

Effects of Forest Fragmentation on Seed Dispersal and Seedling Establishment in Ornithochorous Trees

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Abstract: *Habitat fragmentation increases seed dispersal limitation across the landscape and may also affect subsequent demographic stages such as seedling establishment. Thus, the development of adequate plans for forest restoration requires an understanding of mechanisms by which fragmentation hampers seed delivery to deforested areas and knowledge of how fragmentation affects the relationship between seed-deposition patterns and seedling establishment. We evaluated the dispersal and recruitment of two bird-dispersed, fleshy-fruited tree species (*Crataegus monogyna* and *Ilex aquifolium*) in fragmented secondary forests of northern Spain. Forest fragmentation reduced the probability of seed deposition for both trees because of decreased availability of woody perches and fruit-rich neighborhoods for seed dispersers, rather than because of reductions in tree cover by itself. The effects of fragmentation went beyond effects on the dispersal stage in *Crataegus* because seedling establishment was proportional to the quantities of bird-dispersed seeds arriving at microsites. In contrast, postdispersal mortality in *Ilex* was so high that it obscured the seed-to-seedling transition. These results suggest that the effects of fragmentation are not necessarily consistent across stages of recruitment across species. Habitat management seeking to overcome barriers to forest recovery must include the preservation, and even the planting, of fleshy-fruited trees in the unforested matrix as a measure to encourage frugivorous birds to enter into open and degraded areas. An integrative management strategy should also explicitly consider seed-survival expectancies at microhabitats to preserve plant-population dynamics and community structure in fragmented landscapes.*

Keywords: cantabrian forests, *Crataegus monogyna*, *Ilex aquifolium*, matrix reforestation, seed dispersal, seedling emergence, structural fragmentation

Efectos de la Fragmentación del Bosque Sobre la Dispersión de Semillas y Establecimiento de Plántulas en Plantas Ornitócoras

Resumen: *La fragmentación del hábitat incrementa la limitación en la dispersión de semillas a través del paisaje y puede también afectar estados demográficos posteriores como el establecimiento de las plántulas. De este modo, el adecuado desarrollo de planes de restauración de bosques, requiere del conocimiento de los mecanismos por los cuales la fragmentación dificulta la dispersión de semillas hacia áreas deforestadas y la transición de la fase de semilla a la fase de plántula. Evaluamos la dispersión y reclutamiento en dos plantas de fruto carnoso dispersadas por aves (*Crataegus monogyna* y *Ilex aquifolium*) en bosques secundarios fragmentados del norte de España. La fragmentación del bosque redujo la probabilidad de deposición de semillas en ambas especies por medio de la reducción de perchas y la disponibilidad de frutos para los dispersantes, más que a través de reducciones en la cobertura forestal por sí misma. Los efectos de la fueron más allá de la fase de dispersión en *Crataegus* debido a que la cantidad de plántulas fue proporcional a la cantidad de semillas dispersadas que llegaban a los microhábitats. Por el contrario, en *Ilex* la transición semilla-plántula se interrumpió debido a una alta mortalidad postdispersiva. Estos resultados sugieren que los efectos de la fragmentación no son necesariamente consistentes a través de los diferentes estados de*

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reclutamiento en diferentes especies. La gestión del hábitat encaminada a superar las barreras para la recuperación de los bosques debe incluir el mantenimiento, e incluso el plantado, de plantas productoras de fruto carnoso en la matriz no forestal, como una medida para favorecer la entrada de frugívoros en las áreas degradadas. Además, una estrategia de manejo integral en paisajes fragmentados debe considerar explícitamente las expectativas de supervivencia de las semillas para preservar la dinámica de poblaciones y la estructura de las comunidades de plantas.

Palabras Clave: Bosques Cantábricos, *Crataegus monogyna*, dispersión de semillas, fragmentación estructural, germinación de semillas, *Ilex aquifolium*, reforestación

Introduction

Understanding how anthropogenic landscape alterations affect the persistence of populations is a central task of conservation biology (Harrison & Bruna 1998; Lindenmayer & Fischer 2006). In the case of woody plants, population regeneration and spread demand the coupling of seed-dispersal and seedling-establishment processes (Schupp & Fuentes 1995; Howe & Miriti 2004; Hampe et al. 2008). Empirical evidence suggests that habitat fragmentation can disrupt either one or both of these demographic stages and therefore constrain population persistence as well as plant species' ability to recolonize suitable sites (e.g., Benitez-Malvido 1998; Bruna 2002; Honnay et al. 2005). Nevertheless, it remains an open question whether recruitment failure in fragmented landscapes is caused by increased limitation of seed dispersal or by postdispersal processes (i.e., seed survival, germination, or seedling establishment) (e.g., McEuen & Curran 2004; Honnay et al. 2005; Cordeiro et al. 2009).

In plants dispersed by animals, behavior, foraging decisions, and habitat preferences exerted by frugivores shape the spatial patterns of seed deposition (Westcott & Graham 2000; Westcott et al. 2005; Russo et al. 2006). Thus, one would expect changes in habitat composition and configuration caused by fragmentation to affect seed deposition patterns by modifying the population size or the spatial behavior of frugivores (e.g., Cordeiro & Howe 2003; Morales & Carlo 2006). For example, frugivorous mammals and birds commonly avoid open, deforested areas and, even when they are able to use the un-forested matrix they tend to use small tree clumps or remnant trees scattered throughout the landscape (Galindo-González et al. 2000; Sekercioglu et al. 2007; Herrera & García 2009). Thus, more seeds are expected to be dispersed under woody perches in cover-rich neighborhoods (García & Chacoff 2007; Carlo & Morales 2008). Alternatively, the presence of food resources may increase the likelihood of frugivores entering open, degraded areas, especially when food resources at the landscape scale are scarce, patchy, or highly attractive (Eshiamwata et al. 2006; Herrera & García 2009). Frugivore-generated seed fall through the fragmented landscape thus seems to depend on the interaction among the spatial configurations of perching structures, protective cover, and fruit supply. Nevertheless, forest fragmentation might simultaneously

modify all these structural habitat features and, despite their importance for conservation purposes, the relative role of each feature in driving patterns of seed dispersal remains unclear.

Seed-dispersal templates by themselves may fail to determine recruitment patterns across a fragmented landscape if processes such as predation and germination constrain seed-to-seedling transitions (Howe & Miriti 2004; but see Valdivia & Simonetti 2007). Nevertheless, these effects could also be strengthened by the same fragmentation scenario that previously hampered seed dispersal (Santos & Tellería 1994; García & Chacoff 2007). Accordingly, establishing how fragmentation modifies the foraging behavior of dispersers and subsequently filters the seed pool available for recruitment is necessary for understanding the overall effect of fragmentation on animal-dispersed plant populations.

We evaluated the effects of structural fragmentation of forest (i.e., the loss of forest continuity occurring at a fine spatial scale and representing the change in degree of isolation of individual plants [Lord & Norton 1990]) on seed dispersal by frugivores and whether and how these same effects influenced the seed-to-seedling transition. We analyzed the spatial patterns of seed deposition and seedling establishment of two bird-dispersed trees in temperate forests of northern Spain. Structural fragmentation of forest is known to disrupt processes involved in plant recruitment (Cain et al. 2000; García & Chacoff 2007; Kirika et al. 2008). Our aim was to develop forest conservation and restoration guidelines by answering the following questions: (1) How correlated are seed-dispersal patterns and seedling establishment in a structurally fragmented forest, (2) which mechanism underlying the structural fragmentation of forest better explains the magnitude of recruitment, and (3) are effects of forest fragmentation different for seed dispersal and seedling establishment?

Study Site

The study was conducted in secondary-growth forests in the Sierra de Peña Mayor-Trigueiro (43°17' N, 5°30' W, 900-m asl) in the Cantabrian Range (Asturias, northwestern Spain). The climate of the region is Atlantic, with a mean annual temperature of 13 °C and rainfall (approximately 1300 mm) distributed throughout the year. The

forests are mainly composed of fleshy-fruited trees such as holly (*Ilex aquifolium*), hawthorn (*Crataegus monogyna*), yew (*Taxus baccata*), rowans (*Sorbus* spp.), and hazel (*Corylus avellana*). The canopy of these forests is uniform and 5–15 m high. The understory is almost negligible, with only a few scattered saplings (<0.5 m tall), heaths, and forest herbs. Secondary-growth forests occur as fringe patches, adjacent to mature forests of beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*), and as small fragments embedded in a dominant matrix (75% cover) of stony pastures and heathlands (*Erica* spp., *Ulex europaeus*). Isolated trees or small groups of remnant hawthorns and hollies also occur scattered throughout the matrix.

Study Species

We focused on two fleshy-fruited, bird-dispersed tree species: hawthorn (*Crataegus monogyna* Rosaceae; *Crataegus* hereafter) and holly (*Ilex aquifolium* Aquifoliaceae; *Ilex* hereafter). These species account for approximately 60% of the total forest cover in the study site. *Crataegus* is a deciduous tree with single-seeded, red drupes, and *Ilex* is a dioecious evergreen that bears red berries with 2–4 pyrenes (more detailed information about seeds traits is in García et al. [2005]). Ripe fruits of both species are available for bird dispersal from September to January. The crop size of individual trees is highly variable among years, which results in strong changes in community-wide fruit availability (Herrera & García 2009).

All fleshy-fruited tree species in the study site are mainly consumed by a common guild of avian frugivores

composed of resident (*Turdus merula*, *T. philomelos*, and *T. viscivorus*) and overwintering migrant (*T. iliacus*, *T. pilaris*) thrushes, which present no significant preferences for a given plant species (Martínez et al. 2008). These birds interact with the target tree species as legitimate seed dispersers (sensu Jordano 2000) (i.e., they swallow fruits and regurgitate or defecate the intact seeds in their droppings and do not act as pulp or seed predators (Martínez et al. 2008)). Mammals, such as foxes (*Vulpes vulpes*) and badgers (*Meles meles*), may also occasionally consume fallen fruits or fruits from basal branches. Nevertheless, the relative contribution of mammal dispersers to the total, animal-generated seed rain in the study site is negligible (Martínez et al. 2008). After deposition by birds, seeds of all target species are found in multispecific clumps and may suffer predation by rodents (*Apodemus* spp.) during late winter (García et al. 2005). The seed bank is therefore transient, short lived, and contains seeds defecated by birds and depulped seeds from fruits dropped beneath tree canopies (García et al. 2005). Seedlings emerge from April to June.

Methods

Sampling Framework

In September 2006 we established a rectangular, 400 × 440 m study plot in which the amount of forest cover varied from densely covered areas to areas of scant cover and isolated remnant trees (Fig. 1a). Along this gradient the amount of forest cover negatively correlated to the number of forest patches ($R^2 = 0.54$; $F_{1,165} = 199.7$;

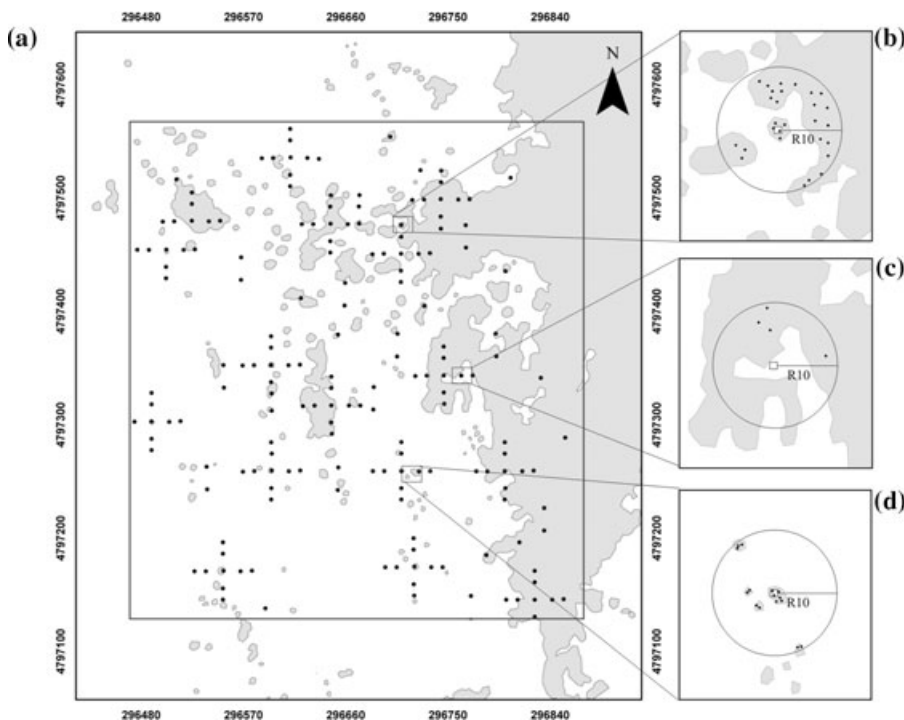


Figure 1. (a) Study plot at the Sierra de Peña Mayor (Asturias, Spain). (b)–(d) A set of potential configurations of sampling stations in microhabitat and 10-m radius neighborhood (R10). (b) Sampling station in covered microhabitat in a fruit-rich and moderate-cover neighborhood. (c) Sampling station in uncovered microhabitat in a fruit-poor, cover-rich neighborhood. (d) Sampling station in covered microhabitat in a fruit-rich neighborhood with a low level of cover. The number of black points in b–d represents fruit availability. Dots in left panel are the 50 × 50 cm sampling stations of 2006. Grey shading represents forest-canopy cover.

$p < 0.0001$) and to the density of forest perimeter ($R^2 = 0.41$; $F_{1,165} = 99.9$; $p < 0.0001$) in 10 m-radius circular plots surrounding a given number of focal points across the plot ($n = 167$; Fig. 1a). Thus, we ensured suitability of this study plot to represent a gradient of forest fragmentation, including to the three major processes of landscape change: habitat loss, increased habitat isolation, and increased edge (Lindenmayer & Fischer 2007).

Within this plot we established 167 sampling stations in September 2006 and 181 stations in September 2007. Sampling stations were a subset of a different design in the same study plot in which sampling occurred at different distances from target trees and along randomly positioned transects. Differences between years in the spatial position of the sampling stations derived from the use of different target trees (i.e., original trees were replaced with the nearest fruiting tree). Some target trees were replaced ($n = 7$) because they did not bear fruit during the second sampling year. To choose subset stations, we used a stratified, arbitrary sampling design in which we selected stations throughout the entire study area that were a minimum of 10 m apart (Fig. 1a). At these stations we measured seed deposition by avian dispersers and seedling establishment of *Crataegus* and *Ilex*. All sampling stations were located, by field observation, on a detailed orthophoto 1:5000 scaled map that was then used to develop a geographic information system (GIS) of the study plot from which we could obtain the exact geographical coordinates of all sampling stations.

Bird-Generated Seed Rain

In September 2006 and 2007 we established in each sampling station a 50 × 50 cm permanent ground quadrat. From these quadrats, we collected all bird-dispersed seeds in successive fortnightly surveys ($n = 10$) (early September to late January). Thus, we accounted for the entire period in which fleshy fruits are available to frugivores and the entire dispersal season (Martínez et al. 2008). Seeds from bird droppings are intact, free of pulp residuals, and therefore easily distinguished from mammal feces. For each sampling quadrat, we estimated the seed-rain density as the cumulative number of seeds at the end of the dispersal season. Previous work at this site compared seed abundance between paired, excluded-from-predators seed traps and open quadrats, and researchers found a negligible loss of seeds from quadrats for the target species (García et al. 2005). Thus, we are confident our method of seed collection in open quadrats provides estimates of seed-deposition densities that allow for evaluation of spatial patterns of seed rain.

Seedling Establishment

Contiguous to each seed quadrat, we established another 50 × 50 cm quadrat, where we surveyed the emergence of seedlings of *Crataegus* and *Ilex*. We positioned the

seedling quadrat to ensure a canopy cover similar to that above the seed-sampling quadrat. Each seedling quadrat was visited fortnightly from early May to late June of 2007 and 2008 ($n = 4$), the season in which most emergences take place (García et al. 2005). Each emerged seedling was individually identified by positioning it within the quadrat with x, y coordinates (two-dimensional accuracy ≤ 1 cm) and was mapped on a drawing template to differentiate between seedlings emerging simultaneously from the same point. For each sampling quadrat, we estimated the density of first-year seedlings as the cumulative number of emerged seedlings at the end of each season.

Fragmentation Correlates on Recruitment

Each sampling station was characterized by several structural variables that correlate directly to habitat fragmentation and that are expected to affect recruitment. The first variable corresponded to the microhabitat structure (i.e., the structural traits of the area above the 50 × 50 cm sampling quadrats in which seeds were deposited and seedlings emerged) (Figs. 1b–d). We assigned each sampling quadrat to one of the following microhabitat types: fruiting tree (any fleshy-fruited plant species); nonfruiting tree (any nonfleshy-fruited species and fleshy-fruited plants bearing no fruits), open pasture and open rocky ground. Each sampling station was assigned to only one microhabitat category.

A second set of variables represented the habitat features of the neighborhood surrounding sampling stations (Figs. 1b–d). We incorporated into the GIS the digitized forest cover (of all plant species) and the position, identity, and fruit crop size for all individual trees of fleshy-fruited species in the study plot. Individual trees were identified at the beginning of each dispersal season (early September 2006 and 2007), and estimates of crop size were made on a semilogarithmic scale and assigned a score of between 0 and 5 (0, no fruits; 1, 1–10 fruits; 2, 11–100; 3, 101–1,000; 4, 1,001–10,000; 5, > 10,001 (see Carlo et al. 2003 for a similar procedure). Once the GIS layers were completed, we delimited a circular plot of 10 m radius (hereafter R10) as the immediate neighborhood of each sampling station (Figs. 1b–d). This neighborhood scale strongly influences the functional response of frugivorous birds to habitat fragmentation in the study site (García & Chacoff 2007; Carlo & Morales 2008). For each R10, we measured from the GIS layers tree cover (sum of square meters occupied by tree canopy of all species either fleshy fruited or not) and the total abundance of fleshy fruits at the beginning of the dispersal season; semilogarithmic-scaled estimates of crop size were translated into the average value between intervals of minimum and maximum values for a given semilogarithmic score (e.g., a score of three matched to 550 fruits), except for crops with a score of five for which we arbitrarily used a value of 25,000.

Statistical Analyses

The change in the position of sampling stations between years did not affect the frequency of microhabitats ($\chi^2 = 0.753$; $p > 0.05$) or the forest cover (unpaired t test; $t = -0.418$; $p > 0.05$) sampled across the study plot every year. We thus assumed that the environmental gradients covered by the sampling stations represented similar fragmentation scenarios in both study years. Nevertheless, the positioning differences led us to perform separate analytical models for the two study years. We also performed separate analysis for each target species.

Our first goal was to examine the correlations among seed rain, seedling emergence, and the amount of forest cover. For this, we used the Spatial Analysis by Distance Indices (SADIE, Perry et al. 1999). This is a spatially explicit methodology developed to quantify correlations between geo-referenced count data sets that are free of statistical constraints due to spatial autocorrelation. SADIE provides an association index, X_p (Winder et al. 2001) and measures the degree of spatial association or dissociation between two variables sampled at the same points. This index ranges between +1 (complete spatial association) and -1 (complete dissociation). Zero indicates spatial independence. The statistical significance of X_p is quantified by the Dutilleul method (Dutilleul et al. 1993), which corrects the amount of degrees of freedom in the presence of spatial autocorrelation. We used X_p to measure, for each target species, the spatial association among the distribution of seed-rain density, seedling emergence, and forest cover at R10. Analyses were conducted with the software SadieShell (version 1.2.2, Perry et al. 1999).

To disentangle the relative effect of each correlate of structural fragmentation (i.e., microhabitat type, forest cover within R10, and fruits within R10) on seed rain and seedling emergence, we used path analysis (Quinn & Keough 2002), which allowed the various direct and indirect causal relationships between a group of predictor (fragmentation correlates) and response variables (seed rain and seedling emergence) to be explored simultaneously. This methodology allows one to discern the effects of each predictor variable irrespective of each other given that some of them may covary. Thus, we sought to verify the direct, independent effect of each fragmentation correlate on seed dispersal (e.g., effect of the amount of forest cover independent of fruit availability and microhabitat); the effects of bird-generated seed rain on seedling emergence independent of fragmentation degree; and the effect of each fragmentation correlate on seedling emergence independent of seed dispersal. We also verified the indirect, dispersal-mediated effects of fragmentation correlates on seedling emergence. Direct effects were measured with standardized partial regression coefficients between a predictor variable and a response variable (i.e., direct link), whereas indirect effects

were calculated by adding the products of all standardized partial regression coefficients over all paths between predictor and response variables. Path coefficients were obtained from Monte Carlo methods. To accept or reject a model, we used the goodness of fit provided by the Akaike's information criterion (AIC). All path analyses were performed in SEPATH module (Statistica, version 6.0; Statsoft, Tulsa, Oklahoma).

Given the gradient-like structure of our sampling framework (Fig. 1), the presence of large-scale spatial structures in the data may exaggerate the net effects of explanatory variables in the path analysis. We checked for the presence of significant spatial structures in the response variables with Moran's I correlograms (Legendre & Legendre 1998). We found a significant gradient-like structure in seed-rain density (data not shown), so we applied a trend surface analysis (TSA) (Legendre & Legendre 1998) to this variable to remove the spatial trend (detrending was corroborated by Moran's I correlograms on TSA residuals, data not shown). Thus, path analysis involving seed-rain density as a response variable was performed with these spatially independent residuals.

Original data were log (for linear measurements) or arcsine transformed (for percentages) if necessary to normalize the data. On the basis of differences in seed-rain and seedling-emergence density between different microhabitat types, we considered the microhabitat structure in the path analysis a binomial variable with a value of 1 or 0, for microhabitats with both fruiting and nonfruiting trees and for microhabitats with both open pasture and rocks, respectively.

Results

Seed density was spatially related to the net amount of forest cover in the area surrounding the sampling station in all cases except for *Crataegus* in 2007 (Table 1). Seedling emergence exhibited a similar pattern; all pairwise comparisons were significant. As such, the association index X_p showed a significant seed-seedling spatial coupling in all but one pairwise comparison (Table 1). There was also spatial coupling between *Crataegus* and *Ilex* seed rain for both years (after Bonferroni correction, $p < 0.0001$).

Seed-rain density differed significantly among microhabitats types in both study years for *Crataegus* and *Ilex*. Seed rain was higher under fruiting than nonfruiting trees (Table 2). Sampling quadrats under these microhabitats received many more seeds of both species than those on bare soil and rocks, even when located in neighborhoods with poor canopy cover (Table 2; Fig. 2). Furthermore, all stations under this type of microhabitat received some seed, whereas the majority of stations in open and rocks received no seeds (Table 2). Thus, two groups of microhabitats were distinguished according to their

Table 1. Spatial analysis by distance index (SADIE) accounting for the spatial association between forest cover and both seed rain and seedling emergence and between seeds and seedlings of *C. monogyna* and *I. aquifolium* in 2006 and 2007.^a

Spatial association	Year	Seeds		Seedlings	
		<i>C. monogyna</i>	<i>I. aquifolium</i>	<i>C. monogyna</i>	<i>I. aquifolium</i>
Forest cover & seed rain and emergence	2006	0.379 ^b	0.591 ^b	0.285 ^b	0.193 ^b
	2007	0.089	0.342 ^b	0.312 ^b	0.524 ^b
Seed and seedling	2006	0.483 ^b	0.133		
	2007	0.205 ^b	0.561 ^b		

^aValues represent the association index X_p (see text for details).

^bSignificant values after Bonferroni sequential adjustment ($p < 0.05$).

functional role as seed-dispersal foci: those with fruiting and nonfruiting trees (hereafter, covered microhabitats) and those with open interspaces and rocks (hereafter, uncovered microhabitats). Moreover, seed-rain density was higher in those stations surrounded by neighborhoods with high levels of canopy cover and, especially, in fruit-rich neighborhoods, the latter both for stations under covered and uncovered microhabitats (Fig. 2). Pattern of seedling emergence followed a similar trend to that of seed dispersal, although density and frequency of seedlings were much lower than seed density (Table 1).

Path models used to reveal the relative role of each factor explaining initial recruitment retained all variables included in the basic a priori model (i.e., forest cover in R10, fruits in R10, microhabitat features) and showed similar trends to explain seed-rain density and seedling emergence patterns in both years (Fig. 3). Path models showed that seed density for both *Ilex* and *Crataegus*

was mainly determined by the microhabitat structure because it showed the highest total effect relative to other variables (Table 3). In all models covered microhabitats had higher seed densities (Table 3; Fig. 3). Fruits in the neighborhood (R10) had a positive, significant effect on seed rain, whereas forest cover in the neighborhood (R10) had negative, significant effects on seed rain in all models. When the indirect effects of forest cover were accounted for through fruits and microhabitat, however, the global effect of the amount of forest cover was positive (Table 3). This was because the cumulative positive indirect effects of forest cover across these two factors were stronger than the negative direct effects by themselves (Table 3). With regard to seedling emergence, causal models included all a priori variables, but only microhabitat and seed density were significant to any extent. In *Crataegus* in both years, seedling emergence was positively related to seed density, which indicates

Table 2. Mean (SD) number of seeds and seedlings per sampling quadrats in each microhabitat of *C. monogyna* and *I. aquifolium* in 2006 ($n = 167$) and 2007 ($n = 181$).*

	<i>C. monogyna</i>		<i>I. aquifolium</i>	
	2006	2007	2006	2007
Seeds				
covered				
fruiting tree	22.5 (32.5) [34, 0.9]	27.9 (38.6) [44, 0.9]	24.8 (62.4) [34, 0.9]	25.6 (43.3) [44, 1.0]
nonfruiting tree	4.6 (5.1) [25, 0.8]	8.5 (12.0) [27, 0.8]	17.6 (32.8) [25, 0.8]	10.5 (5.6) [27, 0.8]
uncovered				
open	0.6 (1.1) [88, 0.3]	0.9 (1.8) [97, 0.4]	0.8 (3.2) [88, 0.2]	0.3 (0.9) [97, 0.1]
rock	2.0 (6.6) [20, 0.4]	1.5 (3.0) [13, 0.5]	0.2 (0.5) [20, 0.1]	1.0 (1.5) [13, 0.4]
Seedling				
covered				
fruiting tree	8.0 (10.3) [34, 0.7]	3.4 (4.8) [44, 0.6]	0.8 (1.8) [34, 0.2]	1.2 (2.4) [44, 0.3]
nonfruiting tree	0.7 (1.5) [25, 0.3]	2.5 (5.1) [27, 0.4]	0.5 (1.2) [25, 0.3]	0.6 (1.3) [27, 0.2]
uncovered				
open	0.3 (1.8) [88, 0.1]	0.1 (0.3) [97, 0.1]	0.0 (0.1) [88, 0.0]	0.0 (0.3) [97, 0.0]
rock	0.0 (0.0) [20, 0.0]	0.1 (0.3) [13, 0.1]	0.0 (0.0) [20, 0.0]	0.0 (0.0) [13, 0.0]

*The number of sampled quadrats and the proportion containing at least one seed or seedling are shown, respectively, in brackets.

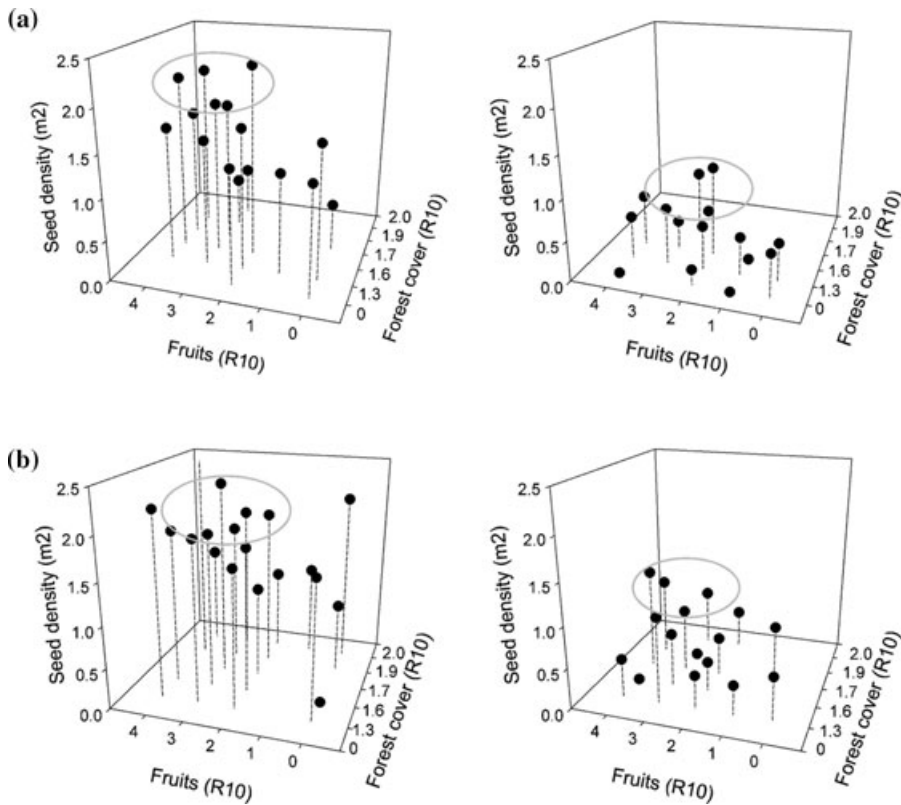


Figure 2. Density of seed rain of *Crataegus* as a function of forest cover and fruit availability (both log transformed) in covered microhabitats (left) and uncovered microhabitats (right) in (a) 2006 and (b) 2007. Dots represent mean seed density of a given value of cover (at R10, i.e., sampling stations in 10-m radius neighborhood) and fruit availability (at R10). Ellipses highlight points of highest seed deposition.

that more seedlings emerged in stations that received more dispersed seeds and in stations with covered microhabitats. In *Ilex* seedling density was only affected by microhabitat and only in 2007 (Table 3). The effect of forest cover (R10) on seedling emergence was not significant in all species and years.

Discussion

Forest structural fragmentation reduced the probability of seed deposition of both *Crataegus* and *Ilex* throughout the landscape. Furthermore, the effects of forest fragmentation went beyond dispersal to recruitment stages

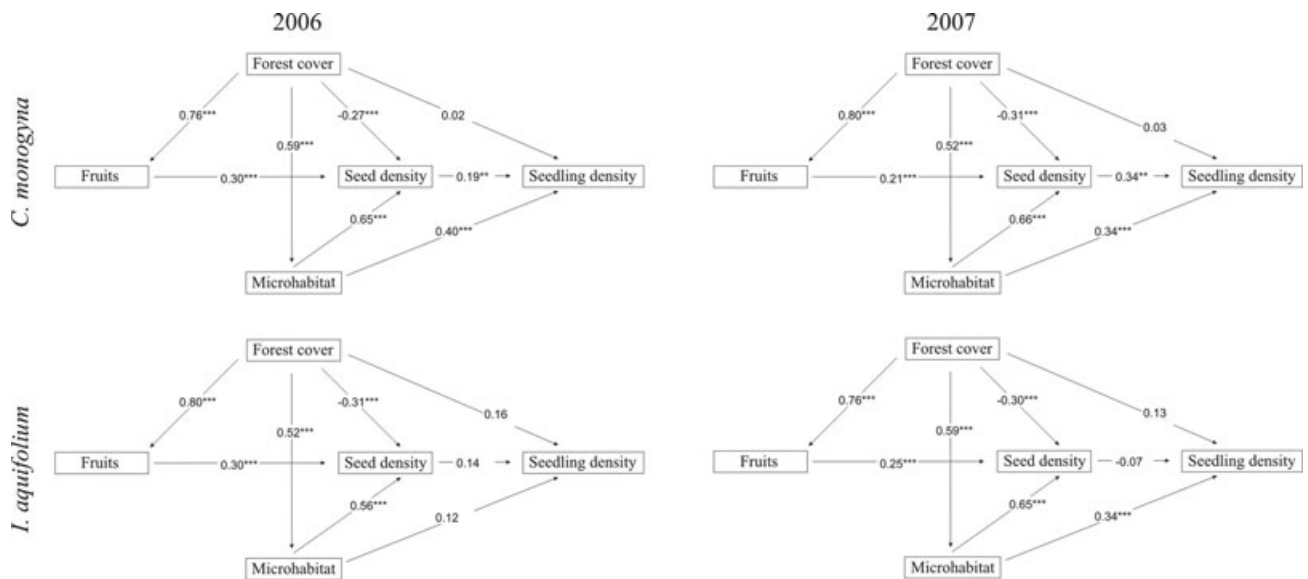


Figure 3. Structural equation models (SEM) of neighborhood and microhabitat effects on the residuals of seed-rain density and seedling emergence of *Crataegus* and *Ilex* plants in 2006 and 2007 after controlling for spatial effects. Numbers are partial regression coefficients (see Methods). Values without asterisks are not significant (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Table 3. Direct, indirect, and total effects of each variable on seed density and seedling density for *Crataegus* and *Ilex* tree species.^a

	2006			2007		
	direct	indirect	total	direct	indirect	total
<i>Crataegus monogyna</i>						
seed density						
forest cover	-0.27 ^b	0.61	0.34 ^b	-0.31 ^b	0.50	0.19 ^b
through fruits		0.23			0.16	
through microhabitat			0.38			0.34
fruits	0.30 ^b		0.30 ^b	0.21 ^b		0.21 ^b
microhabitat	0.65 ^b		0.65 ^b	0.66 ^b		0.66 ^b
seedling density						
forest cover	0.02	0.18	-0.16	0.03	0.07	0.10
through microhabitat			0.23		0.17	
through seed density			-0.05		-0.10	
seed density	0.19 ^b		0.19 ^b	0.34 ^b		0.34 ^b
microhabitat	0.40 ^b		0.40 ^b	0.34 ^b		0.34 ^b
<i>Ilex aquifolium</i>						
seed density						
forest cover	-0.30 ^b	0.56	0.26 ^b	-0.31 ^b	0.55	0.24 ^b
through fruits		0.19			0.24	
through microhabitat			0.37		0.30	
fruits	0.25 ^b		0.25 ^b	0.30 ^b		0.30 ^b
microhabitat	0.65 ^b		0.65 ^b	0.56 ^b		0.56 ^b
seedling density						
forest cover	0.13	0.21	0.08	0.16	0.02	0.14
through microhabitat			0.19		0.06	
through seed density			0.02		-0.04	
seed density	-0.07		-0.07	0.14		0.14
microhabitat	0.34 ^b		0.34 ^b	0.12		0.12

^aDirect effects were measured by standardized partial regression coefficients between a predictor variable and a response variable (i.e., the direct link), whereas indirect effects were calculated by adding the products of all standardized partial regression coefficients over all paths. Direct effects correspond to path coefficients. Indirect effects correspond to the sum of products of the coefficients along all possible routes from the explanatory variable to seed density. Total effects are the sum of direct and indirect effects.

^bSignificance at $p < 0.001$.

because seedling establishment was positively correlated with availability of bird-dispersed seeds. Nevertheless, in *Ilex* the effects of fragmentation constrained the seed-to-seedling transition, probably through seed predation and other mortality factors. Our results highlight that the species-specific coupling between seed dispersal and seedling establishment must be taken into account to predict plant population and community responses to fragmentation gradients.

The sharp decrease we found in number of seeds dispersed by birds along the gradient of forest fragmentation, in both species and years, is similar to the decrease reported elsewhere (e.g., Cordeiro & Howe 2003; Gray et al. 2006; García & Chacoff 2007). The fact that forest cover and seed rain were correlated apparently contrasts with the negative direct effect of forest cover evidenced by the path analysis. This can be explained because the overall effect of the amount of forest cover involved indirect positive effects (i.e., availability of fruits and covered microhabitats) that were even stronger than direct effects themselves (Table 3). Thus, both presence of woody perches (either fruiting or not) and availability of fleshy fruits in their neighborhood, rather than in the remaining forest cover by itself, were the key factors driving seed

dispersal throughout the fragmented landscape. These results are in line with previous work in the same system, which suggests that frugivory on *Crataegus* trees is affected by presence of tree cover in the neighborhood, and more seeds are likely to be dropped away from mother plants where forests are relatively intact (García & Chacoff 2007). Our findings discern how such a cover effect might be related to wider availability of fruit resources rather than simply to amount of canopy. Thus, by explicitly assessing the relative roles of perching and the fruiting neighborhood on probability of seed arrival into degraded matrix, irrespective of the correlated tree cover, our results expand on previous works (e.g., Guevara & Laborde 1993; Graham 2001; Carlo & Morales 2008; Herrera & García 2009).

The density of dispersed seeds and seedling establishment in *Crataegus* were positively related across the fragmented area. As suggested by path analysis, density of emerged seedlings was related to density of dispersed seeds, independent of habitat features. That is, patterns of recruitment of this plant species were strongly shaped by activity of frugivorous birds throughout the landscape. In addition, seed-to-seedling concordance suggests that postdispersal losses were not strong enough to erase the

spatial template of propagules created by birds in *Crataegus* (García et al. 2005; Hampe et al. 2008). In *Ilex*, conversely, the weak link between dispersal and seedling emergence suggested that postdispersal factors were the ultimate drivers of initial recruitment.

Seed predation by rodents is considered the most important factor explaining dispersal-recruitment mismatches (Hulme 1998), and predation is comparatively much higher in *Ilex* than in *Crataegus* because *Ilex* seeds are more palatable to predators (García et al. 2005). Thus, although we did not explicitly measure seed predation, the correlation between forest fragmentation and *Ilex* seedling emergence at the landscape scale, suggests that the same situation that promotes seed dispersal might also increase predation rates (Santos & Tellería 1994; García & Chacoff 2007). Another explanation is that *Ilex* seedling emergence may be more dependent on the number of seeds falling from mother trees than on the seed rain generated by birds (Hampe et al. 2008). Dispersal limitation may lead to dense seedling clumping under parent plants, as was indicated in the path analysis by the positive effect of microhabitat structure on seedling density. This direct role of fruiting trees as recruitment foci would also explain, indirectly, the correlation between dispersed seeds and seedling emergence, at least in 2007, because birds dropped most seeds in those sites already receiving seed input from fallen fruits.

Management Strategies to Increase Plant Recruitment in Fragmented Landscapes

Seed dispersal by animals could be used to lower the costs of restoring forests and plant populations within a reasonable time frame (Wunderle 1997). Unfortunately, there is a generalized lack of information and guidelines on how conservation plans can take advantage of frugivory and seed-dispersal networks to recover degraded habitats. It has been assumed that the proportion of remaining forest cover could overcome, by itself, barriers to forest recovery in fragmented areas by attracting seed-dispersing frugivores. Nevertheless, our results suggest that forest fragmentation reduced probability of seed deposition for both trees as a function of decreased availability of woody perches and fruit-rich neighborhoods, rather than as a function of reductions in tree cover itself. In this sense, our results suggest that presence of scattered and remnant tree cover, and especially that providing fruit resources in unforested matrix, is the most important factor driving seed dispersal through the entire fragmented landscape. Hence, preserving and strategically increasing fruiting trees in the landscape matrix would ensure and increase seed delivery to early-successional patches (Herrera & García 2009) and enhance reproductive connectivity across the landscape (Aldrich & Hamrick 1998). The long-term persistence of birds in fragmented landscapes

might also be ensured by enhanced habitat quantity and quality (Sekercioglu et al. 2007).

Our results also show that management strategies that exclusively focus on seed dispersal by birds would not guarantee recruitment in some species. Consequently, besides fostering seed delivery into degraded areas, management actions must consider seed-survival expectancies to reinforce the role of birds in maintaining the structure of plant communities and ecosystem resilience (Wunderle 1997; Lundberg & Moberg 2003). A plausible action could be to make microhabitats with high seed deposition (i.e., habitats under the canopy of fleshy-fruited plants in fruit-rich neighborhoods) (Figs. 1b & 2) more favorable for seedling survival by, for example, excluding seed predators (Holl 1999). This could be especially important for the heavily depredated *Ilex* species.

Many tropical and temperate forests are dominated by woody plants whose seeds are dispersed by fruit-eating animals (Jordano 2000), and after dispersal the seeds of these plants suffer strong predation (Hulme & Kollmann 2005). These forests are currently faced with high levels of anthropogenic degradation and fragmentation that unequivocally affect tree recruitment processes driven by dispersers and predators (Tylianakis et al. 2008). Given the common pattern of landscape alteration worldwide (Lindenmayer & Fischer 2007) and the predictable responses of vertebrate frugivores to habitat and fruit distributions (Carlo & Morales 2008), we argue that our results may transcend the peculiarities of the system studied and provide general insights on the fine-scale mechanisms controlling tree recovery in fragmented scenarios. We encourage conservation biologists and land-use planners to take advantage of frugivore plant systems in efforts to recover plant populations and communities in degraded areas.

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