

ECOSCIENCE



Volume 15 • (2) • 2008

Differential seed dispersal patterns generated by a common assemblage of vertebrate frugivores in three fleshy-fruited trees¹

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Abstract: We analyzed the role of birds and mammals as seed dispersers of 3 fleshy-fruited tree species, hawthorn (*Crataegus monogyna*), holly (*Ilex aquifolium*), and yew (*Taxus baccata*), in a temperate secondary forest in northwestern Spain. Seed dispersal patterns were assessed from direct observations of the disperser birds (thrushes, *Turdus* spp.), from the collection of bird and mammal defecations; and from seed rain estimates in fixed plots. Some highly specific interactions emerged, especially for the pairs *Turdus iliacus*–*Ilex* and *T. philomelos*–*Taxus*, due to dispersers' fruit preferences and because some fruit species were more consumed than others. Seeds removed by mammals (mainly fox, *Vulpes vulpes*, and badger, *Meles meles*) were deposited in large faecal clumps that were mainly found in open areas, whereas those removed by birds appeared in smaller clumps, located mostly in covered microhabitats. Flocking species (*T. viscivorus*, *T. pilaris*, and *T. iliacus*) flew longer distances after fruit consumption, whereas *T. merula* and *T. philomelos* (less gregarious and with resident populations) tended to fly shorter distances, generating a 2-peaked frequency distribution of flight distances. The refuge provided by the tree canopy seemed to be an important cue for the first perch used by birds after leaving the feeding tree. Seed rain of *Ilex* mainly occurred beneath conspecifics and yews; *Taxus* seeds were mainly found under conspecifics; and no microhabitat was clearly dominated by *Crataegus* seeds. In general, this study reveals that similar bird species differed in the quantity and quality (microhabitat and distance travelled) components of their dispersal effectiveness. At the same time, mammals and flocking species emerge as important dispersal vectors implicated in long-distance dispersal.

Keywords: *Crataegus monogyna*, *Ilex aquifolium*, mammals, seed dispersal, *Taxus baccata*, thrushes.

Résumé : Nous avons analysé le rôle des oiseaux et des mammifères comme agents de dispersion des graines de 3 espèces d'arbres à fruits charnus, l'aubépine monogyne (*Crataegus monogyna*), le houx commun (*Ilex aquifolium*) et l'if commun (*Taxus baccata*) dans une forêt tempérée d'origine secondaire au nord-ouest de l'Espagne. Les patrons de dissémination des graines ont été étudiés par des observations directes des agents disperseurs aviaires (grives et merles, *Turdus* spp.), de la collecte de fèces d'oiseaux et de mammifères et par des estimés de la pluie de semences dans des parcelles fixes. Des interactions très spécifiques sont apparues, particulièrement pour les paires *Turdus iliacus*–*Ilex* et *T. philomelos*–*Taxus* en raison des préférences fruitières des oiseaux et parce qu'en général certains fruits étaient plus consommés que d'autres. Les graines emportées par des mammifères (principalement le renard, *Vulpes vulpes* et le blaireau, *Meles meles*) ont été déposées dans de gros amoncellements de fèces qui ont été retrouvés principalement dans des secteurs ouverts, alors que les graines emportées par des oiseaux ont été retrouvées dans de plus petits amoncellements localisés surtout dans des microhabitats couverts. Les espèces grégaires (*T. viscivorus*, *T. pilaris* et *T. iliacus*) ont parcouru de plus grandes distances après avoir consommé des fruits, alors que *T. merula* et *T. philomelos* (moins grégaires et avec des populations résidentes) ont eu tendance à parcourir de plus courtes distances, produisant une distribution de fréquences des distances de vol à 2 pics. Les refuges procurés par la canopée des arbres ont semblé être un signal important pour le premier perchoir utilisé par les oiseaux après le départ de l'arbre fruitier. Les semences d'*Ilex* ont été retrouvées principalement sous des arbres de la même espèce et sous des ifs, les graines de *Taxus* ont été retrouvées elles aussi principalement sous des arbres de la même espèce alors que les graines de *Crataegus* n'étaient dominantes dans la pluie de semences d'aucun des microhabitats. En général, cette étude révèle que les espèces similaires d'oiseaux diffèrent dans les composantes de quantité et de qualité (le microhabitat et la distance parcourue) de leur efficacité de dispersion. En même temps, les mammifères et les oiseaux grégaires apparaissent comme des vecteurs de dispersion importants impliqués dans la dissémination des graines sur de longues distances.

Mots-clés : *Crataegus monogyna*, dissémination des graines, grives et merles, *Ilex aquifolium*, mammifères, *Taxus baccata*.

Nomenclature: Cramp, 1988; Tutin *et al.*, 1964–1980.

Introduction

Seed dispersal is the process of seed movement away from the parent plants to new locations, conditioning seed

survival expectation. In fleshy-fruited plants, the spatial distribution of seeds generated in this process, *i.e.*, the seed rain, depends to a large extent on the behaviour of seed dispersers (Murray, 1988; Schupp, Milleron & Russo, 2002; Wang & Smith, 2002; Westcott *et al.*, 2005). Dispersers determine the quantity (number of seeds removed) and the quality (survival probability of seeds in later plant stages) of seed dispersal (Schupp, 1993; Jordano & Schupp, 2000). Both theoretical and empirical studies have demonstrated

¹Rec. 2007-04-12; acc. 2007-08-29.

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DOI 10.2980/15-2-3096

the potential impact of the spatial distribution of seeds in determining the structure and dynamics of plant populations and communities (Nathan & Muller-Landau, 2000; Levin *et al.*, 2003; Levine & Murrell, 2003; Potthoff *et al.*, 2006). However, the role of dispersers in determining community seed rain patterns remains poorly known, and comparisons among coexisting plant species and dispersal vectors are still scarce (but see Izhaki, Walton & Safriel, 1991; Jordano & Schupp, 2000; Poulsen *et al.*, 2002; Clark *et al.*, 2005); this scarcity is especially important given the emerging evidence suggesting distance-related differences among disperser species (Jordano *et al.*, 2007; Spiegel & Nathan, 2007).

One method of studying seed rain patterns is based on the collection of seeds in permanent plots or seed traps (Jordano & Schupp, 2000; Alcántara *et al.*, 2000; García, Obeso & Martínez, 2005a,b). However, obtaining accurate estimates of seed rain becomes a difficult task when the main dispersal vectors are vertebrates, which often deposit seeds in clumped and non-random ways (Clark *et al.*, 2004; Russo, Portnoy & Augspurger, 2006; Jordano *et al.*, 2007). For instance, seed traps and permanent plots tend to be ineffective in open microhabitats. Most of them receive no seeds, resulting in zero-inflated samples that cause biased estimates of seed density. In general, these methods do not provide information about the distance and direction of the dispersal displacements, nor about the timing of these events. In multispecific seed rains, contagious seed deposition patterns result from coincident dispersal events involving different species. This could be a consequence of co-dispersal (different species being dispersed jointly) or the result of a succession of independent dispersal events focused on some target microsites (Herrera, 2002). In addition, variations in the composition of disperser assemblages and their effect on seed rain may remain obscure with these passive methods.

Alternatively, seed rain may be inferred from frugivore behaviour, including foraging and post-foraging activities such as fruit consumption and refuge preferences (Hoppe, 1987; Chavez-Ramirez & Slack, 1994; Westcott & Graham, 2000; Holbrook & Smith, 2000; Gómez, 2003; Russo, Portnoy & Augspurger, 2006). Previous studies examining the foraging patterns of vertebrate dispersers in plant communities have demonstrated that the nature of the plant–frugivore interaction is generalized. Plants are usually visited by different dispersers that consume several fruit species during a short time interval (Jordano, 1987; Westcott *et al.*, 2005). However, certain fruit preferences also exist, *i.e.*, frugivores show distinct intra- and inter-specific biases that may affect dispersal (*e.g.*, fruit colour, fruit and seed size: Sallabanks, 1993; Gervais, Noon & Willson, 1999; Herrera, 2002; Martínez, García & Obeso, 2007).

In addition, disperser behaviour away from source trees also affects seed fate. The distance and direction of disperser movements, together with gut passage times, ultimately determine where seeds are delivered (Hoppe, 1987; Westcott & Graham, 2000; Holbrook & Smith, 2000; Gómez, 2003; Westcott *et al.*, 2005). Non-random use of space by dispersers has been widely demonstrated, *i.e.*, birds usually perch in covered microhabitats (*e.g.*, plants with fruits that provide food, resting roosts, and protec-

tion from predators) and tend to avoid open microhabitats (reviewed in Schupp, Milleron & Russo, 2002); some mammal species behave similarly (Poulsen *et al.*, 2002; Russo, Portnoy & Augspurger, 2006). In the same way, variations in seed rain composition through the fruiting season may result in a multispecific seed deposition pattern at the end of the dispersal period. Therefore, the resulting seed rain is heterogeneous in space and time (Loiselle & Blake, 1999; Jordano & Schupp, 2000; Clark *et al.*, 2004; 2005).

In this study, we analyze the interactions between 3 fleshy-fruited tree species, the hawthorn (*Crataegus monogyna*), the holly (*Ilex aquifolium*), and the yew (*Taxus baccata*), and their disperser bird (thrushes, *Turdus* spp.) and mammal species in a temperate secondary forest, abandoning thus the usual approach that commonly focuses on only one species in one of the sides of the interaction pairs (*i.e.*, one plant species and its disperser assemblage, as in for instance Jordano *et al.*, 2007; Spiegel & Nathan, 2007). We examine how foraging and post-foraging behaviour of individual disperser species affects fruit removal and seed deposition patterns on these tree species. The combination of seed rain estimates in fixed plots with direct observation of bird behaviour and collection of seeds from mammal and bird faeces allowed us to (i) estimate the preference of mammals and birds for different tree species; (ii) examine the distribution of bird-mediated dispersal distances; (iii) compare the delivery of seeds to different microhabitats by both kind of dispersers; and (iv) assess the correspondence between post-foraging bird movements and the pattern of seed fall observed.

Methods

STUDY SITE

This study was conducted during 2 consecutive fruiting seasons at 2 sampling sites, Peña Mayor and Teixeu (both ~4 ha), located in Peña Mayor Range (Asturias province, northwestern Spain). Both sites are situated on northern-oriented slopes at 1000 m asl, and the distance between them is ~1.5 km. The sites contain secondary forest stands composed of fleshy-fruited species (*Crataegus monogyna*, *Ilex aquifolium*, and *Taxus baccata*), together with *Corylus avellana* and mature deciduous forest stands of *Fagus sylvatica*. Different stand types are usually contiguous in a successional gradient, and both are embedded into a matrix of pasture valleys and rocky slopes.

PLANT AND FRUGIVORE SPECIES

We studied the disperser assemblage and the seed deposition patterns of 3 fleshy-fruited tree species: *Crataegus monogyna* (Rosaceae; *Crataegus* hereafter), a deciduous shrub or small tree whose fruits are single-seeded drupes that are red when ripe; *Ilex aquifolium* (Aquifoliaceae; *Ilex* hereafter), a dioecious evergreen tree that produces red berries containing 2–4 pyrenes (Obeso, 1998); and *Taxus baccata* (Taxaceae; *Taxus* hereafter), a dioecious evergreen tree with arilated seeds that we will denote as “fruits” hereafter. In the Cantabrian range (northwestern Spain), fruit ripening occurs in early September, November, and August, respectively for *Crataegus*, *Ilex*, and *Taxus*.

Fruits are mainly consumed by thrushes (*Turdus* spp., Turdidae): *Turdus merula*, *T. pilaris*, *T. viscivorus*, *T. iliacus*,

and *T. philomelos* (Snow & Snow, 1988). These species are overwintering migrants that arrive in northwestern Spain during the autumn in a sequential way: *T. philomelos* and *T. merula* (in early October), *T. pilaris* and *T. viscivorus* (November), and *T. iliacus* (at the end of November). There are also resident populations in the area for *T. merula*, *T. philomelos*, and *T. viscivorus* (see Santos, 1982 for a detailed description of their migration phenology).

Thrushes interact with the target tree species as “legitimate seed dispersers” (Jordano & Schupp, 2000), *i.e.*, they swallow the whole fruit and then regurgitate or defecate the seeds intact and viable. All these species are very similar in their physiology and size. Thus, it is expected that gut retention times and number of fruit consumed per feeding event will not vary greatly among them (see Herrera, 1984; Barnea, Harborne & Pannell, 1993). Seeds from uneaten fruits that fall beneath the canopy of the parent tree are eventually dispersed by carnivorous mammals, like *Vulpes vulpes* and *Meles meles*, viverrids, and mustelids.

FRUIT AND MICROHABITAT AVAILABILITY

The availability of different fruits to dispersers was estimated by measuring crop size (fruit crop ripened). When most of the fruits of the target species were ripe but before the massive fruit consumption by frugivores started (September for *Crataegus* and *Taxus* and November for *Ilex*), we recorded the number of fruits on 5 branches per tree ($n = 14$ trees per species, site, and year). The branches were located at different canopy orientations. To obtain the mean crop size of each tree, the mean number of fruits per branch was multiplied by the number of branches with fruits (all fruits were counted in trees with small crop size, *i.e.*, ≤ 900).

The relative abundance of microhabitat types in the watching patches (see below) was estimated visually by identifying the percentage of each microhabitat type and counting the number of adult trees of all species in randomly selected plots of 20×20 m ($n = 4$ plots per patch). The 5 watching patches covered the landscape variability present in the study zone and its physiographic structure, ranging from old forest, *Fagus*-dominated patches (those located within the seed rain sampling sites), to patches with only secondary forest of fleshy-fruited trees interspersed within a matrix of open pasture and rocky zones (the other 3 watching patches). On average, open microhabitats represented 63.5% of the sampled area (pastures 50.0% and rocks 13.5%). Microhabitats with tree cover made up 36.5% (*Corylus* 9.8%, *Crataegus* 3.7%, *Fagus* 2.0%, *Ilex* 17.9%, and *Taxus* 3.1%).

FEEDING AND POST-FORAGING BIRD BEHAVIOUR

We conducted direct field watches within the 2 study sites and at 3 additional patches (all ~ 1 ha) located in the same area and separated from each other by 0.5 to 1.6 km. Periods of continuous observations ranged from 1 to 5 h, 0930–1700 Greenwich Mean Time (GMT) ($n = 82.5$ and 50 h of observation from October to January in 2003–2004 and 2004–2005, respectively), after waiting 10 min to avoid the inclusion of movements caused by observer arrival. The location of the watching points allowed us to see the entirety

of each study patch without interrupting the normal behaviour of the birds. During each watching period, we recorded birds feeding on fruits in any tree in the patch, identifying them to the species level. We considered that there was a feeding event when a bird ingested at least one fruit.

To explore the potential influence of animal behaviour on the seed deposition patterns, we studied post-foraging movements of birds. For each sighted bird feeding in a focal tree species, we tried to record the distance travelled in a movement bout, *i.e.*, the distance between the feeding tree and the first landing perch after leaving it, and the type of microhabitat where they perched, as specified in the previous section. Because gut retention times are frequently short, *i.e.*, they usually range between 1 and 30 min, modal values are near the minor end of this interval (Herrera, 1984; 2002), we expected the first perch to serve as a good proxy of seed dispersal. Distance travelled was classified using the following intervals: < 2 m, $2 - < 5$ m, $5 - < 15$ m, $15 - < 30$ m, $30 - < 50$ m, $50 - < 100$ m, $100 - < 200$ m, $200 - < 300$ m, and > 300 m. To improve the sample size, we also included some chance observations of feeding events recorded in the study patches during 2002, as well as some recorded in sites in the area but not in the observation patches during 2003 and 2004 (204 individual observations in a total of 999, *i.e.*, 20.4%).

SEEDS IN FAECES

During the sampling period, we collected all mammal faeces found along transects comprising the observer movement among the 5 watching patches described above and within them (thus, the total length was 1.6 km, 10 m width, and the total effort was 8 visits per month); the samples were stored at 2 °C before processing. We estimated the percentage of animal remains and counted the number of seeds of each tree species per excrement. We also included mammal faeces found in other sites with similar forest composition and physiographic features (30% of the samples were collected at Aramo and Sueve during 2002 with a similar design but less effort [2 visits per month], see García, Obeso & Martínez, 2005a for a description). The number of seeds of each tree species in bird droppings was directly counted in the field. For that, we randomly sampled the different microhabitats studied during the dispersal season of each tree species.

SEED DISPERSAL

Seed rain was evaluated in the following microhabitats based on the type of vegetation cover, distinguishing among tree species and between female and male individuals in dioecious ones: (1) “*Corylus*”, (2) “*Crataegus*”, (3) “*Fagus*”, (4) “*Ilex* female”, (5) “*Ilex* male”, (6) “*Taxus* female”, (7) “*Taxus* male”, (8) “gap”, *i.e.*, open gaps in the forest, (9) “pasture”, herbaceous vegetation, and (10) “rock”, stones and rock substrate. We categorized types 1–7 as “covered” microhabitats and types 8–10 as “open” microhabitats.

In September 2003, we established fixed 0.5×0.5 -m quadrats in the area ($n = 7$ quadrats per microhabitat and site). For covered microhabitats, quadrats were located beneath trees ≥ 10 cm DBH, ≥ 5 m apart from other con-

specific trees, and with very little or no canopy overlap among them. For open microhabitats, quadrats were randomly selected while ensuring that all quadrats were > 2 m apart. During the dispersal season (September to January in 2003–2004 and September to March in 2004–2005), we collected once per month all dispersed seeds from the quadrats. These samples were oven dried at 60 °C for 24 h, and all seeds were identified to the species level and counted. Then, we calculated the cumulative number of seeds of each target species deposited per quadrat. We considered the possible underestimation of seed rain due to undetected seed removal from sampled surfaces to be negligible due to the scarce seed removal by rodents during the sampling period and because of previous validation using seed traps (see García, Obeso & Martínez, 2005a,b). Seeds showing signs of rodent predation (open husks, teeth marks) were counted as part of the pool of dispersed seeds, reducing thus any underestimation derived from seed predation, given that most seeds are consumed *in situ*.

STATISTICAL ANALYSES

DIETS AND DIETARY OVERLAP ESTIMATES

Feeding preferences for different trees among bird species were tested using a Chi-square statistic. To measure the degree of specialization, the reciprocity between each tree and bird species was calculated. Here, reciprocity is defined as the percentage of fruit feeding records from a tree species by a determined bird species and the percentage of feeding records of the bird species that correspond to the same tree species (Herrera, 1984).

Because this approach ignores food availability, we used the consumer's electivity (preference for food) in our analysis, adjusting for the availability of that resource in the environment (Lawlor, 1980a,b; Gotelli & Graves, 1996). We estimated the dietary overlap among bird species using the Schoener index (Schoener, 1974):

$$R_0 = 1 - \frac{1}{2} \sum_{i=1}^n |e_{ij} - e_{ik}|$$

where R_0 is the fruit resource overlap and e_{ij} and e_{ik} are the electivities for the i fruit species consumed by the j and k bird species. Resource electivities were estimated as $e_{ij} = p_{ij}/R_i$, where p_{ij} is the proportion of i fruit species consumed by the j bird species and R_i is a measure of the availability of i fruit species, calculated by multiplying crop size estimates by the mean relative abundance of each tree species in the observation patches (see Fruit and microhabitat availability). The index ranges between 0, corresponding to a situation of no overlap among species, and 1 (indicating complete overlap). We also estimated the overlap in post-foraging microhabitat use among birds species, considering p_{ij} as the proportion of the i post-foraging microhabitat used by the j bird species and R_i as the relative cover of the i microhabitat in the study sites.

Following Ricklefs and Lau (1980), we used Monte Carlo methods to generate expected resource (fruit or post-foraging microhabitat) overlap between frugivorous species given the observed resource availability. We simu-

lated the expected resource use by frugivores using the Randomization Algorithm 3 (RA3) in Lawlor (1980a). This procedure retained the observed niche breadth for each species and allowed them to use all resources. All the electivities of each consumer, both zero and non-zero, were randomly reassigned to the set of resource states 1000 times to estimate a reference distribution for the Schoener index (E_{ij}). The number of E_{ij} greater or lower than the observed overlap values was counted. We considered the observed overlap value was significant at the 5% level if it was less or greater, respectively, than the percentiles 2.5 or 97.5 of the reference distribution. In this case, we rejected the null hypothesis and concluded that the observed dietary overlap between frugivores was different from that expected under the assumption of resource consumption proportional to their availability in the environment.

POST-FORAGING BEHAVIOUR

Kruskal–Wallis one-way nonparametric analysis of variance and Chi-square tests were used respectively to analyze differences among bird species in flight distances and microhabitat use after fruit feeding (Zar, 1996). Also, to examine if bird movement among microhabitats was random or not, we compared the post-foraging habitat selected by birds (observed frequencies) with microhabitat availability (expected frequencies, see Fruit and microhabitat availability) using Chi-square tests. When a microhabitat is preferred, more bird movements are directed to that microhabitat in relation to its availability in the area, whereas the converse is true for avoided microhabitats.

SEED RAIN

We tested the effect of microhabitat (fixed factor), site (random factor, nested within microhabitat), and year (random factor, nested within site and microhabitat) on the density of dispersed seeds of each target species in the seed rain. We used Generalized Linear Mixed Models (GLMM) with a logit link function because expected residuals follow a Poisson distribution (Proc GLIMMIX, SAS Institute, 2004). The variance-mean scaling was modified to avoid over-dispersion, and quasi-likelihood methods were used in parameter estimation (McCullagh, 1983). Significance of the fixed factor was evaluated with an F -test in the full model and a Satterthwaite approximation of the degrees of freedom. Random terms significance was assessed using likelihood ratio tests (LRT). To complement the analyses, *a priori* contrasts were performed to examine differences in seed deposition patterns between open *versus* covered microhabitats, fleshy-fruited species *versus* dry-fruited ones, and female *versus* male individuals as target microhabitats.

Results

FORAGING PATTERNS

There were differences among bird and tree species in the total number of feeding events ($\chi^2 = 661.8$, $df = 8$, $P < 0.001$). All fruit species were consumed by almost all bird species (Table I). However, the relative importance of each bird species as a consumer varied among tree species (Table I). Holly was mainly consumed by *Turdus iliacus* and *T. merula*. Yew was largely foraged, especially by

T. philomelos, *T. viscivorus*, and *T. merula*. By contrast, a more equal proportion of bird species fed upon hawthorn fruits, although they were mostly consumed by *T. merula*. Although all bird species consumed several fruit species, they also showed certain fruit preferences. *Turdus philomelos* and *T. viscivorus* mainly foraged on yew, *T. iliacus* preferentially fed upon holly fruits, and *T. pilaris* consumed almost nothing but hawthorn fruits. *Turdus merula* had a wider diet because although it largely consumed yew, holly fruits were consumed about as much as hawthorn fruits.

Substantial plant–bird reciprocity occurred in some of the pairs, such as *Ilex–T. iliacus* (67.9/71.9%) and *Taxus–T. philomelos* (42.1/96.5%), but in general there was no agreement (not shown, but these relationships can easily be derived from Table I). Significant dietary overlap values were found in the following pairs of bird species: *T. philomelos–T. viscivorus*, *T. merula–T. viscivorus*, and *T. merula–T. philomelos* (Table II).

Recorded individuals were generally solitary birds, with the exception of the redwing, the fieldfare, and the mistle thrush, although the last species did show solitary, strongly territorial individuals. Large flocks of fieldfare only occurred in the study site during 2003, and no observations of this species were recorded in 2004. Additionally, in 2003 we recorded 2 ring ouzels (*T. torquatus*) foraging on yews in Peña Mayor that were not shown in Table I.

POST-FORAGING BEHAVIOUR

FLIGHT DISTANCES

In total, pooling data of the 2 y studied and all *Turdus* species, we recorded 924 movement observations. Mean post-feeding flight distance was 33.5 m (SD = 47.2). The frequency distribution of the flight distances had 2 peaks, one at short distance and other at an intermediate distance (Figure 1). These peaks were produced by different bird species, since thrushes differed significantly in the distances travelled in a movement bout (Kruskal–Wallis test = 93.01, df = 4, $P < 0.001$). *Turdus viscivorus*, *T. pilaris*, and *T. iliacus* were the species that flew longer distances, with 41% of their flights > 50 m length. *Turdus merula* and *T. philomelos* had the shortest displacement distances; most were shorter than 15 m (Figure 1). Bird species also displayed long-distance displacement events (> 300 m). However, because these were usually associated with movements among patches, we were unable to distinguish the real distance of displacement.

DESTINATION OF POST-FORAGING FLIGHTS

Bird species differed in the identity of the first perch used after leaving the feeding tree, *i.e.*, *Crataegus*, *Ilex*, and *Taxus* trees ($\chi^2 > 84.5$, df = 18, $P < 0.001$, for all target species). Also, flights by a given bird species to different microhabitats differed significantly from expectation according to availability (*i.e.*, divergence values from zero in Figure 2) ($\chi^2 > 248.3$, df = 6, $P < 0.001$, for all combinations of tree and bird species), with homogeneous behaviour within the assemblage (heterogeneity $\chi^2 = 12.9$, df = 24, $P > 0.95$). Birds tended to fly to covered microhabitats and to avoid open microhabitats (Figure 2). Within the latter, rocks were

TABLE I. Number of feeding events and percentage (in parentheses) of the annual total for all tree and bird species combined.

Bird species	Tree species	2003–2004	2004–2005	Total
<i>T. iliacus</i>	<i>Ilex</i>	45 (5.8)	88 (38.9)	133 (13.3)
<i>T. merula</i>		30 (3.9)	15 (6.6)	45 (4.5)
<i>T. philomelos</i>		0	8 (3.5)	8 (0.8)
<i>T. pilaris</i>		2 (0.2)	0	2 (0.2)
<i>T. viscivorus</i>		1 (0.1)	7 (3.1)	8 (0.8)
<i>T. iliacus</i>	<i>Crataegus</i>	34 (4.4)	3 (1.3)	37 (3.7)
<i>T. merula</i>		46 (5.9)	7 (3.1)	53 (5.3)
<i>T. philomelos</i>		1 (0.1)	1 (0.4)	2 (0.2)
<i>T. pilaris</i>		24 (3.1)	0	24 (2.4)
<i>T. viscivorus</i>		0	26 (11.5)	26 (2.6)
<i>T. iliacus</i>	<i>Taxus</i>	8 (1)	7 (3.1)	15 (1.5)
<i>T. merula</i>		159 (20.5)	4 (1.8)	163 (16.3)
<i>T. philomelos</i>		239 (30.8)	39 (17.2)	278 (27.8)
<i>T. pilaris</i>		0	0	0
<i>T. viscivorus</i>		184 (23.7)	21 (9.3)	205 (20.5)
Total		773	226	999

TABLE II. Overlap values (Schoener index) between thrushes for fruits eaten (left) and post-foraging microhabitat use (right) adjusted by fruit and microhabitat availability. Index significances were calculated with Monte Carlo methods ($n = 1000$ simulations). Boldface figures indicate $P < 0.001$.

Bird species	<i>T. merula</i>	<i>T. philomelos</i>	<i>T. pilaris</i>	<i>T. viscivorus</i>
<i>T. iliacus</i>	0.468/0.604	0.382/0.922	0.235/0.445	0.406/0.806
<i>T. merula</i>		0.914/0.528	0.091/0.511	0.938/0.664
<i>T. philomelos</i>			0.005/0.434	0.976/0.737
<i>T. pilaris</i>				0.029/0.331

more visited than pastures, especially by *T. viscivorus*. Although the residual of flight frequency of *T. viscivorus* was negative for both microhabitats (Figure 2), this was the species that flew most frequently to them, especially when the feeding perch was a hawthorn.

Most of the flights to covered microhabitats were directed to fleshy-fruited trees (97.2%). However, among the non-fleshy-fruited trees, *Fagus* was particularly important, especially when the initial perch was a yew (*T. iliacus* and *T. viscivorus* being the main bird species involved). Flights from hollies were predominantly to conspecifics (54.2%) and yews (23.1%), and they were made by different bird species (*T. iliacus* and *T. pilaris* for holly to holly flights and *T. viscivorus* and *T. merula* for holly to yew flights). There was also a tendency for birds to move towards hollies after foraging on *Crataegus* (52.0%, mainly made by *T. pilaris*, *T. merula*, and *T. iliacus*) and to fly in a similar way to hawthorns (*T. merula* and *T. pilaris*) and yews (*T. iliacus* and *T. viscivorus*). Bird movements from *Taxus* were also predominantly to *Ilex* (42.7%, mainly made by *T. philomelos*, *T. merula*, and *T. iliacus*), followed by *Fagus* (12.9%), *Crataegus* (16.2%; *T. merula* and *T. viscivorus*), and *Taxus* (16.2%; *T. iliacus*, *T. merula* and *T. viscivorus*; Figure 2).

Finally, movements between patches (*i.e.*, bird displacement from a fleshy-fruited tree of the observed patch to another place outside the patch) were mainly carried out by

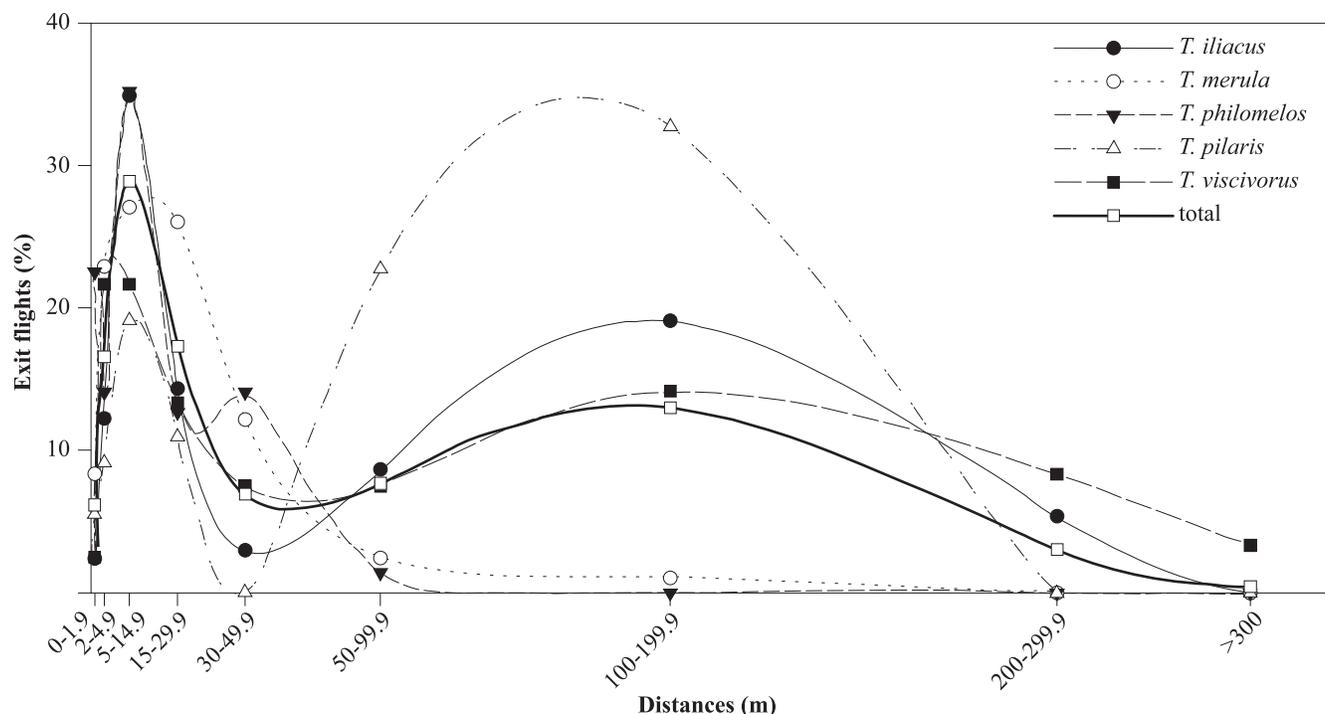


FIGURE 1. Frequency distribution of the total departure flights made by each bird species during 2003–2005 in the study sites. Curved lines were obtained by spline interpolation. The thick solid line includes all bird species. Note that movements among patches were not considered.

T. iliacus (64.3%, $n = 135$, data not included in the analysis or in Figures 1 and 2). Overlap values among thrushes for post-foraging microhabitat use were significant in the following pairs of species: *T. philomelos*–*T. iliacus*, *T. viscivorus*–*T. iliacus*, and *T. viscivorus*–*T. philomelos* (Table II).

COMPOSITION OF FAECES

BIRDS

We analyzed 457 bird droppings, of which 71.1% contained at least 1 seed, 27.6% included only soft tissues (*i.e.*, pulps or arils without seeds), predominantly from *Taxus* (79.4%), and the remainder contained only beetle elytra. Droppings were mainly monospecific: no droppings combined seeds from more than 2 species, and only 12.6% had 2 species present. Of the mixed drops, 95.1% included *Ilex* and *Crataegus* seeds together. Within the monospecific drops, 56.9% contained *Ilex*, 24.0% *Crataegus*, 14.3% *Taxus*, and the remainder other fruited species, including *Sorbus aria*, *S. aucuparia*, *Viscum album*, *Rhamnus* sp., *Rosa* sp., and *Rubus* sp. The mean (\pm SD) number of seeds per drop was 2.9 ± 1.8 , but it varied among seed species (*Crataegus*, 2.1 ± 1.1 ; *Taxus*, 2.1 ± 1.8 ; and *Ilex*, 3.4 ± 1.8 ; $F_{2, 263} = 25.7$, $P < 0.001$, model I ANOVA on log-transformed data). There were 11.0% of droppings with ≥ 5 seeds, and the maximum number of seeds found in a single drop was 11 *Ilex pyrenes*.

MAMMALS

We found 158 mammal faeces located in the following microhabitats: rocks (25.8%), paths (23.7%), pastures (17.5%), beneath yews (14.4%), latrines (7.2%), and the rest beneath other trees and shrubs, including hollies, hawthorns, hazels, and heaths. Identity of mammals at the spe-

cies level was determined in 34% of the total excrements found, and they were mainly of fox and badger (58.3% and 22.3%, respectively), but also of viverrids, mustelids, and wild boar. Most of the excrements (55.7%) contained only seeds; 43.0% included both animal remains and seeds; and in 1.3% we found only animal carcasses. Excrements with seeds were mainly monospecific (68.8%); 67.6% of them were of *Taxus*. Seed species more represented in the excrements were *Taxus* (49.1%), *S. aucuparia* (18.0%), *Crataegus* (7.2%), *Rosa* sp. (7.2%), *Rhamnus* (6.3%), and *Ilex* (2.7%). Mammal excrements contained, on average, 67.0 ± 68.2 seeds. In the case of excrements with yew, mean \pm SD and maximum number of seeds were 54.4 ± 54.1 and 346, respectively.

SEED RAIN

There were significant differences in the density of dispersed seeds among microhabitats for all tree species studied (Table III). We also found significant differences between years and sites in *Taxus* seed densities, and between years in *Ilex* seed densities (Table III). Covered microhabitats received more seeds than open microhabitats (*a priori* contrasts, $F_{1, 270} > 10.08$, $P < 0.001$, for all target species). Most of the dispersed seeds in the latter were found in gaps in the forest, followed by rocks and pastures (Figure 3). Within the covered microhabitats, fleshy-fruited species received most seeds; few seeds were found beneath dry-fruited species (*a priori* contrasts $F_{1, \geq 28} > 8.55$, $P < 0.001$, for all target species). Nevertheless, *Fagus* received predominantly holly and yew seeds, whereas *Corylus* received mainly holly seeds. *Crataegus* dispersed seeds were found in all the microhabitats, but predominantly beneath yews, hollies, hawthorns, and hazels. In contrast, *Ilex pyrenes*

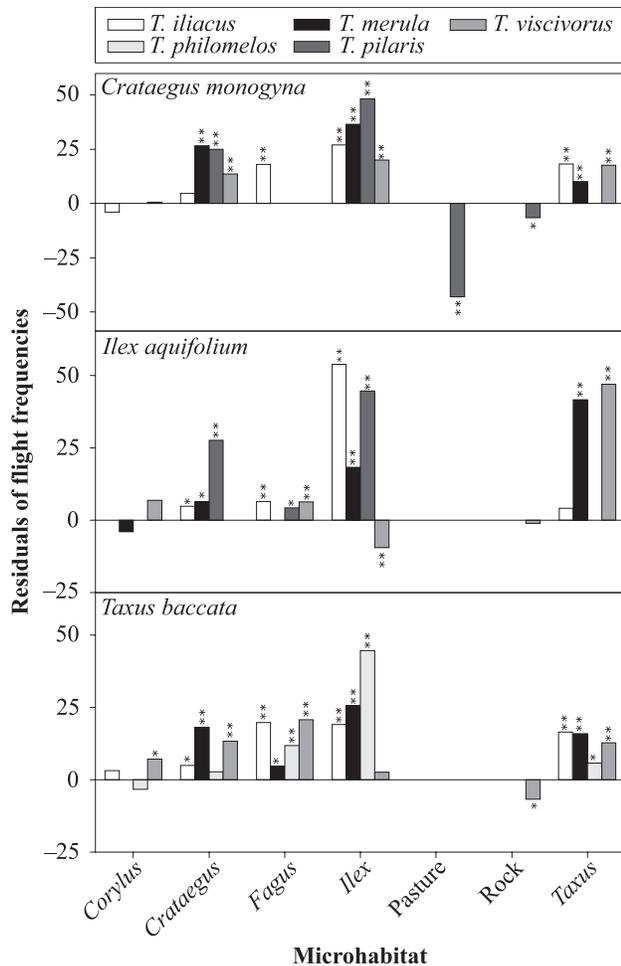


FIGURE 2. Difference between the proportion of exit flights by thrushes to 7 microhabitats after feeding on *Crataegus*, *Ilex*, and *Taxus* trees (observed frequencies) and the availability of those microhabitats (expected frequencies). Positive percentages indicate that proportionately more bird movements went to that microhabitat in relation to its availability (preferred microhabitats), whereas negative percentages indicate that proportionately fewer birds flew to that microhabitat in relation to its availability (avoided microhabitats). Deviations are shown only for those combinations of bird species and microhabitats that contributed > 5% of the total bird movements by species. Note the different scale axis of *Crataegus monogyna* relative to the scale drawn for the other tree species. Significant values * $P < 0.05$, ** $P < 0.01$.

were mainly dispersed beneath conspecifics and yews, and *Taxus* seeds were in large part found under conspecifics (Figure 3). Density of seeds beneath male trees tended to be different from that deposited under females, but it depended on the seed species considered. Conspecific seeds were mainly found beneath female trees, although significant differences were only found for *Taxus* (*a priori* contrast, $F_{1,5.8} = 59.3$, $P < 0.001$). Heterospecific seeds were less abundant beneath female *versus* male trees, but this difference was only significant in *Ilex* (*a priori* contrast, $F_{1,3.6} = 14.9$, $P < 0.05$).

Discussion

In this study, we found that seed dispersers differed in their components of dispersal effectiveness due to specific

TABLE III. Generalized linear models evaluating the effects of microhabitat (fixed factor) together with those of site (random factor, nested within microhabitat) and year (random factor, nested within site and microhabitat) on the density of seeds of the different target species in the total seed rain. All models assumed a Poisson error distribution in the response variable and used a logit link function. Table entries give degrees of freedom (df: effect, error; error df estimated with Satterthwaite approximation) and F -values for the fixed factor, estimated after fitting all random terms, and change in deviance for random factors. Significant P -values are shown in boldface.

Target species: <i>Crataegus monogyna</i>			
	df	F	P
Fixed effect			
Microhabitat	9, 12.17	5.4	0.004
Random effects change in deviance (χ^2 ; df = 1)			
Site [Microhabitat]	0		1
Year [Site[Microhabitat]]	1.72		0.19
Target species: <i>Ilex aquifolium</i>			
	df	F	P
Fixed effect			
Microhabitat	9, 4.19	8.62	0.023
Random effects change in deviance (χ^2 ; df = 1)			
Site [Microhabitat]	0		1
Year [Site[Microhabitat]]	75.88		< 0.001
Target species: <i>Taxus baccata</i>			
	df	F	P
Fixed effect			
Microhabitat	9, 10.38	31.68	< 0.001
Random effects change in deviance (χ^2 ; df = 1)			
Site [Microhabitat]	20.68		< 0.001
Year [Site[Microhabitat]]	43.53		< 0.001

patterns of fruit removal (quantity component of dispersal effectiveness) and habitat selection for seed delivery (quality component). These results suggest that a specific seed rain may emerge for tree species differing in the composition of their disperser assemblage. We inferred the spatial patterns of seed deposition of 3 fleshy-fruited species (*Crataegus*, *Ilex*, and *Taxus*) using 2 complementary approaches, one based on bird behaviour observations and bird and mammal defecations and another based on seed rain estimates. In general, these approaches matched and complemented each other, such that the 2 approaches allowed us to draw conclusions about different aspects of the dispersal process and to propose a mechanistic explanation for seed rain formation.

Although all fruit species were consumed by almost all bird species, certain species-specific fruit preferences also showed up. To some extent, the temporal overlap between fruit maturation and bird arrival during migration determines the intensity of species interactions such as dispersal (Gutián *et al.*, 2000). Plant and bird species with intense early (*Taxus* and *T. philomelos*) or late (*Ilex* and *T. iliacus*) fruit maturation and migration peaks were more closely related (*i.e.*, high reciprocity values). This close relation was also found by Gutián and Bermejo (2006) between *Ilex* and *T. iliacus*. By contrast, resident bird species like *T. merula* and tree species with a gradual dispersal period such as *Crataegus* showed a less intense coupling (Gutián *et al.*, 2000). In this sense, highest dietary overlap values were found among bird species with resident populations, indicating similar habitat perception and resource consumption patterns.

The quality component of dispersal effectiveness is determined both by the treatment of seeds within the gut

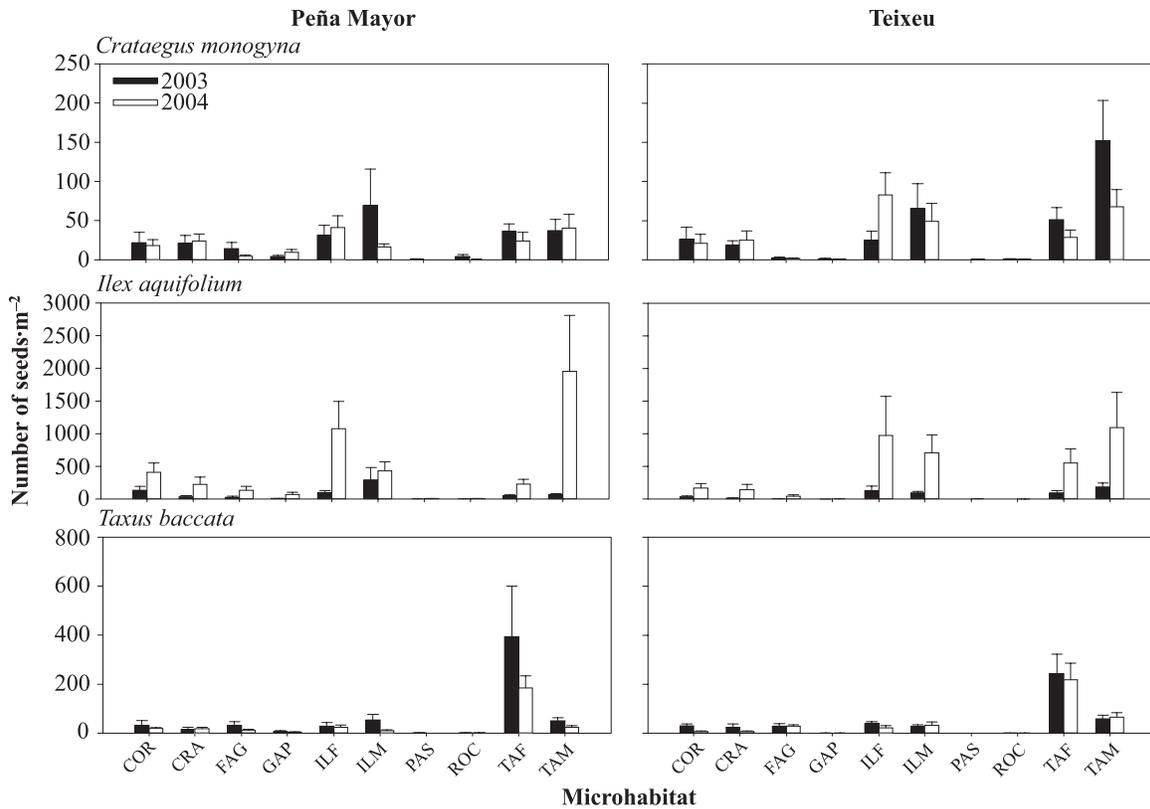


FIGURE 3. Observed seed densities (mean + SE) of the target species (*Crataegus*, *Ilex*, and *Taxus*) at 10 microhabitats in the 2 study sites (Peña Mayor and Teixeu), during 2003–2004 and 2004–2005. Note that the scale is different among tree species. *Corylus* (COR), *Crataegus* (CRA), *Fagus* (FAG), gap (GAP), *Ilex* female (ILF), *Ilex* male (ILM), pasture (PAS), rock (ROC), *Taxus* female (TAF), and *Taxus* male (TAM).

and by the sites where seeds are deposited (Schupp, 1993). In this study, seed treatment within the gut was not evaluated, but it is likely to be equivalent among bird species given the relatively small seed sizes and fast gut passage times (Barnea, Harborne & Pannell, 1993; Loiselle & Blake, 1999; Jordano & Schupp, 2000), although this is not clear in the case of yew (Thomas & Polwart, 2003; and see below). To examine the potential influence of animal behaviour on seed deposition patterns we studied post-foraging bird movements (distance and microhabitat effects) within the environment and clumping of seeds in defecations of birds and mammals.

We found differences among bird species in the flight distances travelled after feeding on fruits; these differences seem to be related to the gregariousness of bird behaviour. The fact that the data came from different observation patches suggests that the results were independent of physiographic features of the study site. Flocking species (*T. viscivorus*, *T. pilaris*, and *T. iliacus*) flew longer distances after feeding, and therefore may contribute more to long dispersal events. By contrast, *T. merula* and *T. philomelos* (less gregarious species) tended to fly short distances, leading to a more aggregated seed deposition pattern around the parent trees. As a consequence, the frequency distribution of post-foraging flights had 2 peaks, one near the source tree and the other at an intermediate distance. Because bird species also differed in their contribution to fruit removal, we hypothesize differences in the dispersal curves among the target tree species.

Differential habitat use by avian frugivores during their post-foraging movements has been previously reported (Loiselle & Blake, 1999; Jordano & Schupp, 2000; Fuentes *et al.*, 2001; Clark *et al.*, 2005). Covered microhabitats, and especially fleshy-fruited perennial trees (*Ilex* and *Taxus*), were the most visited microhabitats in our case. This indicates that not only food availability, but also the protection provided by the tree canopy is an important cue for birds. Among the open microhabitats, rocks were the most visited by birds, especially by *T. viscivorus*. In southern Spain, Jordano and Schupp (2000) found a similar result in the microhabitat selection patterns of the *Prunus mahaleb* disperser bird assemblage. Although they found that *T. viscivorus* predominantly flew to *Pinus*, this species also moved to rocks more often than other species (with the exception of *Phoenicurus ochruros*, not present in our study site). In northern Spain, Fuentes *et al.* (2001) have shown the importance for *P. mahaleb* of landscape-scale factors, such as distance to nesting sites, in determining bird post-foraging movements. These aspects and others related to landscape structure have been ignored in the current study and remain a question for future research at this site.

The analysis of the excrements of birds and mammals revealed that both disperse seeds mostly in monospecific packs. Only in the case of *Ilex* and *Crataegus* was the phenomenon of co-dispersal relatively frequent. These results reinforced diet estimates obtained from observational data of bird feeding behaviour. On the other hand, clumping of seeds and microhabitat seed deposition patterns differed

between mammals and birds, as found in other studies (Clark *et al.*, 2005). Seeds removed by birds appeared in smaller clumps and were predominantly found in covered microhabitats, whereas those removed by mammals were deposited in large faecal clumps that were mainly found in open areas. These kinds of factors are usually ignored when using seed plots to monitor seed rain.

Due to the differences in clump size, seeds removed by mammals should be more affected by density-dependent processes (*e.g.*, post-dispersal seed predation and intra- and inter-specific seedling competition for resources) than those removed by birds (Loiselle, 1990). Also, we can expect differences in their survival resulting from their exposure to different environmental conditions (open *versus* covered areas). For example, rodent predation or fungal pathogens tend to be higher in covered than in open microhabitats (Hulme & Benkman, 2002). Also, given the longer gut passage times and sizable home ranges of the disperser mammal species, mammal vectors promote long-distance dispersal events, allowing the colonization of new sites and enhancing genetic interchange among populations (Levin *et al.*, 2003). These long distance events are also important in shaping the fat tails of dispersal shadows, important for fast population migration (Clark *et al.*, 1998).

We found a characteristic seed deposition pattern among microhabitats for the 3 tree species studied, as previously demonstrated for a smaller sample of microhabitats by García, Martínez, and Obeso (2007). As expected, this pattern was also subject to variation among sites and years, accounting possibly for variations in seed production. Seed rain of *Ilex* mainly occurred beneath conspecifics, and yews; *Taxus* seeds were mainly found under conspecifics; and no microhabitat was clearly dominated by *Crataegus* seeds. *Taxus* and *Ilex* produce large crops that attract respectively early and late migratory bird species, yet many of their removed seeds were deposited under them. By contrast, *Crataegus* is consumed sporadically by bird dispersers and its seeds were deposited in a wide diversity of sites, but only a low percentage were deposited under its own canopy. In fact, the entire *Ilex* and *Taxus* crop was removed by birds during the 2 study years (authors, pers. observ.), whereas only 67% of the *Crataegus* crop was removed (Martínez, García & Obeso, 2007). On the other hand, we found different densities between female and male individuals: heterospecific seeds tended to be more frequent beneath males, while the opposite was true for conspecific seeds. This reinforces earlier assessments of the importance of the protection provided by the tree canopy. Other microhabitats, like dry-fruited species, also received dispersed seeds, although their role in seedling establishment remains a possible question for future studies.

Post-foraging bird movements reflected the observed seed deposition patterns for *Ilex* and *Crataegus*. However, in the case of *Taxus*, bird movements among microhabitats did not match the observed yew seed deposition patterns: yew seeds were mainly found under conspecifics, but bird movements from yews were predominantly to hollies. This might be accounted for by 2 non-exclusive explanations: (1) birds tended to return to yews following the use of a

different tree species as first perch and (2) yew seeds were dispersed under the parent before moving to another perch. If *Taxus* seeds pass through the digestive system faster than those of the other species (*e.g.*, due to laxative effect of the pulp; Herrera, 1984; Thomas & Polwart, 2003), then the chance of being defecated or regurgitated when the bird is still on the tree is higher for *Taxus*, leading to an overestimation with respect to post-foraging flights. Thus, a high proportion of bird droppings include arils without seeds.

This study reveals that similar bird species (all of the genus *Turdus*, with similar size and physiology) differed in the quantity and quality components of their dispersal effectiveness. The operation of mammals as dispersal vectors made the dispersal process even more complex. Characteristic seed deposition patterns for *Crataegus*, *Ilex*, and *Taxus* resulted from the behaviour of their particular dispersers. However, identification of these patterns is just a first step towards properly evaluating the differential effectiveness of these dispersers in terms of dispersal quality since we need information on the survival of seeds throughout their progression to adults in each microhabitat. Also, it is necessary to assess the long-term importance of both groups of dispersers, given the tendency of mammal dispersers to produce long-distance dispersal events, making the colonization of new habitats more likely.

Acknowledgements

We thank F. González for helpful comments on the manuscript and statistical advice. M. Bañuelos made numerous suggestions that improve the manuscript. Comments and suggestions by the editor, J. Kollmann, and three anonymous referees are also acknowledged. A. Valdés helped during the lab work. We acknowledge a PFPU (MEC) grant to I. Martínez, a contract from the “Ramón y Cajal” programme (MCYT, Fondo Social Europeo) to D. García, and support from project CGL2004-2936 (MEC).

Literature cited

- Alcántara, J. M., P. J. Rey, F. Valera & A. M. Sánchez-Lafuente, 2000. Factors shaping the seedfall pattern of a bird-dispersed plant. *Ecology*, 11: 1937–1950.
- Barnea, A., J. B. Harborne & C. Pannell, 1993. What part of fleshy fruits contain secondary compounds toxic to birds and why? *Biochemical Systematics and Ecology*, 21: 421–429.
- Chavez-Ramirez, F. & R. D. Slack, 1994. Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe juniper. *Oikos*, 71: 40–46.
- Clark, C. J., J. R. Poulsen, E. F. Connor & V. T. Parker, 2004. Fruiting trees as dispersal foci in a semi-deciduous tropical forest. *Oecologia*, 139: 66–75.
- Clark, C. J., J. R. Poulsen, B. M. Bolker, E. F. Connor & V. T. Parker, 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology*, 86: 2684–2694.
- Clark, J. S., C. Fastie, G. Hurtt, S. T. Jackson, C. Johnson, G. A. King, M. Lewis, J. Lynch, S. Pacala, C. Prentice, E. W. Schupp, T. Webb III & P. Wyckoff, 1998. Reid’s Paradox of rapid plant migration. *BioScience*, 48: 13–24.
- Cramp, S., (ed.), 1988. *The Birds of the Western Palearctic*, Vol. V. Oxford University Press, Oxford.

- Fuentes, M., J. M. Guitián, P. Guitián, T. Bermejo, A. Larrinaga, P. Amézquita & S. Bongiorno, 2001. Small-scale spatial variation in the interactions between *Prunus mahaleb* and fruit-eating birds. *Plant Ecology*, 157: 69–75.
- García, D., I. Martínez & J. R. Obeso, 2007. Seed transfer among bird-dispersed trees and its consequences for post-dispersal seed fate. *Basic and Applied Ecology*, 8: 533–543.
- García, D., J. R. Obeso & I. Martínez, 2005a. Rodent seed predation promotes differential seedling recruitment among bird-dispersed trees in temperate secondary forests. *Oecologia*, 144: 435–446.
- García, D., J. R. Obeso & I. Martínez, 2005b. Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: Does scale matter? *Journal of Ecology*, 93: 693–700.
- Gervais, J. A., B. R. Noon & M. F. Willson, 1999. Avian selection of the color-dimorphic fruits of salmonberry, *Rubus spectabilis*: A field experiment. *Oikos*, 84: 77–86.
- Gómez, J. M., 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography*, 26: 573–584.
- Gotelli, N. J. & G. R. Graves, 1996. *Null Models in Ecology*. Smithsonian Institution Press, Washington, DC.
- Guitián, J. & T. Bermejo, 2006. Dynamics of plant–frugivore interactions: A long term perspective on holly–redwing relationships in northern Spain. *Acta Oecologica*, 29: 97–103.
- Guitián, J. M., P. Guitián, I. Munilla, J. Guitián, T. Bermejo, A. R. Larrinaga, L. Navarro & B. López, 2000. Zorzales, Espinos y Serbales: Un estudio sobre el consumo de frutos silvestres de las aves migratorias en la costa occidental europea. Universidad de Santiago de Compostela, Santiago de Compostela.
- Herrera, C. M., 1984. A study of avian frugivores, bird-dispersed plants, and their interactions in Mediterranean scrublands. *Ecological Monographs*, 54: 1–23.
- Herrera, C. M., 2002. Seed dispersal by vertebrates. Pages 185–208 in C. M. Herrera & O. Pellmyr (eds.). *Plant–Animal Interactions: An Evolutionary Approach*. Blackwell Publishing, Oxford.
- Holbrook, K. M. & T. B. Smith, 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia*, 125: 249–257.
- Hoppes, W. G., 1987. Pre- and post-foraging movements of frugivorous birds in an eastern deciduous forest woodland, USA. *Oikos*, 49: 281–290.
- Hulme, P. & C. W. Benkman, 2002. Granivory. Pages 133–154 in C. M. Herrera & O. Pellmyr (eds.). *Plant–Animal Interactions: An Evolutionary Approach*, Blackwell Publishing, Oxford.
- Izhaki, I., P. B. Walton & U. N. Safriel, 1991. Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *Journal of Ecology*, 79: 575–590.
- Jordano, P., 1987. Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. *American Naturalist*, 129: 657–677.
- Jordano, P. & E. W. Schupp, 2000. Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, 70: 591–615.
- Jordano, P., C. García, J. A. Godoy & J. L. García-Castaño, 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the USA*, 104: 3278–3282.
- Lawlor, L. R., 1980a. Structure and stability in natural and randomly constructed competitive communities. *American Naturalist*, 116: 394–409.
- Lawlor, L. R. 1980b. Overlap, similarity, and competition coefficients. *Ecology*, 61: 245–251.
- Levin, S. A., H. C. Muller-Landau, R. Nathan & J. Chave, 2003. The ecology and evolution of seed dispersal: A theoretical perspective. *Annual Review of Ecology, Evolution and Systematics*, 34: 535–604.
- Levine, J. M. & D. J. Murrell, 2003. The community-level consequences of seed dispersal patterns. *Annual Review of Ecology Evolution and Systematics*, 34: 549–574.
- Loiselle, B. A., 1990. Seeds in droppings of tropical fruit-eating birds: Importance of considering seed composition. *Oecologia*, 82: 494–500.
- Loiselle, B. A. & J. G. Blake, 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. *Ecology*, 80: 330–336.
- Martínez, I., D. García & J. R. Obeso, 2007. Allometric allocation in fruit and seed packaging conditions the conflict among selective pressures on seed size. *Evolutionary Ecology*, 21: 517–533.
- McCullagh, P., 1983. Quasi-likelihood functions. *Annals of Statistics*, 11: 59–67.
- Murray, K. G., 1988. Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs*, 58: 271–298.
- Nathan, R. & H. C. Muller-Landau, 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15: 278–285.
- Obeso, J. R., 1998. Patterns of variation in *Ilex aquifolium* fruit traits related to fruit consumption by birds and seed predation by rodents. *Écoscience*, 5: 463–469.
- Potthoff, M., K. Johst, J. Gutt & C. Wissel, 2006. Clumped dispersal and species coexistence. *Ecological Modelling*, 198: 247–254.
- Poulsen, J. R., C. J. Clark, E. F. Connor & T. B. Smith, 2002. Differential resource use by primates and hornbills: Implications for seed dispersal. *Ecology*, 83: 228–240.
- Ricklefs, R. E. & M. Lau, 1980. Bias and dispersion of overlap indices: Results of some Monte Carlo simulations. *Ecology*, 61: 1019–1024.
- Russo, S. E., S. Portnoy & C. K. Augspurger, 2006. Incorporating animal behavior into seed dispersal models: Implications for seed shadows. *Ecology*, 87: 3160–3174.
- Sallabanks, R., 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology*, 74: 1326–1336.
- Santos, T., 1982. Migración e invernada de zorzales y mirlos (género *Turdus*) en la Península Ibérica. Ed. Univ. Complutense, Madrid.
- SAS Institute, 2004. *SAS/STAT User's Guide, Version 9.1*. SAS Institute, Cary, North Carolina.
- Schoener, T. W., 1974. Some methods for calculating competition coefficients from resource utilization spectra. *American Naturalist*, 108: 332–340.
- Schupp, E. W., 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, 107/108: 15–29.
- Schupp, E. W., T. Milleron & S. E. Russo, 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. Pages 19–33 in D. J. Levey, W. R. Silva & M. Galetti (eds.). *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford.
- Snow, B. & D. Snow, 1988. *Birds and Berries*. T and AD Poyser, Calton.

- Spiegel, O. & R. Nathan, 2007. Incorporating dispersal distance into the disperser effectiveness framework: Frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, 10: 718–728.
- Thomas, P. A. & A. Polwart, 2003. *Taxus baccata* L. *Journal of Ecology*, 91: 489–524.
- Tutin, T. G., V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters & D. A. Webb, 1964–1980. *Flora Europaea*, Volumes 1–5. Cambridge University Press, Cambridge.
- Wang, C. W. & T. B. Smith, 2002. Closing the seed dispersal loop. *Trends in Ecology & Evolution*, 17: 379–385.
- Westcott, D. A. & D. L. Graham, 2000. Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia*, 122: 249–259.
- Westcott, D. A., J. Bentrupperbäumer, M. G. Bradford & A. McKeown, 2005. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, 146: 57–67.
- Zar, J. H., 1996. *Biostatistical Analysis*. 3rd Edition. Prentice Hall, Upper Saddle River, New Jersey.