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# The role of remnant trees in seed dispersal through the matrix: Being alone is not always so sad

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## ABSTRACT

Remnant trees within the non-forest matrix are common structures of forest landscapes which have high conservation value due to their supposed roles as biological legacies and stepping stones in fragmented forest scenarios. Fleshy-fruited remnant trees are dispersal foci for many forest plants, as seeds accumulate under their canopies after visitation by forest frugivores. Despite this recognized effect, little is known about the relative role of remnant trees in maintaining their seed dispersal function after forest fragmentation. In this work, conducted in the Cantabrian Range (Northern Spain), seed deposition by frugivorous birds and post-dispersal seed predation by rodents were compared beneath the canopies of hawthorn (*Crataegus monogyna*) trees scattered in the non-forested matrix, to those embedded in forest patches. We studied two years which had strong differences in community-wide fruit abundance (high in 2004, and low in 2005). Hawthorn and holly (*Ilex aquifolium*) seeds dominated the seed rain. The density of dispersed seeds differed between years and tree type, with higher values under patch trees relative to remnant ones. However, the effect of tree type depended on both the year and the seed species, as larger differences were found in the year of high fruit availability, and with holly seeds. Higher levels of post-dispersal seed predation on holly seeds also contributed to offset the differences between tree types. Our results suggest that remnant trees, by functioning as dispersal foci, facilitate the dispersal of the two most abundant plant species for forest succession through the matrix. More importantly, we demonstrated that in years of low fruit availability in which forest frugivores are forced to exploit scattered fruit resources, the role of remnant trees may even be equivalent to that played by forest trees.

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## 1. Introduction

Remnant trees, i.e. isolated scattered trees persisting in a degraded habitat matrix originally occupied by forests, are a common feature in many fragmented forest landscapes worldwide (Manning et al., 2006). They have been recognized as a conservation target because of their supposed positive effect on the maintenance of local biodiversity and ecosystem functioning (Franklin et al., 2000; Manning et al., 2006). First,

they allow the persistence in the degraded matrix of a portion of the original forest richness, both of tree species (Harvey and Haber, 1999) and many species that use the trees as feeding, nesting or establishment sites (Fischer and Lindenmayer, 2002a; Lumsden and Bennett, 2004). Second, and from a functional viewpoint, they preserve basic levels of many forest ecological conditions, from soil features (e.g. soil compaction and nutrient content, Rhoades et al., 1998) to the threshold rates of many ecological processes, such as those driven by

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the movement of different organisms across the matrix (e.g. animal foraging and dispersal, Metzger and Décamps, 1997; Fischer and Lindenmayer, 2002b). Therefore, remnant trees act as biological legacies, since they represent persisting organically-generated patterns which drive ecosystem functioning and recovery (Franklin et al., 2000; Elmquist et al., 2002; Keeton and Franklin, 2004), while also acting as stepping stones by increasing the overall connectivity of a fragmented landscape (Manning et al., 2006).

In tropical and temperate landscapes, many remnant trees are fleshy-fruited plants occasionally visited by frugivorous vertebrates that arrive from forest fragments to feed and rest within their fruiting canopies (e.g. birds, Cardoso da Silva et al., 1996; Eshiamwata et al., 2006; bats, Estrada and Coates-Estrada, 2002; primates, Anderson et al., 2007). As a consequence, high-density clumps of seeds defecated or regurgitated by frugivores are typical under remnant trees (Guevara and Laborde, 1993; Holl, 1998; Galindo-González et al., 2000; Slocum and Horvitz, 2000; Pausas et al., 2006). These clumps, or dispersal foci, are usually multispecific, as they receive seeds from fruits picked from the remnant tree together with seeds carried by animal vectors from non-con-specific plants in the nearby forest fragments (e.g. Guevara and Laborde, 1993; Carrière et al., 2002a; Pausas et al., 2006; Zahawi and Augspurger, 2006). Therefore, dispersal foci are sometimes considered a keystone structure for the recovery of forest communities (Guevara et al., 1986, 1992; Slocum, 2001; Martínez-Garza and González-Montagut, 2002; Zahawi and Augspurger, 2006; but see Manning et al., 2006 for a review). Although existing findings demonstrate the role of fleshy-fruited remnant trees as seed dispersal foci in the degraded matrix, by simply comparing seed rain beneath remnant trees with that in the open matrix, these studies do not assess how important remnant trees are in maintaining the quantitative and qualitative patterns of community-wide seed dispersal. To do this, a direct comparison of seed clumping patterns is needed, both in terms of clump size and species composition, between trees scattered in the matrix and trees standing within the forest. Given the reluctance of many frugivorous forest vertebrates to exploit the degraded matrix in fragmented forest landscapes extensively (e.g. Cardoso da Silva et al., 1996; but see Tschardt et al., 2008 for other functional groups), a reduced function as seed dispersal foci would be expected in remnant trees relative to trees within fragments.

Discerning the comparative role of remnant trees as seed dispersal foci also requires the consideration of the intrinsic factors controlling the visitation rate and foraging time of vertebrate frugivores in the trees. First, frugivores may be affected by the availability of fruits at the scale of individual trees, i.e. the crop size, being disproportionately attracted to those trees with larger crop sizes and thus generating denser seed clumps beneath them (Alcántara et al., 2000). Second, frugivores may also be affected by the availability of fruits at the scale of the whole landscape, widening their foraging range in events of community-wide fruit shortage, when fruit resources are scattered and less abundant (e.g. Holbrook et al., 2002; Ingle, 2003; Eshiamwata et al., 2006). Thus, increased use of remnant trees as fruit feeding sites and, therefore, weaker differences between remnant trees and

patch trees in their role of dispersal foci would be expected in the case of: (1) larger crop sizes in remnant trees relative to forest trees, and/or (2) events of low fruit availability at the landscape scale.

To investigate the relative role of remnant trees as seed dispersal foci within the matrix of a fragmented landscape, we studied seed deposition under the bird-dispersed hawthorn tree (*Crataegus monogyna* Jacq.) in mid-elevation wood-pastures of the Cantabrian Range (Northern Spain). In a previous study, García and Chacoff (2007) demonstrated that hawthorns growing in highly fragmented landscape contexts suffered a decreased magnitude of frugivory by avian seed dispersers, as well as increased post-dispersal predation on seeds dispersed under their canopies. In this paper, we assessed the role of remnant trees as tree recruitment foci by explicitly evaluating the demographic outcome of frugivory, in terms of the seed rain deposited under fruiting trees combined with the filtering effects of seed predation. Specifically we asked: (1) Do remnant trees act as seed dispersal foci? (2) How much functionality as dispersal foci do remnant trees retain relative to trees within the forest? (3) Are the effects of remnant trees on initial seed deposition offset by the demographic filtering of post-dispersal predation? and (4) Do inter-annual changes in individual and community-wide fruit production affect the relative role of remnant trees as seed dispersal foci?

## 2. Study site and system

Our study was carried out from 2004 through to 2005 in the Sierra de Peña-Mayor, Asturias, Spain (43°17'N–5°30'W, elevation 900 m a.s.l.) which is a secondary mountain of the Cantabrian Range (Fig. 1; see García and Chacoff, 2007 for detailed map). The climate of the region is Atlantic, with a mean annual temperature of 13 °C and rainfall (ca. 1300 mm) distributed approximately evenly throughout the year. As in many other parts of the Cantabrian Range, historical deforestation for cattle grazing has transformed the once extensive mid-elevation forests into a heavily fragmented wood-pasture (García et al., 2005a). The current physiognomy of the study site is a highly variegated landscape (*sensu* McIntyre and Hobbs, 1999), that is, a mosaic composed of a few large forest fragments made up of hardwood species (*Fagus sylvatica* L. and *Fraxinus excelsior* L.), fringe fleshy-fruited, bird-dispersed trees (holly *Ilex aquifolium* L., hawthorn *C. monogyna* Jacq., yew *Taxus baccata* L., and rowans *Sorbus* spp.), numerous small forest fragments of mostly fleshy-fruited trees, and a dominant (ca. 75% cover) matrix of stony pastures and heathlands (*Erica* spp., *Ulex europaeus* L.) with variable densities of scattered remnant trees.

We focused on hawthorn (*Crataegus*; hereafter) as the target tree species for the following reasons: (1) individual *Crataegus* trees occur across the complete gradient of habitat fragmentation, from trees completely isolated in the non-forest matrix to trees embedded in forest fragments; (2) *Crataegus* accounts for the largest proportion of retained paddock trees in the matrix relative to other species such as *I. aquifolium* and *T. baccata* (*Ilex* and *Taxus*, respectively, hereafter), and it is the main fruit resource and perching structure for avian



**Fig. 1** – Hawthorn (*Crataegus monogyna*) remnant tree in the Sierra Peña-Mayor, Asturias (Spain).

frugivores within the matrix; (3) the seed rain accumulated under *Crataegus* canopies within the forest contains a large proportion of seeds of other fleshy-fruited tree species (García et al., 2007), thus potentially being a good surrogate of the community-level dispersal template; and (4) *Crataegus* and the co-dispersed trees are species whose recruitment in these temperate forests is limited more by the availability of dispersed seeds than by the availability of microsites for establishment (García et al., 2005b), and thus a pivotal role for seed dispersal in the patterns of forest regeneration can be expected.

*Crataegus* is a deciduous small tree that commonly grows up to 10-m in height. Reproductive plants bear panicles of 5–6 single-seeded fruits. Other fruit species in the area with overlapping phenologies are the 3–4 seeded *Ilex* drupes and the one-seeded *Taxus* arils. All these species bear red fruits, and present similar fruit size, seed mass, seed nutrient content and seed toxicity (see García et al., 2005b for a detailed description of seed features). In the study site, the fruits of these species are heavily consumed by a shared guild of frugivorous thrushes composed of resident (*Turdus merula*, *T. philomelos* and *T. viscivorus*) and migrant (*T. iliacus*, *T. pilaris*) species. Birds defecate and/or regurgitate intact seeds, acting as legitimate seed dispersers (*sensu* Jordano, 1994) that account for almost all the animal-generated seed rain under these trees. Due to the foraging activity and post-foraging movements of thrushes within forests, seeds are seldom deposited in open gaps, but mostly occur under the canopy of fleshy-fruited trees in multispecific seed clumps (García et al., 2007). Seed dispersal by frugivorous mammals (badger *Meles meles*, fox *Vulpes vulpes*) is very occasional in *Crataegus* and *Ilex*. In fact, a previous study in the same study site showed that less than 3% of ca. 10,000 seeds of fleshy-fruited trees found in 158 mammal feces belonged to these two species (Martínez et al., 2008).

After dispersal, seeds are frequently preyed upon during winter by rodents, such as woodmice (*Apodemus sylvaticus*) and yellow-necked mice (*A. flavicollis*).

### 3. Methods

#### 3.1. Selection of focal trees

In September 2004, we selected 60 individual *Crataegus* trees as focal trees, comprising 30 trees clearly embedded in forest fragments (hereafter *patch* trees), and 30 trees clearly isolated in the non-forest matrix (hereafter *remnant* trees). Remnant trees were chosen as having no other tree canopy present within a 5-m radius. In addition, within a 50-m radius (calculated from a geographic information system derived from orthophoto 1:5000 maps in which focal trees were georeferenced and tree cover digitised), the percentage of tree cover was much lower in remnant ( $13.28\% \pm 3.53$ ) than in patch trees ( $34.25\% \pm 3.53$ ) (one-way ANOVA;  $F_{1,58} = 17.66$ ,  $P < 0.0001$ ). Both remnant and patch trees were distributed over an area of 75 ha, with no spatial segregation between tree types across the studied extent.

When focal trees were re-sampled in September 2005, 21 of the 60 initial focal trees did not bear fruit during this second sampling year, and were thus replaced by the nearest fruiting *Crataegus*. In this way, we ensured similar spatial configurations and similar tree cover values around focal trees between years (paired *t* test:  $t < 1.7$ ,  $P > 0.10$ ;  $N = 21$  trees).

#### 3.2. Fruit availability at the focal tree and the landscape scale

We were interested in checking the effect on seed deposition under focal trees of the fruit availability of each individual

tree every fruiting year (i.e. fruit crop size). We estimated the crop size of each focal tree in September of each study year by counting all ripe fruits on 15 randomly selected fruiting branches, and the number of fruiting branches per tree, then extrapolating the number of fruits to the whole tree crown.

We were also interested in examining how interannual differences in the availability of fruit resources at the landscape scale may affect the use made of remnant trees by avian seed dispersers at the study site. Thus, for both fruiting years, we monitored the abundance of fleshy-fruits over the whole landscape covered by our sampling. In October of each fruiting year, we randomly established 740 sampling plots of  $10 \times 10$ -m over the whole sampling extent, in each of which we counted the number of individual fruiting trees of all species and visually estimated the individual crop size by means of a logarithmic fruit abundance index (FAI: 0 = no fruits; 1 = 1–10 fruits; 2 = 11–100; 3 = 101–1,000; 4 = 1001–10,000; 5 > 10,000; see Saracco et al., 2004 for a similar procedure). We calculated the density of fruits (fruit  $\times$  m<sup>-2</sup>) of each species on each sampling plot from the summed crop size of all individuals within the plot (we used the intermediate raw value of each logarithmic rank except for the 5th rank, for which we used a value of 25,000 fruits).

### 3.3. Seed rain density and composition

For 5 months (early September to late January) in both sampled years, we established three  $50 \times 50$ -cm quadrats and collected all bird-dispersed (regurgitated or dropped) seeds under the canopy of focal trees in successive fortnightly surveys. We calculated the specific seed rain density as the cumulative number of seeds of each tree species deposited per quadrat through the season, averaging the values of each three quadrats into a single value per focal tree. We considered that seed collection in open quadrats provided estimates of seed density reliable enough for the evaluation of the spatial patterns of seed rain for a number of reasons. First, no diurnal bird or mammal species was observed eating seeds on quadrats during the sampling period. Second, seeds showing signs of predation by nocturnal rodents (open husks or teeth marks) were also counted as part of the pool of dispersed seeds (see also Alcántara et al., 2000). And third, a previous study in the same study site (García et al., 2005c), compared seed density in open quadrats to that in paired seed traps which were protected against seed removal, and evidenced negligible loss of seeds from quadrats for most seed species, as well as showing the open quadrats to be highly accurate in capturing fine-scale spatial variability in seed dispersal patterns.

Seed rain composition was evaluated by means of the proportion of heterospecific seeds in the seed rain (i.e. the proportion of seeds belonging to species other than *Crataegus* deposited under focal trees; see García et al., 2007). This parameter is an unequivocal measure of the ability of a focal tree to act as dispersal focus for seeds coming from sources other than its own canopy. Seed rain sampling revealed very low frequencies of occurrence of *Taxus* and *Sorbus* spp. seeds (<2.2% of 9490 seeds). Thus, we only considered *Ilex* seeds as seeds from different species and calculated, for each quadrat,

the quotient between the cumulative density of *Ilex* seeds and the sum of cumulative densities of *Ilex* and *Crataegus* (i.e. proportion of heterospecific). We averaged the values of the proportion of heterospecific seeds of each three quadrats into a single value per focal tree.

### 3.4. Post-dispersal seed predation by rodents

From late December to late January of 2004 and 2005, we carried out manipulative field sampling to evaluate post-dispersal predation rates on *Crataegus* and *Ilex* seeds under focal trees. We placed two seed depots (one per seed species) adjacent to each one of the three  $50 \times 50$ -cm quadrats where we previously collected seed rain under each focal tree. Each seed depot consisted of 10 seeds glued with a low odour, rain-proof thermoplastic glue, to a  $10 \times 6$ -cm<sup>2</sup> plastic mesh nailed to the ground (see García et al., 2005b for similar procedures). We averaged the values of predation rate of each three depots into a single value per species, focal tree and year. We used seeds extracted from bird feces collected the previous autumn at the study site. Depots were monitored after 2 and 4 weeks and removed after the second monitoring. Seeds were glued firmly to the plastic mesh, so that seed disappearance owing to abiotic factors (wind, rain) and secondary dispersal were considered negligible. Seed predation rate was calculated, for each species, as the proportion of consumed seeds relative to the initial number of seeds in the depot.

### 3.5. Seeds available for recruitment

We evaluated the importance of remnant trees as recruitment foci with respect to patch trees by taking into account the losses that post-dispersal seed predation by rodents caused on the initial seed rain. A previous study in the same study site suggests that the number of seeds that survive predation by rodents is a good proxy for the number of seedlings which will establish in the long term at a given site (García et al., 2005b). Thus, we calculated, for each focal tree, seed species (*Crataegus* and *Ilex*), and year, the density of seeds available for recruitment by multiplying the specific seed rain density by the specific probability of post-dispersal survival (1 – seed predation rate). The proportion of heterospecificity in the seeds available for recruitment after seed predation was also quantified from the estimated densities of *Crataegus* and *Ilex* surviving seeds.

### 3.6. Statistical analysis

To check for the effect of tree type (i.e. remnant vs. patch trees) on the seed rain density and the density of seed available for recruitment after seed predation we used a general linear mixed model (GLMMs) with the GLIMMIX procedure of the SAS 9.1 statistical package (SAS Institute 2000). GLMMs were performed separately for each seed species including tree type and year as fixed factors. Year was considered to be a fixed factor because 2004 and 2005 were not chosen randomly, but corresponded to years with large differences in fruit availability at the landscape scale (see Section 4, and also Fedriani, 2005 for a similar procedure). Tree identity was included in the models as a random factor in order to control

the potential pseudoreplication bias associated with the fact that a portion of the individual trees was repeatedly sampled whereas another portion was replaced by the nearest neighbor tree in the second year (Millar and Anderson, 2004). We also checked for the effect of tree crop size on the seed rain density by including this parameter in the model as a continuous covariate. We used the Akaike's information criterion (AIC) to select the best model from the set of candidate models, performed by sequentially removing non-significant effects of factors or interactions. The AIC approach takes into account both the change in deviance induced by a model and its degrees of freedom, and considers the best approximating and most informative model to be that with the lowest AIC value (Burnham and Anderson, 1998). Differences in crop size between tree types and years were analyzed with similar GLMMs. When a significant difference was detected, a post hoc test (Tukey-Kramer's honestly significant difference) was used to identify groups that differed. Means are given  $\pm 1$  SE throughout the text. Prior to all analyses, we tested the normality of distribution of errors for dependent variables and, when necessary, transformed data to the log- or arc-sine square root. All variables fitted to normal distributions, and thus models were performed by considering identity link functions and normal distribution of the error term.

#### 4. Results

##### 4.1. Fruit availability at the focal tree and the landscape scales

Individual crop size was similar between remnant and patch trees ( $F_{1,118} = 3.45$ ,  $P > 0.05$ ) but differed significantly between years, being higher in 2004 than in 2005 ( $F_{1,118} = 16.26$ ,  $P < 0.001$ ). No significant effect on crop size of the interaction between tree type and year was encountered ( $F_{1,118} = 0.90$ ,  $P > 0.05$ ). Fruit availability at the landscape scale greatly differed between the two study years, with average fruit density being seven-fold higher in 2004 ( $139.12 \pm 11.27$  fruits  $m^{-2}$ ) than in 2005 ( $20.64 \pm 4.15$  fruits  $m^{-2}$ ; Fig. 2). Therefore, it was possible to rank the sampled fruiting events as high (2004) and low (2005) fruit production years. In addition to the inter-annual differences in the overall fruit production, differences in the relative contribution of the main fleshy-fruit species (i.e. *Ilex* and *Crataegus*) were also found. Thus, the lower *Ilex* fruit production in 2005 relative to *Crataegus* led to an increased proportion of *Crataegus* in the overall fruit production, from 46.7% to 98.3% (Fig. 2).

##### 4.2. Effect of tree type on seed rain density, seed predation and seeds available for recruitment

Seed rain densities of both *Ilex* and *Crataegus* were significantly lower under remnant trees than under patch trees (Fig. 3A; Table 1). The effect of tree type on seed rain density was stronger in 2004 than in 2005, and stronger on *Ilex* than on *Crataegus* seed species. In fact, a highly significant interaction between tree type and year was found in the *Ilex* species (Table 1) owing to the differences in seed rain density between remnant and patch trees being 2.5 times larger in 2004 than in

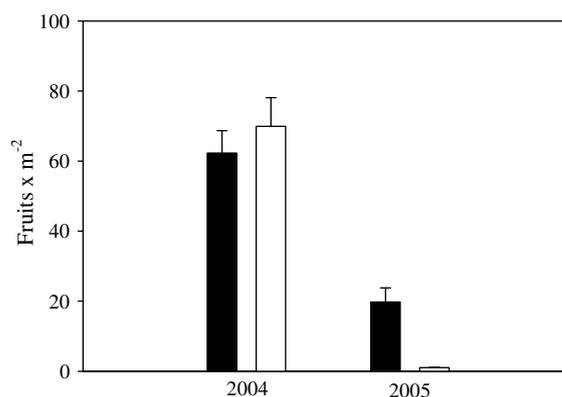


Fig. 2 – Density of fleshy-fruits of *Crataegus* (black bars) and *Ilex* (white bars) in the two study years calculated from 720, 10 × 10 m plots distributed over the entire study site. Means  $1 \pm$  SE are shown.

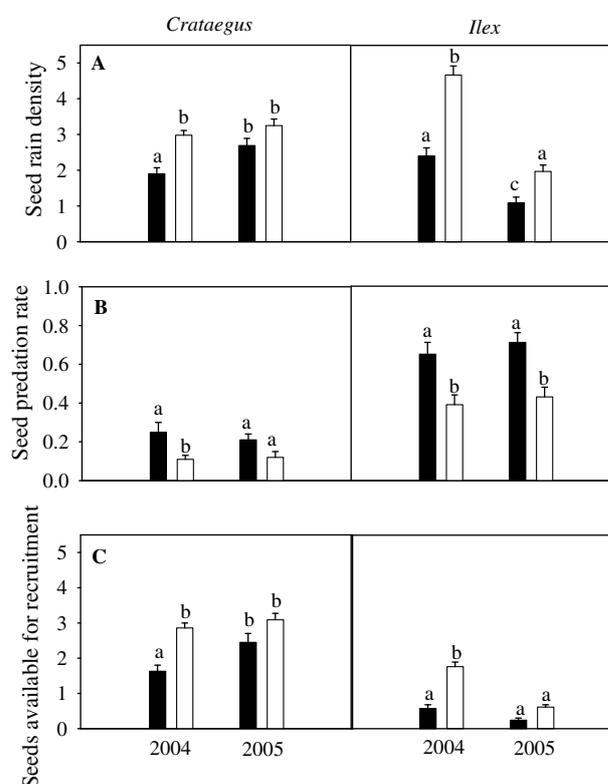


Fig. 3 – Mean ( $\pm 1$  SE) values of seed rain density (A), seed predation rate (B) and the density of seeds available for recruitment (C) under remnant (black bars) and patch trees (white bars), for different years and seed species. All variables were log-transformed except seed predation rate. Bars with the same letter do not differ significantly among year and tree type ( $P > 0.05$ ). Means  $1 \pm$  SE are shown.

2005. Seed rain density of *Ilex* in remnant trees in 2004 was similar to patch trees in 2005 (Tukey-Kramer test,  $t = 1.41$ ,  $P > 0.05$ ; Fig. 3A). The effect of tree type on *Crataegus* seed rain density was also stronger (2.1 times) in 2004 than 2005, a year in which no differences between tree types were found. Sim-

**Table 1 – General linear mixed models examining the effect of tree type, year (both variables considered as fixed factors) and their interaction on seed rain density and the estimated number of surviving seeds (both log-transformed) for *Crataegus* and *Ilex* species. Original global models included the focal tree identity as a categorical random factor and the individual crop size as a continuous covariate.**

Effect	<i>Ilex</i>			<i>Crataegus</i>			
	d.f.	F	P	d.f.	F	P	
Seed rain density	Tree type	1	53.09	<0.0001	1	20.71	0.0001
	Year	1	96.15	<0.0001	1	8.97	0.0063
	Tree type × year	1	11.24	0.0026	1	2.59	0.1209
Seeds available for recruitment	Tree type	1	58.44	<0.0001	1	22.62	<0.0001
	Year	1	64.20	<0.0001	1	7.69	0.0106
	Tree type × year	1	19.08	0.0002	1	2.70	0.1135

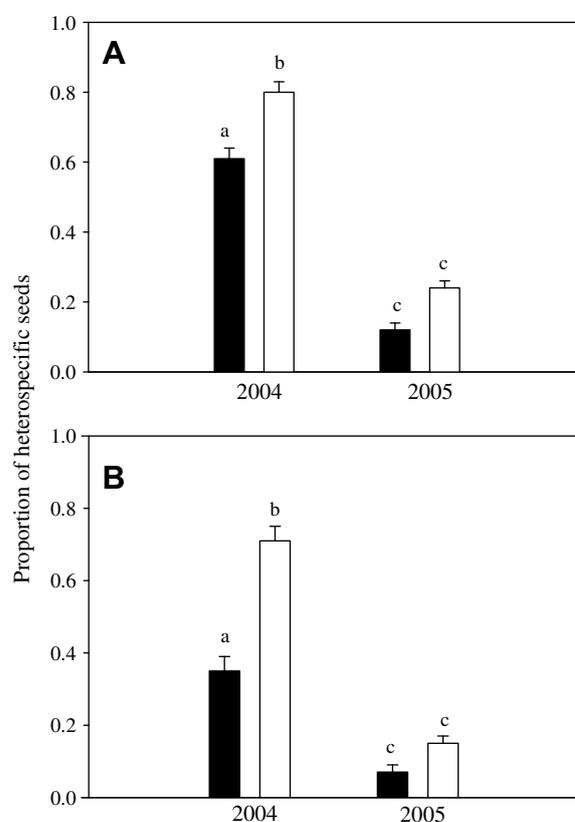
ilar seed rain density in both years for this species promoted no significant interaction term between year and tree type (Table 1; Fig 3A). Moreover, seed rain density in remnant trees in 2005 was similar to patch trees in 2004 (Tukey–Kramer test,  $t = -1.29$ ,  $P > 0.05$ ) (Fig. 3A). No significant effect of tree crop size on seed rain density, or interaction in terms of crop size × tree type or crop size × year, were found, either for *Ilex* or for *Crataegus*.

Predation rate by rodents differed markedly between seed species, being higher in *Ilex* than in *Crataegus* (Fig. 3B). Seed predation was stronger under remnant trees than under patch trees, for *Ilex* in 2004 ( $F_{1,58} = 10.60$ ,  $P < 0.001$ ) and 2005 ( $F_{1,58} = 14.50$ ,  $P < 0.001$ ), and for *Crataegus* in 2004 ( $F_{1,58} = 6.85$ ,  $P < 0.01$ , Fig. 3B).

The differences between tree type and year in the density of seeds available for recruitment followed similar trends to those of initial seed rain density, with lower values under remnant trees than under patch trees. However, as a consequence of the selective seed predation rate by rodents, *Ilex* suffered a larger reduction of seed abundance under remnant trees than did *Crataegus* (Fig. 3C). In the case of *Ilex*, a highly significant interaction between tree type and year was encountered (Table 1). This was due to the effect of tree type on the density of seeds available for recruitment, 3.1 times stronger in 2004 than 2005, a year in which there were no significant differences between tree type (Fig. 3C). The estimated density of seeds surviving predation under remnant trees in 2004 did not differ from that under patch trees in 2005 (Tukey–Kramer test,  $t = 1.59$ ,  $P > 0.05$ ). In the case of *Crataegus* seeds, no significant interaction between tree type and year was encountered (Table 1) but, similarly to *Ilex*, no differences in the density of seeds available for recruitment between tree types were found in 2005. The density of seeds available for recruitment under remnant trees in 2005 was similar to that under patch trees in 2004 (Tukey–Kramer test,  $t = 0.31$ ,  $P > 0.05$ ).

#### 4.3. Effect of tree type on seed rain composition

The proportion of heterospecific seeds was larger in 2004 than in 2005 ( $F_{1,118} = 275.91$ ,  $P < 0.0001$ ), and in patch relative to remnant trees ( $F_{1,118} = 21.18$ ,  $P < 0.0001$ , Fig. 4). Significant differences between tree types occurred in 2004, both before and after seed predation, but not in 2005 (Fig. 4).



**Fig. 4 – Proportion of heterospecific (i.e. proportion of seeds different to *Crataegus*; see Section 3 for details) ( $\pm 1$  SE) seeds in the initial seed rain (A) and in the seeds surviving to post-dispersal predation (B) under remnant (black bars) and patch trees (white bars), for different years. Other symbols and bars as in Fig. 2.**

## 5. Discussion

### 5.1. Remnant trees as seed dispersal foci

Beneath the canopies of *Crataegus* trees scattered in the deforested matrix of the Cantabrian Range, a significant number of bird-dispersed seeds belonging to the main fle-

shy-fruited species in the area were found to accumulate. As such, remnant *Crataegus* trees acted as community-wide seed dispersal foci, similar to paddock trees or artificial perches in tropical pastures (Guevara and Laborde, 1993; Holl, 1998; Slocum and Horvitz, 2000; Carrière et al., 2002a,b; Zahawi and Augspurger, 2006; Kelm et al., 2008) and isolated trees in old, abandoned Mediterranean fields (Pausas et al., 2006). Seed aggregation under remnant canopies is a consequence of the use of remnant trees by avian frugivores, not only as a foraging habitat in which fleshy-fruits are offered (McClanahan and Wolfe, 1993; Carrière et al., 2002a; Lumsden and Bennett, 2004), but also as a stop-over in which to rest or protect themselves when flying through the open matrix (e.g. Guevara et al., 1992; Guevara and Laborde, 1993; Carrière et al., 2002a).

Our approach evaluated the seed rain under remnant trees as well as under trees within forest fragments distributed across the same landscape. Thus, we were able to assess how much of the original ecological function of forest tree canopies as seed dispersal foci was fulfilled by remnant trees in a fragmented landscape. In this sense, our findings of reduced seed rain under remnant trees relative to trees embedded in the forest seem to suggest a diminished functional role of remnant trees. This difference probably resulted from the reluctance (although not complete avoidance) of frugivorous birds to exploit fruit resources in the open matrix (Price et al., 1999; Graham, 2001). Nevertheless, our interannual comparison also suggested that during periods of community-wide fruit shortage, remnant trees not only partially maintained their seed dispersal service through the fragmented landscape, but their ecological role may even be equivalent to that exerted by patch trees. This emphasizes that the role of scattered *Crataegus* trees varies through both time and space, as once predation was taken into account, the number of seeds available for recruitment was similar in both remnant and patch trees.

### 5.2. Fruiting landscape and the functional role of remnant trees

We detected neither differences in individual fruit crop size between remnant and patch trees nor an effect of individual crop size on the seed rain deposited under focal trees. Thus, tree isolation affected the seed rain density independently of the number of fruits produced by each tree each fruiting year.

Our study covered two fruiting seasons with strong differences in the community-wide fruit abundance (high in 2004, and low in 2005) and, as expected, the effect of tree type on seed rain density was influenced by changes in the landscape-wide fruit (and seed) availability. In 2004, a year with larger community-wide fruit production, we encountered stronger differences, with higher seed densities in patch relative to remnant trees. In 2005, a year when fruit availability at the landscape scale declined dramatically, smaller or no differences in seed rain between tree types were found (see Fig. 3).

Two compatible mechanisms, related to the differential response of frugivorous birds to the heterogeneity in fruit resources at the landscape scale, may underpin the

interannual differences in the role of remnant trees as dispersal foci. First, in years of low resource availability, frugivores may be forced to use fruit resources scattered through the matrix, leading to either increases in visitation frequency to remnant trees (Eshiamwata et al., 2006; Sekercioglu et al., 2007) and/or the average time spent foraging in remnant trees (Morales and Carlo, 2006). Second, frugivores may be forced to use the scattered perches provided by remnant trees more extensively; perches thus acting as stepping stones, facilitating movement between fruiting patches in forest fragments (Date et al., 1991; Graham, 2001; but see also Goodwin and Fahrig, 2002). Both processes are possible explanations in the case of frugivorous thrushes, as they are birds with a marked ability to modify the grain of their foraging range and to exploit fruit resources in a hierarchical, scale-dependent manner (Rey, 1995; Tellería and Pérez-Tris, 2003; García and Ortiz-Pulido, 2004).

Regarding interannual variations in fruit abundance between species, *Ilex* showed the strongest reduction in fruit production in 2005 compared to 2004. Thus, while *Crataegus* fruits (and seeds) enhanced their relative contribution to the community-wide fruit production, *Ilex* fruits decreased from 52% in 2004 to less than 2% in 2005. This differential interannual variation in fruit production also explains why there were virtually no differences in *Crataegus* seed density between years as a consequence of the higher use of *Crataegus* fruits as a major fruit resource in periods of shortage of *Ilex* fruits. In fact, no differences between patch trees in 2004 relative to isolated trees in 2005 for *Crataegus* were encountered.

### 5.3. Post-dispersal seed predation and seed survival

The removal experiment showed a consistently higher predation on *Ilex* than on *Crataegus* seeds, as previously found in the same system (García et al., 2005b, 2007). Our data also showed consistently higher post-dispersal seed predation under remnant trees than under patch ones. This concurs with other studies in temperate habitats that have shown an increase in post-dispersal seed predation as cover decreased and habitat isolation increased (Jules and Rathcke, 1999; Donoso et al., 2003; García and Chacoff, 2007). When differences in predation on the two tree species and the degree of tree isolation were interpreted together, we found that lower predation on *Crataegus* seeds allowed this species to maintain its spatial patterns of seed deposition, and become a dominant component of the seed rain in both tree types and years. Conversely, higher predation rates on *Ilex* offset, at least in 2005, the differences between tree types in seed rain density. Thus, the interannual difference in the role of remnant trees as dispersal foci, when evaluated in terms of density of seeds available for recruitment, depended not only on the interannual differences in landscape fruit availability outlined above, but also on the selective filter of spatially heterogeneous seed predation.

### 5.4. Conservation implications: remnant trees and conservation of seed dispersal across the fragmented landscape

Our results show a clear influence of remnant trees in facilitating the movement of seed vectors, i.e. frugivorous birds,

through the whole extent of the fragmented landscape, and thus suggest a concomitant effect on the long-term dynamic of plant populations. Indeed, seed dispersal has been widely recognized as a key process within degraded landscapes that is diminished by habitat fragmentation and which controls plant population and community persistence (Higgins et al., 2003; Pearson and Dawson, 2005). More importantly, our comparative results on seed dispersal under remnant and patch trees highlight the importance of considering the role played by structural features of the degraded matrix in buffering the negative effects of habitat fragmentation (Murphy and Lovett-Doust, 2004; Bender and Fahrig, 2005). Clearly, the present study supports the idea that, thanks to the role of remnant trees as stepping stones for avian frugivores, the matrix does matter in terms of seed dispersal through the whole fragmented landscape (Tewksbury et al., 2002; García and Bañuelos, 2003).

Besides the role in enhancing the functional connectivity of the degraded landscape for seed dispersal process, by acting as seed and seedling nucleation foci, remnant trees may foster the regeneration of woody communities in deforested lands (Zahawi and Augspurger, 2006; Kelm et al., 2008). This is particularly important in the historically managed and fragmented Atlantic temperate forest of the Cantabrian Range in Northern Spain. In these forests, about 80% of forest cover has been cleared (García et al., 2005a). Therefore, we would advocate an integrated land-management approach which tries not only to maintain, but also to increase, the presence of scattered trees over the deforested matrix. This would accelerate the re-establishment of forest in deforested sites as the availability of perching structures through the matrix could reduce the effect of distance on seed input from forests. Moreover, the same remnant trees that act as dispersal foci for the seeds of other forest species into the matrix, may also act as nurse plants, facilitating the establishment of seedlings and juvenile trees from these seeds under their canopies. In fact, prickly trees like hawthorn and holly act as nurse plants for some forest tree species in the Cantabrian Range, such as the yew *T. baccata*, by providing seedlings with defence against browsing and trampling (García and Obeso, 2003). Thus, by accelerating secondary succession in deforested matrix through a process of facilitation mediated by seed dispersers (Méndez et al., 2008), remnant trees should also be considered as essential tools of passive restoration in fragmented landscapes.

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