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INFLUENCE OF FOREST FRAGMENTATION ON SEED CONSUMPTION AND DISPERSAL OF SPANISH JUNIPER *Juniperus thurifera*

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Abstract

We examined the effects of fragmentation on Spanish juniper Juniperus thurifera *in central Spain by comparing eight small forest fragments (SF: 0·2–16 ha) with two large forests (LF: 150 and 270 ha). Wood mice* Apodemus sylvaticus, *the only rodent seed eaters, were 8·9 times more dense in SF, whereas thrushes* Turdus *spp., the main avian seed dispersers, were 4·6 times more abundant in LF. Finches (seed eaters) were scarce in both forest groups. Mean fruit abundance was significantly higher in LF. Seed consumption was mainly by mice in SF and by finches in LF. Thrush pellets with intact seeds, seedling abundance and the proportion of trees with nearby seedlings, were all higher in LF. This evidence points to a decrease in the dispersal efficiency of Spanish juniper in SF. We suggest that the processes leading to reduced dispersal ability might be inherent to fragmentation and represent a threat for the survival of fruit-bearing plants in patchy environments.*

Keywords: fragmentation, Spain, Spanish juniper, *Juniperus thurifera*, thrushes, wood mice.

INTRODUCTION

Habitat fragmentation occupies a central place in conservation biology (Soulé, 1986). The responses of species to fragmentation are highly variable, depending on the species characteristics and on the particular pattern of fragmentation involved. Plant persistence, for example, can be affected through a direct response to habitat reduction (Dzwonko & Loster, 1989), but it may also be negatively affected by interspecific interactions, namely by population changes of animal species that act as dispersers, seed eaters or browsers, or by bringing seeds from surrounding habitats (Janzen, 1983, 1986).

In the agricultural landscapes of central Spain, islands of stable habitats (such as shelterbelts, forest fragments and shrubland patches) surrounded by agricultural matrices usually support high densities of wintering wood mice *Apodemus sylvaticus* (Alcántara, 1986; Díaz, 1992). Mice are omnivorous and highly efficient food searchers (Hansson, 1985; Santos & Tellería, 1991), hence they are expected to act destructively as consumers of seeds and fruits in these isolated habitats. Tellería *et al.* (1991) showed that the density of wintering mice in holm oak *Quercus ilex* woodlots increases as forest size decreases, and suggested that regeneration and long-term persistence of plant species whose propagules are consumed might be threatened within the fragments.

In this paper we analyse some effects of forest fragmentation on the dispersal ecology of Spanish juniper *Juniperus thurifera* in an area of central Spain. In this area, Spanish juniper is a scarce tree species in forests dominated by holm oaks and is the only fruit-producing tree whose seeds are dispersed by wintering birds. Its persistence is therefore likely to be influenced by the increased numbers of mice and by the potential changes in the abundance or behaviour of their dispersal agents. Within this context, we hypothesized two negative effects of fragmentation on the dispersal of Spanish juniper: (1) an increase of fruit and seed consumption by rodents and a decrease of fruit consumption by frugivorous birds; (2) a decrease in seedling recruitment, as a result of the reduced seed dispersal.

STUDY AREA

The study was carried out in Lerma (central Spain: 42°5'N, 3°45'W) during winter 1989–90. Average altitude is 850 m and climatic conditions are inland mediterranean, with long, cold winters (Font, 1983). The region is covered by ploughed agricultural landscape, where small woodlots are isolated remnants of the original forest. Sampling was carried out in two sets of forests. A first set of eight small forests (SF 1–8, 0·2, 0·3, 0·6, 1·2, 1·3, 2·0, 12 and 16 ha, respectively) was sampled in an area (Santa Cecilia) with numerous small woodlots embedded in a matrix of crop fields. Distances between SF ranged from 100 m to 1·3 km and shapes were either square (two fragments) or rectangular (six fragments). We also studied two large forests (LF1, 150 ha and LF2, 270 ha) in Quintanilla del Agua, about 15 km from Santa Cecilia; these allowed us to sample dispersal and predation patterns indicative of the 'natural' situation previous to fragmentation and could thus be considered as controls.

LF1 and LF2 were 2 km apart and moderately rectangular in shape.

Firewood extraction is fairly intense throughout the study area, but our observations show that this does not selectively affect the density or size structure of the tree stratum in the forests studied. Seedlings are very vulnerable to grazing (Ceballos & Ruiz, 1979) but sheep and rabbits *Oryctolagus cuniculus* were rarely recorded in these woods. Fire damage from stubble burning, however, is a potential disturbance.

Tree composition in the forests is dominated by holm oaks (27·3–31·3% cover in LF and 20–87% in SF; mean 33·4%), Spanish juniper being a minor species (3–5·8% cover in LF and 0·3–7·5% in SF; mean 2·7%). The shrub layer is mainly formed by species of the genera *Cistus, Genista, Thymus* and *Lavandula*. Sparse grasses grow in these woodlots, mostly in cleared areas.

BIOLOGY OF SPANISH JUNIPER

The Spanish juniper, a monoecius, long-lived tree around 4–5 m tall, is a Tertiary relict which is distributed throughout the western Mediterranean Basin, with its main quarters in the central Spanish highlands (Ceballos & Ruiz, 1979). The genus *Juniperus* has animal-dispersed fleshy cones (hereafter called fruits) (Herrera, 1987; Snow & Snow, 1988). The main dispersers in Europe are small and medium-sized passerines (e.g. robin *Erithacus rubecula* and thrushes *Turdus* spp.) (Herrera, 1981*a,b*; Debussche & Isenmann, 1985*a,b,c*; Snow & Snow, 1988). Rodents are well-known consumers of both fruits and seeds (Gilbert, 1980; Holthuijzen & Sharik, 1985).

Germination rate of Spanish juniper is low, and regeneration and growth very slow (Ceballos & Ruiz, 1979). It flowers in spring and ripe fruits are available during the autumn–winter period of the following year (Ceballos & Ruiz, 1979). In late January 1990 we recorded the proportion of trees bearing ripe fruits in a sample from the two LF (181 trees) and all SF (214 trees) taken from both the interior and edges of the forests. The means were almost the same (45·9% and 45·8% in LF and SF respectively), although there was much greater variability among SF (15·4–73·7%) than in LF (44·2–48·5%).

METHODS

Rodent and bird abundance

Rodents were recorded in the previous winter (early March 1989) from snap-traps placed in all the woods (for details see Tellería *et al.*, 1991), and from tawny owl *Strix aluco* pellets that were collected and examined.

We studied wintering birds through December 1989–March 1990. All forests were censused twice, the two LF and the 12- and 16-ha SF stands by means of the line-transect method (Järvinen & Väisänen, 1975), using a 50-m main belt width. Untransformed main belt densities (number of birds/10 ha) were compared with the densities obtained by searching for birds throughout the rest of SF. The elongated shape and small size of these woodlots allowed us to census their total area by walking straight through them. The total area surveyed was 92 ha in LF and 32·2 ha in SF.

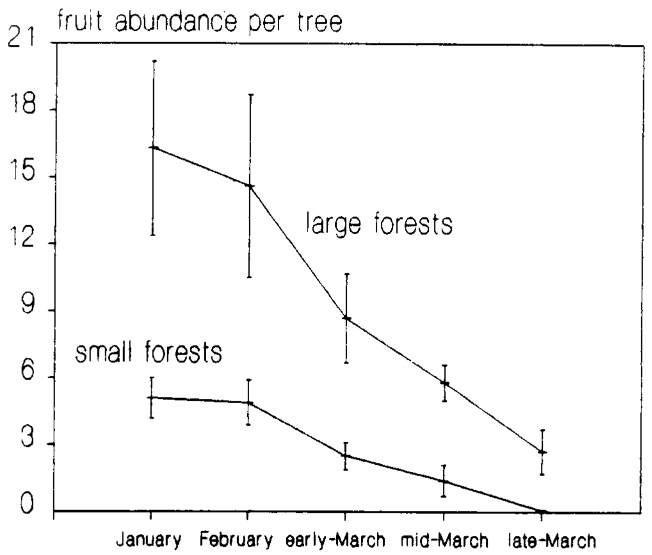

Fig. 1. Temporal changes in the mean abundance (and standard deviation) of juniper fruits in Lerma. Fruit abundance is the average of the mean number of fruits per tree obtained in eight small and two large forests.

Fruit abundance and seed consumption

We sampled fruits and seeds under the canopy of individual junipers in each forest. For each of four 15 × 15 cm random plots beneath each tree (total area 0·09 m^2), we recorded (a) the number of fresh fruits; (b) the number of intact, undamaged seeds; (c) the number of seeds damaged by rodents and (d) the number of seeds consumed by birds; (c) and (d) were added for each tree, thus providing a total seed consumption estimate. The four plots were pooled into a single sample per tree.

Undamaged seeds are left by both mice and birds. Mice tend to eat mainly the outer pulp early in the winter, leaving the seeds intact and then, in late winter, they eat the seeds. Intact seeds are also left in thrush pellets. Seeds consumed by birds and rodents were readily distinguished, since mice obtain the seeds (endosperm) by chewing the husk, while birds usually crack seed husks longitudinally in two halves. The number of half-husks found (attributed to birds) was

Table 1. Densities (no. birds/10 ha) and numbers (in brackets) of avian frugivores and seed eaters in LF (92 ha censused) and SF (32·2 ha censused)

Species	Large forests	Small forests
Erithacus rubecula	4·0 (37)	1·2 (4)
Turdus merula	2·8 (26)	2·2 (7)
Turdus iliacus	5·9 (54)	—
Turdus philomelos	16·8 (155)	3·1 (10)
Turdus viscivorus	0·4 (4)	—
All frugivores	30·0 (276)	6·5 (21)
Fringilla coelebs	6·5 (60)	0·6 (2)
Carduelis chloris	0·1 (1)	—
All seed eaters	6·6 (61)	0·6 (2)

Table 2. Mean values (and standard deviations) of Spanish juniper seeds recorded in 0·09 m^2 samples at the end of March in the small and large forests

Number of junipers sampled in brackets. Mann-Whitney U-tests compare mean SF and LF for proportions of undamaged and consumed seeds (see Methods)

	Area	Undamaged seeds	Consumed seeds		
			Mice	Birds	Total
Small forests					
SF$_1$ (2)	0·2	3·0 (1·1)	3·5 (2·1)	1·0 (0·0)	4·5 (2·1)
SF$_2$ (5)	0·3	21·4 (15·5)	17·2 (27·3)	0·4 (0·9)	17·6 (28·2)
SF$_3$ (7)	0·6	8·3 (10·7)	6·1 (8·4)	1·9 (3·3)	8·0 (8·3)
SF$_4$ (6)	1·2	26·2 (28·8)	4·7 (6·6)	12·8 (29·5)	17·5 (35·2)
SF$_5$ (7)	1·3	14·9 (13·7)	40·6 (34·2)	5·0 (5·4)	45·6 (32·7)
SF$_6$ (5)	2	18·8 (19·9)	48·6 (67·1)	0·2 (0·5)	48·8 (67·1)
SF$_7$ (6)	12	60·7 (33·1)	51·5 (34·2)	1·0 (0·9)	52·5 (34·3)
SF$_8$ (6)	16	21·0 (14·8)	63·8 (78·7)	1·0 (2·0)	64·8 (78·8)
Large forests					
LF$_1$ (27)	150	26·9 (37·1)	0·3 (0·9)	7·0 (21·2)	7·3 (21·2)
LF$_2$ (12)	270	28·4 (25·7)	0·4 (1·2)	32·4 (47·0)	32·8 (47·9)
		$z = 0·914$ $p = 0·361$[a]	$z = 1·958$ $p = 0·025$[b]	$z = 1·697$ $p = 0·045$[b]	$z = 0·914$ $p = 0·361$[a]

[a] Two-tailed test.

[b] One-tailed test.

therefore divided by two to obtain an estimate of the actual number of damaged seeds.

We sampled fruit abundance five times (251 trees in LF and 276 trees in SF), between the end of January up to the end of March 1990 (Fig. 1), encompassing the period of maximum fruit consumption and seed dispersal. Seed abundance was sampled on this last date (see Table 2 for sample sizes), so the numbers of seeds recorded can be considered as accumulated values at the end of the dispersal season. Seed consumption was then estimated for each forest as the ratio between the mean number of seeds taken by mice or birds and the mean total number of seeds. LF and SF data were compared by means of Mann-Whitney U-tests.

We also obtained an index of seed-dispersing activity by recording the presence of thrush pellets that included intact seeds in all SF (below 39 trees) and in the two LF (63 trees).

Fruit removal

Patterns of fruit consumption were studied by estimating the rates of fruit removal by birds and mice in late February 1990. We set a group of three fruits on the ground (close to the trunk) and on the branches (staked by wire) of 88 junipers in SF and 61 in LF (see Denslow & Moermond, 1982, for a similar procedure). The branches were generally slender and chosen randomly within convenient reach. We assumed that the distribution of branch diameters was the same in both forest groups and that it did not influence the identity or frequency of consumers (Denslow & Moermond, 1982; Santos & Tellería, 1991). These 'experimental' fruits were made available during a moonless night for rodents and the previous or subsequent day for birds. Fruit removal from any tree was scored when at least one fruit (out of a group of three) was taken or damaged. The effect of substratum (branches/ground), forest size (SF/LF) and consumer (mice/avian), and the interactions between these factors on the removal of experimental fruits, were analysed using log-linear models (Dixon, 1985).

Seedling recruitment

Seed and seedling mortality may be disproportionately high under and nearby the parent plants where most of the seeds usually fall (Howe, 1986). We therefore assessed seedling recruitment up to 10 m radius from the edge of tree canopy for each of 64 trees in LF and 65 trees in SF.

RESULTS

Rodent and avian abundance

Wood mice abundance was 2·2–19·2 times higher (mean 8·9) in each SF than in any LF (Tellería *et al.*, 1991). Other rodent species were restricted to scarce grass patches (the common vole *Microtus arvalis*) or hibernated throughout the winter (the garden dormouse *Eliomys quercinus* according to records from trapping in spring). The examination of tawny owl pellets also showed that the wood mouse was the main rodent species in the area.

Among birds, song thrushes *Turdus philomelos*, redwings *T. iliacus* and robins were the main avian frugivores and seed dispersers. The chaffinch *Fringilla coelebs* was the only abundant seed-eating species (Table 1), though other birds presumably capable of destroying juniper seeds (P. Jordano, pers. comm.), such as hawfinches *Coccothraustes coccothraustes* and greenfinches *Carduelis chloris*, were occasionally seen. Abundances of each group differed between forest sets. The mean number of bird dispersers was 4·6 times as abundant in LF than in SF, while consumers were 11 times as high (Table 1).

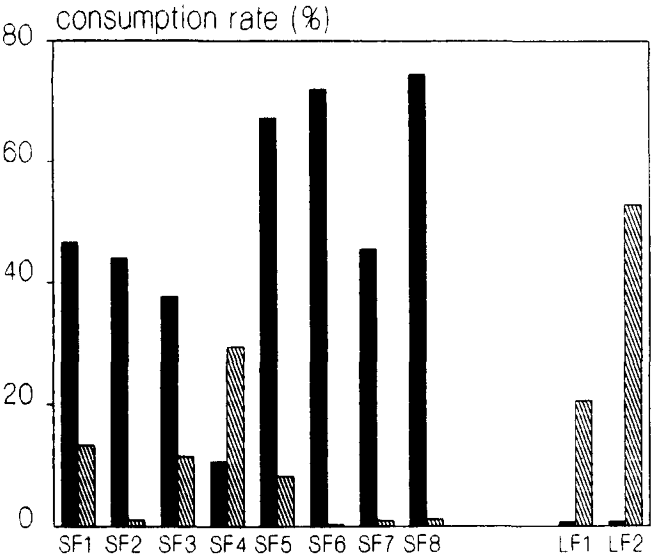

Fig. 2. Consumption rates of juniper seeds by mice (■) and birds (▨) in Lerma (see Table 2). SF: small forests; LF: large forests.

Table 3. Log-linear analysis of the experimental rates of fruit removal in relation to substratum, forest size and consumer
N and R are the numbers of fruit groups placed and removed respectively. The interaction effects of two-, three- and four-factor terms involving removal are shown at the bottom of the table (d.f. = 1 for all terms).

Consumer	Forest size	Substratum	N	R	% R
Mice	Large forest	Branches	61	2	3·3
		Ground	61	4	6·6
	Small forests	Branches	87[a]	8	9·2
		Ground	88	36	40·9
Birds	Large forest	Branches	61	10	16·4
		Ground	61	15	24·6
	Small forests	Branches	88	2	2·3
		Ground	88	3	3·4

Removal with: Substratum: G = 18·44 ***; Forest size: G = 0·14 ns; Consumer: G = 5·80 *; Substratum–Forest size: G = 0·67 ns; Substratum–Consumer: G = 1·35 ns; Forest size–Consumer: G = 45·29 ***; Substratum–Forest size–Consumer: G = 1·08 ns.

[a] Loss of one fruit group.

Fruit and seed consumption

The season in which juniper fruits were available (mid-October to early April), is roughly coincident with the presence of their bird dispersers in the study area (personal observations; Santos, 1982). Juniper fruits naturally fall to the ground from early autumn thus making a high percentage available to ground-dwelling consumers from the beginning of the dispersal season (October).

The abundance of fruit decreased continuously during the study period (Fig. 1). Significantly more fruit overall was recorded per forest (mean of trees sampled) in LF (z = 1·958, p = 0·05) a well as at the beginning (26 January; z = 1·958, p = 0·05) and at the end (30 March; z = 2·089, p = 0·04) of the period.

Mouse-damaged seeds were more abundant in SF than in LF, whereas bird-damaged seeds were more abundant in LF than in SF (Table 2), and this difference was also shown in the proportions of total available seeds consumed by mice and birds (z = 2·933, p = 0·001, one-tailed test) (Fig. 2). Although the combined effect of birds and mice did not differ significantly between SF and LF (Table 2), the proportion of seeds consumed was higher in all the SF than in one LF, and in four SF than in the other LF.

Many seeds remained undamaged under the trees, both in SF and LF. The mean number of these intact seeds on the ground at the end of March was similar in both forest sets (Table 2). Pellets were scarce or absent in most SF whereas a majority of LF junipers had thrush pellets under their canopies (Fig. 3).

The removal of experimental fruits varied significantly with substratum (19·5% of fruit groups were removed from the ground and 7·4% from branches) and with consumer (removal rate was 16·8% for mice and

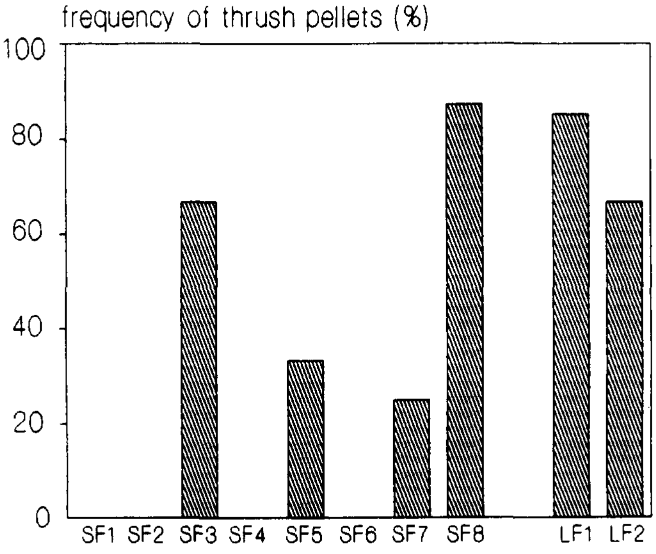

Fig. 3. Percentage of junipers with presence of thrush pellets in Lerma. SF: small forests; LF: large forests.

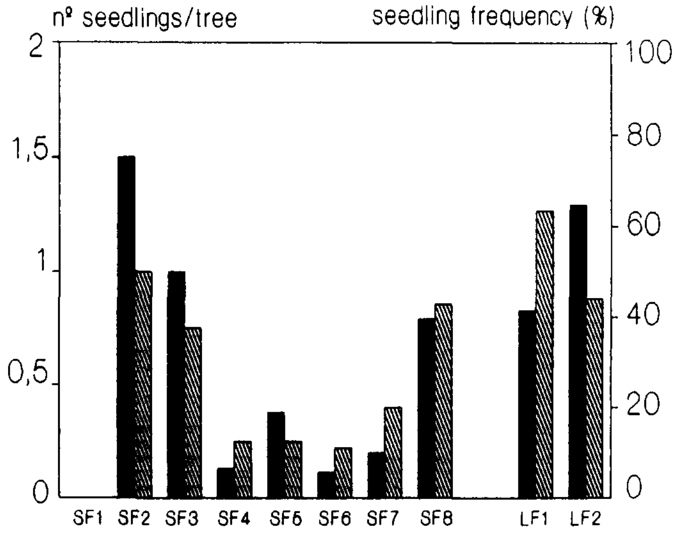

Fig. 4. Mean abundance (mean number of seedlings per tree: ■) and frequency of seedlings (in percentages: ▨) in Lerma. SF: small forests; LF: large forests.

10·1% for birds), but was independent of forest size (12·7% in LF and 14·0% in SF; Table 3). There was, however, a significant interaction of forest size and consumer on removal, mice removing 25·1% of the fruit groups in SF and 4·9% in LF, and birds removing 2·8% and 20·5% respectively. This corroborates the patterns expected from rodent and avian abundances in both forest groups.

Seedling recruitment

The mean density of seedlings was lower in six out of eight SF than in the two LF, and seedlings were totally absent in one SF (Fig. 4); the number of seedlings ranged from 0 to 11 seedlings/tree in LF and from 0 to 5 in SF. The frequency of trees with seedlings present was higher in the two LF than in seven out of eight SF (Fig. 4). Thrush pellet and seedling frequencies showed a significant association in the forests studied (Spearman rank coefficient = 0·595, $n = 10$, $p = 0{\cdot}037$; one-tailed test).

DISCUSSION

Fruit feeding and seed dispersal

Large forests

The numbers of avian dispersers, and the frequency of thrush pellets, were relatively high in LF compared with SF while mice were relatively scarce and consumed less fruits than birds. Most of the undamaged seeds counted under the canopy of trees in LF, as well as most of the experimental fruits removed, could therefore be assigned to bird frugivores. The relatively high frequency of thrush pellets in LF also indicates that effective seed dispersal took place.

Thrushes are common and abundant wintering passerines in extensive Spanish juniper woodlands (Santos, 1982; Santos *et al.*, 1983) and other *Juniperus* habitats (Juana & Santos, 1981; Snow & Snow 1988). However, our four-year records of the intra- and inter-annual variations in wintering populations of these frugivores and of marked temporal variability in the fruit production in the study area (see also Santos, 1982; Herrera, 1988) suggest that dispersal efficiency of Spanish juniper can vary greatly between years in LF.

Small forests

There were marked changes in numbers of consumers and dispersers, and these were reflected in the distinct patterns of fruit and seed consumption in SF. The lower avian removal of experimental fruits (Table 3), and the low frequency of thrush pellets, was consistent with the 4·6-fold decrease in the abundance of bird dispersers relative to LF. On the other hand, the higher rodent removal of experimental fruits in SF (25·1% versus 4·9% in LF) and the direct evidence obtained from destroyed seeds were consistent with the nine-fold increase of mice abundance in SF. These results supported our hypothesis of increased seed consumption and decreased dispersal in small woodland fragments.

The lower abundance of frugivorous birds in SF might be related to fragmentation itself, as has been recorded for avian and other vertebrate frugivores in small patches of tropical forests (Willis, 1979; Terborgh & Winter, 1980; Lovejoy *et al.*, 1983). The concentrations of mice in SF strongly deplete the limited fruit crop throughout the winter, mainly on the ground, but also the more accessible fruits on the branches (Santos & Tellería, 1991). The low density of avian frugivores in SF could therefore be interpreted as the result of competition with mice (Smith & Balda, 1979). The direct influence of increased populations of fruit eaters, or other damaging animals, on dispersal agents feeding on the same plants has indeed been recorded in some instances (Manzur & Courtney, 1984; Christensen & Whitman, 1991). Nevertheless, the available evidence is inconclusive, and further data are needed to assess the influence of mice on the abundance of bird frugivores in SF.

Fragmentation and persistence of Spanish juniper

The stocks per tree of undamaged seeds that have lost the fleshy covering, and therefore are not dispersed by thrushes (Herrera, 1984), were similar in both forest groups. The open ground under the junipers does not seem to be a suitable microhabitat for establishment (Ceballos & Ruiz, 1979; Howe & Smallwood, 1982). Hence, these undamaged seeds represent a loss of dispersal efficiency in SF. Undamaged seeds recorded in LF under junipers are similarly unavailable for recruitment. However most of these were the result of fruit consumption by thrushes which suggests that at least part of the seed crop was dispersed to places suitable for establishment (Howe & Smallwood, 1982; Howe, 1986).

Thus the reduction in fruit removal associated with fragmentation greatly impairs seed dispersal, and could thus reduce the establishment of seeds and the natural regeneration of junipers. Although other factors potentially affecting seedling establishment (e.g. water stress, competition; see Fenner, 1985) were not studied, our results are consistent with this interpretation, since there is a marked fall in recruitment in the majority of small fragments (Fig. 4).

Winter concentrations of small mammals in uncultivated tracts are common in temperate agroecosystems (Ryszkowski, 1982; Yahner, 1982, 1983; Tellería *et al.*, 1991). Conversely, a loss of avian frugivores is to be expected in the remnants of natural habitats, since frugivores rely on superabundant food supplies (Herrera, 1984, 1985; Howe, 1986; Snow & Snow, 1988). Therefore, the processes addressed in this study, namely (1) the decrease of dispersal agents, (2) the increase of seed consumption and (3) the resulting reduction in dispersal and establishment as a result of woodland fragmentation, may be a more general phenomenon and conservation issue in temperate latitudes.

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