

Seed Dispersal Patterns by Large Frugivorous Mammals in a Degraded Mosaic Landscape

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Abstract

Seed dispersal by Red fox (*Vulpes vulpes*), Stone marten (*Martes foina*), and Wild boar (*Sus scrofa*) was analyzed in an extensively degraded mosaic landscape in Sierra Nevada (SE Spain). The main objective was to determine whether seed dispersal by mammals was related to habitat degradation within a mosaic of adjacent degraded patches mixed with native forest and thereby to determine the potential role of mammals as seed dispersers in degraded landscape units. For three consecutive years, mammal feces were collected in the fruit production period, extracting all seeds of woody species found therein and analyzing their viability. Feces were collected in three different plots for each of five different landscape units: shrubland, native forest, and dense, cleared, and fenced reforestation stands. Seeds from 16 woody species (which represent more than a half of the total fleshy-fruited

woody species available) were recorded, although some agrarian species are also introduced in a low percentage of the scats. Seeds showed a high viability rate for all dispersed species, irrespective of the mammal disperser. No differences in species composition appeared in the overall landscape units or in the seed density between degraded habitats. Due to the small patch size, the high viability of dispersed seeds, and the large home range of the large mammals, these three animal species act as efficient seed dispersers for a diverse assemblage of woody plant species regardless of the habitat type within this degradation framework. This fact has important consequences for the biodiversity recuperation in these degraded habitats, principally in pine plantations.

Key words: Mediterranean habitats, Red fox, seed dispersal, seed viability, Sierra Nevada, Stone marten, Wild boar.

Introduction

Animal dispersers (e.g., birds, mammals, ants) are key in the configuration of plant communities, expanding existing populations, founding new ones, and creating a soil seed bank (Harper 1977; Fenner 1992; Venable & Brown 1993; Schupp & Fuentes 1995). Therefore, seed dispersers are among the first landscape architects because their activity determines the diversity, abundance, and spatial distribution of seed banks available to build plant communities (Herrera 1985).

Previous studies on the importance of zoochorous seed dispersal for the regeneration of woody species have been performed in undisturbed habitats such as the tropics (Dalling et al. 1998; Clark et al. 1999), central Europe (Heinken et al. 2002), or Mediterranean habitats (Debusche & Isenmann 1989; Herrera 1989). These studies provide valuable information concerning the importance of zoochory for regeneration of well-conserved plant communities. In fact, there is a solid body of knowledge on the ecology of seed dispersal by animals in Mediterranean

ecosystems (e.g., Herrera 1995 and references therein). However, little of this knowledge has been applied to restoration practices in these environments (but see Tellería et al. 2005). This “applied approach” to seed dispersal ecology is necessary to identify which combinations of disperser assemblages and landscape scenarios are the best for effective plant regeneration (Méndez et al. 2008).

In Mediterranean ecosystems, the long and intense human presence and an intense perturbation regimen have resulted in several phases of habitat degradation (Terradas 2001; Valladares et al. 2004). Therefore, the heavily used Mediterranean landscape does not correspond to a “fragment-matrix” structure (based on the classical Theory of Island Biogeography by MacArthur & Wilson 1967) but rather is composed of a mosaic of adjacent patches with different types of degradation (the “mosaic concept”; Wiens 1995). In the specific case of the Mediterranean mountains, the mosaic landscape is composed of patches of native mountain forest mixed with two types of landscape units degraded by human management: pine reforestation stands (with different degrees of management) and postfire shrublands. However, little information is available on how seed dispersal varies among different habitats in a mosaic landscape composed of adjacent patches with different types of degradation (but see Heinken et al. 2002; Schaumann & Heinken 2002).

Large carnivorous and omnivorous mammals (mammals hereafter) are considered potential seed dispersers of

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fleshy-fruited plants in Mediterranean habitats (Herrera 1989; Jordano et al. 2007). Furthermore, mammals have large home ranges and high retention time in the gut, which enable frugivorous mammals to be key vectors for long-distance dispersal (Hickey et al. 1999; Otani 2002; Jordano et al. 2007). These long-distance dispersal events determine the colonization capacity of vacant sites and the expansion of plant populations to different habitats (Cain et al. 2000; Nathan 2006). In this context, we examined, at the landscape level, the role of mammal endozoochory in relation to woody species biodiversity restoration within a mosaic of adjacent degraded patches mixed with native forest. With respect to selection of the landscape unit by seed dispersers in a mosaic landscape, we propose two alternative hypotheses: (1) the composition and structure of the landscape unit (the spatial pattern) will affect the seed dispersal (the process, *sensu* Turner 1989). Different plant species composition and structure of landscape units may impose diverging abundance and/or activity of mammals, leading to different density and diversity in dispersed seeds. In this case, we propose that the native forest would be expected to have a higher number of seeds dispersed by mammals because fleshy-fruited trees and shrubs are the most abundant here and mammals would presumably be spending more time foraging than in degraded landscape units. Alternatively, (2) the seed dispersal rate may be similar among the different habitats because patches are small in size and close together and the home ranges of mammals are broader than the distance between patches, in which case mammals might be expected to explore all landscape units within the mosaic landscape in a similar way. Because Mediterranean mountains are usually surrounded by extensive agricultural zones, we were also interested in the extent to which mammals introduce seeds of agrarian species into the landscape (Heinken et al. 2001, 2002, 2006).

In particular, we asked, (1) How efficient are mammals as seed dispersers of woody plants? Answering this question led us to determine: (a) the diversity and abundance of the dispersed seeds of woody species and (b) the viability of seed dispersal by mammals. (2) Do mammals disperse seeds in the same way among different habitats or do some landscape units have higher probabilities of receiving more or different seeds? (3) Do mammals introduce agrarian species from the anthropogenic landscape? In this case, are all habitats receiving a similar amount of seeds?

The novel aspect of our work is the systematic comparison of endozoochorous seed dispersal of woody species by a complete mammal disperser guild in habitats with different degrees of degradation. The identification of habitat and species selection patterns by mammals would provide a fuller understanding of the consequences of seed dispersal by mammals, allowing restorers to determine whether a certain habitat may be naturally restored or, on the contrary, which type of restoration practices would be necessary.

Methods

Study Site and Animal Species

The present study was conducted at the Sierra Nevada National Park (Granada province, SE Spain), surrounding the Trevenque Peak area (lat 37°5'N, long 3°28'W, 1,600–1,900 m above sea level), from September 2004 to February 2007. The climate is continental Mediterranean, with annual rainfall of 818 ± 86 mm ($\bar{X} \pm SE$ for 1990–2006) concentrated in autumn and spring. Winters are cold, whereas summers are hot and dry, mean temperatures of coldest (January) and hottest month (July) being 3.6 and 21.5°C, respectively. The bedrock is calcareous, and the predominant soils are regosols and cambisols (Delgado et al. 1989). The study area was a mosaic landscape composed of patches of five different landscape units: fragments of native forest and four degraded habitats (dense, cleared, and fenced reforestation stands as well as shrubland). The native forest was composed mainly of *Pinus sylvestris* var. *nevadensis* mixed with other trees such as *Taxus baccata* or *Acer opalus* ssp. *granatense* (mean tree density >4 m high was 114 individuals/ha) and a dense shrubby understory composed of different fleshy-fruited shrub species (*Berberis vulgaris* ssp. *australis*, *Crataegus monogyna*, *Juniperus communis*, and *Lonicera arborea*). Dense reforestation stands contained *Pi. sylvestris* and *Pi. nigra* with mean densities of 1,041 individuals/ha. Fenced stands were reforestation with exclosures against big ungulates (such as Wild boar) and with the same tree density as dense reforestation stands. Within cleared reforestation stands, timber was harvested in the year 2000, reducing tree densities to 521 individuals/ha. Shrubland was a postfire area dominated by *C. monogyna*, *Prunus ramburii*, *Salvia lavandulifolia*, and *Erinacea anthyllis*, with widely scattered trees. Other fleshy-fruited tree and shrub species present in the study area were *Sorbus aria*, *Arctostaphylos uva-ursi*, *Amelanchier ovalis*, and *Rubus ulmifolius*. Four *Rosa* species were present in the study area, but, because species identification using seeds is problematic, all *Rosa* species were pooled. Fleshy-fruited species (trees and shrubs) were principally found in native forest and shrubland, being very scarce in reforestation stands. The whole study area was composed of these five habitats, which are represented at a broad regional scale in Mediterranean mountains.

Each landscape unit was represented by three plots of similar size, with a mean value of 0.53 ha/plot and an average distance between the three plots of the same landscape unit of 688 m. Plot surface areas were calculated by Geographic Information System (GIS) using Global Positioning System (GPS) data (Leica SR 500; Leica Geosystems, Switzerland). The sum of the 15 plots was around 8 ha. The five different landscape units were mixed and close to each other, occupying an area of about 300 ha (near 2 × 2 km; Appendix).

The principal seed disperser mammals in the study area were Red fox (*Vulpes vulpes*), Stone marten (*Martes foina*), and Wild boar (*Sus scrofa*). Their diet is opportunistic and diverse, adaptable to the seasonal food availability in

Mediterranean areas (Rau et al. 1985; Calisti et al. 1990; Fedriani 1996; Schaumann & Heinken 2002), which makes them occasional seed dispersers (Herrera 1989). These species have overlapping feeding habits (Padial et al. 2002).

Collection of Feces

From September 2004 to April 2006, during the time of fruit production and seed dispersal, study plots were crossed by the same inspection route weekly, and all fresh fox and marten feces found were collected. In the same period, the third year (2006–2007; hereafter, 2006), the entire plot surface was inspected at roughly 10-day intervals to collect seed density data also, removing all fresh fox and marten feces detected in the plots. Evidence from the previous year led us to collect Wild boar feces also, although the literature does not consider this animal as efficient endozoochorous seed disperser for woody species (but see Génard & Lescourret 1985; Massei & Genov 2004). All habitats were carefully inspected to detect all feces independently of the habitat heterogeneity or disperser identity.

After the species producing each scat was morphologically identified, the substrate where it was deposited was recorded, assigning four categories: bare soil, rock, grass, and shrub. We kept the sample in an individual breathable plastic bag, carried it to laboratory, oven-dried it at 40°C for 3 days, and stored at room temperature until examination. Each sample was rehydrated and broken up to remove of all seeds, which were identified to the species level using a reference seed collection compiled from the study area.

Seed Viability Test

Each seed was submerged in water to test viability by the floating method. Floating seeds were assumed to be nonviable and therefore discarded, counting only nonfloating fraction and including them in further analyses. The remaining seeds were stored in a refrigerator at 6°C in petri dishes before the tetrazolium analysis (ISTA 1999), a more effective viability test. We used the six most abundant species found in feces: *Am. ovalis*, *Ar. uva-ursi*, *C. monogyna*, *Rosa* spp., *R. ulmifolius*, and *So. aria*, selecting 30 seeds/disperser from the fraction of the presumably viable seeds. The seed coat and pericarp were removed from all seeds, and endosperm plus embryo fraction were submerged in distilled water for 24 hours and later for 24 hours in a 1% 2,3,5-triphenyl-2H-tetrazolium solution. After this, seeds were then classified in three groups: (1) alive, when seeds were totally dyed; (2) limited viability, when red and white spots were distributed in the different tissues making the evaluation difficult; and (3) not viable, when the embryo was not dyed.

Statistical Analyses

Analyses and all data contained in this article were performed only for noncracked seeds and determined “viable”

by the flotation method. We used two different approaches: qualitative, using the number of species from 3 years of collection, and quantitative, using the seed density only with data from the 2006 period. This was because during 2004 and 2005, we only sampled study plots, whereas in 2006, the whole plot surface was exhaustively inspected and thus dispersed seeds could be related to a specific plot surface for seed density measures. Species richness was calculated using rarefaction curves. For these analyses, we used EstimateS Win 7.5.0 (Colwell 2005). Because the normality and homoscedasticity requirements for analysis of variance (ANOVA) were not fulfilled, to test differences between habitats in number of dispersed seeds, the semiparametric multivariate analysis of variance approach of Anderson (2001), permutational multivariate analysis of variance (PERMANOVA), was used, with Bray–Curtis distances (Quinn & Keough 2002) and 10,000 Monte Carlo permutations of raw data (Anderson & Ter Braak 2003). This approach allows the testing of a multivariate dataset to one or more factors in an ANOVA experimental design on the basis of any distance measure using permutation methods (Anderson 2001; McArdle & Anderson 2001). PERMANOVA were performed using the program PERMANOVA 1.6 (Anderson 2005). In the same way, for a qualitative approach, a cumulative number of species over 3 years were used.

Results

A total of 303 scats were analyzed, 196 of them containing at least one seed of woody species. The relative importance of disperser animals, with respect to the number of scats found, was 47.8% for Red fox, 34.6% for Stone marten, and 17.6% for Wild boar. The number of scats analyzed and seeds found are shown in Table 1 for all areas. In total, seeds from 16 different woody plant species were extracted from the feces. The proportions of scats with one, two, and three seed species were 61, 31.3, and 7.2%, respectively. The mean number of species per fecal sample was 1.47 ± 0.6 SD. Of the species present in the study area, the most abundant seeds found in feces were from *Rubus ulmifolius* (10,401 seeds), *Arctostaphylos uva-ursi* (1,225 seeds), *Rosa* spp. (723 seeds), and *Crataegus monogyna* (590 seeds), present in 10.2, 14.5, 23.8, and 16.5% of the scats, respectively. Among the species not present in the study area, the one most dispersed was *Ficus carica*, a cultivated tree, with 1,931 seeds present in a total of seven scats. Agrarian species appeared only in the 5% of the scats.

Results of the tetrazolium viability test showed a high viability rate for almost all species, the percentage of live seeds ranging between 69.2% (*Amelanchier ovalis* dispersed by fox) and 100% (*C. monogyna* by Wild boar; Fig. 1). *Arctostaphylos uva-ursi* was the only species having low seed viability (24 and 32% of viable seeds dispersed by fox and marten, respectively). This was due to

Table 1. Number of scats (*n*) from fox (*Vulpes vulpes*) and marten (*Martes foina*) analyzed over the 3-year study period (2004–2006) and from Wild boar (*Sus scrofa*) in 2006 plus the identity and number of the seeds found.

	Fox			Marten			Wild Boar	Mean Seeds per Scat
	2004	2005	2006	2004	2005	2006	2006	
<i>n</i>	15	31	91	14	34	48	33	
Species present in the study areas								
<i>Rosa</i> spp. (Rosaceae)	102	26	298	37	—	260	1,434	47
<i>Crataegus monogyna</i> (Rosaceae)	41	2	383	151	13	—	31	13
<i>Rubus ulmifolius</i> (Rosaceae)	1,906	465	4,105	1,570	412	1,943	—	306
<i>Arctostaphylos uva-ursi</i> (Ericaceae)	20	94	737	2	262	110	—	28
<i>Amelanchier ovalis</i> (Rosaceae)	—	799	78	—	627	54	—	50
<i>Sorbus aria</i> (Rosaceae)	—	19	140	—	7	26	—	12
<i>Juniperus communis</i> (Cupressaceae)	21	—	—	29	—	—	—	7
<i>Lonicera arborea</i> (Caprifoliaceae)	—	8	—	—	—	—	—	8
<i>Taxus baccata</i> (Taxaceae)	1	—	—	—	—	—	—	1
<i>Rubia peregrina</i> (Rubiaceae)	—	—	—	—	—	1	—	1
Species not present in the study areas								
<i>Ficus carica</i> (Moraceae)	506	397	478	—	—	550	—	276
<i>Vitis vinifera</i> (Vitaceae)	3	61	69	—	—	14	—	21
<i>Prunus avium</i> (Rosaceae)	—	31	91	—	—	2	—	11
<i>Cucurbita melo</i> (Cucurbitaceae)	—	—	3	—	—	—	—	3
<i>Pr. domestica</i> (Rosaceae)	—	—	1	—	—	—	—	1
<i>Malus domestica</i> (Rosaceae)	—	—	1	—	—	—	—	1
Total seeds	2,600	1,902	6,384	1,789	1,321	2,960	1,465	

a low seed filling instead of a gut transit effect because most of seeds analyzed were empty (despite not floating) and all filled seeds were dyed. The Wild boar feces displayed a high rate of cracked *C. monogyna* seeds (visual estimate of 90–95% damaged). No cracked seeds were found for the other dispersers.

Rarefaction curves indicated sufficient yearly sampling effort for all habitats to represent species richness in the

seeds dispersed by mammals. The species presence in each habitat is listed in Table 2, and number of species and seeds per scat are shown in Figure 2. Substrate where feces were principally deposited was bare soil (80.5%), followed by rock, shrub, and grass (7.3, 6.5, and 5.6%, respectively), and no differences were found among the five landscape units ($\chi^2 = 14.3$, $df = 12$, $p = 0.2$), using the total number of scats found during the 3 years and all the dispersers

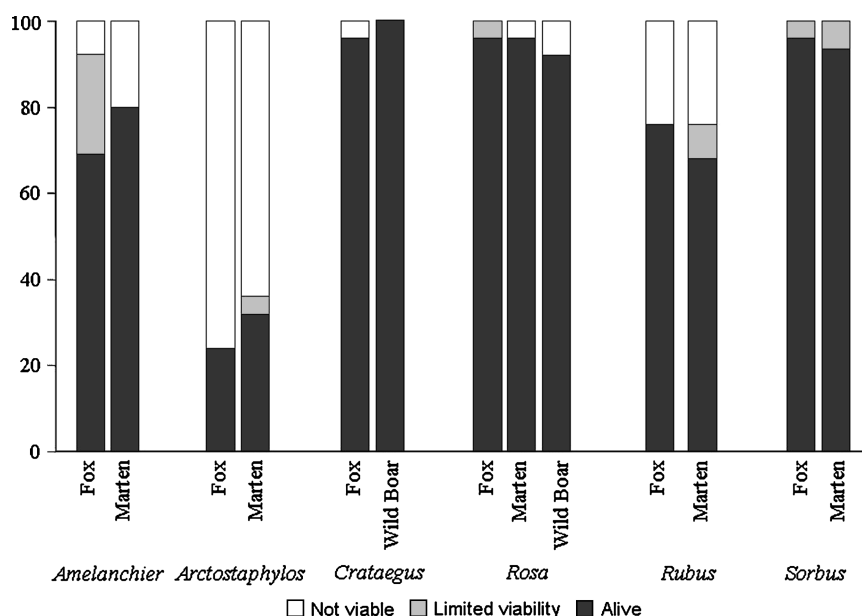


Figure 1. Seed viability percentage of the six most abundant dispersed species examined by the tetrazolium method. Black bars represent viable seeds dyed with tetrazolium, gray bars represent seeds partially dyed (i.e., limited viability), and white bars represent nonviable seeds.

Table 2. List of species found on the different landscape units studied.

Species	Native	Dense	Cleared	Fenced	Shrubland
Species present in the study areas					
<i>Rosa</i> spp. (Rosaceae)	□ ×	□ ×	□ ×	□ ×	□ ×
<i>Crataegus monogyna</i> (Rosaceae)	□ ×	×	□ ×	□ ×	□ ×
<i>Rubus ulmifolius</i> (Rosaceae)	×	×	□ ×	□ ×	□ ×
<i>Arctostaphylos uva-ursi</i> (Ericaceae)	□ ×	×	×	□ ×	×
<i>Amelanchier ovalis</i> (Rosaceae)	□ ×	×	□	□ ×	□ ×
<i>Sorbus aria</i> (Rosaceae)	□ ×	×	□ ×	×	×
<i>Juniperus communis</i> (Cupressaceae)	□ ×	×	□ ×	□	×
Species not present in the study areas					
<i>Ficus carica</i> (Moraceae)		×	×		×
<i>Vitis vinifera</i> (Vitaceae)		×	×		×
<i>Prunus avium</i> (Rosaceae)	×	×		×	×

Presence of adults of fleshy-fruited plant species is indicated with the symbol □ and mammal-dispersed seeds of woody species with the symbol ×. Rare species, such as *Taxus baccata*, *Lonicera arborea*, *Cucurbita melo*, *Prunus domestica*, and *Malus domestica*, were not included.

pooled. From a qualitative approach, mammals deposited the same species throughout all habitats, irrespective of the degradation level (PERMANOVA, $F = 0.61$, $p(\text{MC}) = 0.7$), using the 3-year cumulative number of species. Quantitatively, seed density differed among habitats, using pooled species and only 2006 data (PERMANOVA, $F = 6.33$, $p(\text{MC}) = 0.0009$). Pairwise a posteriori comparisons showed differences between native forest and the rest of landscape units (Table 3), seed dispersal being lower in forest (Fig. 2). This is probably because *R. ulmifolius* was very scarce in native forest, where mainly species with a low number of seeds per fruit appeared, thus lowering the seed density in native forest. Agrarian species showed no differences (PERMANOVA, $F = 1.07$, $p(\text{MC}) = 0.42$) for the 3-year cumulative number of species or for seed density (PERMANOVA, $F = 0.82$, $p(\text{MC}) = 0.6$) among landscape units.

Discussion

Diversity and Abundance of Dispersed Seeds

According to our results, mammals disperse seeds of 16 woody species in the study area, which represent more than a half of the total fleshy-fruited woody species available in the study area (Mendoza 2008). This number of species is lower than in nondegraded, high-diversity Mediterranean forest habitats (27 species, Herrera 1989) but higher than in other studied areas (12 species in central

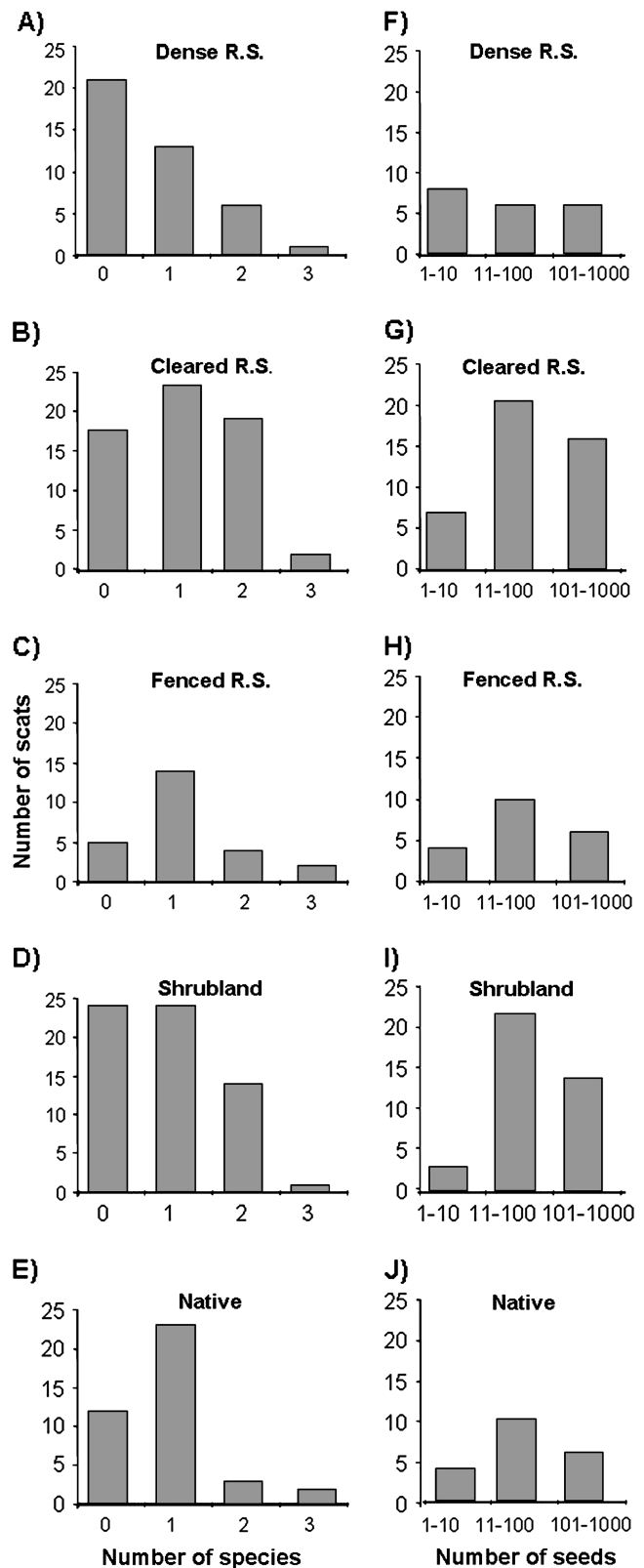


Figure 2. Number of scats in each studied landscape unit. Figures A to E represent number of scats with different numbers of species. Figures F to J represent frequency of scats with different numbers of seeds.

Table 3. Pairwise a posteriori comparisons of seed density in the five landscape units using a semiparametric multivariate analysis of variance (PERMANOVA).

Factor	<i>t</i>	<i>p</i> (MC)
Cleared, dense	2.34	n.s.
Cleared, fenced	1.96	n.s.
Cleared, native	4.84	0.006
Cleared, shrubland	1.27	n.s.
Dense, fenced	0.57	n.s.
Dense, native	2.89	0.007
Dense, shrubland	1.87	n.s.
Fenced, native	3.36	0.003
Fenced, shrubland	1.31	n.s.
Native, shrubland	5.11	0.001

p(MC) represents Monte Carlo *p* values after 9,999 permutations.

Europe, Schaumann & Heinken 2002; 6 species in Chile, Silva et al. 2005). Thus, frugivory by mammals is a common phenomenon in our study area, fleshy fruits being an important part of the diet for foxes and martens (see also Herrera 1989; Schaumann & Heinken 2002; Traba et al. 2006 for other Mediterranean habitats). Red foxes and Stone martens were the most abundant dispersers and are the best studied in this sense (Heinken et al. 2002; Padial et al. 2002; Schaumann & Heinken 2002; Traba et al. 2006), whereas Wild boar has been considered to function mainly as an epizoochorous disperser (Heinken et al. 2006). Endozoochory by Wild boar has been described principally for small seeds (Génard & Lescourret 1985; Herrera 1989; Heinken et al. 2001, 2002). Our results show Wild boars to be important endozoochorous dispersers, even for relatively large seeds such as *Crataegus monogyna* (5.63 ± 0.7 mm) or *Rosa* spp. (5.22 ± 0.5 mm). Even though a large number of *C. monogyna* seeds were cracked, seed viability was not reduced, making Wild boar a legitimate seed disperser for this species.

Quantitatively, *Rubus ulmifolius* was the species with the highest number of dispersed seeds, probably due to the high number of seeds per fruit. *Rosa* spp. and *C. monogyna* were the species present in a major number of scats; both species are also very abundant in the seedling and sapling bank in our study system (García et al. 2000; Quero et al. 2008; Mendoza 2008). The only fleshy-fruited tree species, *Sorbus aria* (with 0.9% of the total seeds dispersed) and *Taxus baccata* (with only one record) were hardly dispersed by mammals. The rest of the woody dispersed species were fleshy-fruited shrubs.

Mammals as Vectors for Agrarian Species

The appearance of species originating from outside the study area was in a very low percentage of the scats (5%). These plant species (mainly fig, *Ficus carica*; sour cherry, *Prunus avium*; and grape, *Vitis vinifera*) are cultivated some kilometers away from the study area shows that mammals can act as long-distance dispersal vectors.

Nevertheless, all these species are components of the Mediterranean flora (Herrera 1985). Mammals dispersed agrarian species in the same way in all landscape units, but the effect would be important mainly in reforestation stands, where the species richness is lower and its effects on community dynamics would be higher. Both Red fox and Stone marten have previously been indicated as principal allochthonous seed dispersers in Mediterranean areas (Guix et al. 2001), but our results show only Red fox as the major disperser of agrarian species in our study system.

Viability of Dispersed Seeds

The tetrazolium test results showed a high viability rate for all dispersed species, except *Arctostaphylos uva-ursi*, irrespective of the dispersing species. Mammal digestion normally increases seed germination (Aronne & Russo 1997; Traveset et al. 2001; Schaumann & Heinken 2002; Verdú & Traveset 2004), but seeds often respond differently to the gut passage relating to such factors as the quality of other foods eaten (e.g., degree of acidity; Traveset et al. 2001) or seed size (Verdú & Traveset 2004), physically and/or chemically affecting the structure of seed coat. The high viability rate found for most species in our study system indicates that fox, Stone marten, and Wild boar are legitimate seed dispersers of a broad array of woody species, most of which are dominant in the seedling and sapling bank of the woody community in our study system (Quero et al. 2008). These results support the conclusions of Traba et al. (2006) for Red fox and of Schaumann and Heinken (2002) for Stone marten and provide new data for Wild boar.

Another important factor that should be taken into account is the seed density in the feces. The high number of seeds of some species dispersed in the same scat (i.e., cases such as *R. ulmifolius* or *F. carica*) boosts competition once seedlings have emerged, reducing the recruitment probabilities (density-dependent effects for seedling establishment; Janzen 1970; Connell 1971). However, only a low percentage of the total scats had a high number of seeds, most of them ranging between 0 and 20 seeds. This fact may favor species with only one or two seeds per fruit, such as *C. monogyna*, because intraspecific seedling competition would be lower than in other cases, as in *R. ulmifolius* or *F. carica*, which had higher seed densities and probably increased seedling competition. The other species presented low-to-moderate numbers of seeds per scats, thus limiting potential density-dependent negative consequences for seedlings.

Mammalian Dispersal in a Degraded Mosaic Landscape

Qualitatively, mammals dispersed a very similar sample of woody species (6–8; Table 2), irrespective of the landscape unit. Quantitatively, mammals dispersed even more seeds

in degraded habitats (plantations and postfire shrubland) than in native forest. The small size and spatial proximity of patches allowed mammals to explore all the landscape units due to the large home range and flexible use of different habitat types by foxes, martens, or Wild boars (Cavallini & Lovari 1994). This is a key fact, which indicates that mammals constitute a major vector for seed dispersal and colonization regardless of the degradation level of the habitat. These findings are novel because they demonstrate for the first time that mammals deposited a very similar pool of species in all habitats comprising a mosaic landscape, whether native forest, reforestation stands, or shrubland.

Although mammals tend to disperse fewer seeds than birds in Mediterranean mountains, mammals are responsible for most of the long-distance seed dispersal (Jordano et al. 2007). Furthermore, there is a major difference between mammals and avian dispersers because birds normally avoid habitats that they find unattractive, such as reforestation stands (Debussche & Isenmann 1994; Pausas et al. 2006). Thus, mammals are strongly maintaining the seed movement among landscape units, favoring the transport from native forests and shrublands, which acted as a net seed source of fleshy-fruited seeds, to pine plantations, which acted as seed sink (because fruit production is negligible).

Because this kind of mosaic landscape is the result of land use changes in mountain ecosystems, and because Red fox, Stone marten, and Wild boar are widespread mammals, these results could be generalized to a great part of anthropogenically influenced landscapes in Mediterranean ecosystems.

Implications for Practice

- In modified Mediterranean mountain ecosystems, large mammals dispersed a diverse and viable pool of fleshy-fruited woody species through different habitats in a mosaic landscape.
- Due to their long-distance dispersal, mammal seed dispersal may also be crucial for the introduction of immigrant seeds from fleshy-fruited woody species from nearby well-conserved habitats, contributing to passive restoration of degraded areas, particularly pine plantations.
- Mammals might also introduce agrarian species into native and degraded habitats. In every ecosystem, the proportion of native versus agrarian species dispersed needs to be evaluated in order to fully understand the role of mammals as propagule vectors.
- In Mediterranean mountains, a healthy and diverse guild of frugivorous mammals should be used by forest managers as a good indicator of the potential passive recuperation of the biodiversity, especially in pine plantations.

Acknowledgments

We thank N. Villegas and A. Herrero for field and laboratory work, S. Hitos for chemical advice, and F. J. Bonet for plot surfaces measures. C. M. Herrera gave us helpful comments, as well as J. Kanowski and two anonymous reviewers. D. Nesbitt improved English of this article. This study was supported by project MMA 24/2003 to R.Z., FPI-MEC grant to L.M. (BES-2006-13562), and FPU-MEC grant to I.M. (2002-0626). We are also very grateful to the Direction of the Sierra Nevada National Park for permission for the fieldwork, constant support, and facilities.

LITERATURE CITED

- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**:32–46.
- Anderson, M. J. 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, Auckland, New Zealand (available from <http://www.stat.auckland.ac.nz/~mja/Programs.htm>) accessed 13 October 2008.
- Anderson, M. J., and C. J. F. Ter Braak. 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* **73**:85–113.
- Aronne, G., and D. Russo. 1997. Carnivorous mammals dispersers of *Myrtus communis* (Myrtaceae) in the Mediterranean shrublands. *Plant Biosystems* **127**:781–788.
- Cain, M. L., B. G. Milligan, and A. Strand. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* **87**:1217–1227.
- Calisti, M., B. Ciampalini, S. Lovari, and M. Lucherini. 1990. Food habits and trophic niche variation of the Red Fox *Vulpes vulpes* (L., 1758) in a Mediterranean coastal area. *Revue d'Ecologie (Terre Vie)* **45**: 309–320.
- Cavallini, P., and S. Lovari. 1994. Home-range, habitat selection and activity of the Red Fox in a Mediterranean coastal ecotone. *Acta Theriologica* **39**:279–287.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* **80**:1475–1494.
- Colwell, R. K. 2005. *EstimateS*: statistical estimation of species richness and shared species from samples. Version 7.5 (<http://viceroy.eeb.uconn.edu/estimates>) accessed 13 October 2008.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in forest trees. Pages 298–312 in P. J. den Boer and G. R. Gradwell, editors. *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Dalling, J. W., S. P. Hubell, and K. Silvera. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology* **86**:674–689.
- Debussche, M., and P. Isenmann. 1989. Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. *Oikos* **56**:327–338.
- Debussche, M. J., and P. Isenmann. 1994. Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. *Oikos* **56**:327–380.
- Delgado, R., G. Delgado, J. Párraga, E. Gámiz, M. Sánchez, and M. A. Tenorio. 1989. Mapa de suelos, hoja 1027 (Güejar Sierra). Instituto para la Conservación de la Naturaleza, Madrid, Spain.
- Fedriani, J. M. 1996. Dieta del zorro en Doñana. *Doñana Acta Vertebrata* **23**:144–152.

- Fenner, M. 1992. Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, United Kingdom.
- García, D., R. Zamora, J. A. Hódar, J. M. Gómez, and J. Castro. 2000. Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. *Biological Conservation* **95**:31–38.
- Génard, M., and F. Lescourret. 1985. Le sanglier (*Sus scrofa* L.) et les diaspores dans le sud de la France. *Revue d'Ecologie (Terre et Vie)* **40**: 343–353.
- Guix, J. C., M. Soler, M. Martín, M. Fosalba, and A. Mauri. 2001. Introducción y colonización de plantas alóctonas en un área mediterránea: evidencias históricas y análisis cuantitativo. *Orsis* **16**:145–185.
- Harper, J. L. 1977. Population biology of plants. Academic Press, London, United Kingdom.
- Heinken, T., H. Hanspach, D. Raudnitschka, and F. Schaumann. 2002. Dispersal of vascular plants by four species of wild mammals in a deciduous forest in NE Germany. *Phytocoenologia* **32**:627–643.
- Heinken, T., R. Lees, D. Raudnitschka, and S. Runge. 2001. Epizoochorous dispersal of bryophyte stem fragments by roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). *Journal of Bryology* **23**: 293–300.
- Heinken, T., M. Schmidt, G. Oheimb, W. U. Kriebitzsch, and H. Ellenberg. 2006. Soil seed banks near rubbing trees indicates dispersal of plant species into forest by wild boar. *Basic and Applied Ecology* **7**:31–44.
- Herrera, C. M. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos* **44**:132–141.
- Herrera, C. M. 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. *Oikos* **55**:250–262.
- Herrera, C. M. 1995. Habitat-consumer interactions in frugivorous birds. Pages 341–367 in M. L. Cody, editor. *Habitat selection in birds*. Academic Press, New York.
- Hickey, J. R., R. W. Flynn, S. W. Buskirk, K. G. Gerow, and M. F. Willson. 1999. An evaluation of mammalian predator, *Martes americana*, as a disperser of seeds. *Oikos* **87**:499–508.
- ISTA (International Seed Testing Association). 1999. Proceedings of the International Seed Testing Association. *Seed Science and Technology* **27**(Suppl.).
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**:501–528.
- Jordano, P., C. García, J. A. Godoy, and J. L. García-Castaño. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of National Academy of Sciences* **104**:3278–3282.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.
- Massei, G., and P. V. Genov. 2004. The environmental impact of wild boar. *Galemys* **16**:135–145.
- McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* **82**:290–297.
- Méndez, M., D. García, F. T. Maestre, and A. Escudero. 2008. More ecology is needed to restore Mediterranean ecosystems: a reply to Valladares and Gianoli. *Restoration Ecology* **16**:210–216.
- Mendoza, I. 2008. Regeneración de la biodiversidad de especies leñosas en un marco de degradación de hábitats mediterráneos de montaña: combinación de interacciones ecológicas y manejo humano. Ph.D. dissertation. University of Granada, Granada, Spain.
- Nathan, R. 2006. Long distance dispersal of plants. *Science* **313**:786–788.
- Otani, T. 2002. Seed dispersal by Japanese marten *Martes melampus* in the subalpine shrubland of northern Japan. *Ecological Research* **17**:29–38.
- Padial, J. M., E. Ávila, and J. M. Gil-Sánchez. 2002. Feeding habits and overlap among red fox (*Vulpes vulpes*) and stone marten (*Martes foina*) in two Mediterranean mountain habitats. *Mammalian Biology* **67**:137–146.
- Pausas, J. G., A. Bonet, F. T. Maestre, and A. Climent. 2006. The role of the perch on the nucleation process in Mediterranean semi-arid old-fields. *Acta Oecologica* **29**:346–352.
- Quero, J. L., L. Gómez-Aparicio, R. Zamora, and F. Maestre. 2008. Shifts in the regeneration niche of a endangered tree (*Acer opalus* ssp. *granatense*) during ontogeny: using an ecological concept for application. *Basic and Applied Ecology* **9**:635–644.
- Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologist. Cambridge University Press, Cambridge, United Kingdom.
- Rau, J. R., J. F. Beltrán, and M. Delibes. 1985. Can the increase of fox density explain the decrease of lynx numbers at Doñana? *Revue d'Ecologie (Terre Vie)* **40**:145–150.
- Schaumann, F., and T. Heinken. 2002. Endozoochorous seed dispersal by martens (*Martes foina*, *M. martes*) in two woodland habitats. *Flora* **197**:370–378.
- Schupp, E. W., and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* **2**: 267–275.
- Silva, S. I., F. Bozinovic, and F. A. Jaksic. 2005. Frugivory and seed dispersal by foxes in relation to mammalian prey abundance in a semi-arid thornscrub. *Austral Ecology* **30**:739–746.
- Tellería, J. L., A. Ramírez, and J. Pérez-Tris. 2005. Conservation of seed dispersing migrants in Mediterranean habitats: shedding light on patterns to preserve processes. *Biological Conservation* **124**: 493–502.
- Terradas, J. 2001. Ecología de la vegetación: de la ecofisiología de las plantas a la dinámica de comunidades y paisajes. Ediciones Omega, S.A., Barcelona, Spain.
- Traba, J., S. Arrieta, J. Herranz, and M. C. Clamagirand. 2006. Red fox (*Vulpes vulpes* L.) favour seed dispersal, germination and seedling survival of Mediterranean Hackberry (*Celtis australis* L.). *Acta Oecologica* **30**:39–45.
- Traveset, A., N. Riera, and R. E. Mas. 2001. Ecology of fruit-colour polymorphism in *Myrtus communis* and differential effects of birds and mammals on seed germination and seedling growth. *Journal of Ecology* **89**:749–760.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* **20**:171–197.
- Valladares F., J. J. Camarero, F. Pulido, and E. Gil-Pelegrín. 2004. El bosque mediterráneo, un sistema humanizado y dinámico. Pages 13–25 in F. Valladares, editor. *Ecología del bosque mediterráneo en un mundo cambiante*. Ministerio de Medio Ambiente, EGRAF, S.A., Madrid, Spain.
- Venable, D. L., and J. S. Brown. 1993. The population dynamic functions of seed dispersal. *Vegetatio* **107**:31–55.
- Verdú, M., and A. Traveset. 2004. Bridging meta-analysis and the comparative method: a test of seed size effect on germination after frugivores' gut passage. *Oecologia* **138**:414–418.
- Wiens, J. A. 1995. Landscape mosaics and ecological theory. Pages 1–21 in L. Hansson, L. Fahring, and M. Gray, editors. *Mosaic landscapes and ecological processes*. Chapman & Hall, London, United Kingdom.

Appendix. Aerial photograph of the study area with polygons delimitating the five habitats and the three replicates of each habitat ($n = 15$).

