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Dispersal of Spanish juniper *Juniperus thurifera* by birds and mammals in a fragmented landscape

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Dispersal of Spanish juniper *Juniperus thurifera* was examined in a farming landscape of central Spain to study the effects of fragmentation on the dispersal effectiveness of the different dispersers, and the consequences for the plant. The study was conducted in two large forests (LF; 280 and 150 ha) representative of unfragmented conditions, and 18 small isolated fragments (0.1–3 ha) which were classified in two groups: 1) F1, forest remnants with both high juniper cover and cone production ($N = 5$); and 2) F2, remnants in which fragmentation has caused a heavy reduction in junipers ($N = 13$). Cone production, disperser abundances and quantity of dispersal by birds (*Turdus* thrushes) and mammals (carnivores, rabbits and sheep) were estimated throughout two study years. Dispersal by thrushes was measured in three types of trees representing a decreasing attraction focus to birds: Spanish junipers with cones (SJ1), Spanish junipers without cones (SJ2) and holm oaks (HO).

Cone production greatly decreased from LF to F1 and F2 in both study years, affecting F2 dramatically. Thrush abundances were similar in LF and F1, but thrushes lacked or were very scarce in F2. Carnivores showed an even distribution throughout the whole area, but herbivores were relatively scarce in F2 fragments, especially rabbits, which were lacking in the fragments under 0.6 ha. Patterns of seed deposition around trees showed decreasing dispersal activity of thrushes from SJ1 (83.1% of the examined trees had seed-packets–thrush pellets) to SJ2 (53.6%) and HO (23.6%). Both distribution patterns and density of pellets were roughly similar in LF and F1, but pellets were only recorded in one (SJ1) out of 159 trees examined in F2, supporting thrushes behaved as specialist feeders and thus avoided the patches devoid of juniper cones. Average densities of pellets in LF reached 397.6 pellets ha^{-1}, surpassing at least 30 times the quantitative effectiveness (seed-packets ha^{-1}) of mammal dispersers. Juniper seeds were present but very scarce in the mammal faeces collected in both fragments F1 and F2. Overall, the quantitative effectiveness of carnivores was nearly 4 times lower in the fragments than in LF, and that of herbivores 11 times lower. This result is consistent with the lower availability of juniper cones in the fragments and, together the distribution of mammal abundances, fits the prediction that mammals (except rabbits) moved among landscape patches according to the total availability of food supplies.

Overall, results showed that dispersal of Spanish juniper in fragments F2 is seriously impaired by the loss of their main dispersers (thrushes), and that recruitment became dependent upon mammal dispersers with a low quantitative effectiveness, namely carnivores and sheep.

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Habitat fragmentation is a central conservation problem to forest organisms in the temperate zone (Harris 1984, Wilcove et al. 1986). The reduction of available habitat and the increasing distances among habitat remnants seem to be the main causes of the dramatic loss of species recorded in forest fragments (Andrén

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1994). Other more subtle effects, such as alteration of keystone processes in the life-cycles of the species, may also be very important in determining the survival of species in fragments (Janzen 1983, Terborgh 1986, Feinsinger 1987, Jennersten 1988, Aizen and Feinsinger 1994, Turner 1996). In the case of zoochorous plants, seed dispersal may be affected by the loss or rarefaction of dispersers in small and/or isolated habitat patches (Janzen 1983, Howe 1984, Johnson 1988, Van Ruremonde and Kalkhoven 1991, Estrada et al. 1993).

Over much of northern-central Spain, the original forest has been greatly fragmented by agricultural use (Tellería et al. 1995, Santos and Tellería 1998). In this area, the Spanish juniper *Juniperus thurifera*, an endozoochorous, endemic species of this southwestern corner of the Palearctic (Ceballos and Ruiz 1979, Gómez 1991), is a scarce tree in holm oak *Quercus ilex* dominated woodlands which seems to be greatly affected by fragmentation (Santos and Tellería 1994). Former studies suggest that high predation rates on juniper cones and seeds significantly decrease seedling recruitment in small fragments (Santos and Tellería 1994). Few data are available, however, on the way fragmentation affects the ability of Spanish juniper to disperse among fragments despite the importance of dispersal in reinforcing very small populations or recolonizing fragments in which juniper became extinct (Hanski 1989, Eriksson 1996).

The main dispersers of junipers (*Juniperus* spp.) in Spain are wintering thrushes (*Turdus* spp.; Jordano 1993, Santos and Tellería 1994) and medium-sized carnivorous mammals (Mustelidae, Viverridae and foxes; Herrera 1989), but dispersal by rabbits and domestic goats and sheep has also been recorded (Muñoz 1993, Heras et al. 1994). Given the influence of habitat structure on the movements of many dispersers (Hoppes 1987, Van Ruremonde and Kalkhoven 1991, Schupp 1993), habitat changes associated with fragmentation might affect the post-feeding behaviour and dispersal effectiveness of frugivores. The effectiveness of Spanish juniper dispersers might thus be very different in continuous forest and in isolated forest patches spread over the agricultural matrix. The different patterns of feeding movements expected for mammals and thrushes suggest that fragmentation will have a greater effect on the behaviour and effectiveness of avian rather than mammal dispersers. Previous studies carried out in fragmented landscapes of central Spain, have shown that food resources are abundant and diverse in winter both for carnivores (e.g., rabbits, large numbers of small mammals, juniper cones, acorns, and some fleshy fruits scattered over the landscape patches; Tellería et al. 1991, 1995, Santos and Tellería 1994, 1997, and unpubl.) and for domestic ungulates that forage in herds upon fallow land, shrubland and forest patches. Since juniper cones represent only a minor part of the food available to carnivores and ungulates, their visit rates to forest fragments will be relatively independent of the size of cone crops or even of the presence/absence of Spanish junipers within the fragments. These mammals have thus the potential to be efficient dispersers of juniper seeds among all forest tracts. However, this expectation does not apply to rabbits, which rarely move from forest fragments where they burrow.

In contrast, wintering thrushes show frequent functional responses to variation in the availability of some single food items, such as juniper cones (Santos 1982, Snow and Snow 1988, Jordano 1993), by tracking their abundance among regions, landscapes patches and intra-habitat patches (De Juana and Santos 1981, Jordano 1993, Herrera 1995). Food supplies available for wintering thrushes are almost restricted to juniper cones in large areas of central Spain because of the scarcity of other alternative fruits and the scarcity of ground invertebrates. Some studies in southern Spain have in fact shown that thrushes are more or less monophagous on junipers in winter (Jordano 1993), even subsisting almost exclusively on a juniper diet when other food supplies are not available (Zamora 1990). Therefore, thrushes will be more selective dispersers of Spanish junipers than mammals since they will move from patch to patch looking for juniper cones and dispersing juniper seeds. Hence, the size of cone crops will influence their visit rates to forest tracts.

In this paper, we try to evaluate the role of both disperser groups, mammals and thrushes, for the ability of Spanish juniper to survive in or colonise a landscape of isolated forest fragments. We predict that 1) if thrushes behave as specialist feeders on juniper cones, they will move among trees (intra-habitat scale) and among fragments (landscape scale) with adequate supplies of edible cones, whereas fragments without junipers or with small cone crops will be avoided. This means that thrushes will mostly influence recruitment within those Spanish juniper populations isolated in forest fragments. On the other hand, their effect on colonization of fragments in which juniper is rare or absent will be negligible. Furthermore 2) since mammals (mainly carnivores and ungulates) use fragments as part of their home ranges where they search for a broader array of resources than thrushes, they will move seeds to forest fragments in which junipers are scarce or absent, thus favouring the colonisation processes.

Methods

Study area

The study was conducted in an agricultural landscape located in central Spain, around Lerma (42°5′N, 3°45′W; 850 m a.s.l.), from late autumn to early summer for two annual cycles (1994–95 and 1995–96), coinciding with the availability of ripe juniper cones on branches and the ground. The climate is inland Mediterranean (Font 1983), with long, cold winters. Forest extends over < 10% its former area in Lerma, occupying the landscape as small woodlots. In this region, the forest is dominated by several Mediterranean oak species, mainly the holm oak *Quercus ilex*, whereas the Spanish juniper *Juniperus thurifera* is a scarce but locally abundant tree. Apart from Spanish juniper, endozoochorous plants are restricted in Lerma to wild rose *Rosa canina* and juniper *J. communis*, but the fleshy fruits of these species make up a negligible portion of the available fruits. Cone production of Spanish juniper shows strong between-year variation in the study region, but was high in the study years (Santos and Tellería 1994, unpubl.). Field data were recorded in eighteen forest fragments ranging from 0.1 to 3 ha, and in two large forests stretching over 280 and 150 ha (Table 1). Cover values range from 90% to 20% for the tree stratum, and from 7.5% to 0.03% for Spanish juniper (Santos and Tellería 1998; Table 1).

We examined the dispersal of juniper seeds both on a landscape and intra-habitat scale. To study dispersal on a landscape scale, we classified the forests into three types according to their size and cone availability (Table 1): 1) LF, the two large forests, with high Spanish juniper cover (average 4.4%) and abundant cone production; 2) F1 (N = 5), fragments with high juniper cover (> 1%, average = 3.6%), including mature trees with good cone production; and 3) F2 (N = 13), fragments with a low juniper cover (< 1%, average = 0.23%), largely young trees with scarce cone production. We considered LF as control forests, representative of unfragmented conditions for all study purposes. To test for the effects of isolation alone, discounting the influence of low cone production (F2), we compare LF with F1.

To assess seed deposition patterns by the thrushes within forest fragments (intra-habitat scale), we assumed that, within forests, thrushes use the trees for feeding and/or perching according to the following gradient of decreasing preference (see prediction 1): Spanish junipers with cones (SJ1) > Spanish junipers without cones (SJ2) > oak trees (mainly holm oaks; HO). Since the use of trees as attraction foci influences the spatial pattern of seed distribution (Hoppes 1987, Guevara and Laborde 1993), the consumption of juniper cones and consequently the quantity of seed dispersal by thrushes would decrease within forests (habitat scale) from SJ1 to SJ2 and HO.

Estimation of cone crops

Ripening of juniper cones occurred both in 1994 and 1995 by late autumn (mid-November) when we initially estimated cone production in each forest from estimates in individual trees. At that time most cones were still

Table 1. Vegetation composition and cone production (average production per tree) in the forest types studied in Lerma (LF, large forests; F1, fragments with large cone crops of Spanish juniper; F2, fragments with small cone crops or absence of cone production). Area: forest size (in ha); (N_1, N_2): number of juniper trees in which cone crop was recorded in 1994–95 (N_1) and 1995–96 (N_2). Cover figures are given in percentages. Crop LA/LW: mean cone crop by juniper in late autumn (LA) and late winter (LW).

		Area (ha)	Tree cover (%)	Spanish juniper cover (%)	(N_1, N_2)	Cone crop size	
						1994–95 LA/LW	1995–96 LA/LW
LF	1	280	32.3	3	(10, 7)	7120/3635	3580/1375
	2	150	29.8	5.8	(10, 6)	11732/9981	13211/4352
F1	3	2.0	37.1	1.3	(3, 2)	2684/410	3640/2072
	4	0.3	90	2	(4, 4)	4739/2526	13085/2838
	5	0.2	20	2	(2, 2)	4034/1206	3943/1902
	6	0.6	25	7.5	(4, 3)	4384/2473	3286/1642
	7	1.3	50	5.3	(4, 4)	5356/2396	2414/1263
F2	8	0.7	50	0.5	(1, 1)	115/76	1611/0
	9	0.8	53.3	0.3	(1, 1)	a/11278	1646/206
	10	0.7	40	0.1	(1, 1)	422/80	150/120
	11	0.1	20	0.1	(1, 1)	350/29	100/64
	12	0.3	50	1	(1, 0)	17/0	
	13	3.0	27	0.06	(1, 1)	1087/0	2600/867
	14	0.2	55	0.5	(1, 2)	70/47	1639/1653
	15	0.5	40	0.03	(1, 1)	28/17	32/40
	16	0.3	20	0.1	(0, 0)		
	17	0.3	60	0.1	(0, 0)		
	18	0.8	65	0.03	(0, 0)		
	19	0.4	36.7	0.1	(1, 0)	45/55	
	20	0.1	30	0.03	(0, 0)		

a: no sampled.

Table 2. Densities of thrushes (*Turdus* spp.) in the forest types (LF, F1 and F2; see Table 1) studied in Lerma in two study years (EW: early winter; LW: late winter). Census area (in ha), number of thrushes recorded (No.) and mean density per forest (D: thrushes 10 ha^{-1}) are given. All individuals recorded in the F2 forests were blackbirds.

		Winter 94–95		Winter 95–96	
		EW	LW	EW	LW
LF	Area	42.5	42.5	42.5	42.5
	No.	37	38	22	33
	D	8.9	9.2	5.2	7.6
F1	Area	24	4.4	13.8	15.2
	No.	53	0	15	19
	D	52.9	0	15.9	18.9
F2	Area	23.1	14.3	26.2	15.5
	No.	7	2	10	1
	D	1.7	1.9	7.1	0.8

attached to branches, and cone and seeds remains on the ground with signs of consumption by mice, the main cause of juniper loss through predation (Santos and Tellería 1994), were absent or very scarce in an overwhelming majority of trees. We thus assume that the data recorded provide reliable estimates of cone production. Estimates were carried out again in late winter (late February–mid-March) in 1995 and 1996. We assessed mean cone crops for each forest from individual trees selected at random (see sample sizes in Table 1). The scarcity of fruiting junipers in F1 and in F2 made random sampling unfeasible in many of these fragments. In fact, in most F2 fragments with cone crops we were able to estimate only the crop of a single juniper. We sampled individual juniper trees with a 30 cm-diameter by 15 cm-high cylindrical frame, taking eight random samples per tree, four from the ground under the canopy, and four from the peripheral layer of the crown where cones are located (for details see Santos and Tellería 1994, 1997). We used crown areas and "parental shadows" (ground area beneath the canopy) to estimate absolute cone crops per tree from the four samples recorded in each location (canopy and ground). We added the samples to estimate the number of cones m^{-2} per location (canopy and ground) and extrapolated to the whole area for each tree (see Holthuijzen and Sharik 1985, Holthuijzen et al. 1987, and Santos and Tellería 1994, 1997 for a similar procedure). Finally, we obtained the average production/tree for each fragment.

Thrush and mammal abundances

We censused wintering thrushes at least twice per study year, in late autumn-early winter and in late winter (surveyed areas in Table 2). Large forests (LF) were censused using line-transects (Järvinen and Väisänen 1975) with a main belt 50 m wide. We compared the main belt densities (number of thrushes 10 ha^{-1}) with the densities recorded in the fragments (F1 and F2) by searching for thrushes throughout the overall area. The presence or absence of thrush species in the fragments was also reported from visits over 15 min (F1: 34 samples in each year – from 5 to 8 visits per forest and year; F2: 59 samples in 1994–95 and 81 in 1995–96 – from 2 to 9 visits per forest and year). The absolute frequencies (of forests with and without thrushes; hereafter incidence) were used to compare the intensity or frequency of use between fragment types (F1 and F2). The term incidence is applied in the same sense in other analyses. In addition to thrushes, no other frugivorous birds, except robins *Erithacus rubecula*, overwinter in Lerma (Santos and Tellería 1994, unpubl.). Robins were not considered in our analyses, as they only sporadically feed on juniper cones due to gape size limitations (large Spanish juniper cones are 8–13 mm in diameter; unpubl. for the study area).

A general survey of wild mammals carried out in the summer of 1994 (Santos and Tellería 1998) showed the presence in Lerma of a handful of carnivores (red fox *Vulpes vulpes*, wild cat *Felis sylvestris*, stone marten *Martes foina*, and badger *Meles meles*) and herbivores (wild boar *Sus scrofa*, roe deer *Capreolus capreolus* and rabbit *Oryctolagus cuniculus*) with the potential to disperse juniper seeds. Relative abundance and distribution among forest types of these species was obtained in the two study years, together with evidence of their dispersal activity (see below).

Seed dispersal by thrushes and mammals

We evaluated evidences of trush dispersal twice in each study year, roughly at the same dates that cone crops and trush densities were estimated. Thrushes feeding on juniper fruits produce pellets containing intact seeds (Snow and Snow 1988, unpubl. for *J. thurifera*). We obtained an index of intensity of use looking for these pellets in the three types of forests (LF, F1 and F2) considered. Within each forest fragment, we sampled the three types of tree (SJ1, SJ2 and HO). Pellets were sampled on the ground, beneath the canopy and in a 1 × 10 m transect located at random compass direction away from the canopy edge of the sampled tree. In order to avoid overlap between different transects, we chose whenever possible, trees whose canopy edges were at least 25 m away from the nearest sampled tree. Sampling areas varied among forest and tree types according to tree size (oak crowns were the largest, and the crowns of SJ1 were larger than thoses of SJ2) and number of sampled trees (see Appendix 1). In order to evaluate the quantitative role of thrushes as dispersers in unfragmented conditions, we estimated the actual density of pellets in LF by weighing the densities associated with each tree type (Appendix 1) with their respective cover values (Table 1; the proportion of SJ1 and SJ2 trees was estimated as 0.5 from a random sample taken in the two large forests; for a similar value in a previous year, see Santos and Tellería 1994). Seed density was obtained by estimating the number of seeds mobilised per pellet from 33 pellets collected from 9 trees.

Evidences of seed dispersal by mammals were assessed twice in each study year, coinciding with the fruiting season of Spanish juniper (November–February) and in April–June. Faeces were sampled in 33 2×250 m fixed transects (located on paths and across the forests) in the large forests (LF) and in 2 m-wide transects along the perimeter and across the greater axis of each F1 and F2 fragment. All forests were surveyed fortnightly in autumn-winter and twice in spring (sampling effort in Table 3). We collected all carnivorous scats found in the samples and 10 faecal pellets (hereafter a faeces unit) from each dropping site for herbivores (sample sizes in Table 4). Roe deer pellets, present in LF, were also included in the analyses. Faeces were examined in the laboratory for juniper seeds and other food items according to the procedure described in Putman (1984). Wild boar faeces, frequent in all forest types, were collected the first year ($N = 37$) but they were discarded from the analyses as all them lacked juniper seeds (pigs digest virtually all seeds eaten; Gérard and Lescourret 1985, Howe 1986). Since sample sizes were very low in F2 for carnivores and herbivores in the first year (21 scats and faeces units each, respectively), the effect of year was not analysed. The quantitative effectiveness of mammals as dispersers in LF was estimated as the density of seed-packets and seeds mobilised, and compared with thrush values. Thrush pellets, carnivore scats and rabbit droppings (discrete clumps containing from 5 to 470 pellets per site) were considered as individual and comparable faecal deposits (hereafter seed-packets), but it was not possible to transform the "continuous" faecal tracks of sheep in comparable density values. Faeces units were converted into seed density from absolute counts carried out at 74 rabbit dropping sites and 30 sheep dropping tracks recorded within transects (average values were 102.1 rabbit pellets/site and 207.1 sheep pellets/track).

Results

Cone production

The mean number of cones per tree in autumn (cone crops before consumption and dispersal) differed among forest types in both study years (two-way ANOVA; $F = 35.924$, $DF = 2$, $p < 0.001$), but differences between years ($F = 0.026$, $DF = 1$, $p = 0.872$) and the forest type-year interaction ($F = 0.335$, $DF = 2$, $p = 0.717$) were not significant. The mean crop size per tree decreased from LF to F1 and F2 in both study years (Table 1, Fig. 1), with significant differences (multiple range tests) among all possible pair-wise comparisons except for F1-1994 vs F2-1995 ($p = 0.09$). Mean crop size per tree in F1 and F2 ranged from being equal to LF, to three orders of magnitude below the values recorded in LF (Table 1). Differences in absolute cone availability were even more dramatic, since the average number of trees per forest type ranged over four orders of magnitude, from ca 13700 Spanish junipers in LF to 40 in F1 and 3–4 in F2 (counted or assessed from a stratified random sampling of trunk density; Santos and Tellería 1998). Forest types thus fit a landscape gradient of attraction foci for dispersers that is maintained throughout the late autumn–winter, since even in late winter many Spanish junipers retained sizeable crops (Table 1).

Table 3. Abundance indexes (no. faeces km^{-1}: carnivore scats, sheep dropping tracks and rabbit dropping sites) of potential mammal dispersers of Spanish juniper in Lerma according to year and forest type (LF, F1 and F2; see Table 1). Results are given separately for carnivores (red fox, stone marten and wild cat), and both large (sheep) and small (rabbit) herbivores that act as seed dispersers. Sampling (2 m-wide transects) effort is given in km. The total numbers of faeces reported from each forest and disperser types are given in Table 4.

	1994–95				1995–96			
	km	Carnivores	Sheep	Rabbits	km	Carnivores	Sheep	Rabbits
LF	66	1.17	1.47	1.03	53.5	0.84	1.10	1.57
F1	16.5	1.27	1.27	1.76	11.4	1.83	2.02	1.23
F2	31.1	0.77	0.58	0.1	29.5	1.93	0.88	0.17

Table 4. Distribution among forest types (LF, F1 and F2; see Table 1) of the carnivorous and herbivorous faeces collected in Lerma during the study period (autumn 1994–summer 1996). Number of faeces (N), number of faeces with intact seeds of Spanish juniper (Nj), an abundance index of these faeces (Ab = Nj km^{-1} sampled × 100; see Table 3) and the proportion of forests with juniper seeds (P) are given for carnivores together (red fox, stone marten and wild cat) and for the three extant species of herbivores. For herbivores a faeces refers to a faeces unit (a group of 10 faecal pellets sampled in a dropping site or dropping track; see methods and Table 3).

		Carnivores	Herbivores			
		Total	Rabbit	Sheep	Roe deer	Total
LF	N	122	152	156	21	329
	Nj	17	101	6	0	107
	Ab	14.2	84.5	5.02	0	89.5
	P	1				1
F1	N	42	43	44	2	89
	Nj	0	3	3	0	6
	Ab	0	10.75	10.75	0	21.50
	P	0				0.6
F2	N	78	8	43	1	52
	Nj	3	1	0	0	1
	Ab	4.9	1.6	0	0	1.65
	P	0.15				0.08
F1,2	Ab	3.4	4.5	3.4		7.9
Ab	(LF/F1,2)	4.2	18.8	1.5		11.3

Thrush and mammal abundance and distribution

Thrushes settled in all forest types of the study area throughout the late autumn and winter (Table 2). The four species recorded, the blackbird *Turdus merula* (56.1% of censused thrushes), the mistle thrush *T. viscivorus* (13.8%), the song thrush *T. philomelos* (20.9%) and the redwing *T. iliacus* (9.2%), were observed in LF and F1. The two first species have moderate (blackbird) or very scarce (mistle thrush) breeding populations exclusively in the large forests of Lerma (Tellería and Santos 1997, unpubl.) so that a high proportion of the increased and expanded winter populations were migrant birds. Song thrushes and redwings are exclusively migrant species in Lerma (Santos 1982).

In LF, thrush numbers were roughly constant troughout the winter every study year but in 1995–96 they were 25% lower than in 1994–95 (Table 2). Thrush abundance did not differ significantly between LF and F1 forests (Mann-Whitney U-test: $Z = 0.775$, $p = 0.4$ for both years), although densities varied greatly in the latter (ranging from 233 to 0 birds 10 ha^{-1} among fragments in a single census), mainly as a consequence of the vagrancy and gregariousness of redwing and song thrush. Thrushes were scarce and represented only by blackbirds in F2. Blackbirds were however absent troughout the two study years in 5 of these fragments, as well as in 3 out of the 4 census seasons in 2 fragments, and in 2 census seasons in the remaining six fragments. Altogether, thrushes occurred in 100% of LF and F1 forests in both study years, but only in 46.2% (1994–95) and 53.8% (1995–96) of F2 forests. A log-linear analysis on the incidence of thrushes per visit to fragments (F1 and F2), according to year and forest type, showed a significant effect of forest type (partial association: $\chi^2 = 45.540$, DF = 1, $p < 0.001$; 57.4% incidence in F1 and 12.1% in F2).

Carnivore scats were collected in the three forest types, but no clear trend was evident from examination of abundance indices, indicating a very widespread and even distribution of mammal activity throughout the whole area (Table 3). The distribution of collected scats shows that carnivores moved across all forest fragments throughout the study period (except one F2 fragment): 100% incidence in F1 and 92.3% in F2 (two-tailed Fisher exact test, $p = 1$). Abundance patterns were clearer for individual herbivores since sheep and specially rabbit faeces were relatively scarce in F2 in both study years (Table 3), and roe deer faeces were almost restricted to LF (Table 4). However, the incidence of herbivorous faeces did not differ significantly (two-tailed Fisher exact test, $p = 0.3$) between F1 (100% incidence) and F2 (69.2%).

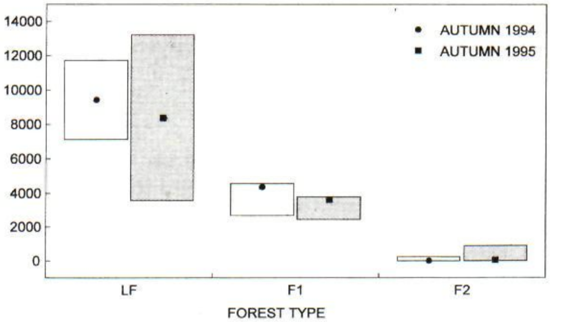

Fig. 1. Variation in cone crop size (mean number of cones per tree) of Spanish juniper *Juniperus thurifera* in Lerma according to forest type and study year (see Table 1). Values represented are the medians and the 25th and 75th percentiles. LF, large forests; F1, fragments with large cone crops; F2, fragments with negligible cone production.

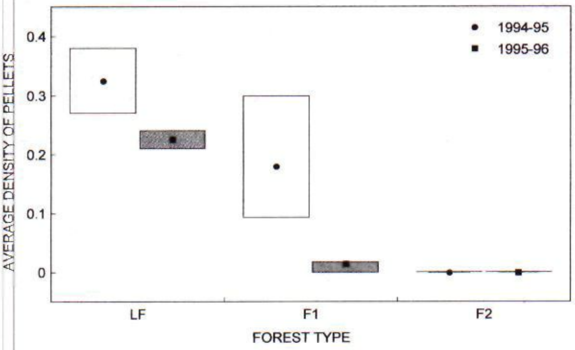

Fig. 2. Variation in density of thrush pellets (mean number of pellets m^{-2}) in Lerma according to forest type and study year; mean values were obtained from the mean number of pellets recorded in the canopy projection of every tree type (SJ1, SJ2 and HO). Values represented are the medians and the 25th and 75th percentiles.

Seed dispersal by thrushes

Changes in the attractiveness to thrushes of the tree types defined (SJ1, SJ2 and HO) and their relation to fragmentation were explored by means of a log-linear analysis of the incidence of thrush pellets under the trees sampled in LF and F1 forests. Tree type (three levels), forest type (two levels) and year (two levels) were included as design variables (see Appendix 1 for sample sizes). F2 forests, with very low cone crops, were excluded since the aim of the analysis was to test for an effect of isolation alone. The results showed a significant effect of tree type in the predicted direction (partial association: $\chi^2 = 49.801$, DF = 2, $p < 0.001$; pellet incidence: 83.1% in SJ1, 53.6% in SJ2 and 23.6% in HO), whereas there was a marginal interaction between tree type and forest type ($\chi^2 = 5.463$, DF = 2, $p = 0.065$; 97%, 51.6% and 13.3% of pellet incidence for SJ1, SJ2 and HO respectively in LF, and 68.8%, 56% and 36% in F1). The effect of the year was also significant ($\chi^2 = 28.430$, DF = 1, $p < 0.001$; pellet incidence: 70.3% in 1994–95 and 34.7% in 1995–96), with a marginal interaction of year and forest type ($\chi^2 = 3.550$, DF = 1, $p = 0.059$; pellet incidence: 63% and 45% for 1994–95 and 1995–96 respectively in LF, and 78.7% and 22.9% in F1) but not with the tree type.

Juniper seed mobilisation by thrushes was evident from the 1180 pellets recorded in 1994–95, and from the 613 ones recorded in 1995–96. Mean densities of pellets beneath the canopy of parent trees were estimated for every forest as the average of mean values for every tree type (Fig. 2, Appendix 1), and compared between LF and F1 forest types with Mann-Whitney U-tests to test for isolation effects alone. No significant difference was evident (1994–95: $Z = 0.387$, $p = 0.698$; 1995–96: $Z = 1.162$, $p = 0.245$). Mobilisation out of the parental shadow (pellets recorded in the transects in both forest types) amounted to 9.3% of the pellets recorded in the first year and 5.4% in the second one; mean densities were ten-fold greater beneath parent canopies (20.2 pellets 100 m^{-2}) than in transects (2.1 pellets 100 m^{-2}). The abundance distribution of the pellets deposited away from parental shadow fitted a decreasing pattern that was similar in large forests and fragments (Fig. 3). Pellet density in LF (unfragmented conditions) varied from 514.2 pellets ha^{-1} in 1994–95 to 281 in 1995–96. The average number of seeds was 2.57 seeds/pellet and ranged from 1 to 5 seeds/pellet (see Table 5 for average values of pellet and seed density).

Pellets were absent in all of the trees examined in F2 fragments, except for one Spanish juniper with cones (SJ1) sampled in the second year (6 pellets; Appendix 1). The influence of year and fragment type (F1 and F2) and their interaction on pellet incidence was analysed with log-linear analysis. Results show that pellet incidence varied significantly between F1 and F2 (partial association: $\chi^2 = 23.646$, DF = 1, $p < 0.001$) but no effect or interaction of year was detected (pellet incidence: 100% and 0% in F1 and F2, respectively, in the first year, and 80% and 8.3% in the second).

Seed dispersal by mammals

Dispersal activity of carnivores was evident in the large forests (LF), since a 13.9% of the scats analysed contained intact juniper seeds (Table 4). The red fox *Vulpes vulpes* was the most important disperser both in number of scats (N = 15) and seeds (N = 778), followed by the stone marten *Martes foina* (one scat with 53 seeds) and the wild cat *Felis silvestris* (one scat with 2 seeds). Undamaged juniper seeds were also frequent in herbivore pellets collected in LF (32.5%), but most were found in rabbit pellets (66.4% of faeces units; 1228

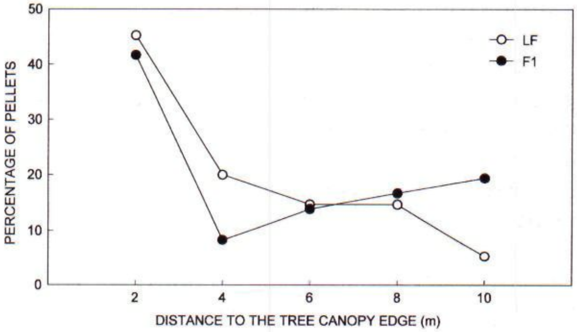

Fig. 3. Distribution of thrush pellets along transects originating at the edge of the canopy of trees in LF and F1. Values were obtained from the pellets recorded in the transects carried out in both juniper tree types (SJ1 and SJ2).

Table 5. Quantitative effectiveness of the Spanish juniper dispersers in Lerma estimated in two large forests (LF; see Table 1) throughout two study years. Thrush pellets and carnivore scats are individual faecal deposits directly convertible in seed-packet and seed densities from count data. A faeces unit are 10 pellets sampled in each dropping site (rabbits) or dropping track (sheep). Faeces units were transformed in seeds ha^{-1} from absolute counts in 74 rabbit sites (average = 102.1 pellets/site) and 30 sheep tracks (average = 207.1 pellets/track). N: number of pellets, scats or faeces units examined for seeds; in brackets, number of samples containing juniper seeds.

	N	No. seeds per seed-packet	Seed-packets ha^{-1}	Seeds ha^{-1}
Thrushes (pellets)	33(33)	2.57	397.6	1021.9
Carnivores (scats)	122(17)	49	0.71	34.9
Sheep (faeces units)	156(6)	1.3	6.73_1	6.73
Rabbits (faeces units)	152(101)	12.1	$4.23–6.36_2$	518.8
Ratio of dispersal effectiveness				
Thrushes/mammals			28.8_3	1.82
Thrushes/carnivores			560	29.3
Thrushes/sheep			59.08_4	151.8
Thrushes/rabbits			$94–62.5_5$	1.97

Hypothetical maximum value (if each seed is considered as an individual seed-packet). Potential maximum value (if the 152 dropping sites censused contained some seed). $_{3,4,5}$ Hypothetical minimum values for assumptions $_1$ and $_{2,1}$ and $_2$, respectively.

seeds). Seeds were extremely scarce in sheep pellets (3.8% of faeces units; 8 seeds) and were not recorded in roe deer (Table 4). Both density of depositions with juniper seeds (these individual seed-packets could not be estimated for sheep; see Methods) and seed density were highest for rabbits, that mobilised most seeds (Table 5), although their deposition patterns were highly clumped.

Percentages of carnivore scats collected in the fragments (F1 and F2 forests) containing intact juniper seeds were 0% in F1 and 3.8% in F2 (Table 4; overall, 315 seeds were mobilised to two fragments into 2 scats of red fox and one of stone marten). The incidence per fragment of these faeces did not differ significantly between F1 and F2 forests (two-tailed Fisher exact p, p = 1). In contrast, the percentage of herbivore faeces with intact seeds was 6.7% in F1 and 1.9% in F2 where overall 15 seeds were recorded in 7 faeces units collected in 3 F1 fragments and 1 F2 fragment. The incidence per fragment of herbivore faeces units with juniper seeds differed significantly between F1 and F2 forests (Fisher exact p, two-tailed p = 0.044). The quantity of dispersal (the number of faeces units with intact seeds km^{-1}) was much lower in fragments (F1 and F2) than in LF (Table 4), although, as mentioned above, mammals showed similar or higher abundance indices (overall number of faeces km^{-1}; see Table 3) in fragments. These results fit our second prediction about the movement patterns of mammals and their potential to disperse seeds to any fragment (F1 or F2). Furthermore, the scarcity of juniper seeds in their diet in the fragmented landscape is attributable to the low representation of forest and resulting lower availability of Spanish juniper in the area surrounding the fragments (from 3 to 5% of forest cover) than in large forests (LF: from 20 to 30%; both ranges estimated from circular samples each with a radius of 3 km centred in each fragment or large forest; for a similar procedure see McCollin 1993).

Discussion

The role of thrushes as seed dispersers

Dispersal of Spanish juniper within LF forest type (intra-habitat scale) depended on a diverse community of birds and mammals, a well-known fact for *Juniperus* (Holthuijzen et al. 1987, Debussche and Isenmann 1989, Herrera 1989, Jordano 1993, Willson 1993, Chávez-Ramírez and Slack 1994, Schupp et al. 1995, 1997). However, thrushes were the most relevant dispersers, based both on the quantity of seeds mobilised, and on the density of seed packages (pellets) involved, which exceeded at least 29 times that of mammals for the whole study period (Table 5). This difference in the dispersal role of both disperser groups is also supported by the records for thrush density in 4 previous winters, which ranged from similar to 4 times higher than those recorded in this study (Santos and Tellería 1994, unpubl.). The potential of thrushes to disperse juniper seeds may thus vary among years because of variations in their abundances and, in fact, both pellet incidence and density were nearly twice greater in the first study year, coinciding with higher numbers of thrushes. Nevertheless, other factors such as embryo abortion and pre-dispersal seed predation by invertebrates, frequent among junipers (Roques et al. 1984, Fuentes and Schupp 1998), may contribute to the variation in the quantitative effectiveness of dispersers by reducing the number of seeds finally available for recruitment. Despite these variations, it is evident that, in terms of quantity of seeds dispersed, mammals play a secondary role compared to thrushes.

The seed fall pattern evidenced by pellet sampling suggests that, at intra-habitat scale (LF), thrushes visited the tree types as expected, so that thrushes must forage and spend most of their time on SJ1, and must perch on SJ2 rather than on HO. This behaviour originated radial seed shadows with seed density decreasing further away from the parent trees, suggesting that, based on the quantity of seeds dispersed, the highest recruitment of Spanish juniper should occur around the more productive trees, and that the holm oaks are the microhabitat with lower probability of recruitment.

Fragmentation per se, i.e. the isolation of healthy, productive juniper populations in tiny forest tracts (F1), had limited influence on thrush occurrence and behaviour, and also on their patterns of seed deposition. Thrush densities were high in F1, although highly variable among forests, years and within-year, contrasting with the apparent regularity of thrush numbers in LF. Yet, both pellet densities and the distribution patterns of pellets among tree types and outside of parental shadows were nevertheless similar in both forest types. Therefore, fragmentation per se was not the cause of either quantitative or qualitative decreases in dispersal effectiveness (see Schupp 1993) by thrushes. *Turdus* thrushes are highly polyphagous (Cramp 1988) but with a strong tendency to frugivory in the overwintering period (Herrera 1981, 1984, Debussche and Isenmann 1985a, b, 1989, Snow and Snow 1988). In their Spanish wintering grounds thrushes tend to monophagous habits as a functional response to clumped distributions of dominant food items, such as juniper cones (Zamora 1990, Jordano 1993) or olives (Rey 1995). This distribution of food supplies is present in the study area, not only among fragments (F1 forest type) but also within continuous forests (LF), in which the patches with high density of Spanish junipers are more or less distant from one another, so that movements among them could be equivalent to movements among fragments of F1 type. Hence, both the similar numbers of birds and the similar densities and distribution patterns of pellets found in LF and F1 suggest that thrushes tracked the local availability of juniper cone crops on a landscape scale, moving among all habitat patches with available cone supplies (LF and F1 forest types), in a similar way to the resource tracking described in localities of southern Spain for other juniper species (Zamora 1990, Jordano 1993).

In the small forest remnants in which fragmentation resulted in minimum or unproductive populations of Spanish juniper (F2 fragments), thrush numbers were very low and, according to our predictions, their quantitative role in the mobilisation of juniper seeds was negligible (Appendix 1). The scarce individuals recorded were all blackbirds, with a majority of solitary males and rare records of up two individuals, probably involving territory-holders (Cramp 1988, Snow and Snow 1988). These territorial and rather sedentary individuals must have the ability to use the food supplies of F2 as generalists, contrasting with the gregariousness and nomadic behaviour of strictly migrant thrushes in Lerma (the redwing and the song thrush), and with the marked restriction of mistle thrush to the large forests (LF). In fact, records of blackbirds feeding in fields or isolated shrubs of wild rose adjacent to fragments were frequent, both in F1 and F2 fragments. These results confirm that thrushes actually behaved as specialist feeders on juniper cones, and that in fragments devoid of attraction to frugivores, such as F2, only generalists, such as the blackbird, are able to overwinter on other food resources. In short, this evidence strongly supports the idea that it is exceptional for juniper seeds to reach these fragments due to the activity of thrush dispersers, and the idea might even be discarded in those fragments where fragmentation or subsequent use by man has totally eliminated the Spanish juniper.

The role of mammals as seed dispersers

The loss of thrushes as seed dispersers in F2 fragments entails an unknown but relevant decrease in the quantitative effectiveness of the dispersal system of Spanish juniper in these small forest fragments. In these fragments, mammals will thus be the only juniper dispersers, with low quantitative effectiveness of seed dispersal and with relevant differences among groups in dispersal quality due to their different movement patterns (Schupp 1993). Rabbits have the ability to disperse seeds of fleshy fruited plants, including juniper species (Muñoz 1993, Heras et al. 1994, Nogales et al. 1995, Schupp et al. 1995, 1997). However, they show highly sedentary habits, with very scarce and short-distance dispersal (a few tens or hundreds of meters; Corbet and Southern 1977, Kolb 1991), and very small home ranges in Mediterranean Spain, well below 1 ha in continuous habitat (Soriguer 1981). In the fragmented landscape of Lerma, 5 out of 6 fragments occupied by rabbits (from 18) ranged in fact between 0.6 and 0.8 ha, but warrens were lacking in the ten fragments under 0.5 ha. Rabbits thus seem to be restricted by fragment size, but the relevant issue for Spanish juniper dispersal and potential colonisation is that of unlikely dispersal outside the colonised fragments (e.g. from F1 to F2).

Carnivores contrast with rabbits by their mobility and large home ranges, associated with the ability to perform long-distance dispersal (Debussche and Isenmann 1989, Willson 1993). The two species concerned here, the red fox and the stone marten (dispersal by wild cats was anecdotal and may perhaps be indirect, related to the consumption of cat prey items; see Nogales et al. 1996), are relevant to the dispersal of many fleshy plants in the Mediterranean region, including several junipers species (Herrera 1989, Debussche and Isenmann 1989). In the case of red fox, which in Lerma dispersed ca 90% of seeds removed by carnivores, home ranges in Spain vary from 100 to 600 ha and average daily movements from 4.9 to 6.7 km (Blanco 1986, Castells and Mayo 1993). In Lerma, evidence of carnivores was recorded over all studied fragments (except in one F2 fragment), supporting thus that both vagility and generalist tracking of resources are also valid in the study landscape. An analysis of the scats collected showed that rodents (voles and mice) were the main component of the diet in Lerma, amounting to 73.3% of occurrence in red fox scats ($N = 165$) and 48.4% in stone marten scats ($N = 31$; seeds of sunflower and grapes, available in the farming matrix, were the other main food items). In Lerma, as well as in similar farming landscapes in central Spain, winter populations of rodents are almost restricted to woodlands (Tellería et al. 1991, Santos and Tellería 1998). Hence, carnivores must mainly look for small mammals in the fragments, and the consumption (and consequential dispersal) of juniper seeds must in most cases be an incidental event, in contrast to the directional consumption and dispersal by thrushes. Furthermore, many of the droppings containing seed loads will be defecated in the agricultural patches, outside the forest remnants, thus limiting even more their role in recruiting small populations of Spanish juniper isolated within the fragments, or in recolonizing forest remnants where junipers have become extinct.

Dispersal by domestic herbivores is less documented than avian and carnivore dispersal, but a positive effect of sheep endozoochory on germination and dissemination of Spanish juniper has been recognised (Borel and Polidori 1983, Heras et al. 1994). Sheep are raised "extensively" in Lerma, so that the dispersal effects associated with their movement patterns are comparable to those of carnivores due to the high managed-vagility and long foregut passage time characteristic of ruminants (Pough et al. 1990). In the fragments studied in Lerma, the frequency of occurrence of juniper seeds was similar for sheep and carnivores (3 faeces units and 3 scats, respectively; Table 4), and the seed numbers involved may be regarded as similar given the scarcity of data (7 seeds multiplied for a factor of ca 20 vs 315 seeds counted in the carnivore scats). In short, sheep admittedly play a role qualitatively similar to carnivores on a landscape level by dispersing juniper seeds among all possible patches (F1 and F2 fragments, shrublands, set-aside fields, and within LF), but data are insufficient to compare the quantitative effectiveness of sheep and carnivores.

Conclusions

Our results support the idea that fragmentation seriously impairs the long-term subsistence of Spanish juniper on many fragmented forest patches in the agricultural landscape. The main reasons for this are 1) the probability of reinforcing small populations of Spanish juniper isolated in forest patches or colonising empty patches (F2 fragments) is drastically diminished by the loss of thrushes, which are the most efficient part of the dispersal system, and 2) it is almost restricted to carnivores and sheep, generalist dispersers with a low quantitative effectiveness. The scarce seeds reaching these forest patches (F2), likewise the small seed crops produced if it is the case, are moreover subjected to a high extinction risk because of the high predation rates juniper seeds are subject to in the fragments (mainly by rodent predation; Santos and Tellería 1994). In contrast with this low seed recruitment and high seed mortality in F2, seedling recruitment actually occurs in F1 forest patches (Santos and Tellería 1994) because the large cone crops produced are sufficient to guarantee that some seeds escape predation. Spanish juniper reproduces only by seeds (Costa et al. 1986), so this tree cannot counteract the effects of high predation pressures by vegetative sprouting, as in the holm oak *Quercus ilex*, a tree with strong clonal propagation (Ceballos and Ruiz 1979) also exposed to heavy rates of seed predation in Lerma (Santos and Tellería 1997). Nevertheless, given the long lifespan of Spanish juniper (until 500 yr old; Ceballos and Ruiz 1979), a low seedling recruitment should be quite enough to ensure their long-term conservation even in fragments with only one surviving tree (Dzwonko and Loster 1989). Seedling recruitment can fail however if seed numbers are low and risks, such as seed predation, seedling mortality (by herbivory and others) and even the felling of the scarce adult trees, are high.

Since fragmentation is advancing in Lerma (Santos and Tellería 1997), and probably over most of central Spain (Santos and Tellería 1998), progressively smaller forest fragments are to be expected, and thus a progressive increase in the number of fragments with weakened juniper populations or totally devoid of any juniper tree (F2). In this scenario, the role of carnivores and sheep appears, in spite of its limitations, to be vital to maintaining the Spanish juniper in the severely fragmented landscapes of central Spain since there will gradually be an increase in the number of fragments in which the bird component of the dispersal system is lost.

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Appendix 1. Number of trees sampled and number of thrush pellets collected according to tree type (SJ1, SJ2, HO), forest type (LF, F1, F2) and year. The area sampled is also given in m^2.

		1994–95			1995–96		
		SJ1	SJ2	HO	SJ1	SJ2	HO
LF	No. trees	20	17	17	13	14	13
	Area	764	550	2153	469	474	513
	No. pellets	632	69	6	270	17	1
F1	No. trees	17	15	15	15	10	10
	Area	571	582	1689	505	386	465
	No. pellets	380	79	14	265	2	52
F2	No. trees	7	10	67	9	11	55
	Area	160	229	2820	213	264	2057
	No. pellets	0	0	0	6	0	0