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DISPERSAL SPECIAL FEATURE

Spatio-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees

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Summary

1. Initial recruitment, or the arrival and establishment of propagules, is the most variable period in the life cycle of long-lived plants, and the extent to which studies of initial recruitment can be used to predict patterns of regeneration remains unresolved.

2. We investigated the spatio-temporal dynamics of initial recruitment across five populations of three fleshy-fruited tree species from contrasting environments. Among-year variation in total seedfall, dispersed seedfall and seedling distributions was examined using analytical approaches that are new to the field and that explicitly incorporate space and allow comparisons among studies.

3. Observed patterns ranged from remarkable across-year consistency in seedfall distributions and strong spatial coupling between seed and seedling stages to extensive variation and almost complete independence of stages. Spatial distributions of frugivore-mediated seedfall were markedly more consistent than those of the total seedfall in two of the five populations. Seedling distributions were generally more variable among years than seedfall distributions.

4. All populations showed a positive relationship between the long-term mean density of recruitment at a given microsite and its year-to-year consistency. This relationship remained valid when considering only microsites away from fruiting tree canopies (i.e. those receiving actually dispersed seeds), and was virtually independent of their distance to the nearest fruiting tree.

5. *Synthesis*. Our results point to the existence of some general rules behind the idiosyncratic recruitment dynamics of perennial plant populations, which should help with projecting spatial patterns of plant establishment in long-lived species. In particular, those microsites that combine a great intensity with a high year-to-year consistency of recruitment should represent potential regeneration 'hotspots' whose identification and characterization can be of great use for the management and conservation of naturally regenerating tree populations.

Key-words: *Faramea occidentalis*, *Frangula alnus*, frugivory, generalized least squares linear models, *Prunus mahaleb*, SADIE, seed dispersal, seedling recruitment, spatial demography

Introduction

The period spanning seed release and early seedling establishment is potentially the most variable and least predictable transition in the life of long-lived plants, and the extent to which information on these early recruitment stages can be used to forecast landscape-scale patterns of regeneration in natural tree populations remains unresolved (Clark *et al.* 1999). Realistic estimates of plant establishment from seedfall or seedling distributions require spatially and temporally extensive sampling (Clark *et al.* 1998; Nathan & Muller-Landau 2000). However, 'the tendency to sample few stands for a single year and to avoid true replication at several spatial scales makes the literature on recruitment inadequate for assessing simple questions of broad interest' (Clark *et al.* 1999, p. 10). One such question is how consistent spatial patterns of propagule arrival and establishment are through time. The probability that a single seed dispersal event, or even all dispersal events to a given microsite during a single

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reproductive period, will result in the establishment of an adult plant is usually extremely small (Howe & Miriti 2004). In addition, any given site may be 'open' for recruitment in some years yet 'closed' in others (Schupp *et al.* 2002). It therefore is important to know whether there are sites that receive *consistently* more seeds than others, or whether patterns of seedfall change from year to year in a completely unpredictable manner. Further, it is important to know whether year-to-year consistency of seed delivery results in differential patterns of plant establishment. If this is the case, then microsites with consistently high seed input could represent 'hotspots' of population regeneration within the landscape, and their existence and spatial distribution would have important implications for management and conservation of naturally regenerating tree populations.

A number of empirical studies have assessed spatial patterns of seedfall and seedling emergence through multiple years, both within and outside the tropics (Houle 1994, 1998; Shibata & Nakashizuka 1995; Iida & Nakashizuka 1997; Nathan *et al.* 2000; DeSteven & Wright 2002; Hampe 2004; Beckage *et al.* 2005; Wright *et al.* 2005). Regardless of the particular species and the processes involved, recruit density and mortality are typically extremely heterogeneous both in space and time. Unfortunately, few studies have searched for relationships between these two components. Wright *et al.* (2005) compared both for 108 tree species growing on Barro Colorado Island and concluded that, at the whole-population level, initial recruitment was more variable in space than across years for all taxa. In contrast, Beckage *et al.* (2005) found that seedling survival of *Acer rubrum* varied seven times more across years than across sampling points. At the microsite scale, Nathan *et al.* (2000) observed that seedfall densities of wind-dispersed *Pinus halepensis* were less variable across years beneath reproductive trees than away from them. It remains unknown, however, how spatial and temporal variation in recruitment dynamics interact across heterogeneous landscapes, which of these components has greater effects on landscape-scale patterns of regeneration in long-lived plants, and under which conditions.

In addition, empirical recruitment studies suffer from two major limitations that have hindered a more general understanding of the long-term dynamics of initial recruitment: (i) The idiosyncratic character of each particular study area and sampling design has so far precluded attempts to compare different studies and thereby inhibited a search for general relationships between the spatial and the temporal heterogeneity of initial recruitment (e.g. whether highly contagious recruit distributions are typically more stable through time than more homogeneous ones). (ii) Realistic interpretations of ecological data across complex landscapes require analytical approaches that work over multiple spatial scales while controlling for spatial autocorrelation of data. In particular, seedfall and seedling distributions are often strongly contagious and thereby inherently subject to spatial autocorrelation, but only two studies on wind-dispersed species (Houle 1998; Nathan *et al.* 2000) have, to our knowledge, ever explored this aspect. Several analytical techniques have recently been proposed for this aim (see e.g. Perry *et al.* 2002; Wagner & Fortin 2005 for reviews), and such new approaches are clearly needed to achieve both unbiased and mutually comparable estimates of recruitment patterns.

Here we quantify among-year variation in the spatial distributions of seedfall and of seedling emergence for five populations belonging to three vertebrate-dispersed woody plant species from a diverse array of environments (tropical moist forest, temperate riparian forest and Mediterranean mountain woodland). We consider that both the seed dispersal and establishment stages are two biologically relevant components of final recruitment patterns, and we use a broadened definition of recruitment encompassing both processes (see e.g. Schupp & Fuentes 1995; Jordano & Godoy 2002; Schupp *et al.* 2002). Among-year variation among cohorts and between recruitment stages is quantified using the Spatial Analysis by Distance Indices (SADIE) technique (Perry *et al.* 1999; Winder *et al.* 2001). This analytical approach overcomes the shortcomings of previous studies mentioned above, as SADIE compares the spatial distributions of geographically referenced census data and produces standardized measures of their similarity that allow a direct comparison of different studies. Based on our five examples, we address the following specific questions: (i) How consistent are spatial patterns of seedfall and of seedling emergence from one year to another? (ii) Are among-year differences in seedfall patterns mostly triggered by variation in individual plant fecundity or by frugivore behaviour? (iii) How strong is the spatial concordance between seedfall and the resulting seedling emergence the following year, and how much does this vary among reproductive seasons? (iv) Does a relationship exist between the long-term abundance of recruits at specific microsites in the landscape and the among-year variation in abundance? Microsites that experience both a great intensity and a high year-to-year consistency of recruitment should represent potential 'hotspots' of initial plant establishment. If so, their identification and characterization might help predict spatial patterns of regeneration in long-lived plants, even if empirical studies can only cover a small part of their generation time.

Methods

STUDY SYSTEMS AND FIELD SAMPLING

Our analysis was based on data from three species for which a detailed biological knowledge of recruitment dynamics has been achieved over multiple years (including phenology, seed dispersers and predators, germination biology, post-dispersal mortality factors, etc.). The following species were investigated: (i) *Prunus mahaleb* L. (Rosaceae, *Prunus* hereafter) grows scattered in open shrublands at mid-elevations in Spanish mountains. Two populations (Calarilla and Nava de las Correhuelas, hereafter Correhuelas) in the 'Sierra de Cazorla, Segura y las Villas' Natural Park (Jaén Province, SE Spain) were studied from 1997 to 1999. (ii) *Frangula alnus* subsp. *baetica* (Rev. & Willk.) Rivas Goday (Rhamnaceae, *Frangula* hereafter) is mostly restricted to headwaters of small creeks in mountains of southern Spain and northern Morocco. Two populations (Aljibe and Puerto Oscuro) in the 'Los Alcornocales' Natural Park (Cádiz

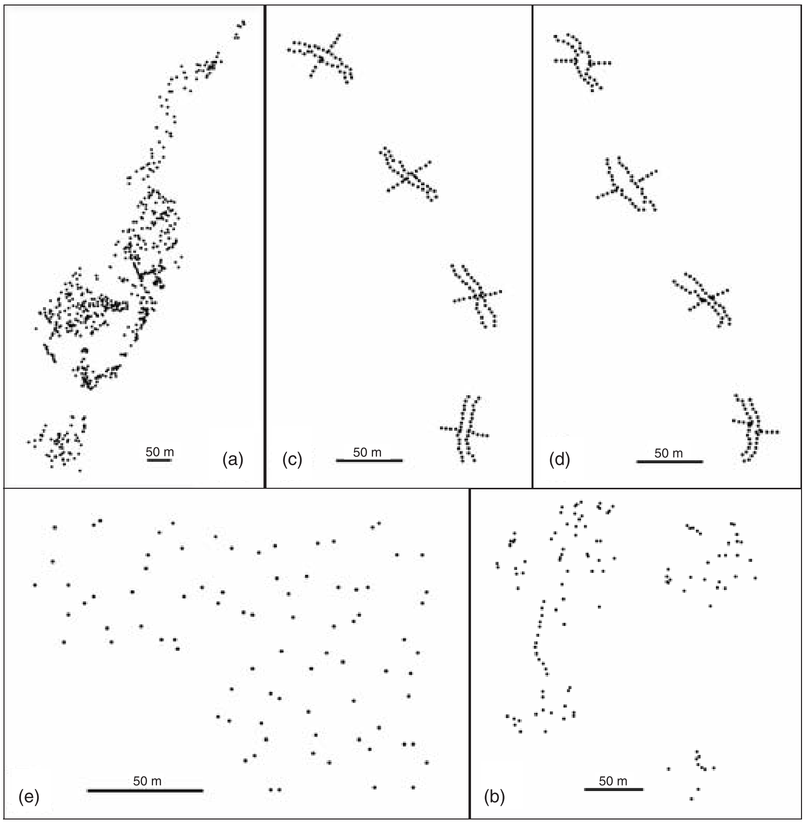

Fig. 1. Spatial arrangements of sampling points used for seedfall and seedling censuses in the five investigated populations: (a) *Prunus* Nava de las Correhuelas (COR); (b) *Prunus* Calarilla (CAL); (c) *Frangula* Aljibe (ALJ); (d) *Frangula* Puerto Oscuro (PTO); (e) *Faramea* (BCI). The complete population areas were covered in the two *Prunus* stands, whereas representative population subsets were censused in *Faramea* and *Frangula* (see Table 1 for further details).

Province, SW Spain) were studied from 2000 to 2003. (iii) *Faramea occidentalis* (L.) A. Rich. (Rubiaceae, *Faramea* hereafter) is widely distributed in the tropical moist forest of the Smithsonian Tropical Research Institute facilities on Barro Colorado Island, Panama, where one population was studied from 1982 to 1986.

The three species differ greatly in the spatial and the demographic structure of their populations and the surrounding vegetation. *Prunus* is patchily distributed in a very heterogeneous landscape of meadows and rocky outcrops intermingled with patches of dense scrub and pine stands. *Frangula* is limited to narrow (usually 10–20 m wide) but dense riparian forests surrounded by sclerophyllous oak woodlands. In contrast to the other two species, it experiences extensive secondary seed dispersal by peak water flow following heavy winter rainfalls (Hampe & Arroyo 2002; Hampe 2004). *Faramea* forms extensive, dense stands in a relatively homogeneous forest with a relatively open understorey. Table 1 and Supplementary Figure S1 in the Online Appendix present numerous details on the populations and the sampling; further detailed descriptions can be found in Schupp (1990, 1992), Jordano & Schupp (2000), Hampe & Bairlein (2000), García-Castaño (2001), Hampe (2004, 2005) and García *et al.* (2007). In particular, no species forms a significant persistent seedbank and therefore seedlings emerging in a given year were related to seeds produced the year before.

Sampling followed similar procedures in all populations and was designed to enable a fine-scale analysis, at the microsite level, of the spatial patterns of seedfall and subsequent seedling emergence. Permanent sampling points were established using stratified random designs (described in detail in the above cited works) aimed at achieving a representative coverage of the target populations and their landscape context (Fig. 1). All points were GIS-mapped and seed traps were placed prior to each fruiting season and censused regularly. In the case of *Frangula* and *Prunus*, these consisted of a pair of aluminium trays (30 × 20 cm for *Frangula*, 32 × 26 cm for *Prunus*) covered with a mesh wire that allowed fruits to pass through but prevented seed predation by rodents. Seedfall censuses were conducted and seeds were categorized by whether they had been handled by frugivores or not (i.e. remained within the intact fruit). Seedling emergence was monitored weekly to fortnightly (*Frangula*) or once per year briefly after the germination period (*Prunus*) in a marked area adjacent to the seed traps that was left untouched throughout the study. For *Faramea,* 1 × 1 m seed traps made of 1.5-mm mesh plastic window screening in a PVC frame were established *c.* 1.5 m above ground level. Seeds were removed weekly from the traps, counted (likewise distinguishing between handled and non-handled seeds) and scattered in a marked plot directly beneath the trap; these plots were then censused for seedling emergence the following wet season. Sampling covered the entire populations in *Prunus* and representative population subsets in the other two species. Overall, we consider that sampling designs were consistent enough to allow reasonable comparisons of the three species.

STATISTICAL ANALYSES

We used the SADIE technique to assess (i) levels of spatial association among seed or seedling distributions recorded in different study years, and (ii) spatial associations between seedfall patterns in a year and seedling patterns the following year. SADIE has been developed for the spatial analysis of ecological data in the form of spatially

Table 1. Principal features of the five investigated populations and the conducted sampling

Species	*Prunus*		*Frangula*		*Faramea*
Approximately plant longevity (years)	80		60		> 150
Start of fruit production (years)	15–20		20		> 20
Fruit type	Drupe		2–3 seeded berry		Drupe
Vegetation type	Open Mediterranean woodland		Riparian forest		Moist tropical forest
Main seed dispersers	Passerine birds (mainly *Sylvia* spp., *Turdus* spp., *Erithacus rubecula*, *Phoenicurus ochruros*)		Passerine birds (mainly *Sylvia* spp., *Turdus* spp., *Erithacus rubecula*)		Monkeys (*Alouatta palliata*, *Cebus capucinus*), Guans (*Penelope purpurascens*)
Persistent seed bank	Negligible		Negligible		Non-existent
Study years	1997–1999		2000–2003		1982–1985
Population	Correhuelas	Calarilla	Aljibe	Puerto Oscuro	Barro Colorado Island
Coordinates	37°56′N, 2°52′W	37°56′N, 2°53′W	36°31′N, 5°36′W	36°30′N, 5°35′W	9°09′N, 79°51′W
Approximately altitude (m, a.s.l.)	1650	1700	450	650	165
Population area sampled (ha)	20.6	5.1	0.5	0.5	6.0
No. fruiting plants	Approximately 200	35	39	67	Approximately 1880
No. sample points	613	120	126 (seedfall) 168 (seedlings)	126 (seedfall) 168 (seedlings)	84
Total area sampled (m^2)	203.5	39.8	62.7	70.7	84
No. years seedfall	3	2	3	3	4
No. years seedlings	3	3	4	4	4
Seed–seedling transitions	2	2	3	3	4
Total recorded seedfall	7619	991	2754	947	3207
Total recorded seedlings	395	36	1787	1354	2381
Percent seeds handled by frugivores	40	36	52	69	74

Information from Croat (1978), Schupp (1990), O'Brien *et al.* (1995), Jordano & Schupp (2000), Hampe & Bairlein (2000), García-Castaño (2001), Hampe (2004, 2005), and unpublished data (*Prunus*: P. Jordano and J.L. García-Castaño; *Frangula*: A. Hampe; *Faramea*: E.W. Schupp).

referenced counts (Perry *et al.* 1999, 2002). Its conceptual approach differs from most other spatially explicit analyses in that it seeks to identify those areas where patches of high- or low density cluster. This is done by ascribing an index to each sampling point that quantifies the degree to which the count at that location contributes to this clustering. The outcome of this interpolation procedure may be presented as a map of density isolines, which is a great advantage over other autocorrelation techniques such as Moran's I that do not allow identification of clusters and gaps in space. Winder *et al.* (2001) have proposed an association test for two SADIE data sets that examines the spatial similarity of their cluster-and-gap distributions. The corresponding association index, X_p, ranges between +1 (complete spatial association) and –1 (complete dissociation), with 0 indicating spatial independence. The extent of association can be tested statistically by a permutation procedure. Because the index itself and its test rely exclusively on the referenced count data without assuming any underlying distribution, outcomes are comparable across populations and sample designs of very different spatial structure, as in the present case. SADIE analyses were conducted with the software SadieShell v1.22 (Conrad 2001). Significance levels of X_p were Bonferroni corrected to account for multiple testing.

We also fit generalized least squares linear models (GLS, hereafter) to address the relationships between the long-term mean abundance of recruits and the among-year variation of recruits at given sampling points while accounting for potential effects of spatial autocorrelation of the data. Contrary to ordinary GLM, this class of extended linear models allows the errors of variables to be correlated and/or to have unequal variances (Pinheiro & Bates 2000), which makes them suitable to control for potential spatial autocorrelation of the census data. Different correlation structures can be incorporated into models and these are then tested against each other to select the model with the greatest explanatory power. We included as independent variables the spatial coordinates of sampling points and the mean number of seeds or seedlings recorded at each sampling point per year ($\log(x + 1)$-transformed). The dependent variable was the coefficient of variation (CV) across years of seed or seedling numbers recorded at a given sampling point ($\log(x + 1)$-transformed). We evaluated several models with different correlation structures (independent, linear, exponential, Gaussian, ratio quadratical and spherical) and found that they produced only very slightly different slope estimates and that their explanatory powers did not differ statistically. Therefore, we report results of the independent models throughout for consistency, although sometimes an alternative model produced a slightly lower AIC value ($\Delta\text{AIC} \leq 2$). It is well known that relationships of the form X vs. Y/X commonly yield r values in the range 0.52–0.63, generally negative, especially when $\text{CV}_X >> \text{CV}_Y$ (Brett 2004). Thus, we tested the significance of the regressions against bootstrapped estimates after 5000 resamplings, as suggested by Brett (2004). GLS and bootstrap analyses were conducted using the nlme and bootstrap packages of R software v2.2.1 (R Development Core Team 2006).

GLS were conducted in a first step involving total seedfall, handled seedfall and seedling emergence across all sampling points. A second analysis considered only frugivore-handled seedfall and those sampling points that were at least 1 m away from the nearest fruiting canopy in order to elucidate whether observed relationships also hold for actually dispersed seeds. In addition to the long-term mean density of recruits, this analysis included the distance of sampling points to the nearest fruiting tree canopy (log-transformed) as a second independent variable. This combination of analyses allowed us to disentangle whether observed trends were primarily due to fruiting patterns or to disperser activity.

Results

AMONG-YEAR VARIATION AND SPATIAL CONCORDANCE OF SEEDFALL AND SEEDLING EMERGENCE

Despite the relatively limited duration of the studies (3–4 years), the extent of among-year variation in seedfall and seedling patterns differed greatly in both among- and within-species. Observed patterns ranged from remarkable among-year consistency in patterns and clear spatial coupling between recruitment stages to extensive variation across years and almost complete independence of stages (see Fig. 2, Table 2 for detailed results).

Prunus

Year-to-year consistency of total seedfall, frugivore-handled seedfall and seedling distributions was considerable in this species. X_p values were significant for all pairwise comparisons between years. Seedfall and seedling emergence were also spatially concordant in three of the four comparisons (and marginally so in the fourth). Although the trend was the same at both study sites, the Calarilla population had consistently, and often markedly, higher X_p values than the Correhuelas population.

Frangula

Patterns were much more complex than in *Prunus*. In the Aljibe population, seedfall was positively associated across all years, and X_p values resembled those of *Prunus* at Correhuelas. In contrast, the Puerto Oscuro population produced similar seedfall distributions in the first two seasons, but a very distinct one in the third. Notably, patterns of frugivore-handled seedfall were – often markedly – more consistent among years than those of the total seedfall in both populations. Patterns of seedling emergence usually changed greatly from year to year. It seems notable, however, that both populations showed remarkably similar X_p values for a given comparison of seedling cohorts. Transitions between seedfall and seedling stages ranged widely from significant association to significant dissociation.

Faramea

Seedfall patterns were consistent in space through three of the four study years, whereas one year deviated somewhat from the general pattern. Total and frugivore-handled seedfall were similar in this species. No seedlings were observed in year 3, which was excluded from the analyses. Two of the three remaining comparisons resulted in significant association of yearly spatial patterns of emergence. As in *Prunus*, however, most X_p values at the seedling stage were smaller than those of the corresponding seedfall stage. Considering the seedfall–seedling transitions, *Faramea* had a marked spatial association in one year, a slight but non-significant one in another, and none at all in the third.

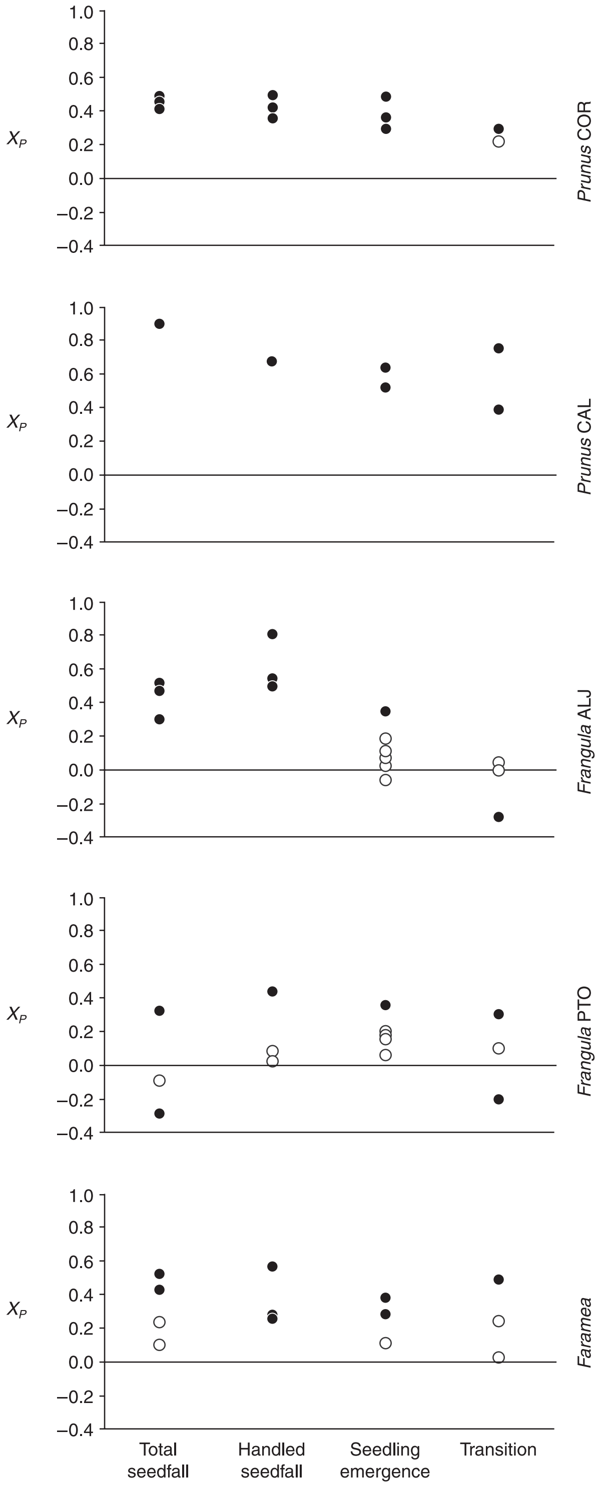

Fig. 2. Spatial Analyses by Distance Indices (SADIE) for total seedfall, frugivore-handled seedfall and seedling data of the five populations, as well as the transition between total seedfall and seedling emergence of the following year. Filled circles indicate significant relationships, empty circles non-significant ones. Detailed results of the pairwise comparisons between study years are shown in Table 1. *X*p is the SADIE statistic for spatial concordance between years (see Statistion a Analysis Section).

LONG-TERM ABUNDANCE AND AMONG-YEAR VARIABILITY OF RECRUITMENT

Despite the wide range of patterns encountered, all populations and recruitment stages showed a significant negative relationship between the across-year mean density of recruits and their among-year variation at a given microsite (Table 3). In other words, greater long-term abundance of initial recruitment was significantly associated in space with greater year-to-year consistency. Although highly significant, the relationship was usually weak ($-0.2 < \text{slope} < 0$ on a log–log scale), except for seedling emergence in the two *Prunus* populations (slopes of –0.26 and –0.51, respectively). Slopes were steeper for handled seedfall than for total seedfall in three of the five populations (Table 3), highlighting the contributions of seed disperser behaviour to this relationship. This interpretation was clearly corroborated by the second GLS that considered only actually dispersed seeds (Table 4). Notably, this second analysis demonstrated that the among-year variation of initial recruitment (including both seedfall and seedling emergence) is markedly more affected and better predicted by the long-term mean recruit density itself than by the distance of sampling points to the nearest fruiting tree canopy. When only the actually dispersed seedfall was considered, seedfall density and distance to the nearest tree were usually not tightly correlated ($-0.27 < r < 0$, $P > 0.05$ for *Faramea* and *Frangula*; $r = -0.30$, $P = 0.001$ for *Prunus* CAL, $r = +0.11$, $P = 0.001$ for *Prunus* COR).

Discussion

AMONG-YEAR CONSISTENCY OF INITIAL RECRUITMENT PATTERNS

Among-year variation in seedfall and seedling distributions is usually ample and spatial concordance between stages is often weak due to secondary movements and mortality of propagules (Schupp & Fuentes 1995; Clark *et al.* 1999). Our analyses across five different populations from three contrasting ecosystems clearly demonstrate that the year-to-year patterns of seedfall and seedling emergence may range from remarkable consistency to almost complete unpredictability both across- and within-species. This diversity seems particularly striking given that our data sets covered only three to four different reproductive events, respectively (i.e. between 5% and 15% of species' average adult lifetimes), and are therefore likely to depict only a limited extent of a population's long-term reproductive variability (Pimm & Redfearn 1988).

Spatial patterns of seedfall were positively related (i.e. spatially concordant) in all populations across most study years, except for the third cohort of the *Frangula* Puerto Oscuro population and, to a lesser extent, the third cohort of the *Faramea* population. In the former case, data on yearly fruit crop sizes of mapped individuals (A. Hampe, unpublished data; see also Hampe 2004) indicate that observed differences in seedfall density at given sampling points can be explained largely by variation in crop sizes of surrounding trees. Comparable data are not available for *Faramea*, but the year

Table 2. Spatial Analyses by Distance Indices (SADIE) for total seedfall, handled seedfall and seedling data of the five populations, as well as the transition between total seedfall and seedling emergence of the following year. Columns indicate the cohorts included in the pairwise tests and the association index X_p as described in Winder *et al.* (2001)

Stage	Cohort	*Prunus* COR	*Prunus* CAL	*Frangula* ALJ	*Frangula* PTO	*Faramea* BCI
Total seedfall	1–2	–	–	–	–	0.36**
	1–3	–	–	–	–	0.10
	1–4	–	–	–	–	0.52***
	2–3	0.45***	0.89***	0.48***	0.32**	0.35***
	2–4	0.48***	–	0.51***	–0.29***	0.43***
	3–4	0.41***	–	0.31**	–0.09	0.23
Handled seedfall	1–2	–	–	–	–	0.26*
	1–3	–	–	–	–	–†
	1–4	–	–	–	–	0.56***
	2–3	0.49***	0.67***	0.53***	0.44***	–†
	2–4	0.42***	–	0.81***	0.08	0.28**
	3–4	0.36***	–	0.55***	0.03	–†
Seedling emergence	1–2	0.36**	0.63***	0.02	0.06	0.38**
	1–3	0.48**	0.63***	0.19	0.19	–†
	1–4	–	–	0.11	0.17	0.28*
	2–3	0.29*	0.51***	–0.05	0.16	–†
	2–4	–	–	0.07	0.18	0.11
	3–4	–	–	0.35*	0.35*	–†
Transition from total seedfall to seedling emergence	1	0.29**	0.38**	0.00	0.30**	0.24
	2	0.22	0.75***	–0.27***	–0.21***	0.03
	3	–	–	0.05	0.10	–†
	4	–	–	–	–	0.49***

Asterisks denote Bonferroni-corrected significance levels of X_p. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. – = no data available.
†No records of either handled seedfall or seedlings in year 3.

Table 3. Relationship between long-term mean density and among-year variation of recruitment at sampling points. The bootstrapped estimates of the linear model slopes are shown with their 1st and 3rd quartile in brackets

	Total seedfall		Handled seedfall		Seedling emergence	
	Intercept	log (density)	Intercept	log (density)	Intercept	log (density)
Prunus COR	0.404	–0.062 [–0.068, –0.055]***	0.418	–0.102 [–0.109, –0.094]***	0.426	–0.256 [–0.289, –0.222]***
Prunus CAL	0.364	–0.103 [–0.135, –0.079]**	0.389	–0.182 [–0.215, –0.134]***	0.497	–0.511 [–0.559, –0.472]***
Frangula ALJ	0.469	–0.095 [–0.105, –0.086]***	0.563	–0.167 [–0.174, –0.160]***	0.476	–0.075 [–0.089, –0.061]***
Frangula PTO	0.481	–0.113 [–0.127, –0.099]***	0.503	–0.133 [–0.146, –0.120]***	0.455	–0.049 [–0.063, –0.037]**
Faramea BCI	0.435	–0.106 [–0.115, –0.098]***	0.438	–0.118 [–0.129, –0.108]***	0.461	–0.093 [–0.106, –0.082]***

Significance levels (tested with randomization, $N = 5000$ resamplings) for the slopes of log (density). **$P < 0.01$, ***$P < 0.001$. All intercepts were highly significant ($P < 0.0001$).

Table 4. Relationship between long-term mean density and among-year variation of recruitment at sampling points, based on actually dispersed seeds (i.e. those ingested and delivered away from fruiting trees). The distance of sampling points to the nearest fruiting tree canopy was included in this analysis. The bootstrapped estimates of the slopes are shown with their 1st and 3rd quartile in brackets

	Prunus COR	*Prunus* CAL	*Frangula* ALJ	*Frangula* PTO	*Faramea* BCI
Intercept	0.401	0.351	0.587	0.552	0.434
log (density)	–0.107 [–0.116; –0.098)***	–0.171 [–0.214; –0.137]***	–0.170 [–0.184; –0.156]***	–0.148 [–0.167; –0.130]***	–0.172 [–0.190; –0.157]***
log (tree distance)	0.016 [0.010; 0.022]**	0.022 [–0.014; 0.060]$^{\mathrm{ns}}$	–0.031 [–0.055; –0.009]*	–0.043 [–0.062; –0.024]**	0.059 [0.031; –0.086]$^{\mathrm{ns}}$

Significance levels (tested with randomization, $N = 5000$ resamplings) for the slopes of log (density) and log (tree distance). *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; ns, not significant. All intercepts were highly significant ($P < 0.0001$).

in question had much smaller fruit crops than the other study years with most trees failing to fruit. Hence, exceptions from the usual year-to-year consistency of seedfall patterns are apparently triggered by variation in fruit production of individual trees rather than by changes in the behaviour of seed-dispersing animals. It seems noteworthy that in both *Frangula* populations the among-year consistency of frugivore-handled seedfall exceeded that of the total seedfall throughout the entire study (Table 2), strong evidence of relatively invariable disperser behaviour (see also Hampe 2008). *Frangula* and *Prunus* are mainly dispersed by relatively stable breeding and early post-breeding bird communities (Hampe & Bairlein 2000; Jordano & Schupp 2000; Hampe 2001), and the major seed dispersers of *Faramea* are also likely to exhibit little year-to-year variation in abundance (Milton 1982; Oppenheimer 1982). Effects of variable disperser service might be greater for plants relying on migrant or overwintering bird communities with strong interannual fluctuations (Jordano 1993). It seems unlikely, however, that they would yield the remarkable extent of temporal variability reported for wind-dispersed species (Houle 1994, 1998; Nathan *et al.* 2000).

We observed a much greater diversity of patterns at the seedling stage. Although among-year consistency of spatial distributions tended to decrease from the seedfall to the seedling stage across all populations, the two *Prunus* stands displayed markedly more consistent seedling distributions than the other two species. Likewise, the spatial concordance between seedfall and seedling patterns was greatest in *Prunus*. The other two species also had similar seedling distributions in some years, but not in others. In the same line, patterns of seedfall and of the resulting seedling cohorts were positively associated in only about half of the comparisons. Our results indicate that in both *Faramea* and *Frangula* the influence of (primary) seed dispersal on subsequent recruitment patterns is very irregular; consequently, dissemination limitation does not seem to be a major determinant of their recruitment patterns in the long-term, although in some years it may shape patterns of seedling emergence. In the case of *Frangula* this result is not surprising given the extensive secondary dispersal of seeds by peak water flows (Hampe & Arroyo 2002; Hampe 2004). In *Faramea*, post-dispersal seed predation might be most responsible for the spatial uncoupling of recruitment stages in two of three cohorts (Schupp 1990, 1992). In contrast, recruitment in the two *Prunus* populations appears to be determined largely by the comparatively consistent seedfall distribution. Two factors might be most responsible for this: (i) The *Prunus* populations experienced the lowest seed dispersal rates of the three species (see Table 1), resulting in a relatively high number of seeds landing beneath maternal trees. (ii) Most dispersed seeds were delivered to a relatively few spots within very heterogeneous landscapes due to marked microhabitat preferences of the main dispersers (Jordano & Schupp 2000). In contrast, both *Frangula* and *Faramea* experienced higher seed dispersal rates and they grow in relatively homogeneous habitats that do not affect disperser behaviour in the way observed in *Prunus* (Schupp 1990; Hampe 2001, 2004).

How much the interpretation of recruitment patterns may be affected by incorporating the spatial arrangement of census data into analyses is clearly demonstrated by the example of *Frangula*. Hampe (2004) examined spatio-temporal variation of seedfall and seedling abundance without explicitly considering sampling point location, instead using Spearman rank correlations. Results indicated great among-year consistency of seedfall and, to a lesser extent, seedling patterns, as well as a consistent lack of spatial concordance between the two recruitment stages. The SADIE approach used here draws a remarkably different and more complex picture that modifies conclusions in no less than four respects: (i) Seedfall patterns of the third cohort in the Aljibe population differed significantly from those of the other cohorts instead of showing a similar pattern; (ii) yearly patterns of seedling emergence were mostly unrelated with each other instead of showing significant consistency throughout the study; (iii) seedfall–seedling transitions ranged from significant spatial association to significant dissociation instead of being consistently weakly related with each other; and (iv) both populations coincided surprisingly well in their X_p values of seedlings and seedfall–seedling transitions, whereas no such coincidence had been detected before. This coincidence is not surprising, however, since the two populations are close to each other and therefore experience very similar precipitation regimes which in turn determine the impact of secondary seed dispersal.

Although seedfall and seedling census data are by their very nature spatially structured and hence susceptible to spatial autocorrelation, few studies have accounted for this by using appropriate analytical techniques (Keitt *et al.* 2002; but see Houle 1998; Nathan *et al.* 2000). To our knowledge, this study is the first to use the SADIE approach for a combined analysis of seedfall and seedling patterns, and it documents how SADIE's improved use of available information may considerably enhance interpretations.

RELATIONSHIP BETWEEN LONG-TERM ABUNDANCE AND AMONG-YEAR CONSISTENCY OF INITIAL RECRUITMENT

The single most basic feature that characterizes the recruitment potential of a microsite within the landscape is the propagule input it receives (Clark *et al.* 1998, 1999; Howe & Miriti 2004). We found that this key feature of microsites was related to the extent of among-year variation of recruitment at these sites, not only across all investigated populations with their sometimes disparate recruitment dynamics but also across the investigated recruitment stages. The often weak (slope usually $-0.2 < \text{slope} < 0$ on a log–log scale) but always highly significant negative relationship indicates that microsites receiving abundant recruits over the relatively long-term have recruit arrival spread more evenly through time than do microsites with little overall recruitment. Successful establishment of long-lived plants is often restricted to a window of particularly favourable conditions (e.g. years with high precipitation, opening of forest gaps, etc.; see e.g. Eriksson & Fröborg 1996;

Schupp *et al.* 2002; Beckage *et al.* 2005), and the likelihood that recruitment events at a given microsite occur during these favourable conditions is a function not only of the absolute number of propagules arriving but also of the distribution of propagule arrival in time. Therefore, those microsites which combine the most intense with the most regular recruitment should represent potential 'hotspots' with a disproportionately high prospect of successful plant establishment in the relatively long-term. Note, however, that this likelihood may be still very small and scarcely detectable in the course of a typical short-term research project (Clark *et al.* 1999; Howe & Miriti 2004).

Importantly, the described effect is not simply generated by a strong difference between high density sampling points beneath fruiting canopies and low density points away from fruiting canopies. Instead, the activity of seed dispersers seems to play a significant role in creating these patterns, as the observed relationship was often stronger when considering only frugivore-handled seedfall instead of total seedfall. More importantly, it also persisted when only actually dispersed seeds (i.e. those ingested and subsequently deposited away from fruiting plants) were considered. It is well known that dispersers deliver seeds preferably to certain microsites in the landscape (Jordano & Schupp 2000; Schupp *et al.* 2002; Carlo & Morales 2008; Levey *et al.* 2008), and our results suggest that these sites are relatively stable from one year to another. Whether a microsite receives many dispersed seeds or not in many cases depends on its structural features, because frugivore movements are often greatly affected by vegetation structure (Jordano & Schupp 2000; Jordano & Godoy 2002). In contrast, we found no clear link between propagule arrival in microsites – neither in mean density nor in among-year variation – and their proximity to fruiting adult trees. Although this result is in clear contrast with patterns observed in some other species (e.g. Houle 1994, 1998; Clark *et al.* 1998; Nathan *et al.* 2000), it is not very surprising. As noted above, in many ecosystems the strong influence of the landscape context on dispersers' post-foraging movements is likely to make habitat structure a more important driver of patterns of seedfall than distance from a fruiting tree. Other forms of spatially contagious seed dispersal created by such processes as dispersal to fruit-processing roosts, dispersal to display sites and others may also frequently obscure the expected steady decline in density of seedfall with distance from the parent (Schupp *et al.* 2002). In addition, the density of fruiting plants in all of our populations should result in a strong overlap of individual seed shadows (Alcántara *et al.* 2000).

On the other hand, the rather shallow slopes of the reported relationship also indicate that year-to-year variation in the spatial distributions of recruits (e.g. due to variation in tree fecundity) most likely does not override the spatial heterogeneity of recruitment events. This result corroborates Wright *et al.*'s (2005) results for numerous animal-dispersed tropical tree species, whereas it contrasts with other observations from populations with a more continuous distribution of fruiting trees, greater variation in fecundity (i.e. pronounced masting) and/or less clumped seed dispersal distributions, such as in *Betula* and other small-seeded, wind-dispersed species (Houle 1994, 1998; Clark *et al.* 1998; McEuen & Curran 2004).

Interestingly, the GLS models showed remarkably similar slopes for seedfall and for seedling emergence both in the *Faramea* stand and in the two *Frangula* populations. This similarity between the two recruitment stages indicates that processes acting on seeds between their dispersal and germination (such as seed mortality or secondary movements on the ground) do not appear to significantly counteract the reported relationship. In other words, although mortality factors such as seed predation are commonly density-dependent within a given year (see e.g. Schupp 1992 for the *Faramea* case) and their impact tends to vary greatly among years, they do not systematically change the way recruitment patterns vary from year to year at a landscape scale (see also García *et al.* 2005). In contrast, the two *Prunus* populations showed a much more pronounced slope at the seedling emergence stage, thereby suggesting (i) that seedling emergence at microsites with low propagule input is not only rarer but also considerably more irregular than seed delivery itself, and (ii) that the effects of post-dispersal processes on recruit distributions change from year to year (and differently for high- and low density microsites). This latter effect might result from the interplay of a very heterogeneous landscape structure and strong yearly variation in the climatic conditions. In fact, differences among microhabitats in post-dispersal seed predation and seed germination rate (García-Castaño 2001; P. Jordano & E. W. Schupp, unpublished data) are likely to vary from one year to another. In principle, seedbank dynamics might also result in a markedly more regular seedling emergence at microsites with higher propagule input; however, a seedbank is almost non-existent in the studied *Prunus* populations (see Table 1).

Recruitment hotspots in populations of long-lived species need to have two major characteristics: First, they must receive a sufficiently high and regular seed input to allow a disproportionately high probability of establishment of recruits. Our study demonstrates that such sites may be present in many natural populations of fleshy-fruited species. Second, recruits established at such sites should not experience a disproportionately high mortality. Therefore, sites located beneath fruiting trees are not likely to represent recruitment hotspots, even though they may receive huge amounts of seeds. Instead, the most likely candidates for hotspots are those sites away from canopies that are relatively often used by seed dispersers (Jordano & Godoy 2002; Schupp *et al.* 2002; Carlo 2005; Kwit *et al.* 2007). Here, seed densities should be high enough to allow regular plant establishment but low enough to escape strong density-dependent mortality; in other words, some intermediate density. Direct identification of such sites as recruitment hotspots would require many years of plant monitoring; indirect evidence for their existence is abundant, however, as a great number of studies have described agglomerations of saplings or adult plants beneath sites known to attract frugivorous seed dispersers (such as perches or roosting sites; see e.g. Verdú & García-Fayos 1996; García *et al.* 2000; Deckers *et al.* 2005; Milton *et al.* 2007).

Conclusion

There has been much interest in whether, and, if so, how, year-to-year variation in reproductive output provides advantages for recruitment in long-lived plants (Kelly & Sork 2002; Wright *et al.* 2005). Little attention has been paid, however, to the long-term demographic consequences of this variation within realistic landscape contexts, despite its relevance for understanding population dynamics of long-lived plants within both natural and managed ecosystems (Clark *et al.* 1999; Howe & Miriti 2004). Studies spanning only a few years can never track real patterns of regeneration in populations with generational turnover of decades or centuries. Year-to-year variation of spatial recruitment patterns has important biological consequences, however, and should not be treated as a noise to be ignored. Our analysis demonstrates that even studies spanning only a few years can help elucidate general relationships behind year-to-year recruitment variability. Here, we have only explored two basic features that influence the recruitment potential of microsites: their propagule input and their proximity to fruiting trees. GIS-based approaches incorporating microsites' abiotic and biotic environments coupled with data collection over more years than our limited sample will greatly contribute to our understanding of how initial recruitment dynamics translate into overall population dynamics of long-lived organisms, and to implement this knowledge into the management and conservation of forest ecosystems.

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Supplementary material

The following supplementary material is available for this article:

Figure S1 Spatial distributions of mean recruit abundance and its among-year CV across the study populations of *Prunus mahaleb*, *Frangula alnus* and *Faramea occidentalis*.

This material is available as a part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2008.01364.x
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