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# Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter?

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## Summary

**1** We explored whether seedling recruitment was spatially predicted by seed rain (spatial concordance) at different scales (microsite, microhabitat and site) in the bird-dispersed trees *Crataegus monogyna*, *Ilex aquifolium* and *Taxus baccata*, in temperate secondary forests in north-west Spain.

**2** We propose that both spatial concordance within each scale and consistency of concordance patterns across scales are dependent on differences between seed rain and post-dispersal processes in the partitioning of spatial variance at each scale.

**3** We measured the density of dispersed seeds, the percentage of post-dispersal seed predation by rodents and the density of emerged first-year seedlings at sampling stations distributed throughout five microhabitats (under canopies of parental trees and in open gaps) and four localities over two seasons.

**4** Seed rain density of all tree species varied most at the microhabitat scale, but microsite and site differences accounted for most of the spatial variance in post-dispersal seed predation and, especially, in seedling establishment.

**5** All three species showed concordance between seed rain and seedling establishment at the microhabitat scale, because strong patchiness in avian-generated seed rain overrode the slight uncoupling effects exerted by the more homogeneous post-dispersal processes. Seed rain was also a good predictor of recruitment of *Ilex* and *Crataegus* at the microsite scale, but, for *Taxus*, the rather homogeneous dispersal across microsites contrasted with the heterogeneous post-dispersal losses. At the site scale, only *Taxus* showed a positive trend of concordance.

**6** Concordance patterns were maintained from microsite to microhabitat in *Crataegus* and *Ilex*, and from microhabitat to site in *Taxus*. Low-variance allocation to the site scale at the seed rain stage precluded complete consistency in *Crataegus* and *Ilex*.

**7** Positive responses of recruitment to seed dispersal depended on both species and scale, resulting in a complex template for dispersal-limitation effects on metapopulations and communities.

*Key-words*: landscape, microhabitat, microsite, post-dispersal seed predation, recruitment, scale-dependency, seed dispersal, spatial heterogeneity

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## Introduction

Plant recruitment is a multi-staged, spatially structured process that determines the distribution, dynamics and genetic structure of plant populations and communities (Schupp 1995; Clark *et al*. 1999; Nathan & Müller-Landau 2000; Levine & Murrell 2003). Spatial patterns of recruitment largely depend on the initial template established by seed dispersal, but are also influenced by successive post-dispersal factors such as seed predation, germination and seedling mortality (Herrera *et al*. 1994; Nathan *et al*. 2000; Wenny 2000; García 2001). Thus, a central question in plant demography is whether recruitment can be spatially predicted from the seed rain (spatial concordance) or whether post-dispersal processes erase seed deposition patterns, leading to independence or even a negative relationship

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between seed rain and recruitment (spatial discordance; Houle 1995; Jordano & Herrera 1995; Schupp 1995; Schupp & Fuentes 1995). Models relating recruitment to the distance from seed sources (Hubbell 1980; Janzen 1980; Connell *et al*. 1984; see reviews in Houle 1995; Nathan & Casagrandi 2004) and others describing recruitment in relation to habitat patchiness (e.g. Jordano & Herrera 1995; Schupp 1995; Schupp & Fuentes 1995) have been used to show that the relationship between seed rain and recruitment depends both on the degree of spatial heterogeneity of post-dispersal losses compared with that of seed rain, and on the correlation between survival expectancies throughout the different recruitment stages. Concordance occurs when seed rain is much more heterogeneous than post-dispersal losses, as, for example, when high seed density under parent plants overwhelms seed and seedling mortality, even if they are density-dependent (e.g. Houle 1995, 1998; Harms *et al*. 2000); it also occurs when survival expectancies are spatially coupled across stages, as when habitat patches that receive more seeds are also the most suitable for avoiding predation or for germination (e.g. Schupp 1995; Wenny 2000; Wenny & Levey 1998). Conversely, highly heterogeneous and uncoupled post-dispersal mortality usually leads to seedling establishment patterns that are discordant with those of the seed rain (e.g. Houle 1992a; Herrera *et al*. 1994; Nathan *et al*. 2000; Rey & Alcántara 2000; García 2001).

A complementary framework for evaluating the importance of seed dispersal for the spatial structure of recruitment explicitly considers the spatial scale at which recruitment patterns emerge. In fact, a multi-scaled perspective makes it possible to elucidate whether different recruitment processes (seed dispersal, seed survival, germination, emergence) are controlled by factors operating at different spatial scales (Schupp 1992; Clark *et al*. 1998; Kollmann 2000). For example, seed rain may show marked variation at a local scale, as in both wind-dispersed trees (for which seed shadows strongly reflect the distribution of parent plants; Houle 1995, 1998; Nathan *et al*. 2000) and avian-dispersed species (in which seeds accumulate disproportionately under bird perches; Herrera *et al*. 1994; Rey & Alcántara 2000; Wenny 2000). However, in the same systems, post-dispersal factors such as seed predation and germination may behave more homogeneously in space than the seed rain, because variation is principally at finer or coarser scales (Houle 1995, 1998; Wenny 2000; García & Houle 2005). These scale differences are important because post-dispersal processes are only involved in uncoupling seed rain and recruitment if the two processes act at the same spatial scale (Houle 1994, 1995; Jordano & Herrera 1995; Kollmann 2000). In addition, the scaling approach is necessary to show whether spatial concordance between seed rain and recruitment occurs at all scales (Houle 1992a; Schupp 1992; Clark *et al*. 1998; see also Wiens 1989).

Our objective was to describe the patterns of concordance between seed dispersal and seedling recruitment in coexisting species, using a multi-scaled spatial design to study three fleshy fruited, bird-dispersed trees in temperate secondary-growth forests in north-west Spain. We investigated (i) the contribution of different spatial scales to the total variance in seed rain, post-dispersal seed predation, and seedling establishment, (ii) whether concordance between seedling density and seed rain is scale-dependent or consistent across scales and (iii) whether both concordance and consistency can be interpreted in terms of differences between seed rain and post-dispersal losses in the variance partitioning across scales. We first present a conceptual framework that assumes that different recruitment processes may show different degrees of spatial heterogeneity because they operate at different scales. In other words, a given process may appear homogeneous at a given scale because a different scale accounts for most of its spatial variance. If spatial patchiness occurs at two scales (e.g. in different patch types within a site as well as different sites within a region; *a–e* and *A* and *B*, respectively, in Fig. 1), seed rain, post-dispersal losses and seedling recruitment may show variability (i.e. different magnitudes for different levels) at both smaller and larger scales.

This leads to two predictions. First, we propose that spatial concordance between seed dispersal and recruitment at a particular scale depends on the similarity in the spatial scales at which seed rain (SR) and post-dispersal losses (PDL) operate. Concordance occurs when seed rain varies most at a smaller scale (Fig. 1-1, large differences among *a–e*, but small differences between *A* and *B*) but post-dispersal mortality varies at a larger scale, acting as a homogeneous filter for seed rain. Conversely, when most of the variation in the seed rain occurs at the larger scale (Fig. 1-2, small differences among *a–e*, but large differences between *A* and *B*), post-dispersal losses acting at the smaller scale produce high variability in recruitment, leading to discordance.

Our second hypothesis is that the consistency of concordance patterns between seed dispersal and recruitment across successive spatial scales depends on the variability of the seed rain at different scales. Post-dispersal losses may tend to vary at a larger scale (as in Fig. 1-1), but seed rain may vary at both smaller and larger scales. When its variance is distributed proportionally across scales (Fig. 2-1, large differences among *a–e* and between *A* and *B*), the concordance pattern is consistent across scales, but when variance in seed rain is mostly accounted for by the smaller scale (Fig. 2-2, large differences among *a–e* but not between *A* and *B*), concordance is only seen at that scale.

## Materials and methods

### STUDY SITES AND SPECIES

The study was carried out in secondary-growth forests in the Cantabrian mountain range (Asturias, Spain) between 2001 and 2003. These forests are dominated by fleshy fruited trees (holly *Ilex aquifolium* L., hawthorn

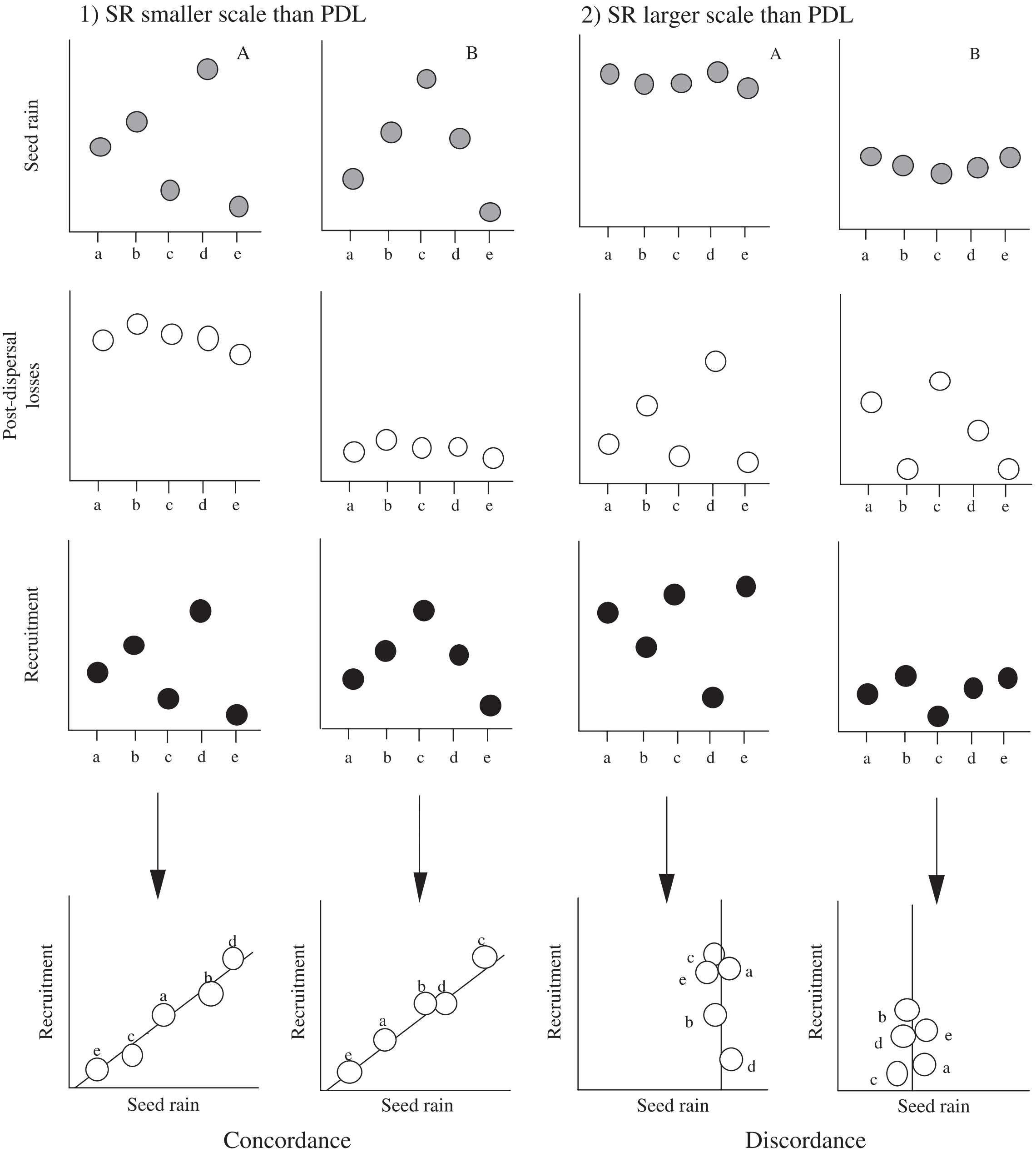

**Fig. 1** Hypothetical relationships between the spatial patterns of seed rain and seedling recruitment (concordance or discordance) as a function of the spatial scale at which seed rain (SR) and post-dispersal losses (PDL, probability of loss) operate. Seed rain, post-dispersal losses and seedling recruitment are represented for different levels at two spatial scales (*a–e* for smaller scale, *A* and *B* for larger scale). In (1) seed rain density varies more at the smaller scale and post-dispersal losses at the larger scale, whereas this is reversed in (2).

*Crataegus monogyna* L., yew *Taxus baccata* L. and rowan *Sorbus* spp.), together with hazel *Corylus avellana* L. Such forests occur as isolated stands in a pasture matrix or as fringe patches between pasture and mature deciduous forests (beech *Fagus sylvatica* L.). The present study focused on three species (*Taxus baccata*, *Ilex aquifolium* and *Crataegus monogyna*, hereafter *Taxus*, *Ilex* and *Crataegus*), chosen because they are the major canopy species at all study sites (Table 1) and share a common guild of avian frugivores that disperse seeds in their droppings (almost exclusively thrushes: *Turdus viscivorus*, *T. iliacus*, *T. philomelos* and *T. merula*).

## SPATIAL SCALING FRAMEWORK

Our analysis considered three scales of observation, representing the three levels of spatial heterogeneity in patch suitability for seeds and seedlings that are commonly used in recruitment studies (e.g. Jordano & Herrera 1995; Russell & Schupp 1998; Kollmann 2000), namely microsite, microhabitat and site. Microsite represents fine-grained heterogeneity over less than a few square metres, and is determined by small-scale features (e.g. distance to tree canopy, canopy density, soil texture, ground cover by herbaceous plants). Microhabitat

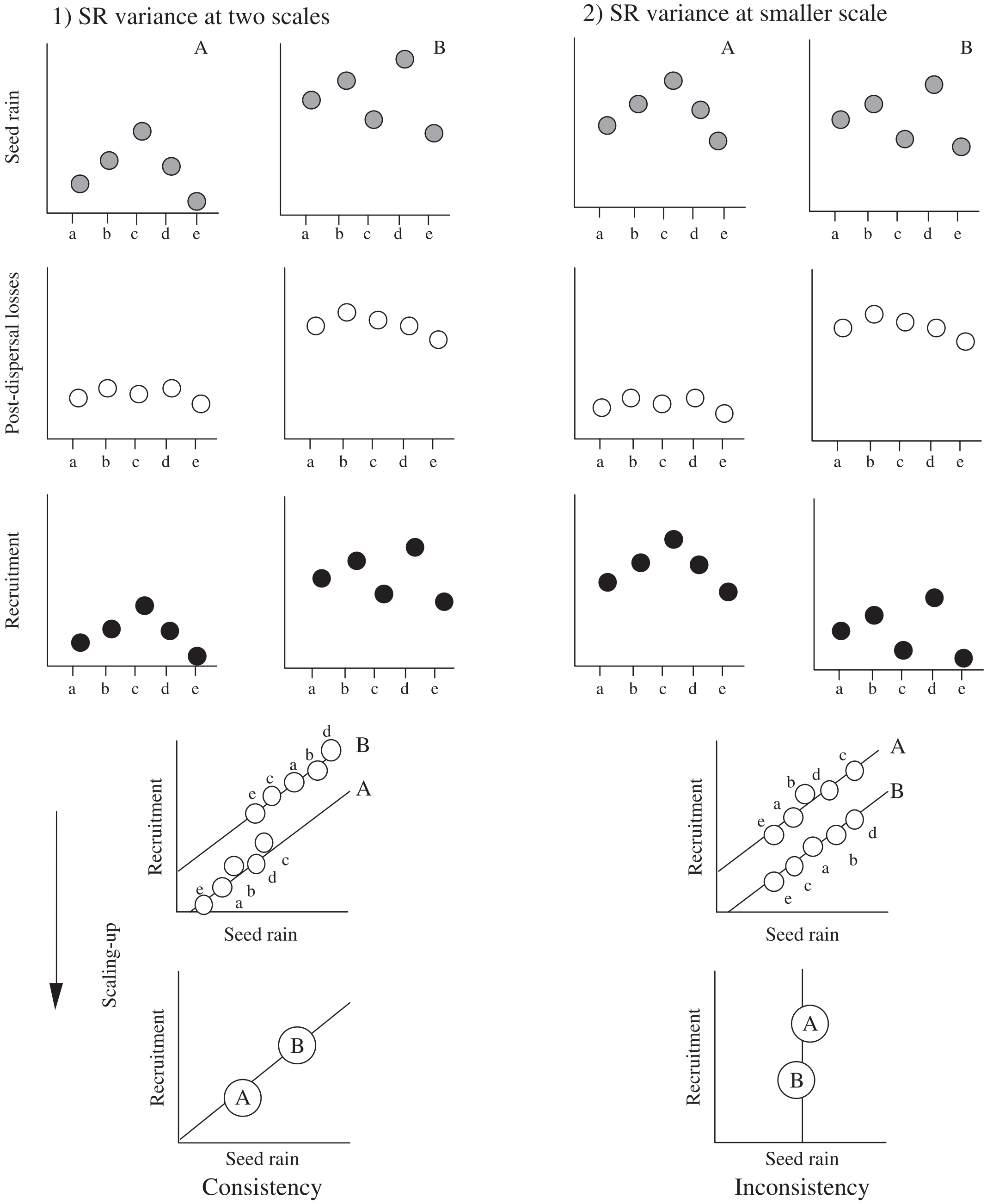

**Fig. 2** Hypothetical framework for the occurrence of concordance between seed rain and seedling recruitment across successive spatial scales (consistency), as a function of the variance partitioning of seed rain density between these scales. Levels of variation within scales are represented as in Fig. 1. In (1) the spatial variance in seed rain is distributed proportionally between both scales whereas in (2) most is accounted for by the smaller scale. For scaling-up, the values of seed rain and recruitment at the larger scale are calculated by averaging between the smaller-scale levels.

**Table 1** Percentage (mean ± SE) cover of different microhabitats (canopy of different tree species and open interspaces between tree canopy) in the four study sites. Mean values were obtained from 10–15 sampling plots (each of 20 × 20 m), arbitrarily distributed throughout each site (see García & Obeso 2003 for methodology)

| | Site | | | |
|---|---|---|---|---|
| Microhabitat | Aramo | Peña Mayor | Sueve | Teixeu |
| *Taxus* | 6.47 ± 1.62 | 10.67 ± 2.23 | 29.70 ± 7.96 | 10.00 ± 2.24 |
| *Ilex* | 15.13 ± 3.17 | 21.80 ± 2.73 | 19.00 ± 3.32 | 10.70 ± 1.61 |
| *Crataegus* | 2.13 ± 0.86 | 12.60 ± 1.33 | 9.20 ± 1.69 | 4.20 ± 1.16 |
| Open gaps | 56.73 ± 5.11 | 38.60 ± 6.43 | 15.30 ± 8.02 | 43.60 ± 5.49 |
| Other | 19.53 ± 5.27 | 16.66 ± 2.99 | 32.40 ± 8.02 | 31.50 ± 5.45 |

corresponds to patches that are physiognomically distinguished by the presence/absence of different vegetation cover or canopy types, or of features such as rocks, and patches extend over areas of 10–100 $m^2$. Site represents coarse-grained heterogeneity occurring at the scale of a region or landscape, covering at least several ha, and representing local habitats separated by topographic features such as hilltops or valley bottoms. These spatial scales are hierarchical, with every site containing a combination of microhabitats as levels of variation within site, and every microhabitat containing a range of microsites.

Sampling was set up at four different sites (Aramo, Peña Mayor, Sueve and Teixeu) located on north-facing slopes at altitudes of between 680 and 1400 m a.s.l. and 5–50 km apart (see García & Obeso 2003 for a comprehensive description of the sites). At each site, we considered five microhabitats representing most of the natural variation in the seed rain of the studied species: under female *Taxus*, under male *Taxus*, under female *Ilex*, under *Crataegus* and in open spaces between tree canopies (Obeso & Fernández-Calvo 2002; García & Obeso 2003). These microhabitats accounted for 68–84% of the total cover at the study sites (Table 1). Open space between canopies was the most common microhabitat at all but one site, whereas yew canopy showed the most variation between sites (Table 1). For each microhabitat, we established 10 permanent sampling stations, ≥ 5 m apart, each extending over an area of 1–2 $m^2$, to represent specific microsites.

### SEED DISPERSAL

The deposition of seeds in avian droppings was monitored at all sampling stations during the dispersal season (September to January) in 2001–02 and 2002–03, by establishing one permanent 50 × 50 cm quadrat per station, at which we collected all dispersed seeds found in successive fortnightly surveys. We calculated the cumulative density of seeds (seeds $m^{-2}$) of each target species deposited per sampling station. Seeds showing signs of predation (open husks, teeth marks) were also counted as part of the dispersed seed pool (see Alcántara *et al.* 2000b; García 2001; García & Obeso 2003 for similar procedures). The sampling method may underestimate actual seed rain, because of undetected seed removal from sampled surfaces by post-dispersal predators. Thus, to validate the use of the quadrats for evaluating spatial variation in seed rain density, we set up two seed traps per sampling station at the Peña Mayor site during 2001–02. Traps consisted of 50 × 25 × 5 cm plastic trays covered with 1.3-cm-diameter mesh, which were fixed to the ground adjacent to the seed quadrat by nailing down the mesh. The contents of the traps were collected at the same time as quadrat surveys were carried out. Seed densities of *Taxus* and *Crataegus* were similar in traps and quadrats (Wilcoxon paired test: $Z = 1.30$, $P > 0.18$, $n = 50$; for both species), whereas *Ilex* seed density was on average 14% lower in the quadrats than in the traps (Wilcoxon paired test: $Z = 4.51$, $P < 0.001$, $n = 50$). On the other hand, quadrats represented a high proportion of the spatial variability in seed rain for all species (regressions between seed density on quadrats and seed density in traps, considering a Poisson error distribution in the dependent variables: *Taxus*: $F_{1,48} = 34.41$, $P < 0.0001$, $R^2 = 0.417$; *Ilex*: $F_{1,48} = 83.45$, $P < 0.0001$, $R^2 = 0.635$; *Crataegus*: $F_{1,48} = 82.97$, $P < 0.0001$, $R^2 = 0.634$). Therefore, given the negligible or low loss of seeds from quadrats by predators and the ability of quadrat sampling to take into account the small-scale variability in seed dispersal, we considered this a reliable method of estimating seed rain density for the multi-scale purposes of this study.

### POST-DISPERSAL SEED PREDATION ESTIMATES

Seed predation was studied by recording removal of seeds of the target species offered simultaneously to predators in the field. In each sampling station we placed eight seed depots composed of plastic mesh (1.5-mm pore diameter) triangles (6-cm side), which were nailed to the ground 50 cm from each other. One seed of each of the three target species was glued to a different vertex of the triangle, using a low-odour, rainproof thermoplastic glue (see Herrera *et al.* 1994; Alcántara *et al.* 2000a for similar methods). The triangles were arranged in two parallel lines passing through the seed rain quadrat, to ensure a uniform, low density of natural seeds around the seed depots. Density mimicked by seed depots (*c.* 15 seeds $m^{-2}$) was within the range of natural densities of all species. Seeds, previously collected from seed rain at the study sites, were considered sound, because empty *Ilex* seeds (identifiable by external aspect and weight; Obeso & Fernández-Calvo 2002) were discarded, and most of the *Taxus* and *Crataegus* seeds were viable (D. García *et al.* unpublished data). Depots were monitored after 2 and 4 weeks and removed after the second monitoring. Seeds were glued firmly to the plastic triangles, so that seed disappearance owing to abiotic factors (wind, rain) was considered negligible. We did not record trampling or digging-up of triangles by animals during experiments. We thus considered that a seed had been subject to predation if it was either missing from the plastic mesh or was still on the mesh but was gnawed and empty. Seed attack was exclusively attributable to forest rodents (woodmouse *Apodemus sylvaticus*, D. García *et al.* unpublished data). Experiments were carried out at all sites in 2002 and 2003, between late January and early March, i.e. after the seed dispersal season. Predation rate was calculated for each species and sampling station as the percentage of seed predation.

### SEEDLING ESTABLISHMENT

For each sampling station, we established a permanent 50 × 50 cm emergence quadrat adjacent to the seed rain quadrat. Quadrats were examined fortnightly between May and September in 2002 and 2003, and the presence of emerged seedlings of all three species was recorded (species were distinguished on the basis of the presence of cotyledons and stem colour; see Peterken & Lloyd 1967; Thomas & Polwart 2003). Each seedling was individually mapped within the quadrat according to its $x$ and $y$ coordinates (two-dimensional accuracy ≤ 1 cm), distinguishing seedlings emerging simultaneously from the same point. The fate of each marked seedling was followed in successive surveys identifying, where possible, the cause of mortality (e.g. clipping by herbivores, trampling, uprooting, drought). We thus estimated the density of first-year seedlings for each station as the cumulative number of emerged seedlings $m^{-2}$ at the end of the survey season. Given the high frequency of surveys and the accuracy of location, we considered that every recorded seedling represented one single individual, and assumed that bias due to confusing a marked seedling with others successively germinating and dying at exactly the same point was negligible.

### STATISTICAL ANALYSIS

#### *Variance partitioning between spatial scales*

We evaluated spatial variation at different scales by means of Generalized Linear Models (GLM Crawley 1993) considering site and microhabitat (nested within site) as the main factors and the density of dispersed seeds, the percentage of seed predation and the density of first-year seedlings as response variables. Poisson and binomial error distributions were considered for density and percentage, respectively. Deviance (sum of squares) quotients provided the percentage of relative variance accounted for by each spatial scale, with error (within subjects) deviance being considered as microsite variance.

#### *Concordance between seed rain and seedling establishment at different spatial scales*

Spatial concordance was evaluated by means of correlation and regression models of seed rain and seedling establishment and the strength of concordance was assessed by the occurrence of significant positive linear relationships (one-tailed tests) and model coefficients of determination ($r^2$; see Schupp & Fuentes 1995). At the microsite scale, covariation was addressed for each species by regressing the residuals of previous GLM models considering site and microhabitat (nested within site) as the main factors and the density of dispersed seeds and the density of first-year seedlings of each sampling station as response variables (Poisson error distributions). In this way, all of the spatial variance in the regression variables was attributable to the microsite scale, stations belonging to the same microhabitat and site being considered as independent samples.

Concordance at the microhabitat scale was addressed by regressing mean values of seedling density for each microhabitat within each site (averaging across sampling stations within each microhabitat) with the corresponding mean values of seed rain. In order to consider the values of similar microhabitats at different locations as independent units, we used the residuals of previous GLM models considering the site effects on, respectively, the density of dispersed seeds and the density of first-year seedlings (Poisson error distributions).

At the site scale, we first correlated the number of seeds and the number of seedlings per $m^2$, averaging across the mean values of the five different microhabitats within site, to interpret the consistency of concordance patterns across scales (Fig. 2). Second, we correlated the numbers of seeds and seedlings per ha, calculated as the sum of the products of the average seed and seedling densities by the proportion of cover for each microhabitat. We thus sought to represent the actual landscape variation for both parameters, accounting for the potential bias due to between-site differences in microhabitat coverage (see also García & Ortiz-Pulido 2004). In order to overcome the shortcomings derived from the small sample size (four sites), we calculated $P$-values for each correlation coefficient ($r$) from a distribution generated by a randomization technique ($n = 600$, $\approx 4! \times 4!$ permutations; Potvin & Roff 1993).

Seed rain density, seed predation rate and seedling density were averaged for the two years of study for each sampling station. This procedure did not allow us to discern how concordance patterns change over time (Houle 1998), but temporal variation in the demographic parameters tested has been shown elsewhere to be non-significant or much lower than spatial variation (D. García *et al.* unpublished data; see also Kollmann *et al.* 1998). On the other hand, as all chosen species have short-lived seed banks (1–3 years; Kollmann 2000; Thomas & Polwart 2003; Arrieta & Suárez 2004), a small proportion of the recorded seedling emergence may correspond to seed cohorts existing prior to sampling. Averaging variables between years should reduce the possible bias derived from assigning a given seedling cohort to previous seed rain, owing to the effects of delayed germination (see Clark *et al.* 1998; De Steven & Wright 2002 for similar procedures).

## Results

### SPATIAL VARIABILITY IN SEED RAIN, POST-DISPERSAL LOSSES AND SEEDLING ESTABLISHMENT

The density of dispersed seeds differed significantly between microhabitats and sites (GLM: site and microhabitat [site] effects $P < 0.0001$, for all species; Fig. 3). Birds dispersed more seeds under the canopies of the fleshy fruited trees than in open gaps (Fig. 3). For *Taxus*, the areas under the same species (both male and female yew) received most of the dispersed seeds. This pattern

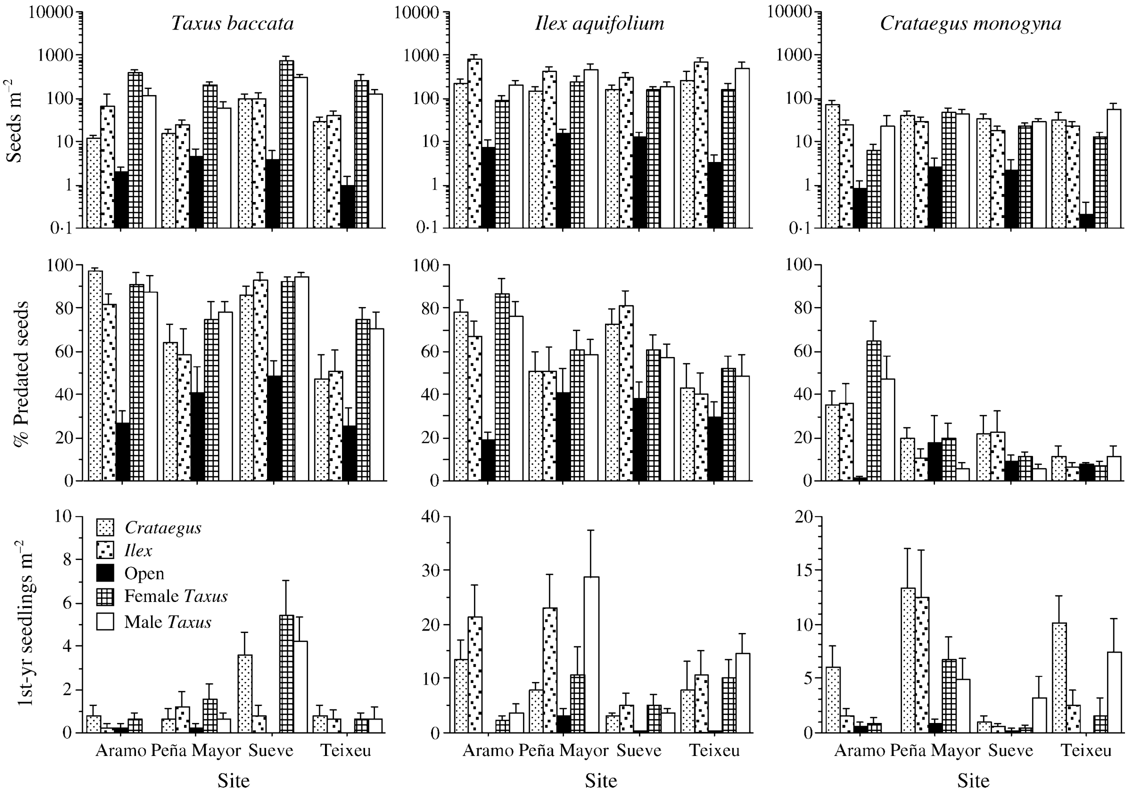

**Fig. 3** Density of dispersed seeds, the percentage of seed predation and the density of emerged first-year seedlings of three fleshy fruited trees in four study sites and five different microhabitats (mean + SE, $n$ = 10 sampling stations per microhabitat). Note the logarithmic scale for seed density.

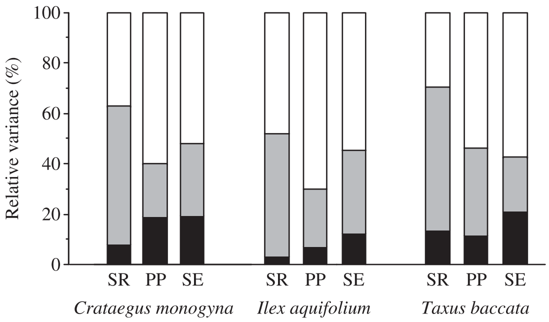

**Fig. 4** Variance in different regeneration parameters (SR: the density of dispersed seeds, PP: percentage of post-dispersal seed predation, SE: the density of emerged first-year seedlings) accounted for by microsite (white bar), microhabitat (grey bar) and site (black bar) for different species, derived from Generalized Linear Models considering site and microhabitat (nested within site) as main factors (error deviance was considered to represent the variance at the microsite scale).

was less marked for *Ilex* and *Crataegus*, for which large numbers of seeds were also deposited beneath other species (Fig. 3). Microhabitat accounted for the highest percentage of variation in seed rain density (≥ 48%, for all species; Fig. 4). In a comparison of demographic stages, seed rain showed the lowest percentage of variation explained by the microsite scale (Fig. 4).

Post-dispersal seed predation by rodents also varied significantly between microhabitats and sites (GLM: site and microhabitat [site] effects $P < 0.001$, for all species; Fig. 3), but these scales together always accounted for a lower percentage of variance than did the microsite (Fig. 4). Differences in microhabitats were mainly due to lower predation in open gaps (Fig. 3). In all cases, site caused more variation at this stage than at the seed rain stage (Fig. 4).

Seedling establishment was significantly affected by microhabitat and site (GLM: site and microhabitat [site] effects $P < 0.0001$, for all species; Fig. 3), but most of the variance was accounted for by the microsite (Fig. 4). Compared with earlier demographic stages, seedling establishment showed a high percentage of variation accounted for by site, especially for *Taxus* (Fig. 4). Microhabitat heterogeneity in the density of first-year seedlings was related to the differences between canopy and open microhabitats (Fig. 3).

### CONCORDANCE BETWEEN SEED RAIN AND SEEDLING ESTABLISHMENT AT DIFFERENT SPATIAL SCALES

When evaluated at the microsite scale, seedling establishment proved concordant with seed rain in *Crataegus* and in *Ilex* (Fig. 5a). Although the seedling density residuals were also significantly related to the seed density residuals in *Taxus*, the regression model explained a low percentage of variation in the dependent variable (Fig. 5a). At the microhabitat scale, all species showed

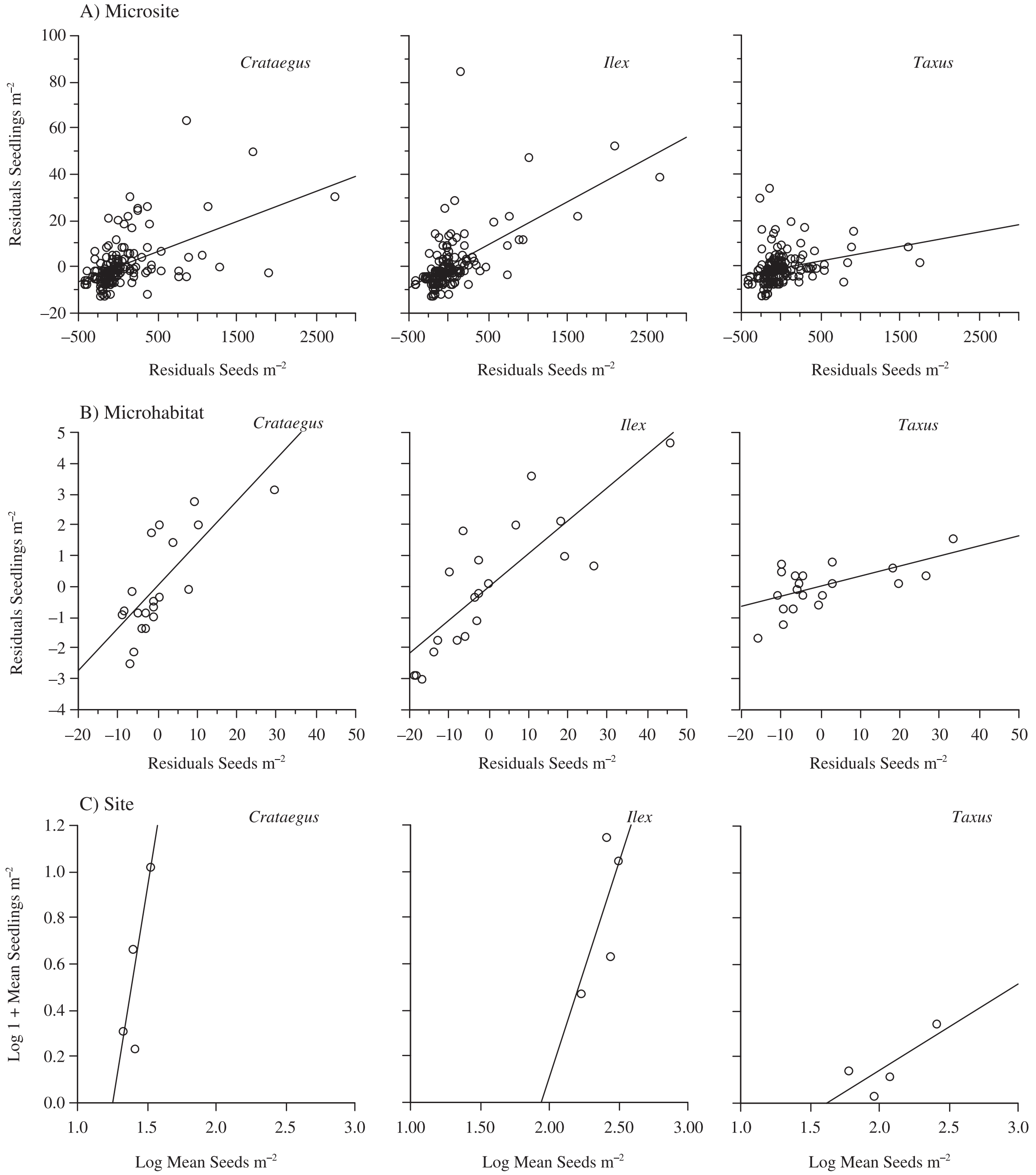

**Fig. 5** Spatial concordance between seed rain and recruitment for different tree species at different scales. (a) The microsite scale, represented by the relationships between the residuals of the density of dispersed seeds and the density of emerged first-year seedlings, after removing microhabitat and site effects (*Crataegus*: $r^2 = 0.271$, $F_{1,198} = 73.96$, $P < 0.0001$; *Ilex*: $r^2 = 0.369$, $F_{1,198} = 115.71$, $P < 0.0001$; *Taxus*: $r^2 = 0.073$, $F_{1,198} = 15.71$, $P < 0.0001$; each point represents a sampling station). (b) Microhabitat, represented by the relationships between the residuals of the above variables, after removing site effects (*Crataegus*: $r^2 = 0.570$, $F_{1,18} = 23.89$, $P < 0.0001$; *Ilex*: $r^2 = 0.671$, $F_{1,18} = 36.67$, $P < 0.0001$; *Taxus*: $r^2 = 0.363$, $F_{1,18} = 10.27$, $P = 0.0025$; each point represents the average between sampling stations within microhabitat and site). (c) Site, represented by the relationships between the density of dispersed seeds and the density of emerged first-year seedlings; both variables are represented on a logarithmic scale (*Crataegus*: $r^2 = 0.751$, $P = 0.069$; *Ilex*: $r^2 = 0.315$, $P = 0.251$; *Taxus*: $r^2 = 0.922$, $P = 0.078$; each point represents a site, the values of both variables were calculated by averaging density values of the different microhabitats within each site).

establishment patterns strongly concordant with seed rain (Fig. 5b).

At the site scale, no significant relationship was found between local values of seed and seedling densities for *Ilex* (Fig. 5c, densities per ha: $r^2 = 0.074$, $P = 0.352$). In the case of *Crataegus*, there was a steep positive relationship between the average seed and seedling densities per m$^2$ (Fig. 5c). However, this trend disappeared when microhabitat coverages were considered in the calculation of seed and seedling densities (densities per ha: $r^2 = 0.255$, $P = 0.385$). For both species, site variance was much lower for seed density than for seedling density (as depicted by the range of values covered by each parameter in the regression plots, Fig. 5c). Comparatively, *Taxus* showed more similar site variances of seed and seedling densities, providing a shallow, near-significant relationship when evaluated both by using the densities of seeds and seedlings per $m^2$ (Fig. 5c), and the densities corrected by microhabitat coverage (densities per ha: $r^2 = 0.964$, $P = 0.108$).

Post-dispersal seed predation rate was spatially independent of seed rain at the microsite scale ($F_{1,198} < 2.10$, $P > 0.15$, for all species). This independence was also evident at the microhabitat scale for *Crataegus* and *Ilex* ($F_{1,18} < 1.72$, $P > 0.20$, for both cases), but not for *Taxus*, for which seed predation rate was positive and significantly related to seed density ($r^2 = 0.276$, $F_{1,18} = 6.89$, $P = 0.016$; regression between residuals of both variables after removing site effects).

## Discussion

### VARIANCE PARTITIONING BETWEEN SPATIAL SCALES FOR DIFFERENT RECRUITMENT STAGES

Spatial variation in seed rain of all three fleshy fruited species was mainly determined by microhabitat differences, namely the contrast between areas beneath parental tree canopies and open pasture. This generalized pattern is probably explained by the fact that all three species are largely dispersed by wintering frugivorous thrushes (*Turdus* sp.) whose post-foraging movements caused a disproportionate seed deposition under fruiting trees (see also Jordano & Schupp 2000; Wenny 2000; García 2001; García & Obeso 2003). However, the nomadic behaviour of these birds allows them to track fruit patches across the regional landscape (Jordano 1993; Rey 1995; García & Ortiz-Pulido 2004), reducing the contrast between sites, as evidenced by low site differences for seed rain of *Ilex* and *Crataegus*. For *Taxus*, however, high fruit production and yew microhabitat coverage at one of the study sites (Sueve, Table 1) probably caused more pronounced between-site differences. Seed deposition varied, to some extent, between microsites probably because of fine-scale structural characteristics, such as fruit availability or canopy density, causing variation in the time spent by dispersers in different trees within a forest patch or even in different branches within a tree (Sallabanks 1993; Masaki *et al*. 1994; García & Ortiz-Pulido 2004).

The spatial pattern of rodent seed predation was poorly explained by site or microhabitat, with most of the variance being accounted for by microsite. This indicates that seed survival was probably affected by fine-scale features such as the distance to rodent burrows, presence of leaf litter and open ground cover (Whelan *et al*. 1991; Myster & Pickett 1993; Manson & Stiles 1998). At the microhabitat scale, the probability of being attacked by rodents was nevertheless higher for seeds under tree canopies than in open gaps, suggesting that rodents avoided patches offering low protection against their predators (as shown in other temperate areas, e.g. Myster & Pickett 1993; Hulme 1996; Manson & Stiles 1998; Hulme & Hunt 1999). For all studied species, differences between sites were greater for seed predation than for seed rain, suggesting that landscape factors may have affected local rodent population sizes (see also Hulme 1996; Kollmann *et al*. 1998).

Our data show that the success of seedling establishment was primarily determined at the microsite scale. Some post-dispersal processes may strengthen the importance of microsite: germination, for example, may be affected by factors that cause variation in temperature, light, humidity and chemical composition of the immediate seed environment, such as soil compaction, the presence of leaf litter or herbaceous plants, and canopy density (Houle 1992b; Molofsky & Augspurger 1992; Verdú & García-Fayós 1996; Arrieta & Suárez 2004). Seedling establishment also differed considerably between sites, suggesting that landscape factors, such as altitude, soil composition, orientation, canopy cover and frequency of disturbance, caused differences in germination and emergence (Houle 1992b; Ashton & Larson 1996). Different post-dispersal filters thus increase the importance of both larger (site) and smaller (microsite) scales in the overall spatial template of recruitment.

### CONCORDANCE BETWEEN SEED RAIN AND RECRUITMENT AT DIFFERENT SPATIAL SCALES

The spatial patterns of seedling establishment reflected the seed distribution generated by avian dispersers, independently of the outcome of the different processes operating between these two stages (Houle 1995; Jordano & Herrera 1995; Schupp & Fuentes 1995). Spatial concordance was, however, species- and scale-dependent. All three species showed clear concordance between seed rain and seedling establishment at the microhabitat scale (highly heterogeneous seed rain compared with relatively homogeneous post-dispersal factors, see Fig. 1-1). In all species, microhabitats that received more seeds also showed more concentrated activity of seed predators, but this was not sufficient to cause uncoupling at the stage between dispersal and predation because, even for *Taxus*, in which predation correlated positively with seed rain at the microhabitat scale, more seedlings were finally recruited under canopy. This generalized concordant pattern contrasts with the common discordance found for avian-dispersed, fleshy fruited woody plants from Mediterranean areas, where strong abiotic constraints on seedling establishment and survival uncouple recruitment from the seed rain (e.g. Jordano & Herrera 1995; Rey & Alcántara 2000; García 2001).

The present results also show that seed rain was a good predictor of seedling establishment at the microsite scale for *Crataegus* and, especially, for *Ilex*. In both species, a large proportion of the variation in seed dispersal occurred at the microsite scale and was not erased by the density-independent seed predation (see Houle 1995, 1998 for similar results with wind-dispersed species). Independence between seed density and predation was also found for *Taxus*, which showed weak concordance at this scale, as judged by the low variance in recruitment (< 10%) explained by the patterns of dispersal. In this case, low concordance may be related to the fact that seed rain scarcely varied at the microsite scale, so that it presented a relatively homogeneous template for post-dispersal losses (Fig. 1-2), rather than to the uncoupling effects of post-dispersal factors (as described for some bird- and wind-dispersed trees, e.g. Nathan *et al*. 2000; Wenny 2000).

In contrast, no clear relationships between recruitment and seed rain were found at the site scale. In *Ilex* and *Crataegus*, the low variance between sites in terms of seed rain, determined by similar average seed density values (Fig. 3) and similar cover of microhabitats accumulating more seeds (Table 1), contrasted with higher heterogeneity at post-dispersal stages (Fig. 1-2). For example, in *Ilex*, sites such as Aramo and Peña Mayor, in which seed densities were similar, showed marked differences in seedling emergence, probably as a result of differences in seed predation (higher in Aramo than in Peña Mayor, Figs 3 & 5). Similarly, small differences in seed density of *Crataegus* at the Peña Mayor and Sueve sites were associated with large differences in seedling emergence at the same sites (Figs 3 & 5). Nevertheless, despite the low statistical power associated with small sample size at the landscape scale, our data suggested a trend of concordance between seed rain and recruitment in *Taxus*. In this species, regional variance in seedling density matched the variance in seed density, even when microhabitat cover was accounted for. This was probably because seed rain mainly occurred under the canopy of conspecific trees and thus variation in seed density across the landscape was more responsive to differences in *Taxus* cover among sites. Consequently, sites such as Sueve, with high seed density at the microhabitat scale and much higher *Taxus* cover than the other sites (Fig. 3, Table 1), promoted strong landscape variance in seed rain that persisted throughout recruitment (see also Herrera *et al*. 1994; Jordano & Herrera 1995).

### CONSISTENCY ACROSS SCALES IN CONCORDANCE PATTERNS

Concordance between seed dispersal and recruitment was not consistent across all scales although particular species showed concordance for different domains of scale (*sensu* Wiens 1989; see also García & Ortiz-Pulido 2004). For example, in both *Crataegus* and *Ilex*, recruitment was clearly concordant with seed rain from the microsite to the microhabitat scale, disappearing only on scaling-up to the site scale. In addition, we found a trend for consistency from microhabitat to site in *Taxus*, despite weak concordance at the smallest scale (see also Schupp 1992). The bottom-up inconsistency of the first two species may be interpreted in terms of how variance in seed rain is accounted for by microhabitat and site; low site variance in seed rain, filtered by more heterogeneous post-dispersal factors, determined high site specificity in recruitment, irrespective of the concordant pattern at the smaller scale (Fig. 2-2). Conversely, in *Taxus*, higher variance at both microhabitat and site scales favoured consistency across the scales studied (Fig. 2-1). Similar reasoning could be applied to explain the microsite–microhabitat consistency in *Ilex* and *Crataegus*.

## Future work

An unresolved question is whether the concordance patterns emerging at a given scale are the result of scale-specific mechanisms or, alternatively, the consequence of the accumulation of similar patterns at immediately smaller scales (Wiens 1989; García & Ortiz-Pulido 2004). In this sense, microsite–microhabitat inconsistency in *Taxus* undoubtedly indicated that recruitment processes are driven by factors acting at the microhabitat scale; although many demographic sieves (e.g. predation, germination) can operate at a smaller scale, they do not compensate for the overwhelming influence of microhabitat-structured seed rain. However, site-scale patterns in *Taxus* may be the result of smaller scale accumulative patterns rather than the result of landscape-scale dispersal processes; if more recruitment is found in a given microhabitat where more seeds are accumulated, then sites with greater cover of the given microhabitat would support more recruitment. Thus, to understand the relative contribution of accumulative scaling patterns compared with scale-specific processes, we need to complete the multi-scaled analysis of post-dispersal factors with studies designed to disentangle the mechanisms underpinning the hierachical nature of seed dispersal, namely, the use of the space by seed dispersers (Sallabanks 1993; Kollmann 2000; García & Ortiz-Pulido 2004).

Concordance between seed rain and recruitment may be also viewed as the expression of the importance of dispersal for plant population dynamics, as positive covariation across space indicates that recruitment is determined by the number of seeds arriving at safe sites (dispersal limitation) rather than by the number of sites suitable for establishment (microsite limitation; Turnbull *et al*. 2000; De Steven & Wright 2002; see also Law *et al*. 2003 for dispersal–competition trade-offs). Identifying the scale and the species for which dispersal limitation occurs is therefore a prerequisite in determining both how specific metapopulation dynamics are affected by within- and between-population demographic effects of seed dispersal (Bullock *et al*. 2002; Freckleton & Watkinson 2002) and how seed dispersal may control commonness and rarity of different species at different spatial scales, determining the structure of local communities as well as regional diversity patterns (Clark *et al*. 1998; Levine & Murrell 2003).

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## References

Alcántara, J.M., Rey, P.J., Sánchez-Lafuente, A.M. & Valera, F. (2000a) Early effects of rodent post-dispersal seed predation on the outcome of the plant–seed disperser interaction. *Oikos*, **88**, 362–370.

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

Arrieta, S. & Suárez, F. (2004) Germination and seed bank depletion of holly (*Ilex aquifolium* L.) in four microhabitat types. *Seed Science Research*, **14**, 305–313.

Ashton, M.S. & Larson, B.C. (1996) Germination and seedling growth of *Quercus* (section *Erythrobalanus*) across openings in a mixed-deciduous forest of southern New England, USA. *Forest Ecology and Management*, **80**, 81–84.

Bullock, J.M., Moy, I.L., Pywell, R.F., Coulson, S.J., Nolan, A.M. & Caswell, H. (2002) Plant dispersal and colonization processes at local and landscape scales. *Dispersal Ecology* (eds J.M. Bullock, R.E. Kenward & R. Hails), pp. 271–302. Blackwell Science, Oxford.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J. & Wyckoff, P. (1999) Interpreting recruitment limitation in forests. *American Journal of Botany*, **86**, 1–16.

Clark, J.S., Macklin, E. & Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs*, **68**, 213–235.

Connell, J.H., Tracey, J.G. & Webb, L.J. (1984) Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecological Monographs*, **54**, 141–164.

Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell, Oxford.

De Steven, D. & Wright, S.J. (2002) Consequences of variable reproduction for seedling recruitment in three neotropical tree species. *Ecology*, **83**, 2315–2327.

Freckleton, R.P. & Watkinson, A.R. (2002) Large-scale spatial dynamics of plants: metapopulations, regional ensembles and patchy populations. *Journal of Ecology*, **90**, 419–434.

García, D. (2001) Effects of seed dispersal on *Juniperus communis* recruitment on a Mediterranean mountain. *Journal of Vegetation Science*, **12**, 839–848.

García, D. & Houle, G. (2005) Fine-scale spatial patterns of recruitment in red oak (*Quercus Rubra*) – What matters most: abiotic or biotic factors? *Écoscience*, **12**, 000–000.

García, D. & Obeso, J.R. (2003) Facilitation by herbivore-mediated nurse plants in a threatened tree *Taxus baccata*: local effects and landscape level consistency. *Ecography*, **26**, 739–750.

García, D. & Ortiz-Pulido, R. (2004) Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography*, **27**, 187–196.

Harms, K.E., Wright, S.J., Calderón, O., Hernández, A. & Herre, E.A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, **404**, 493–495.

Herrera, C.M., Jordano, P., López-Soria, L. & Amat, J.A. (1994) Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs*, **64**, 315–344.

Houle, G. (1992a) Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of north-eastern North America. *Journal of Ecology*, **80**, 99–108.

Houle, G. (1992b) The reproductive ecology of *Abies balsamea*, *Acer saccharum* and *Betula aleghaniensis* in Tantaré Ecological Reserve, Québec. *Journal of Ecology*, **80**, 611–623.

Houle, G. (1994) Spatiotemporal patterns in the components of regeneration of four sympatric tree species – *Acer rubrum*, *Acer saccharum*, *Betula aleghaniensis* and *Fagus grandifolia*. *Journal of Ecology*, **82**, 39–53.

Houle, G. (1995) Seed dispersal and seedling recruitment: the missing link (s). *Écoscience*, **2**, 238–244.

Houle, G. (1998) Seed dispersal and seedling recruitment of *Betula alleghaniensis*: spatial inconsistency in time. *Ecology*, **79**, 807–818.

Hubbell, S.P. (1980) Seed predation and the coexistence of tree species in tropical forests. *Oikos*, **35**, 214–229.

Hulme, P.E. (1996) Natural regeneration of yew (*Taxus baccata* L.): microsite, seed or herbivore limitation? *Journal of Ecology*, **84**, 853–861.

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.

Janzen, D.H. (1980) Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.

Jordano, P. (1993) Geographical ecology and variation of plant–seed disperser interactions: southern Spanish junipers and frugivorous thrushes. *Vegetatio*, **107/108**, 85–93.

Jordano, P. & Herrera, C.M. (1995) Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Écoscience*, **2**, 230–237.

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. (2000) Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 29–51.

Kollmann, J., Coomes, D.A. & White, S.M. (1998) Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. *Functional Ecology*, **12**, 683–690.

Law, R., Murrell, D.J. & Dieckmann, U. (2003) Population growth in space and time: spatial logistic equations. *Ecology*, **84**, 252–262.

Levine, J.M. & Murrell, D.J. (2003) The community-level consequences of seed dispersal patterns. *Annual Review of Ecology and Systematics*, **34**, 549–574.

Manson, R.H. & Stiles, E.W. (1998) Links between microhabitat preferences and seed predation by small mammals in old fields. *Oikos*, **82**, 37–50.

Masaki, T., Kominami, Y. & Nakashizuka, T. (1994) Spatial and seasonal patterns of seed dissemination of *Cornus controversa* in a temperate forest. *Ecology*, **75**, 1903–1910.

Molofsky, J. & Augspurger, C.K. (1992) The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology*, **73**, 68–77.

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. & Casagrandi, R. (2004) A simple mechanistic model of seed dispersal, seed predation and plant establishment: Janzen-Connell and beyond. *Journal of Ecology*, **92**, 733–746.

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.

Nathan, R., Safriel, U.N., Noy-Meir, I. & Schiller, G. (2000) Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. *Ecology*, **81**, 2156–2169.

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.

Peterken, G.F. & Lloyd, P.S. (1967) *Ilex aquifolium* L. *Journal of Ecology*, **55**, 841–858.

Potvin, C. & Roff, D.A. (1993) Distribution-free and robust statistical methods: viable alternatives to parametric statistics. *Ecology*, **74**, 1617–1628.

Rey, P.J. (1995) Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. *Ecology*, **76**, 1625–1635.

Rey, P.J. & Alcántara, J.M. (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology*, **88**, 622–633.

Russell, S.K. & Schupp, E.W. (1998) Effects of microhabitat patchiness on patterns of seed dispersal and seed predation of *Cercocarpus ledifolius* (Rosaceae). *Oikos*, **81**, 434–443.

Sallabanks, R. (1993) Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology*, **74**, 1326–1336.

Schupp, E.W. (1992) The Janzen-Connell model for tropical tree diversity: population implications and the importance of spatial scale. *American Naturalist*, **140**, 526–530.

Schupp, E.W. (1995) Seed–seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, **82**, 399–409.

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

Thomas, P.A. & Polwart, A. (2003) *Taxus baccata* L. *Journal of Ecology*, **91**, 489–524.

Turnbull, L.A., Crawley, M.J. & Rees, M. (2000) Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, **88**, 225–238.

Verdú, M. & García-Fayós, P. (1996) Nucleation proceses in a Mediterranean bird-dispersed plant. *Functional Ecology*, **10**, 275–280.

Wenny, D.G. (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs*, **70**, 331–351.

Wenny, D.G. & Levey, D.J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences USA*, **95**, 6204–6207.

Whelan, C.J., Willson, M.F., Tuma, C.A. & Souza-Pinto, I. (1991) Spatial and temporal patterns of post-dispersal seed predation. *Canadian Journal of Botany*, **69**, 428–436.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.

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