RESEARCH ARTICLE

Matrix effects on plant-frugivore and plant-predator interactions in forest fragments

José M. Herrera · Daniel García · Juan M. Morales

Abstract Structural features of both habitat remnants and surrounding matrix can be important for explaining plant population dynamics and ecosystem functions in human-impacted landscapes. However, little is known about how the structural features of the adjacent matrix affect biotic interactions and whether such context effects are subject to temporal variations. Using the hawthorn *Crataegus monogyna* in northern Spain, we studied matrix effects on two sequential plant-animal interactions, frugivory by birds and postdispersal seed predation by rodents. Using Hierarchical Linear Models, we compared the magnitude of both interactions on trees located in two patch types that strongly differed in structural features of the adjacent matrix habitat: patches totally surrounded by a degraded, structurally contrasted pastures (unconnected patches), and trees growing in patches adjacent to a lowly degraded, structurally similar mature forests (connected patches). We compared outcomes for 2005 and 2006, which were years with strong differences in community-wide fruit and seed abundance. Frugivory rate did not differ between patch types in either year, likely related to high mobility of birds. Seed predation rates were higher in unconnected patches than in connected ones, but only in 2005. We conclude that strong interannual fluctuations in resource availability are not rare in temperate systems and that recruitment rates could be frequently reduced within unconnected patches, thus collapsing plant regeneration processes of hawthorn populations. Overall, our results suggest that generalizations about potential effects of the matrix on plant-animal interactions within remnant patches must consider: (1) species-specific habitat responses of the organisms, (2) suitability of neighbouring habitats in terms of food supply, and (3) temporal variations in plant-resource availability for interacting animals.

Keywords Matrix effects · Cantabrian range · Connectivity · Forest fragmentation · Frugivory · Hierarchical Linear Models · Plant-animal interactions · Seed predation · Spain

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Introduction

Habitat fragmentation severely threatens the maintenance of biodiversity and the functioning of natural systems worldwide (Fahrig 2003). Reduced population size due to habitat loss, metapopulation collapse by increased habitat isolation, and decreased individual fitness due to edge effects are pivotal processes that

frequently lead to the extinction of species in fragmented landscapes (Haila 2002; Fahrig 2003). These effects are mainly expected (and reported) in landscapes where remaining habitat fragments are embedded in a highly contrasting, inhospitable matrix of degraded habitat (e.g., Bayne and Hobson 1997; Sisk et al. 1997). Nevertheless, this binomial habitat versus non-habitat scenario is hardly suitable for many degraded landscapes, thus limiting its potential for a broad application, as well as for the establishment of management guidelines to disturbed landscapes. In fact, most real landscapes are better represented by a continuum mosaic of patches with different degrees of degradation and structural disparity (McIntyre and Hobbs 1999). Therefore, fragmentation research should be able to predict matrix effects not only for original habitat remnants adjoined to highly contrasting patches (e.g., mature forest relative to human-generated pastures), but also for altered, structurally similar patches (e.g., mature forest relative to tree plantations; Estades and Temple 1999; Yamaura et al. 2006), and for natural and low contrasting patches (e.g., mature forest compared with secondary forest; Antogiovanni and Metzger 2005; Nascimento et al. 2006). Matrix effects are suggested to affect biodiversity patterns in landscapes mosaics (e.g., Hesperger and Forman 2003; Yamaura et al. 2006; Hedenås and Ericson 2008; Wiens 2009), although they have been largely ignored in mechanistic, process-based studies.

Plant-animal relationships are pivotal ecological functions affected by habitat fragmentation, with common disruption of mutualisms due to habitat loss or increased isolation, and increased antagonisms due to edge effects (e.g., Jules and Rathcke 1999; García and Chacoff 2007). Recent theoretical and empirical research calls for the inclusion of matrix effects in the analysis of plant-animal interactions in fragmented landscapes (Jules and Shahani 2003; Hesperger and Forman 2003; Antogiovanni and Metzger 2005; Bender and Fahrig 2005; Kupfer et al. 2006, Vasconcelos et al. 2006; Farwig et al. 2009). Depending on its structural features, the matrix that surrounds remnant habitats may support part of the populations of seed dispersers, serve as temporary habitats, and even favor their individual movements when moving across the whole landscape (Estrada and Coates-Estrada 2001; Tewksbury et al. 2002; Luck and Daily 2003). Moreover, some matrix habitats can buffer the increased seed predation and herbivory risk by edge-favoured, generalist vertebrates within fragments (Curran and Webb 2000; López-Barrera et al. 2005). These effects of the matrix habitats on animals should explain why plants inhabiting fragments embedded in structurally complex, highly connective matrix do not suffer strong collapse in regeneration processes (e.g., Takada et al. 2002; Hesperger and Forman 2003; Nascimento et al. 2006). Nonetheless, the true role of matrix effects on plant-animal interactions is far from clarified mainly due to the scarcity of studies that explicitly compare multiple plant-animal interactions functioning in forest fragments that differ in structure of the surrounding matrix.

We studied matrix effects on two plant-animal interactions, frugivory by birds and seed predation by rodents, belonging to the network of hawthorn (*Crataegus monogyna* Jacq., Rosaceae) in fragmented forests of northern Spain. During 2 years, we compared the magnitude of both interactions within forest patches that were totally surrounded by pastures (a highly contrasted or "hard" matrix, *sensu* Stamps et al. 1987) to that within patches adjoined to deciduous forests (a structurally similar or "soft" matrix). We use the term matrix for the non-target habitat of the landscape surrounding patches of a given target habitat, which may be inherently heterogeneous in terms of structural features (Bender and Fahrig 2005). We had two main objectives. First, as different animals interacting with plants may show differential responses to fragmentation (e.g., Steffan-Dewenter et al. 2001; García and Chacoff 2007), we tested whether matrix effects similarly influenced plant-animal interactions involving groups that greatly differ in life-history traits such as mobility and foraging behavior (i.e., birds as seed-dispersers and rodents as seed-predators). Second, the linkage of seed dispersal and predation as two key processes of plant regeneration raises the question as to what extent these processes may be counterbalanced under the same fragmentation scenario. This outcome might be particularly important given that both seed dispersal and seed predation are relevant drivers of recruitment process for our focal species (García et al. 2005a; Herrera and García 2010). Considering the forest-favoured nature of frugivores (García and Chacoff 2007) and the edge-favoured response of seed predators (Jules and Shahani 2003), we expected decreased frugivory rates but increased seed predation rates in unconnected forest patches not adjacent to extensive deciduous mature forest.

Methods

Study site and system

The study was conducted in mid-elevation montane forests at the Cantabrian Range (Asturias, NW Spain) in 2005 and 2006. Historical human disturbance has had strong impacts on the composition and configuration patterns of Cantabrian forests. The current physiognomy of the landscape is characterized by low forest habitat cover (ca. 22%), and a size distribution of remnant forest strongly skewed towards low values (<10 ha, García et al. 2005b). Specifically, the sampling was carried out in the Sierra de Peña Mayor-Trigueiro (43°17′ N, 5°30′ W, 900 m a.s.l.), where the local forest landscape is composed of mature deciduous forests of beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.), and secondary-growth forests. The target habitat of the study was these secondary forests that are mainly composed of fleshly-fruited, bird-dispersed trees such as holly (*Ilex aquifolium* L.), hawthorn (*Crataegus monogyna* Jacq.), yew (*Taxus baccata* L.), and rowans (*Sorbus* spp.). Secondary forests occur as patches totally embedded in human-promoted stony pastures and heathlands (*Erica* spp., *Ulex europaeus* L.), as well as patches adjacent to deciduous, mature forest (Fig. 1). Isolated trees or small groups of remnant hawthorns and hollies also occur scattered throughout the matrix.

We focused on hawthorn (*Crataegus monogyna* Jaqc., Rosaceae) as the target plant species. Reproductive plants bear single-seeded drupes that turn red during ripening (September to December) and are arranged in panicles of 5–6 fruits. Fruits are mainly consumed by frugivorous birds, almost exclusively resident (blackbird *Turdus merula*, mistle thrush *T. viscivorus*, song thrush *T. philomelos*) and migrant (redwings *T. iliacus*, fieldfare *T. pilaris)* thrushes (Martínez et al. 2008). Thrushes are thus a key component in driving all the animal-generated seed rain in our study site (Martínez et al. 2008). Further, thrushes act as legitimate seed dispersers (*sensu* Jordano 2000) by swallowing the whole fruit and then regurgitating or defecating the seeds intact and viable. Foxes (*Vulpes vulpes*) and badgers (*Meles meles*) may also occasionally consume fruits from basal branches or fruits fallen to the ground, although their relative contribution to the total, animal-generated seed rain in the study site is negligible (Martínez et al. 2008). After dispersal (January to March), seeds are almost exclusively consumed by the woodmouse (*Apodemus sylvaticus*), yellow-necked mouse (*A. flavicollis*), and the bank vole (*Clethrionomys glareolus*), which do not act as seed dispersers (García et al. 2005a).

Patch and tree selection

We studied patches that were totally surrounded by stony pastures (hereafter, unconnected patches) and patches adjacent to extensive mature deciduous forest (hereafter, connected patches). Distance of unconnected patches to mature forest ranged from 60 to 75 m. We selected this terminology for patch types because extensive deciduous forest may act as an ecological corridor by facilitating animal movement (and therefore their ecological interactions with plants) through the landscape (Tewksbury et al. 2002). In September 2005, we selected three patches of each type within an area of 250 ha in the study site, and tried to avoid spatial segregation between patch types by locating both types of patches over a similar spatial extent (Fig. 1). The topographic information about each patch (patch area and perimeter) was calculated by a Geographic Information System (GIS) established from digitized 1:5000-scale orthophotomaps. To evaluate several structural and biological characteristics of patches not provided by GIS, we established in each patch 10–15 non-overlapping circular plots of 10-m radius, arbitrarily distributed to cover the different sectors of each patch. In these plots, we visually estimated cover (%) of each tree species surrounding each focal tree in the field (see García and Chacoff 2007). We also estimated for each circular plot the fruit availability of each individual fleshy-fruited tree by using a logarithmic Fruit Abundance Index (FAI: 0, 1: ≤10 fruits, 2: 10–100, 3: 101–1000, 4: 1001–10000, 5 >10000) considering individuals of height ≥1.5 m and dbh ≥10 cm (see Herrera and García 2009). To measure fruit abundance more accurately, we assigned the FAI index following the semi-logarithmic scale described above to a subsample of trees with known actual crop size ($n = 136$). Then, by fitting data to an exponential model ($y = 1.765 \times e^{1.924x}$; $R^2 = 0.80$; $n = 136$) we extrapolated the number of fruits for each individual tree and thus calculated the number of fruits within each circular plot (10-m radius). Finally, data from

Fig. 1 Map of Peña Mayor site depicting location of the six holly-hawthorn patches under study (labelled patches). *Light grey* areas correspond to mature forest, *darker grey* areas to secondary-growth forests, and *white area* correspond to non-forest matrix (stony pastures, heathlands and human settlements). *White triangles* within forest patches correspond to target trees (to simplify only trees for 2005 are shown)
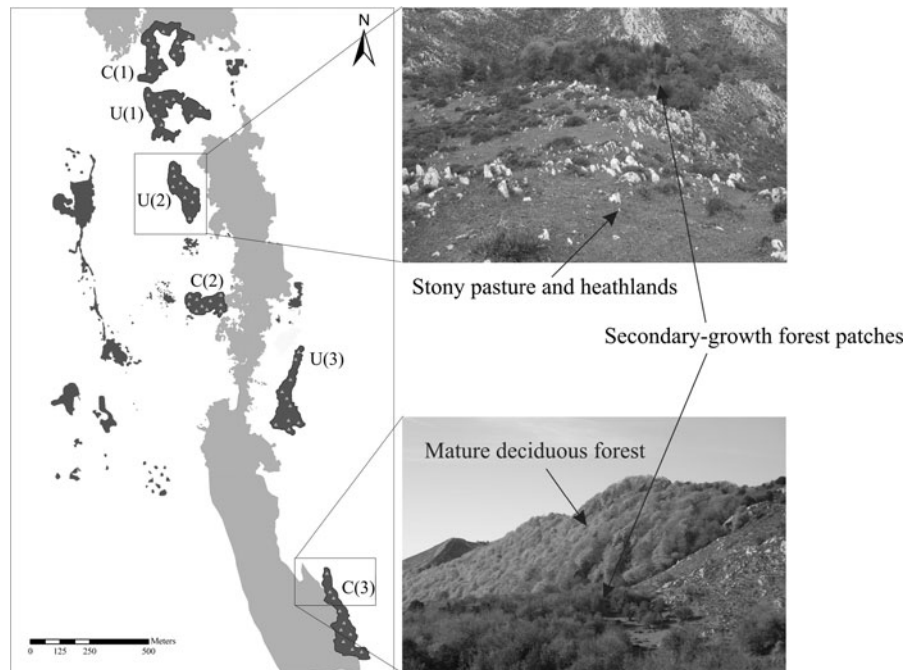
circular plots were extrapolated to the whole patch area from the average fruit availability per m² and the average tree canopy cover of the different plant species (Table 1). These measures were exclusively used to ensure no differences in patch quality in terms of fruit-resource availability between patch types.

In September 2005, we selected a total of 10 individual fruiting hawthorns (dbh >10; crop size >1000 fruits) within each patch to be used as target trees in which we estimated the magnitude of frugivory and seed predation. Distances among trees within a patch were ≥10 m. All trees were georeferenced using a Global Positioning System (GPS) receiver (accuracy ±1 m). For each tree, we estimated the number of ripe fruits (i.e., crop size) by counting all fruits in 15 randomly selected fruiting branches and the total number of fruiting branches per tree, and then extrapolating to the number of fruits in the whole tree crown (see Herrera and García 2009). Crop sizes were estimated as they can exert strong influence on the degree of plant-disperser interaction from individual trees. Thirty trees from the previous year's pool produced no fruits in 2006, and thus they were replaced by the nearest fruiting hawthorn to maintain the spatial framework of the study.

Measuring interactions

Frugivory by birds

In September of 2005, we established three 50 × 50 cm permanent sampling quadrats beneath each tree. In these quadrats, we collected all fallen hawthorn fruits and counted the number of fruits pecked by thrushes. Fallen, pecked fruits result from handling failures from birds when perching and pecking fruits on branches, and pecked fruits are easily recognizable by the V-shaped beak marks on the fruit coat (see Sallabanks 1993). Data from the three quadrats were pooled into a single sample per tree. Plant-frugivore interaction was estimated as the cumulative number of pecked fruits with respect to the total number of fallen fruits at the end of the dispersal season (see Sallabanks 1993; García and Chacoff 2007). To validate this parameter as an estimate of the intensity of fruit consumption by birds, during 2006 in 16 independent control hawthorn trees, we simultaneously calculated frugivory intensity by using sampling quadrats but also by means of labelled fruiting branches. We marked five fruiting branches per tree and counted all fruits present. Bird-removed fruits are easily distinguishable from abiotically fallen fruits because fruit petioles

Table 1 Structural and biological features of the studied holly-hawthorn patches in the Cantabrian range (Asturias, northern Spain), 2005–2006

Patch type	Area (ha)	Adjacency perimeter (%)	Fleshy-fruited tree cover (%)	Fleshy-fruits abundance (fruits per m²)		Dispersed seeds abundance (seeds per quadrat)	
				2005	2006	2005	2006
C(1)	25	18.3	66.9 ± 0.8	2.9 ± 1.5	14.2 ± 5.6	25.0 ± 5.1	71.3 ± 17.3
C(2)	15	12.1	51.7 ± 0.5	56.3 ± 7.2	48.5 ± 13.3	18.0 ± 5.4	108.8 ± 49.8
C(3)	25	30.0	55.8 ± 1.2	26.9 ± 12.2	41.9 ± 15.7	24.4 ± 6.6	17.7 ± 6.5
U(1)	23	0	69.7 ± 2.9	2.8 ± 1.7	65.8 ± 17.4	38.8 ± 14.8	139.1 ± 52.9
U(2)	14	0	49.8 ± 1.9	39.7 ± 9.3	62.0 ± 16.8	30.0 ± 13.4	31.7 ± 3.7
U(3)	19	0	70.3 ± 0.9	60.0 ± 9.5	48.6 ± 11.5	43.0 ± 6.9	48.5 ± 12.6

Mean values ± 1 SE are reported. Adjacency perimeter was estimated as the percentage of total patch perimeter adjoined to mature deciduous forests. Holly-hawthorn patches were differentiated into patches adjacent to extensive patches of mature deciduous forest (connected patches; C), and patches surrounded by a pasture matrix (unconnected patches; U)

remain attached to the branches when birds remove fruit, whereas petioles fall attached to the fruit otherwise (J.M.H and D.G personal observation). The rate of fruit removal by birds was calculated as the ratio of fruits removed from branches at the end of the dispersal period with respect to the initial number of fruits monitored per plant. The rate of fruit removal on labelled branches was correlated positively with the proportion of beak-marked fruits in sampling quadrats located beneath control target trees ($R^2 = 0.28$; $P < 0.05$; $n = 16$). Thus, we ensured that our indirect estimate was representative of fruit consumption and therefore a good approximation of plant-frugivore interaction on each individual tree throughout the dispersal season (Sallabanks 1993; García and Chacoff 2007).

Seed predation by rodents

We investigated the plant-predator interaction by evaluating the magnitude of seed predation in three experimental seed depots beneath each focal tree in 2005 and 2006. Each depot consisted of 10 seeds of *Crataegus* selected from a pool of bird-dispersed seeds previously collected in the study area. Seeds were glued with a low odor, rain-proof thermoplastic glue to a $10 \times 6 \ cm^2$ plastic mesh nailed to the ground (García et al. 2005a; García and Chacoff 2007). We revisited seed depots fortnightly (from January to March) assuming that a seed had been preyed on by rodents when it was missing from the plastic mesh or still on the mesh but gnawed and empty (Alcántara et al. 2000). We considered that

seed attack was exclusively attributable to rodents because of consumption of seeds by birds on the ground is highly infrequent in our study site (we did not find sign of either predation nor feces attributable to granivorous birds) and seed removal by ants was precluded by the small size and scarcity of granivorous ants in the area. Seed predation rate was calculated as the proportion of preyed seeds per individual tree (average among trials per tree).

Prior to the predation sampling period and concurrent with the collection of fallen fruits for frugivory sampling, we counted all seeds located inside sampling quadrats irrespective of tree species. Rodents rarely prey directly on fallen fruits (whether pecked by birds or not), and thus the cumulative number of seeds per quadrat would directly estimate availability of food resources for rodents beneath the canopy of focal trees (Table 1). The high frequency of sampling, relatively low predation rate at the beginning of the dispersal season, and rare secondary seed dispersal guaranteed negligible seed losses from quadrats (as validated by the use of seed traps; García et al. 2005c).

Statistical analysis

The sampling design with trees as sample units might increase Type-I error rates when testing effects of patch type due to pseudoreplication (Hurlbert 1984). Thus, to test matrix effects for potentially non-independent responses by individual trees within a given patch, we used Hierarchical Linear Models (HLM; Raudenbush and Bryk 2002). HLMs provide a framework for testing the significance of multiple

variables simultaneously at multiple levels—each of the levels with more than one variance component—and yield estimated parameters free of statistical constraints due to spatial pseudoreplication (Raudenbush and Bryk 2002). HLMs use nested regression equations to investigate associations between variables at different scales within a hierarchical data set. Accordingly, we considered that our sampling design could be expressed as a hierarchical process as both frugivory and seed predation magnitudes on a given tree might respond to tree individual traits (i.e., fruit or seed availability), but that responses also might be conditioned by patch-level traits.

Based on our sampling design, we assumed two, nested, hierarchical levels of analysis. Level-1, the individual tree level, represented the relationship between responses and tree individual traits in a linear form through a simple linear regression,

$$Y_{ij} = \beta_{0j} + \beta_{1j}X_{ij} + r_{ij} \tag{1}$$

where Y_{ij} is a measured response variable i (i.e., plant-frugivore and plant-predator interaction rate) that is observed in sample i belonging to a group (patch) j, and where r_{ij} is the random error term. Note that the response variable Y is therefore associated not only with the individual i observations, but it is nested within the j groups or level-2 traits (patch level) leading residuals to be correlated and not independent (Hurlbert 1984). To cope with this pseudoreplication bias, the level-1 relationships are modelled not around an overall intercept and slope, but around the intercept and slope of each of the $j = 1,…, J$ level-2 groups. As a result, to obtain an overall estimate of the relationships between the response variable and the predictors, we use the j first-level regression coefficients to form two, higher-level regressions:

$$\beta_{0j} = \gamma_{00} + \gamma_{01}W_j + u_{0j} \tag{2a}$$

$$\beta_{1j} = \gamma_{10} + \gamma_{11}W_j + u_{1j} \tag{2b}$$

where γ_{00} and γ_{01} are the level-2 coefficients for the intercept and slope, respectively, of these level-2 regression models. W_j is a level-2 predictor, and behaves as the X_{ij} does in Eq. 1. The level-2 random effects u_{0j} and u_{1j} are assumed to be distributed as multivariate normal with means of zeros and variances of σ_{00} and σ_{11}, respectively. Linking the above equations we obtain a combined model that simultaneously

describes the relationship between all predictors and response variables including their error terms at the two levels (Raudenbush and Bryk 2002; McMahon and Diez 2007):

$$Y_{ij} = \gamma_{00} + \gamma_{01}W_j + \gamma_{10}X_{ij} + \gamma_{11}W_jX_{ij} + u_{oj} \\ + u_{ij}X_{ij} + r_{ij} \tag{3}$$

Note that changes in the intercept parameter would be interpreted as differences in the average interaction rate in both types of patches. Conversely, changes in the slope indicate that the linear relationships between individual-tree interaction rate and level-1 traits is stronger in a given patch type. Level-1 traits were the crop size at individual trees for frugivory, and seed availability on sampling quadrats for seed predation rate. The Level-2 trait was patch type (connected or unconnected) for both plant-animal interactions. Both response variables, i.e., frugivory rate (manipulated fruits over total fruits) and seed predation rate (predated seeds over total seeds in depots) were fitted to a Binomial distribution. Potential differences in crop size and seed availability at individual trees, as well as fruit availability at the patch scale as a function of patch type, were similarly fitted by means of a HLM approach. The partial replacement of trees (see *Patch and tree selection*) led us to fit separate analytical models for each year. All models were fit by using HLM 6.06 statistical package. Other analysis such as differences in fruit and seed availability between years, and the relationship between predictor and response variables with no consideration of patch nature, was performed in JMP statistical package (SAS Institute Inc. 2000). Means ± 1 SE are reported throughout the text.

Results

Fruit and seed availability

There were strong, annual differences in community-wide fruit availability at the landscape scale (ANOVA; $F_{1,136} = 81.8$; $P < 0.001$) with fruit being twice as abundant in 2006 (54.4 ± 13.3 fruits per m^2) compared to 2005 (28.7 ± 8.7 fruits per m^2). However, there were no differences between patch types in fruit abundance in 2005 (unconnected: 28.2 ± 4.7, connected: 34.3 ± 7.3; HLM, t-ratio $= 0.8$; $P = 0.643$)

or in 2006 (unconnected: 50.62 ± 15.14, connected: 51.1 ± 13.6; t-ratio = 0.1; $P = 0.841$). In 2005, crop sizes of focal trees were marginally higher in unconnected patches (4476.3 ± 782.5 fruits) than in connected patches (5514.1 ± 810.0 fruits; HLM, t-ratio = 2.9; $P = 0.034$), but no differences were encountered in 2006 (unconnected: 4592.7 ± 802.2, connected: 4963.7 ± 788.2; HLM, t-ratio = -0.1; $P = 0.871$).

The abundance of dispersed seeds beneath focal trees varied between years (ANOVA; $F_{1,111} = 14.0$; $P < 0.001$; Table 1), being lower in 2005 (29.9 ± 3.8 seeds per quadrant) than in 2006 (71.4 ± 14.0 seeds per quadrant), and thus mirroring fruit abundance at the landscape scale. In 2005, seeds mostly corresponded to *Crataegus* (25%) and *Ilex* (75%). In 2006, seed mostly were *Crataegus* (15%), *Ilex* (85%), and *Taxus* (5%). Abundance of dispersed seeds did not differ between patch types in 2005 ($F_{1,56} = 0.12$; $P > 0.05$) or in 2006 ($F_{1,56} = 0.23$; $P > 0.05$). Overall, there were no differences in seed abundance beneath target trees as a function of patch type in 2005 (unconnected: 37.8 ± 5.3, connected: 22.5 ± 5.1; HLM, t-ratio = 0.6; $P = 0.543$) or 2006 (unconnected: 76.0 ± 19.0, connected: 66.9 ± 19.8; t-ratio = 0.5; $P = 0.630$; Table 1).

Adjacency effects on plant-animal interactions

The proportion of beak-marked fruits (i.e., frugivory rate) averaged 0.36 ± 0.02 in 2005 and 0.21 ± 0.01 in 2006. Models indicated no differences in the average of plant-frugivore interaction rate between patch types in 2005 (HLM; t-ratio = -0.143; $P = 0.892$; Table 2; Fig. 2a) or 2006 (t-ratio = 0.227; $P = 0.832$; Table 2; Fig. 2b). Furthermore, there were no effects of patch type on the slope from the frugivory magnitude and its response to crop size in 2005 (HLM; t-ratio = 0.046; $P = 0.956$; Table 2; Fig. 2a) or in 2006 (t-ratio = 0.527; $P = 0.935$; Table 2; Fig. 2b). An overall positive effect of crop size on frugivory rate –with no consideration of patch type—was encountered in 2005 ($R^2 = 0.25$; $F_{1,56} = 9.91$; $P < 0.01$) but not in 2006 ($R^2 = 0.01$; $F_{1,56} = 0.49$; $P = 0.480$).

Post-dispersal seed predation by rodents averaged 0.11 ± 0.21 in 2005 and 0.15 ± 0.21 in 2006. There were differences in the average predation rate between patch types in 2005 (HLM; t-ratio = 2.491; $P = 0.034$; Table 2; Fig. 2c) but not in 2006

(t-ratio = 0.855; $P = 0.441$; Table 2; Fig. 2d). Thus, as connected patches were coded as 1 and unconnected patches as 2, the coefficient for patch type (γ_{01}; Table 2) implies that average seed predation rate was 0.59 times higher in unconnected patches (in 2005) relative to that in connected patches. Conversely, there were no significant relationship between seed availability and seed predation rate in 2005 (HLM; t-ratio = -0.860; $P = 0.438$; Table 2; Fig. 2c) or in 2006 (t-ratio = -0.844; $P = 0.447$; Table 2; Fig. 2d).

Discussion

Growing research demonstrates that matrix habitats can influence ecological processes such as plant-animal interactions within remnant habitat patches in fragmented landscapes. By comparing both frugivory by birds and seed predation by rodents on hawthorn trees in patches that differed in the nature of the surrounding matrix, we determined that only average seed predation rate was influenced by the matrix. Furthermore, this effect was temporally inconsistent likely related to annual changes in resource (i.e., seeds) availability at the landscape scale. Therefore, complex interactions among the species-specific life-history traits of animals and the spatio-temporal variations in the availability of plant resources could be major determinants of matrix effects on plant-animal interactions in heterogeneous landscapes.

Depending on its structure and composition, the matrix can offer food resources and even breeding areas to frugivores, leading them to tolerate, exploit food resources, and even increase in abundance in matrix habitats (e.g., Estrada and Coates-Estrada 2001; Luck and Daily 2003; Yamaura et al. 2006). The adjacency to structurally similar, highly connective matrix thus has been suggested to influence plant-disperser interaction rates within remnant habitat patches (Tewksbury et al. 2002). However, contrary to our expectations, we detected no effect of the surrounding matrix on the response of frugivores. This outcome can be explained by several interrelated reasons. First, although frugivorous thrushes are affected by fine-scale habitat features such as presence of protective canopy surrounding feeding trees, they seem able to cope with large-scale habitat fragmentation and patch isolation due to their great mobility

Table 2 Results from Hierarchical Linear Models that tested effects of patch type on average frugivory and seed-predation rates (intercept estimates) and on the relationship among individual (tree) traits and plant-animal interaction rates (tree crop size for frugivory, and dispersed seeds abundance for seed predation)

Statistic	Frugivory rate				Seed predation rate			
	For intercept (β_{0j})		For slope (β_{1j})		For intercept (β_{0j})		For slope (β_{1j})	
	Intercept (γ_{00})	Patch type (γ_{01})	Intercept (γ_{10})	Patch type (γ_{11})	Intercept (γ_{00})	Patch type (γ_{01})	Intercept (γ_{10})	Patch type (γ_{11})
2005								
Coefficient	−2.414	−0.272	0.599	0.029	−3.069	0.586	0.748	−0.352
Standard error	3.481	1.875	0.984	0.627	0.451	0.235	0.766	0.410
t-ratio	−0.694	−0.143	0.650	0.046	−6.807	2.491	0.976	−0.860
P	0.562	0.892	0.551	0.956	**0.000**	**0.034**	0.385	0.438
2006								
Coefficient	−3.648	0.490	0.518	−0.050	−3.358	1.942	0.526	−1.021
Standard error	2.765	2.162	0.749	0.570	2.557	2.270	1.399	1.210
t-ratio	−1.319	0.227	0.692	3.485	−1.313	0.855	0.376	−0.844
P	0.258	0.832	0.527	0.935	0.259	0.441	0.726	0.447

Statistics are presented for both study years (2005 and 2006)
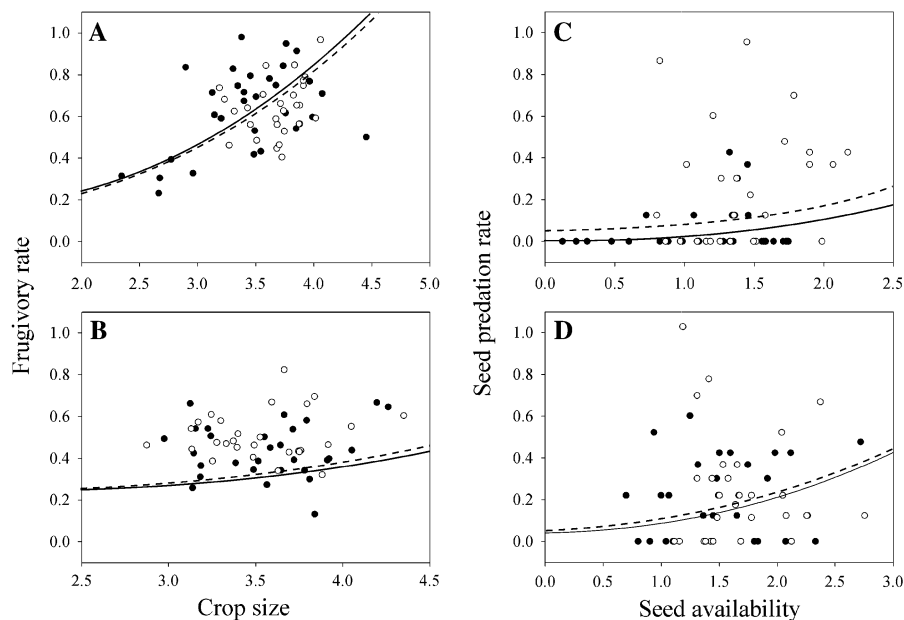
Significant values are shown in boldface

Fig. 2 Relationship between frugivory rate (proportion of beak-marked fruits) and the individual crop size (log-transformed) of focal trees (**a**, **b**), and seed predation rate (proportion of predated seeds relative to those offered in seed traps) and seed abundance (log-transformed) (**c**, **d**). Data for 2005 (*upper panels*) and 2006 (*lower panels*) are presented for trees in unconnected patches (*filled circles*) and in connected patches (*open circles*). Regression lines from Hierarchical Linear Models are shown for connected patches (*solid line*) and unconnected patches (*dashed line*)

(García and Chacoff 2007; Lehouck et al. 2009). Hence, frequent inter-patch movements by frugivores would lead to similar frugivory rates among habitat patches and thus plant-frugivore interactions will be retained even where the modified habitat matrix differs greatly from remnant habitat patches (Bender

and Fahrig 2005). Another, non-exclusive explanation is that presence of scattered, individual trees in the study site is actually enriching the structure of the apparently homogeneous pasture matrix. Scattered trees not only offer fleshy-fruited resources for avian frugivores, but also safe stop-over sites in which to rest when flying through the landscape, probably enhancing landscape connectivity for seed dispersal (Herrera and García 2009). In this way, scattered trees might be blurring the boundaries between patches and matrix habitats leading frugivorous birds to perceive the landscape as a continuum rather than as discrete habitat patches (McIntyre and Hobbs 1999). Finally, mature deciduous forest provides scarce resources for frugivorous birds given that few fleshy-fruits occur there. Although frugivorous birds seem indifferent to the adjoined matrix habitat, our results still suggest that frugivorous birds respond to fine-scale factors, such as the individual crop size of trees, especially during events of reduced fruit availability at the landscape scale (Ortiz-Pulido and Rico-Gray 2000).

In both years, seeds within unconnected patches suffered stronger predation (on average) than those located within connected patches. These results closely match with previous studies showing increased seed predation rates in more isolated, edge-increased habitat fragments, through demographic responses by increased population sizes of rodents (Khidas et al. 2002; Tallmon et al. 2003), or even compensatory functional responses of the local populations of these seed predators (García and Chacoff 2007). Nevertheless, effects of the matrix habitats on plant-predator interactions were temporally inconsistent; the difference in seed predation rates between patch types was significant in 2005 but not in 2006. We suspect that this temporal inconsistency was conditioned by the variations between years in seed abundance at the landscape scale (much lower in 2005 than in 2006), indicating that the activity of seed predators is markedly affected by the spatio-temporal variations in food resources (Jules and Rathcke 1999; Tallmon et al. 2003). In years of seed shortage, rodents populating unconnected patches would have limited seed availability but also reduced capacities to track alternative resources in adjacent habitats given the high degree of isolation of unconnected patches (Mills 1995). As a result, seed predation rates on *Crataegus* would be relatively higher within unconnected than connected patches

(García et al. 2007; Martínez and González-Taboada 2009). Alternatively, events of high seed availability at the landscape scale, especially involving more preferred species such as *Ilex aquifolium*, would make seed resources more similar in unconnected and connected patches, reducing differences in predation pressure between patch types.

Conclusions

Our results suggest that species-specific life-history traits such as foraging behaviour and mobility of interacting animals translate into differences in matrix effects among plant-animal interactions. Whereas no adjacency effects on frugivory were detected, a significant influence on seed predation on hawthorns trees was found, at least in years of seed-resource shortage. Given that strong interannual fluctuations in fruit and seed resources are not rare in temperate systems, the need for considering matrix effects on plant population dynamics and community structure seems justified. Recruitment rates could be frequently reduced within unconnected patches, thus collapsing hawthorn regeneration. Moreover, taking into account that prickly trees like hawthorns commonly act as nurse plants for other forest tree species in the Cantabrian Range like yew (*Taxus baccata*) and holly (*Ilex aquifolium*), frequent recruitment failures of hawthorn might affect long-term diversity of plant species in fragmented forests (Santos and Tellería 1994; Steffan-Dewenter et al. 2001; García and Chacoff 2007; Cordeiro et al. 2009). Our results therefore suggest that generalizations about potential effects of matrix habitats on plant-animal interactions within remnant patches must consider: (1) species-specific habitat perception of the organisms, (2) suitability of neighbouring habitats in terms of food supply, and (3) temporal variation in resource availability.

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