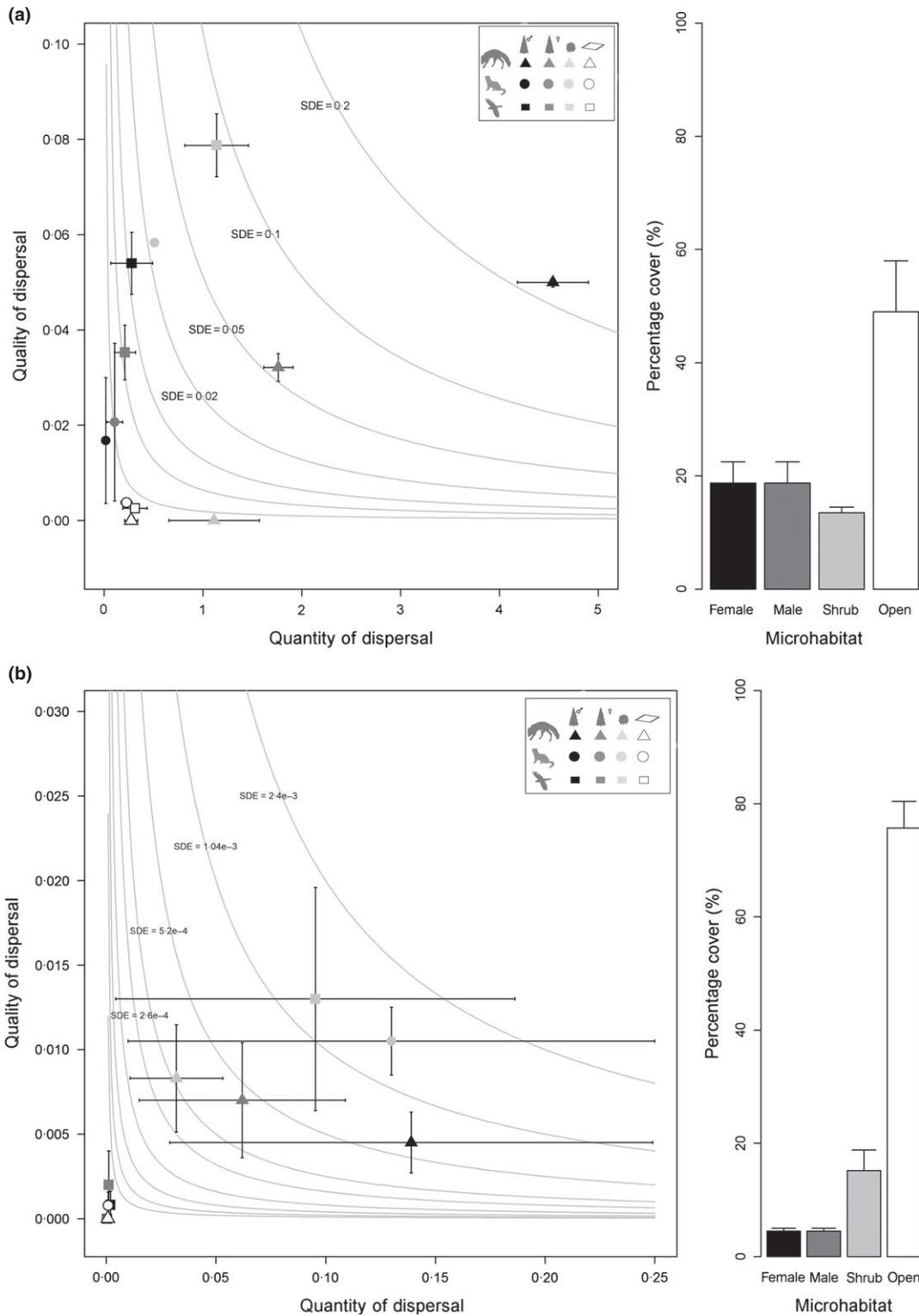
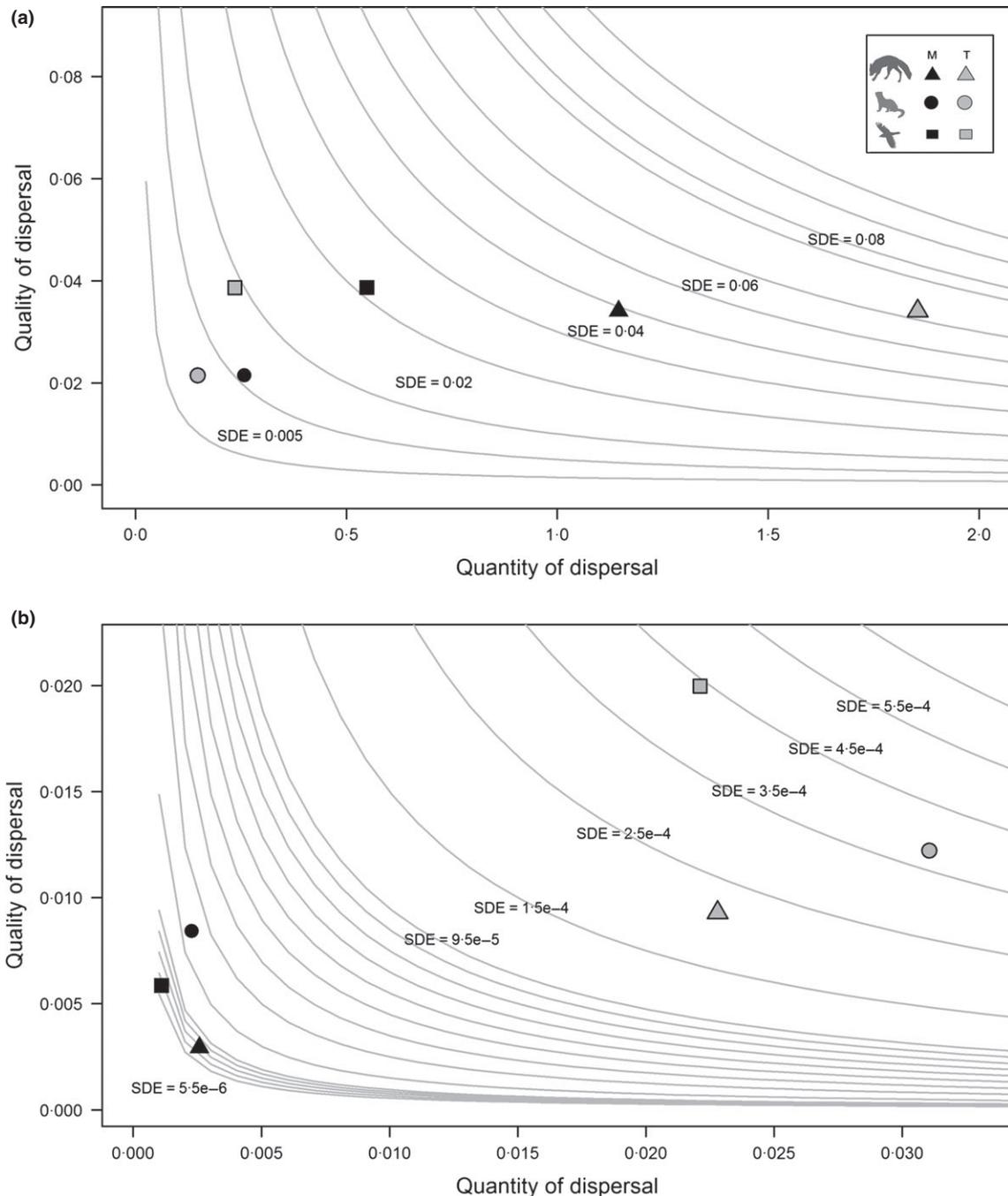


Fig. 3. Seed dispersal effectiveness (Mean  $\pm$ SE of quantity and quality of dispersal) indexed by seedlings per square metre generated for each disperser in each microhabitat in woodland remnants (a) and old fields (b), with the relative cover of each microhabitat shown on the right.

SHIFTS IN SEED DISPERSAL EFFECTIVENESS AND ITS IMPLICATIONS

Thrushes are small-to-medium-sized dispersers, strongly frugivorous, which have been previously described as the main

dispersal agents in forested environments with high availability of fruits (Jordano *et al.* 2007; McConkey & Brockelman 2011). Our results support such a statement, with thrushes contributing to *c.* 75% of total recruitment in woodlands. Such great contribution to recruitment was



**Fig. 4.** Overall seed dispersal effectiveness (seedlings) generated for each disperser in remnant woodlands (a) and recently colonized old fields (b), after pooling the SDE in all microhabitats, weighted by their relative cover in each habitat. Maranchón and Torremocha del Pinar study sites are indicated in black and grey, respectively.

mainly due to the amount of seeds dispersed by thrushes (dispersal quantity) that was approximately three times greater than the contribution of the two species of carnivores combined. Thrushes track fruit abundance, selecting patches and trees with larger crops (García, Zamora & Amico 2011) and feeding heavily on juniper fruits during the dispersal season (Escribano-Avila *et al.* 2012; Tellería, Carrascal & Santos 2014). Additionally, thrushes perform

flights between neighbouring perches, usually dispersing seeds from tens to a few hundred of metres, contributing to seedling recruitment around the canopy of conspecifics (Breitbach *et al.* 2012). This has likely favoured the spatial aggregation observed in the study area in remnant woodlands (Gimeno *et al.* 2011) and may promote spatial genetic structure at the local scale (Jordano *et al.* 2007). At the same time, the short-distance dispersal of thrushes and their avoidance of areas

with sparse vegetation (Jordano 1993; García, Zamora & Amico 2010) made thrushes less effective in old fields, where carnivores contributed *c.* 80% of recruitment.

Larger seed dispersers are not constrained by gape width (Wheelwright 1985) and mobilize more seeds per visit and over longer distances than smaller seed dispersers (Jordano & Schupp 2000; Spiegel & Nathan 2007; Escribano-Avila *et al.* 2012). These size-related features help to explain the greater contribution to plant recruitment of carnivores compared to thrushes in old fields. Carnivores are medium-to-large-sized dispersers, 25 times bigger than thrushes (average body mass) leading to the dispersal of bigger seeds, which have higher probability of recruitment than the smaller seeds dispersed by thrushes (Escribano-Avila *et al.* 2013). Carnivores are opportunistic frugivores, for which juniper fruits represent only a minor fraction of their diet. They prefer to feed on small mammals and arthropods (Genovesi, Secchi & Boitani 1996; Díaz-Ruiz *et al.* 2013) and actively search for those prey in their wide home ranges (Genovesi, Sinibaldi & Boitani 1997; Dekker, Stein & Heitkönig 2001). Such behaviour makes carnivores to be less reliable dispersers, as highlighted elsewhere (Escribano-Avila *et al.* 2013), but also favours long-distance seed dispersal, frequently exceeding 1–2 km from mother trees (González-Varo, López-Bao & Guitián 2013). This probably increased the amount of seeds dispersed by carnivores in old fields. Additionally, carnivores deposit their scats mostly under shrubs due to their scent-marking behaviour, used for territorial demarcation, generating a recruitment pattern not related spatially to former established junipers. This could help to explain the random spatial distribution of Spanish junipers previously observed in old fields in our study area, in contrast to the aggregated distribution observed in woodlands (Gimeno *et al.* 2011). Thus, carnivores play a critical role in moving seeds between woodland remnants and old fields due to their feeding behaviour and body size, favouring the colonization process, the genetic connectivity between remnant and expanding populations and, overall, the recovery of these degraded areas (Matías *et al.* 2010; López-Bao & González-Varo 2011; Peredo *et al.* 2013).

Debussche & Lepart (1992) suggested that the combination of different dispersal types for a given plant species may be a common feature, one being dominant at the local scale and the other at a larger scale, thus related to successional and invasive process, respectively. This pattern matches the functional complementarity detected for the dispersal community of Spanish juniper which seems to be driven by dispersers' feeding behaviour and movement range related to body size: small strongly frugivorous dispersers were responsible for dispersal services at the local scale, leading to population growth, while bigger generalist dispersers promoted dispersal at the larger scale, driving population expansion (Jordano *et al.* 2007; Spiegel & Nathan 2007).

#### THE LACK OF FUNCTIONAL REDUNDANCY ON DISPERSAL COMMUNITIES: IMPLICATIONS FOR FOREST REGENERATION AND RESILIENCE CAPACITY

Functional redundancy between components seems to be a common feature of ecosystems, which assures functionality even after some species become extinct (Lawton & Brown 1993). However, recent studies evaluating functional redundancy of seed dispersal communities, either with partial (Albrecth *et al.* 2013; Bueno *et al.* 2013; García *et al.* 2013) or with comprehensive measures of seed dispersal effectiveness (Brodie *et al.* 2009; Calviño-Cancela & Martín-Herrero 2009; McConkey & Brockelman 2011), have found that different dispersers provide complementary rather than redundant services to their host plants. Our results reinforce this evidence, and this is, to our knowledge, the first in which the contribution of the main dispersal guilds to plant recruitment has been comprehensively evaluated in different ecological contexts spatially replicated.

The lack of redundancy in dispersal communities can compromise plant recruitment if key dispersal species are lost (Traveset, González-Varo & Valido 2012 and references therein) which in degraded environments may seriously constrain the possibility of ecosystem recovery (Valiente-Banuet & Verdú 2013). In our study system, the extinction or severe decline of thrushes or carnivores would significantly compromise regeneration dynamics. Thus, the maintenance of a diverse dispersal community that includes species with a wide range of feeding behaviour (specialized and generalist frugivorous), movement patterns and body size may favour ecosystem recovery, providing resilience to anthropogenic-driven perturbations.

#### CONCLUSIONS

For natural vegetation recovery to proceed unaided in the newly available habitats derived from land abandonment, the ecological services provided by functionally diverse communities of animal seed dispersers become essential, in order to (i) secure recruitment in extant populations (e.g. remnant forests), which are the main seed sources in the landscape, and (ii) promote seed arrival in old fields, favouring colonization and expansion in newly available habitats. Small strongly frugivorous dispersers (e.g. passerine birds) and large generalist frugivores with long-distance movements (e.g. carnivorous mammals) can play these roles, enhancing ecosystem resilience. Thus, the conservation of a functionally diverse dispersal community should be considered a management priority for biodiversity conservation and passive restoration of woodlands and forests dominated by fleshy fruited species, especially in human-perturbed landscape mosaics which are highly frequent in developed countries.

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## Data accessibility

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.68gm7> (Escribano-Avila et al. 2014).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** Model comparison of predicted and independent seedling emergence.