Basic and Applied Ecology **8** (2007) 533–543

Basic and Applied Ecology

www.elsevier.de/baae

GfÖ Ecological Society of Germany, Austria and Switzerland

Seed transfer among bird-dispersed trees and its consequences for post-dispersal seed fate

Daniel García[*], **Isabel Martínez**, **José Ramón Obeso**

Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, 33071 Oviedo, Spain

Received 14 February 2006; received in revised form 2 November 2006; accepted 10 November 2006

KEYWORDS
Background seed density;
Contagious seed dispersal;
Density-dependent mortality;
NW Spain;
Post-dispersal seed predation

Summary

We investigated seed transfer, i.e. the seed movement away from a source canopy to areas beneath heterospecific canopies, among the ornithochorous tree species *Taxus baccata*, *Ilex aquifolium* and *Crataegus monogyna* in temperate secondary forests in NW Spain, by analysing the composition of multispecific seed rain beneath the canopy of each species, at four sites and for 2 years. To evaluate the consequences on seed fate, we estimated predation by rodents in manipulated seed rains, representing variable levels of relative proportion and total density for combinations of a preferred species paired with a less-preferred species. Seed rain under *Taxus* canopies was dominated by *Taxus* seeds, which occurred in low proportion under heterospecific canopies. *Ilex* seeds dominated the areas under *Ilex* but accounted for 20–40% of seeds under heterospecific trees. *Crataegus* seeds were not dominant in any of the microhabitats. The probability of being deposited beneath a heterospecific canopy was much higher for *Ilex* and *Crataegus* than for *Taxus*. The effects of seed rain composition on post-dispersal seed predation were species-specific. *Taxus* seeds experienced lower predation when occurring in a background of seeds dominated by heterospecific, *Ilex* or *Crataegus*, seeds. *Crataegus* seeds escaped predation more successfully in high-density patches, independently of seed clump composition. Predation on *Ilex* seeds was independent to both the density and the composition of seed clump. Seed transfer among heterospecific tree species may contribute to shape the template of propagule abundances from which forest will develop, by generating seed combinations favourable to escape from predation.

Zusammenfassung

Wir untersuchten den Samentransfer, d. h. die Samenbewegung von einer Quellbaumkrone in die Bereiche heterospezifischer Baumkronen, bei den ornithochoren Baumarten *Taxus baccata*, *Ilex aquifolium* und *Crataegus monogyna* in

---

[*] Corresponding author. Tel.: +34 985 104788; fax: +34 985 104777.
E-mail address: danielgarcia@uniovi.es (D. García).

1439-1791/$ - see front matter © 2006 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.
doi:10.1016/j.baae.2006.11.002

gemäßigten Wäldern des südlichen Spaniens indem wir die Zusammensetzung des vielartigen Samenregens unter den Baumkronen einer jeden Art in vier Probeflächen über zwei Jahre hinweg analysierten. Um die Konsequenzen des Samenschicksals zu evaluieren, schätzten wir die Samenprädation durch Nagetiere in manipulierten Samenregen ab, die variable Stufen der relativen Anteile und Gesamtdichten von Kombinationen aus den bevorzugten Arten gepaart mit den weniger bevorzugten Arten repräsentierten. Der Samenregen unter den *Taxus* Kronen wurde von *Taxus* Samen dominiert, die in geringen Anteilen unter den heterospezifischen Baumkronen auftraten. *Ilex* Samen dominierten die Areale unter *Ilex*, waren aber auch für 20–40% des Samenregens unter heterospezifischen Bäumen verantwortlich. *Crataegus* Samen waren in keinem der Mikrohabitate dominant. Die Wahrscheinlichkeit unter einer heterospezifischen Baumkrone deponiert zu werden war für *Ilex* und *Crataegus* wesentlich höher als für *Taxus*. Die Auswirkungen der Samenregenzusammensetzung auf die post-dispersale Samenprädation waren artspezifisch. *Taxus* Samen erfuhren eine geringere Prädation, wenn sie vor einem Hintergrund von Samen vorkamen, der von heterospezifischen *Ilex* oder *Crataegus* Samen dominiert wurde. *Crataegus* Samen entkamen der Prädation erfolgreicher in Bereichen hoher Samendichte, unabhängig von der Zusammensetzung der Samenansammlung. Die Prädation der *Ilex* Samen war sowohl von der Dichte als auch der Zusammensetzung der Samenansammlungen unabhängig. Der Samentransfer zwischen heterospezifischen Baumarten könnte dazu beitragen, das Muster für die Abundanzen der Nachkommen zu formen, aus der sich Wälder entwickeln, indem er Samenkombinationen generiert, die günstig dafür sind der Prädation zu entkommen.

Introduction

Seed rain, the spatial template of seed distribution generated after dispersal, plays a pivotal role in the spatial dynamics of plant populations, with potential community consequences (Levine & Murrell, 2003; Nathan & Müller-Landau, 2000; Schupp & Fuentes, 1995). This role is mainly associated with the recruitment advantage derived from seeds being deposited far from the area beneath the parent plant, where high propagule aggregation promotes disproportionate mortality by density-dependent pathogens and predators, kin competition and competition by the mother plant (Janzen, 1970; Loiselle, 1990; Terborgh, Pitman, Silman, Schichter, & Nùñez, 2002). Recent research has, however, brought into question whether seed destination after dispersal may be so different from the origin, because high-density seed clumps may occur even far from conspecific – parent or non-parent – plants (Romo, Tuomisto, & Loiselle, 2004; Russo & Augspurger, 2004; Schupp, Milleron, & Russo, 2002). In fact, in communities dominated by vertebrate-dispersed plants, seed rain is an array of overlapping multispecific seed shadows that result from dispersal by frugivores foraging across the canopies of different species (Clark, Poulsen, Connor, & Parker, 2004; Kwit, Levey, & Greenberg, 2004; Schupp et al., 2002).

Seed transfer among coexisting plant species, that is, the seed movement away from a source canopy to areas beneath heterospecific canopies that generates multispecific seed rains, may affect seed fate by several ways. Firstly, the occurrence in the same dispersal patch of different seeds species that share a common seed predator may result in apparent, pre-emptive competition among seed species for the occupancy of an establishment microsite (García, Obeso, & Martínez, 2005a; Hulme, 1996). Secondly, seed transfer can lead to a change of scenario for the density-dependent performance of seed and seedling mortality factors by, for example, further exaggerating a clumped pattern of conspecific seeds fallen beneath the parent and leading to stronger attraction for predators (Kwit et al., 2004; Loiselle, 1990; Russo & Augspurger, 2004; Schupp et al., 2002). This effect is far from straightforward, since seeds of different plant species usually differ in their relative susceptibility to predators, and seed transfer may also introduce favourite seeds in clumps of less preferred seeds. Then, the fate of transferred seeds will depend on the relative background densities of both individual species rather than on the overall seed density (Schupp et al., 2002). In this sense, it is known that the seeds of some species may experience increased attack by predators when occurring in heterospecific clumps (Kwit et al., 2004), whereas other seeds may increase their survival when surrounded by other species (Hoshizaki & Hulme, 2002). The second case may even be interpreted as a sort of associational resistance (*sensu* Wahl & Hay, 1995) in which a given seed species benefits, in terms of survival, from the spatial association with other species. Ultimately, seed benefit or damage will depend on the foraging behaviour of predators in terms of frequency-dependent response, with pro-apostatic selection resulting in increased survival for seed species in low-frequency contexts whereas anti-apostatic selection leading to increased mortality for the rarest species (Celis-Díez & Bustamante, 2005; Celis-Díez, Bustamante, & Vásquez, 2004; Greenwood, 1985; Hulme & Hunt, 1999).

Despite the widespread occurrence of multispecific seed rain, and the accepted importance that it may have as a template for plant communities (Levine & Murrell, 2003; Schupp et al., 2002), few attempts have been made to analyse the consequences of the patterns of seed transfer in terms of seed survival (but see Kwit et al., 2004). In fact, we are not aware of any study in which seed transfer has been investigated in comparative, inter-specific approaches that analyse the effects of modifying both the absolute and the relative densities of seeds for predators. In the present study, we assessed whether different coexisting tree species contribute equally to the generation of multispecific seed rain, testing experimentally the consequences of seed transfer in terms of post-dispersal seed predation. Our study system, the secondary-growth forest of the Cantabrian range, is optimal for evaluating seed transfer effects because it is dominated by fleshy-fruited trees with overlapping fruiting phenologies that share seed dispersers. Moreover, post-dispersal seed predation is a major cause of recruitment losses for these trees (García et al., 2005a). Specifically, we sought to answer the following questions: (1) Do tree species differ in the proportion of heterospecific seeds accumulated beneath their canopies? (2) Do seed species differ in the likelihood of being dispersed to a heterospecific canopy? (3) Does predation vary depending on the absolute and relative quantity of seeds comprising the multispecific seed context?

Material and methods

Study sites and species

This study was carried out in secondary-growth forests of the Cantabrian mountain range (Asturias, NW Spain), between 2001 and 2003. These forests are dominated by fleshy-fruited trees (holly, *Ilex aquifolium* L., hawthorn, *Crataegus monogyna* L., yew, *Taxus baccata* L., and rowans, *Sorbus* spp.) together with hazel, *Corylus avellana* L. They inhabit isolated stands in a pasture matrix or fringe patches between pastures and mature deciduous forests (beech, *Fagus sylvatica* L). Sampling was set up at four different sites, Aramo, Peña Mayor, Sueve and Teixeu, located on northern-oriented slopes at altitudes of 680–1400 m a.s.l. (see García et al. (2005a) for a comprehensive description).

We focused on three fleshy-fruited species: *T. baccata* (Taxaceae; hereafter *Taxus*), *I. aquifolium* (Aquifoliaceae; hereafter *Ilex*) and *C. monogyna* (Rosaceae; hereafter *Crataegus*). Together these species account for a high degree of canopy cover in all study sites (25–60%). *Ilex* was the most abundant species in terms of tree density, followed by *Crataegus* and *Taxus* (García et al., 2005a). All species bear red fruits, and their fruiting phenologies overlap partially (August–November for *Taxus*, October–January for *Ilex*, September–December for *Crataegus*). The average crop size per plants is ca. 4400, 2600 and 2300 fruits/year in *Taxus*, *Ilex* and *Crataegus*, respectively (authors' unpublished data). The one-seeded *Taxus* arils are 8–12 mm in diameter, the 3–4 seeded *Ilex* drupes are 7–10 mm and the one-seeded *Crataegus* drupes are 7–12 mm. The mean seed dry weights are 66.3, 28.2, and 87.1 mg, respectively, for *Taxus*, *Ilex* and *Crataegus*. The fruits of these species are mainly consumed by a common guild of avian frugivores composed of resident (*Turdus merula*, *Turdus philomelos* and *Turdus viscivorus*) and migrant thrushes (*T. iliacus*, *T. pilaris*). These birds pick the fruits directly from branches, swallowing them whole and regurgitating or defecating in their droppings the intact seeds. Foxes *Vulpes vulpes* and badgers *Meles meles* may also occasionally consume fruits, but their relative contribution to the total seed rain is very low because of their low densities (authors' unpublished data). After dispersal, the seeds of these species experience selective predation, in the order *Taxus* > *Ilex* > *Crataegus*, by the woodmouse *Apodemus sylvaticus* and the yellow-necked mouse *Apodemus flavicollis*, which are almost the only predators (García et al., 2005a). The predation preference ranking is the inverse of that of seed protection against predators, measured as the mass of woody coat per mass unit of the edible fraction (García et al., 2005a).

Multispecific seed rain composition as a surrogate of seed transfer

Previous work had shown that 90.8% of seeds of these fruit-bearing species are deposited beneath the canopies of these species, and few seeds are dispersed in open gaps or stony meadows (1.1%), or areas beneath non-fleshy-fruited species such as *C. avellana* and *F. sylvatica* (8.1%, authors' unpubl. data; García, Obeso, & Martínez, 2005b). Besides, the densities of seeds dispersed beneath male individuals (*Taxus* and *Ilex* are dioecious) had been found to be similar to those deposited under female trees because male trees are used by frugivorous birds for shelter (both species are perennial; García et al., 2005b; Obeso & Fernández-Calvo, 2002). Therefore, we restricted our seed rain study to areas beneath fruiting canopies of the target species. At each site, we chose arbitrarily ten focal fruiting trees of each species, ⩾10 cm DBH; ⩾5 m apart and with no or very low canopy overlap among species, and established a sampling station extending over an area of 1–2 m^2 beneath each tree. We monitored the seed rain in all sampling stations during the dispersal season (late September to early January) in 2001–2002 and 2002–2003, by establishing one permanent $50 \times 50\,cm^2$ quadrat per station, from which we collected all fallen fruits and regurgitated or dropped seeds found in successive fortnightly surveys. The high frequency of sampling and the lower predation rate during the fall (the abundance of dispersed seeds peaks usually in November, when predation is still low) made the possible underestimation of seed rain due to undetected seed removal from sampled surfaces negligible (see García et al. (2005a, b), for a validation of this methodology using seed traps). In any case, those fruits or seeds showing signs of predation (open husks, teeth marks) were also counted as a part of the pool of dispersed seeds (see also Alcántara, Rey, Valera, & Sánchez-Lafuente, 2000; for a similar procedure). We counted the cumulative number of seeds of each target species deposited per sampling station.

Seed transfer among species was inferred from two complementary approaches based on the co-occurrence of seeds of the different species in the multispecific seed rain. Firstly, we calculated the *proportion of seeds in the seed rain*, as the proportion of seeds of a target species relative to the total number of seeds of all species found. We calculated this proportion for each sampling station and every target seed species (*Taxus*, *Ilex*, *Crataegus*; $n = 30$ sampling stations per site per year). Secondly, for each seed species, site and year, we calculated the *probability of being dispersed beneath a heterospecific canopy,* by relating the number of seeds dispersed beneath the canopy of heterospecific trees to the total number of seeds of the target species found in all sampling stations. In both proportions, the total number of seeds included seeds dispersed by birds and seeds within fallen fruits, making our estimation of biotic dispersal among heterospecific canopies more conservative.

In order to evaluate the spatial configuration of the fruiting trees of the different species within each site, we measured the distance from each sampling station to the nearest fruiting heterospecific canopy of the two corresponding species. We inferred spatial clumping within- and among tree species by comparing the distance to the nearest heterospecific fruiting canopy among combinations of paired species (from *Taxus* to *Ilex*, from *Taxus* to *Crataegus*, from *Ilex* to *Crataegus*).

Predation on experimental multispecific seed rain

In late January 2004, we set up a field experiment to evaluate seed survival of several target species in different contexts of mimicked multispecific seed rain. We paired seed species considering a preferred species (i.e. *Taxus*) in relation to a less-preferred species (i.e. *Ilex, Crataegus*), and we established four combinations of seeds for paired species, representing crossed treatments of relative proportion (low, high; the low treatment for a given species representing the high treatment for the paired species) and total seed density (low, high). Thus, considering the pair *Taxus–Ilex*, the treatments were generated as follows: low total density (10 seeds), (i) 2 *Taxus*+8 *Ilex* seeds (low proportion of *Taxus*, high proportion of *Ilex*), (ii) 8 *Taxus*+2 *Ilex* seeds (high proportion of *Taxus*, low proportion of *Ilex*); high total density (50 seeds), (iii) 10 *Taxus*+40 *Ilex* seeds (low proportion of *Taxus*, high proportion of *Ilex*), (iv) 40 *Taxus*+10 *Ilex* seeds (high proportion of *Taxus*, low proportion of *Ilex*). Both proportions and densities established in the experiment were within the range of seed densities found in the field (García et al., 2005a, b). The same numbers of seeds and proportions were used for the *Taxus–Crataegus* combination. Seeds were offered to predators in the field in seed depots consisting of the seeds of a given treatment glued to a $20 \times 20\,cm^2$, 1.5-mm pore plastic square mesh nailed to the ground. We used seeds found on the ground in birds faeces collected during the previous autumn in the study sites. We used a low odour, rainproof thermoplastic glue and fixed the seeds on to the mesh by forming a regular grid in which the two species were alternated at random. Fifteen depots (replicates) of each treatment were placed in each of two study sites (Peña Mayor and Teixeu). Putting seed depots in the field involved a variable local seed background for each experimental replicate. To reduce this variability, each seed depot was placed in the centre of a $50 \times 50\,\mathrm{cm}^2$ area previously cleared of all seeds occurring in the natural seed rain, in order to homogenize seed availability in the immediate surroundings. Moreover, to match as closely as possible the composition of experimental patches and that of the surrounding natural seed rain, treatments representing a high proportion of *Taxus* (ii, iv above) were placed beneath the canopy of 15 different fruiting *Taxus*, and those representing a high proportion of *Ilex* (i, iii above) were placed beneath the canopy of 15 different fruiting *Ilex*. Trees were $\geqslant 5\,\mathrm{m}$ apart, and many of them had been used as seed rain sampling stations in previous years. An analogous design was used for the *Taxus*–*Crataegus* combination.

Depots were monitored after two and four weeks and removed after the second monitoring. Seeds were glued firmly onto the plastic mesh, so that seed disappearance due to wind and rain could be considered negligible. We thus considered that a seed had been consumed if (1) it was missing from the plastic mesh; or (2) it was still on the mesh but gnawed and empty. The predation rate was calculated, for each species, as the proportion of consumed seeds relative to the initial number of seeds of each species in the depot.

Statistical analysis

We tested the effects of canopy tree species (fixed factor) together with those of site (random factor, nested within canopy species) and year (random factor, nested within site and canopy species) on the proportion of seeds of the different seed species in the total seed rain with generalized linear mixed models (GLMM) considering binomial distributions in the dependent variables and logit link functions (Proc GLIMMIX, SAS Institute, 2004). The probability of being dispersed beneath a heterospecific canopy was compared among seed species, sites and years by means of a multivariate contingency table (generalized logits model) that considered seed destination as a dichotomous response variable (conspecific vs. heterospecific canopy), fitted to a binomial distribution with logit link function (Proc CATMOD, SAS Institute, 2004).

We compared, in each study site, the nearest distance to the heterospecific fruiting canopy among combinations of paired species (*Taxus*–*Ilex*, *Taxus*–*Crataegus*, *Ilex*–*Crataegus*) by one-way ANOVA with type III sum of squares (due to the unbalanced nature of the data). Distance was log-transformed for normality and homoscedasticity requirements.

The experimental results were analysed separately for each tree species and site, by means of generalized linear models using the proportion of the target species and the total density as main fixed factors and the predation rate of the target species as response variables (binomial distributions, logit link function, Proc GENMOD, SAS Institute (2004)). The model evaluating predation on *Taxus* seeds incorporated an additional source of variation (the context species, fixed factor) representing the identity of the heterospecific background generated by either *Ilex* or *Crataegus* seeds. Thus, it considered all experimental replicates of both paired combinations.

Results

Seed transfer among species

Taxus seeds dominated the seed rain beneath *Taxus* canopies. At least 20% of seed rain under *Ilex* and *Crataegus* canopies corresponded also to *Taxus* seeds at Sueve, but this percentage was lower for the remaining sites (Fig. 1). The respective proportions of *Taxus* and *Ilex* seeds in the seed rain differed significantly between tree canopies, but this effect was affected by site (Table 1). More than 75% of seed rain beneath *Ilex* canopies belonged to *Ilex* seeds. The seeds of this species also accounted for more than 30% of seed rain beneath *Crataegus* and, depending on the site, beneath *Taxus* canopies (Fig. 1). *Crataegus* seeds always accounted for a low proportion of the seed rain beneath heterospecific canopies. Even beneath conspecific canopy, this species seldom exceeded 50% of the seeds (Fig. 1). The proportion of *Crataegus* seeds in the seed rain differed significantly between tree canopies, sites and years (Table 1). Canopy species accounted for most of the variation in the relative proportion of seeds of each species occurring in the seed rain ($\geqslant 34.2\%$ of total deviance for all species).

Species also differed in terms of the probability of being dispersed beneath a heterospecific canopy (generalized logits model: species effect, Wald $\chi^2 = 748.71$, $P \leqslant 0.0001$, d.f. $= 2$). The percentage of *Ilex* seeds dispersed beneath heterospecific canopies always exceeded 35% (except in Aramo in 2002–2003, Fig. 2). The respective percentages were significantly lower for *Crataegus*, especially, for *Taxus* (except in Aramo, Fig. 2). Site, year and all interactions had significant effects on this

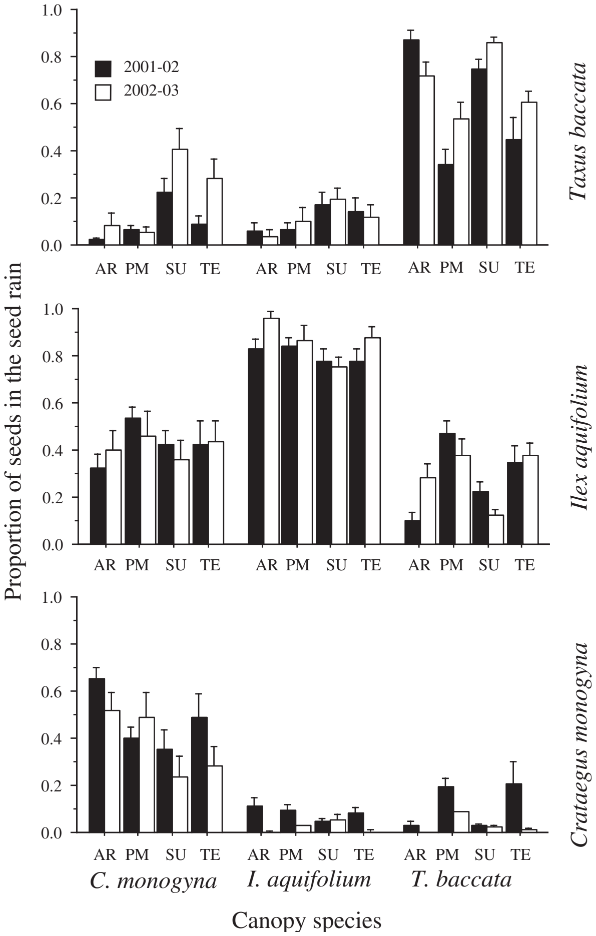

Figure 1. Proportion (mean+SE) of seeds of different target species in the seed rain found beneath different canopy species, in different sites and years (sites: AR, Aramo; PM, Peña Mayor; SU, Sueve; TE, Teixeu).

variable (generalized logits model: $507.22 \geqslant$ Wald $\chi^2 \geqslant 20.21$, $P \leqslant 0.0001$).

The average distance from each sampling station to the nearest heterospecific fruiting canopy was 10.9 m (±0.7SE), with no differences among combinations of paired species (*Taxus–Ilex*, *Taxus–Crataegus*, *Ilex–Crataegus*) in none of study sites (ANOVA: $F_{2,44} \leqslant 2.29$, $P \geqslant 0.11$, for all sites).

Predation on experimental multispecific seed rain

Taxus seeds were heavily consumed, independent of the total density of seeds in the experimental seed depot (Table 2, Fig. 3). However, the probability of predation decreased significantly when *Taxus* seeds were offered in a low proportion, for both total seed densities and at both sites (Table 2, Fig. 3). The probability of removal of *Taxus* seeds was also affected by the identity of the less-preferred background seed species in Peña Mayor site, being higher when surrounded by *Crataegus* than by *Ilex* (Table 2). No effect of proportion of the target species or density was detected for *Ilex* seeds (Table 2, Fig. 3). Rates of removal of *Crataegus* seeds were similar across the different proportion treatments (Table 2, Fig. 3). However, at least in the Teixeu site, the probability of removal significantly decreased in high-density seed depots, independent of the proportion of occurrence (Table 2, Fig. 3).

Discussion

Inter-specific differences in seed transfer

The present study reveals that the patterns of seed transfer from fruiting sources to areas below different species are strongly influenced by the identity of the source. There were large differences in terms of relative importance of conspecific vs. heterospecific seed rain deposited beneath each target species, as well as in terms of destination of the seeds of each particular species. These specific seed transfer patterns were consistent in time but not in space, except in the case of *Crataegus*, in which there was a significant time effect too. Probably, this spatio-temporal variability was due to differences among sites and years in the relative crop size, the density of fruiting individuals and the disperser assemblage composition (Clark et al., 2004; Jordano & Schupp, 2000).

The spatial distribution of fruiting trees of the different species may have strong effects on the composition of the seed rain accumulated beneath a particular canopy (Schupp et al., 2002). Species whose fruiting trees are strongly clumped in space should show shorter dispersal distances (e.g. Serio-Silva & Rico-Gray, 2002) and hence seed rains more dominated by their own seeds than those of species whose fruiting individuals are sparser in space and intermingled with other species. Judging from our data on distances among heterospecific canopies, the different tree species did not show clumped distributions but were intermingled in all study sites, despite differences in total tree density among species (abundances ranked *Ilex* > *Crataegus* ⩾ *Taxus* in all sites, García et al. (2005a)). Thus, we cannot consider the differences in spatial configuration among species a major cause of differences in seed transfer patterns.

Seed transfer patterns may also be interpreted in the light of differences in absolute numbers of

Table 1. Generalized linear models evaluating the effects of tree canopy species (fixed factor) together with those of site (random, nested within canopy) and year (random, nested within site and canopy) on the proportion of seeds of the different target species in the total seed rain

Fixed factor	d.f.	F	P
Target seed species: *Taxus baccata*			
Canopy species	2, 5.6	17.91	**0.004**
Random factors	Change in deviance (χ^2; d.f. $=1$)		
Site [tree canopy species]	18.10		$\leqslant$**0.0001**
Year [site [tree canopy species]]	1.69		0.194
Target species: *Ilex aquifolium*			
Canopy species	2, 5.7	45.68	**0.0003**
Random factors	Change in deviance (χ^2; d.f. $=1$)		
Site [tree canopy species]	8.11		**0.004**
Year [site [tree canopy species]]	1.55		0.213
Target species: *Crataegus monogyna*			
Canopy species	2, 7.08	24.11	**0.0007**
Random factors	Change in deviance (χ^2; d.f. $=1$)		
Site [tree canopy species]	23.91		$\leqslant$**0.0001**
Year [site [tree canopy species]]	19.48		$\leqslant$**0.0001**

All models assumed a binomial error structure in the response variable (logit link function). Significance of random terms was assessed by first determining the deviance of the full model with residual maximum likelihood and next fitting the model without the term of interest. The change in deviance after omitting this term indicates its contribution to model fit and follows a χ^2 distribution with one degree of freedom. Significance of fixed term was tested with F-ratio with inclusion of all random terms and a Satterthwaite approximation of the degrees of freedom. Table entries give degrees of freedom, F-values for fixed factor, and change in deviance for random factors. Significant P values appear in bold face.

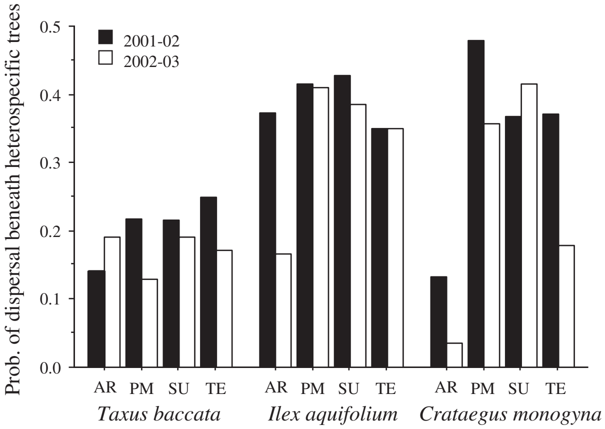

Figure 2. Proportion of seeds (*Taxus*, *Ilex*, and *Crataegus*) collected beneath the canopy of the respective heterospecific trees, in 2 years (see Fig. 1 for site abbreviations).

seeds produced by the different species (Izhaki, Walton, & Safriel, 1991). Considering together adult abundance and individual crop size, *Ilex* and *Taxus* would show rather similar fruit crop sizes at the local scale, but the larger number of seeds per fruit in *Ilex* determines higher seed production and more seeds dispersed per fruit eaten by frugivores. This led to larger quantities of *Ilex* seeds dispersed, which clearly favoured dominance in seed rain (García et al., 2005b). On the other hand, the degree of overlapping of the specific fruiting phenologies may also be involved in inter-specific patterns of seed transfer. *Taxus* ripens early in the autumn, when few other species are available, and this may encourage frugivores to stay longer and move preferentially among fruiting *Taxus*, thereby generating seed rains mainly under yew. A similar situation would occur late in the winter, when *Ilex* fruits are much more abundant than those of *Taxus* and *Crataegus*. Finally, differences in the composition of the disperser assemblage, and the treatment given to the fruit by different frugivores, could underlie differences in seed transfer, as shown for other systems (Clark et al., 2004; Loiselle, 1990; Murray, 1988). In our case, *T. philomelos* and *T. viscivorus*, feeding alone or in small flocks, are the main consumers of *Taxus* arils (unpublished data). These thrushes should favour high clumping under maternal plants due to short seed processing time and long permanence in the perch (see also Murray, 1988; Pratt & Stiles, 1983). *Ilex* was mainly consumed and dispersed by *T. iliacus*, a late-season migrant that forms large flocks which move constantly among fruiting trees and between forest patches (Obeso &

Table 2. Generalized linear models evaluating the significance of the proportion of the target species and the total seed density for the probability of seed removal, in different target species and sites, in the experiments simulating multispecific seed rain

Source	Peña Mayor				Teixeu			
	d.f.	Deviance	*F*	*P*	d.f.	Deviance	*F*	*P*
Target species: *Taxus baccata*								
Proportion of target species	1	3.40	18.56	⩽**0.0001**	1	1.70	5.45	**0.021**
Total density	1	0.20	1.09	0.298	1	0.10	0.32	0.573
Context species	1	2.40	13.11	**0.0004**	1	1.10	3.52	0.063
Proportion × total density	1	0.01	0.05	0.823	1	0.60	1.92	0.169
Proportion × context species	1	0.30	1.64	0.203	1	0.02	0.06	0.807
Total density × context species	1	0.20	1.09	0.299	1	0.90	2.88	0.093
Proportion × total density × context species	1	0.70	3.82	0.053	1	0.70	2.24	0.137
Error	112	20.51			108	33.72		
Target species: *Ilex aquifolium*								
Proportion of target species	1	1.10	1.77	0.189	1	0.04	0.06	0.809
Total density	1	0.60	0.10	0.331	1	0.61	0.90	0.347
Proportion × total density	1	0.06	0.09	0.765	1	0.05	0.07	0.787
Error	56	35.09			54	36.70		
Target species: *Crataegus monogyna*								
Proportion of target species	1	0.23	0.29	0.594	1	0.02	0.04	0.848
Total density	1	0.98	1.25	0.269	1	6.96	13.72	**0.0005**
Proportion × total density	1	0.43	0.55	0.461	1	0.32	0.62	0.434
Error	56	43.94			54	27.38		

The models for *Taxus baccata* include the effect of the identity of the context species (*Ilex aquifolium* and *Crataegus monogyna*). All models assumed the response variable to have a binomial error. Significant *P* values appear in bold face.

Fernández-Calvo, 2002), a fact probably contributing to the widespread dispersal of *Ilex* seeds.

Effects of multispecific seed rain on seed survival

Experiments evidenced that the combination of seeds of different species at variable densities and proportions had significant effects on seed fate. Firstly, *Taxus* seeds were less attacked by rodents when occurring in low proportions far from conspecific plants and in a background dominated by heterospecific seeds. This pattern was, at least in one of study sites, independent of the context species, whether *Ilex* or *Crataegus*, thereby indicating that proportion effects were independent of the microhabitat. The preferred seed species, *Taxus*, therefore gained a survival advantage when dispersed to a background dominated by less-preferred seeds, probably because the seeds were less conspicuous to rodents when surrounded by many *Ilex* or *Crataegus* seeds. This evidence of pro-apostatic selection contrasts with that of previous studies testing frequency-dependent predation for combinations of seeds of different profitability (Celis-Díez et al., 2004; Hulme & Hunt, 1999; but see Hoshizaki & Hulme, 2002). In our study, differences in profitability were probably strong enough to generate differences among species but not to avoid proportion effects. Secondly, our experimental data also confirm a negative density-dependent effect in *Crataegus*, the seeds of which escaped more from predators in high-density patches, independent of the composition of the seed clump (but see Hulme, 1997; for absence of a density effect in this species). This pattern was also independent of microhabitat structural features, occurring beneath both *Taxus* and *Crataegus* canopies. Predator satiation or reluctance to remain exposed for a long time (Janzen, 1971; Myster & Pickett, 1993; Romo et al., 2004) may

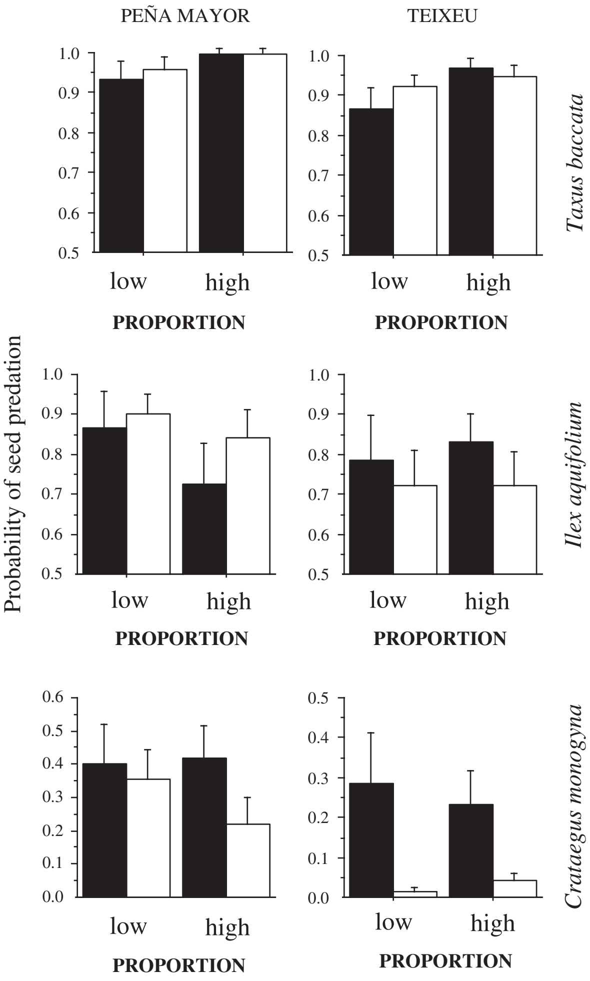

Figure 3. Probability (mean+SE) of seed predation for different target species (*Taxus*, *Ilex*, and *Crataegus*) in different contexts of mimicked multispecific seed rain and different sites. The contexts were generated by combining the seeds of the target species with seeds of a background species in four treatments considering two relative proportions of the target species (low, high) and two total seed densities (10 seeds: black bars, 50 seeds: white bars). *Taxus* target seeds were simultaneously and separately combined with *Ilex* and *Crataegus* background seeds – the results from both combinations are pooled together in the figure. *Ilex* and *Crataegus* target seeds were combined with *Taxus* background seeds.

explain the higher seed survival in high-density clumps dominated by *Crataegus*. Interestingly, a similar effect was found in high-density clumps dominated by the preferred species – high abundance of *Taxus* probably decreased the relatively low attractiveness of the scarce *Crataegus* seeds to an even greater extent. Nevertheless, this density effect varied among sites, and was probably affected by differences in rodent population size or even rodent predation risk (Romo et al., 2004). Unlike *Taxus* and *Crataegus*, no effect of proportion or density was detected for *Ilex* seeds. The effects of seed rain composition are therefore species dependent, as previously shown for density effects (Hulme, 1997; Myster & Pickett, 1993). The role of seed profitability in underpinning these interspecific differences, with highly profitable seeds tending to suffer proportion effects whereas less profitable seeds are prone to density effects, requires further study (see also Hulme & Borelli, 1999; for effects of size-related profitability on density-dependent predation).

Conclusions

Multi-specific seed rains are a common feature of forest systems dominated by vertebrate-dispersed trees, both in tropical (Clark et al., 2004; Schupp et al., 2002), Mediterranean (Izhaki et al., 1991), and temperate systems (Kollmann, 1995; this study). Nevertheless, the phenomenon of co-dispersal of suites of species and how it affects the dynamics of plant populations and communities is still poorly understood (Schupp et al., 2002). This study contributes to fill this gap, revealing that different seed transfer patterns are possible for trees with similar means of dispersal. Whereas in one species (*Taxus)* seed clumps were mostly associated with conspecific trees, in others (*Ilex*, *Crataegus*) seed patches occurred not only under their respective parent canopy, but also beneath heterospecific fruiting trees. More importantly, our data evidence that the composition of multispecific seed rains has post-dispersal consequences that are also species-specific. Aggregated seed dispersal probably determined stronger recruitment limitation in that highly preferred species with few seeds deposited under heterospecific canopies, i.e. in low proportion contexts where survival was enhanced. On the contrary, seed transfer decreased dispersal limitation of less preferred species because scattered deposition enabled some seeds to reach high-density patches that were more favourable for escaping predators. Given that multi-specific seed rains, by offering seed combinations that favour avoidance of post-dispersal predators, have the potential to shape the template of relative propagule abundances, we encourage for a deeper consideration of seed transfer among the mechanisms structuring forest communities, together with late-acting factors such as sapling and young tree competition.

Acknowledgements

We thank Olga Sáez for technical support and Christine Francis for checking the English of the manuscript. Comments by Charles Kwit, Pedro Jordano, Klaus Hövemeyer and two anonymous referees improved previous versions of the manuscript. Natacha P. Chacoff and Fernando González provided some statistical advice. We acknowledge a contract from Programme "Ramón y Cajal" (MCYT, Fondo Social Europeo) to D.G., a grant PFPU (MEC) to I.M., and the project CGL2004-2936/BOS (MEC) to D.G.

References

Alcántara, J. M., Rey, P. J., Valera, F., & Sánchez-Lafuente, A. M. (2000). Factors shaping the seedfall pattern of a bird-dispersed plant. *Ecology, 11*, 1937–1950.

Celis-Díez, J. L., & Bustamante, R. O. (2005). Frequency-dependent seed size selection on *Cryptocarya alba* (Mol.) Looser (Lauraceae): Testing the effect of background. *Biological Journal of the Linnean Society, 84*, 137–142.

Celis-Díez, J. L., Bustamante, R. O., & Vásquez, R. A. (2004). Assessing frequency-dependent seed size selection: A field experiment. *Biological Journal of the Linnean Society, 81*, 307–312.

Clark, C. J., Poulsen, J. R., Connor, E. F., & Parker, V. T. (2004). Fruiting trees as dispersal foci in a semi-deciduous tropical forest. *Oecologia*, *139*, 66–755.

García, D., Obeso, J. R., & Martínez, I. (2005a). Rodent seed predation promotes differential seedling recruitment among bird-dispersed trees in temperate secondary forests. *Oecologia*, *144*, 435–446.

García, D., Obeso, J. R., & Martínez, I. (2005b). Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: Does scale matter? *Journal of Ecology, 93*, 693–704.

Greenwood, J. J. D. (1985). Frequency-dependent selection by seed predators. *Oikos*, *44*, 195–210.

Hoshizaki, K., & Hulme, P. E. (2002). Mast seedling and predator-mediated indirect interactions in a forest community: Evidence from post-dispersal fate of rodent-generated caches. In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed dispersal and frugivory, evolution and conservation* (pp. 227–240). Wallingford: CAB International.

Hulme, P. E. (1996). Herbivory, plant regeneration, and species coexistence. *Journal of Ecology, 84*, 609–615.

Hulme, P. E. (1997). Postdispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. *Oecologia*, *111*, 91–98.

Hulme, P. E., & Borelli, T. (1999). Variability in post-dispersal seed predation in deciduous woodland: Relative importance of location, seed species, burial and density. *Plant Ecology, 145*, 149–156.

Hulme, P. E., & Hunt, M. K. (1999). Rodent post-dispersal seed predation in deciduous woodland: Predator response to absolute and relative abundance of prey. *Journal of Animal Ecology, 68*, 417–428.

Izhaki, I., Walton, P. B., & Safriel, U. N. (1991). Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *Journal of Ecology, 79*, 575–590.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, *104*, 501–528.

Janzen, D. H. (1971). Seed predation by animals. *Annual Review of Ecology and Systematics*, 2, 465–492.

Jordano, P., & Schupp, E. W. (2000). Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, *70*, 591–615.

Kollmann, J. (1995). Regeneration window for fleshy-fruited plants during scrub development on abandoned grassland. *Écoscience*, *2*, 213–222.

Kwit, C., Levey, D. J., & Greenberg, C. H. (2004). Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. *Oikos*, *107*, 303–308.

Levine, J. M., & Murrell, D. J. (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology 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.

Murray, K. G. (1988). Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs*, *58*, 271–298.

Myster, R. W., & Pickett, S. T. A. (1993). Effects of litter, distance, density and vegetation patch type on post-dispersal tree seed predation in old fields. *Oikos*, *66*, 381–388.

Nathan, R., & Müller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, *15*, 278–285.

Obeso, J. R., & Fernández-Calvo, I. (2002). Fruit removal, pyrene dispersal, post-dispersal predation and seedling establishment of a bird-dispersed tree. *Plant Ecology, 165*, 223–233.

Pratt, T. K., & Stiles, E. W. (1983). How long fruit-eating birds stay in the plants where they feed: Implications for seed dispersal. *The American Naturalist*, *122*, 797–805.

Romo, M., Tuomisto, H., & Loiselle, B. (2004). On the density-dependence of seed predation in *Dipteryx micrantha*, a bat-dispersed rain forest tree. *Oecologia, 140*, 76–85.

Russo, S. E., & Augspurger, C. K. (2004). Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters*, *7*, 1058–1067.

SAS Institute. (2004). *SAS/STAT user's guide, version 9.1*. Cary, NC: SAS Institute.

Schupp, E. W., & Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of plant population ecology. *Écoscience*, *2*, 267–275.

Schupp, E. W., Milleron, T., & Russo, S. (2002). Dissemination limitation and the origin and maintenance of species-rich tropical forest. In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed dispersal and frugivory, evolution and conservation* (pp. 19–33). Wallingford: CAB International.

Serio-Silva, J. C., & Rico-Gray, V. (2002). Interacting effects of forest fragmentation and howler monkey foraging on germination and dispersal of fig seeds. *Oryx*, *36*, 266–271.

Terborgh, J., Pitman, N., Silman, M., Schichter, H., & Nùñez, V. P. (2002). Maintenance of tree diversity in tropical forests. In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed dispersal and frugivory, evolution and conservation* (pp. 1–17). Wallingford: CAB International.

Wahl, M., & Hay, M. E. (1995). Associational resistance and shared doom: Effects of epibiosis on herbivory. *Oecologia*, *102*, 329–340.