

# Extensive hydrochory uncouples spatiotemporal patterns of seedfall and seedling recruitment in a 'bird-dispersed' riparian tree

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## Summary

**1** Initial recruitment is by far the most variable and least predictable phase of the plant life cycle. Its dynamics remain little known, particularly in complex seed dispersal systems and over multiple reproductive cycles.

**2** Seeds of the tree *Frangula alnus* are usually dispersed by frugivorous birds. Mediterranean populations, however, are mostly restricted to riparian forests, and their seeds may be re-distributed during the winter by elevated stream water flow. Strength and frequency of peak discharges vary greatly from year to year. I investigated spatiotemporal variation of initial recruitment by monitoring fruit production, seedfall and seedling emergence over 4 years along permanent transects in two *F. alnus* populations growing along small mountain streams in southern Spain.

**3** Seedling abundance varied greatly among years and independently of fruit or primary seedfall abundance. Spatial distributions of both seedfall and seedling emergence were highly consistent among years. Bird-mediated seedfall density decreased exponentially with both increasing distance from the nearest fruiting tree and the decrease of its crop size. Seedling emergence was, however, uncoupled in space from the previous year's seedfall, both across single sample points and entire 60-m transects. Dispersal experiments with seed mimics revealed that flooding caused secondary dispersal of much of the population seed pool over several scores of metres.

**4** Seed re-distribution by water appears to override patterns of primary (bird-generated) seedfall and to determine spatial patterns of seedling recruitment. Seedling emergence is, however, more stable across years than would be expected given the unpredictability of rainfall (and thus stream flow), suggesting that seed deposition may be primarily determined by relatively stable microsite characteristics.

**5** The dynamics of seed rain patterns are of critical importance for plant population demography and spatial structures. The finding that even complex, multistep dispersal systems may produce remarkably consistent year-to-year distributions of recruits has important implications for the interpretation of long-term patterns of riparian plant regeneration at the landscape level and resulting conservation management.

*Key-words:* bird dispersal, hydrochory, hydrology, interannual variation, landscape features, Mediterranean climate, secondary seed dispersal, seed rain, seedling emergence, spatial autocorrelation

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## Introduction

Seed dispersal is a key process in plant population dynamics and demography. It creates the initial

template for population recruitment by allowing seeds to reach suitable microhabitats and to increase their chance of survival and establishment (Nathan & Muller-Landau 2000). The dispersal of seeds to safe establishment sites is often a complicated multistage process, and the processes and treatments a seed experiences during successive stages have important effects on its ultimate fate (Chambers & MacMahon 1994;

Vander Wall & Longland 2004). A detailed knowledge of seed movements is therefore necessary to bridge the gap between studies of seed dispersal and plant demography.

The great spatiotemporal variability inherent in seed dispersal and recruitment processes has largely been ignored (Clark *et al.* 1999a). Studies 'are most often conducted in single populations and single seasons, over short distances and without consideration of the microsite' (Nathan & Muller-Landau 2000, p. 278), yet the phase from seed release until seedling establishment is by far the most variable and least predictable stage of the plant life cycle (Schupp & Fuentes 1995; Clark *et al.* 1999a). This variability appears particularly large in regions of strongly seasonal climate, such as cool temperate forests or semi-arid Mediterranean-type woodlands, where the lag between seed release and germination often amounts to several months and the biotic and abiotic factors that affect seeds during this period may vary considerably in both space and time (Houle 1994, 1998; Jordano & Herrera 1995; Shibata & Nakashizuka 1995; Tomita *et al.* 2002). More spatially extensive and longer duration sampling is therefore needed to adequately describe seed dispersal systems in these regions (Clark *et al.* 1999a).

A number of recent studies that have analysed spatial patterns of seed dispersal and seedling recruitment over multiple years (Streng *et al.* 1989; Houle 1994, 1998; Jones *et al.* 1994; Forget 1997; Clark *et al.* 1998, 1999a; Connell & Green 2000; Nathan *et al.* 2000) all show significant between-year variation in the spatial distribution of both seedfall and seedling emergence. Moreover the two patterns are often uncoupled, presumably due to post-dispersal processes (e.g. seed re-distribution, predation or germination), although these events have rarely been identified in the field (but see Schupp 1995; Jordano & Herrera 1995; Tomita *et al.* 2002).

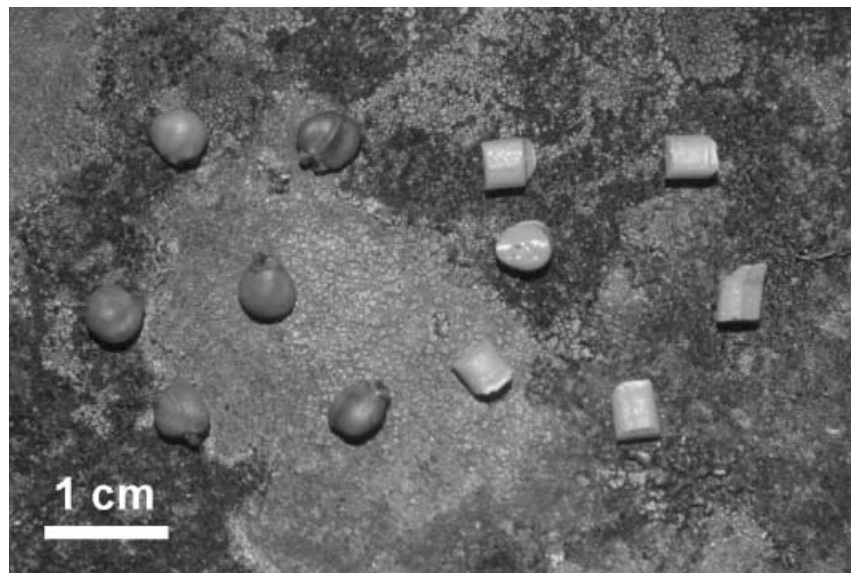
The present study describes the spatial patterns of seedfall and seedling recruitment over 4 years in two populations of the tree *Frangula alnus* ssp. *baetica* (Rev. & Willk.) Rivas Goday ex Devesa (Rhamnaceae). The taxon is endemic to riparian forests, such as in the study area in southern Spain, and is a typical representative of the numerous climatic relict species in these communities that were widely distributed over Europe during the Tertiary, but are today restricted to isolated refugia in the south-western Mediterranean Basin and on the Macaronesian Islands. The species' fruits are regularly consumed, and its seeds dispersed, by members of the resident breeding bird community (Hampe 2001) and elevated stream flow after heavy winter rains appears to re-distribute the bird-dispersed seeds (Hampe & Arroyo 2002; see also Barat-Segretain 1996). Seedfall patterns generated by resident, territorial frugivores are usually heterogeneous in space, but are probably relatively stable among years, although this assumption has never been tested empirically (Schupp & Fuentes 1995; Nathan & Muller-Landau 2000). In contrast, the dispersal of seeds by stream flow is largely determined by precipitation,

which in all Mediterranean-climate regions changes greatly from year to year (Gasith & Resh 1999). Complex dispersal systems with (a variety of) both primary and secondary vectors are generally poorly understood because of lack of data (Levey & Byrne 1993; Vander Wall 2002; Vander Wall & Longland 2004). In particular, patterns of seed dispersal by stream water have never, to my knowledge, been quantified for a population with multi-step dispersal, although their importance for structuring riparian plant communities has been documented by both observational and experimental studies (Nilsson *et al.* 1991; Andersson *et al.* 2000; Merritt & Wohl 2002; Nilsson *et al.* 2002; Shafroth *et al.* 2002). The present study follows the abundance and spatial distributions of seedfall and of seedling emergence over 4 years and examines the degree of spatial coupling between these two demographic stages over three reproductive cycles. It also evaluates the impact of secondary dispersal by water on bird-mediated seedfall in years with different rainfall.

### Study system

*Frangula alnus* Miller is a deciduous shrub or small tree that grows over most of temperate Europe and western Asia (Hampe *et al.* 2003). The subspecies *F. a. baetica* is sparsely distributed across the mountain ranges of southern Spain and northern Morocco. It is a climatic relict of Tertiary origin (Hampe *et al.* 2003), currently in accelerated decline and considered vulnerable according to IUCN standards, and is therefore on the Spanish National Red List (Hampe & Arroyo 2002). Populations grow beside small mountain streams in the understorey of 10–15 m wide riparian forests that extend a few 100 m to a few kilometres along the stream and are surrounded by Mediterranean sclerophyllous and semi-deciduous forests (Hampe & Arroyo 2002). The reproductive biology of *F. a. baetica* has been described in detail by Medán (1994) and Hampe & Bairlein (2000a). Trees can grow up to 15 m tall and live for up to about 60 years. They do not reproduce vegetatively and therefore rely exclusively on regeneration from seed. Mature trees produce black berries that are 8–12 mm wide, usually contain three seeds (see Fig. 1, weight:  $37 \pm 16$  mg, mean  $\pm 1$  SD) and ripen between the end of June and mid-August or September. These are consumed by at least 12 species of the local breeding bird community, but > 95% of the seed dispersal is due to only three species (*Erithacus rubecula* L., *Sylvia atricapilla* L. and *Turdus merula* L.) (Hampe 2001). Seed dispersal by ants does not occur in the study area. A large percentage of the seeds germinate between late April and early June of the year after fruiting and there is no persistent seed bank (A. Hampe, unpublished data). Seedlings, which are easy to recognize shortly after emergence, grow quickly to 3–4 cm tall before unfolding their first leaves.

The study was carried out in two populations (Garganta del Puerto Oscuro and Garganta del Aljibe;



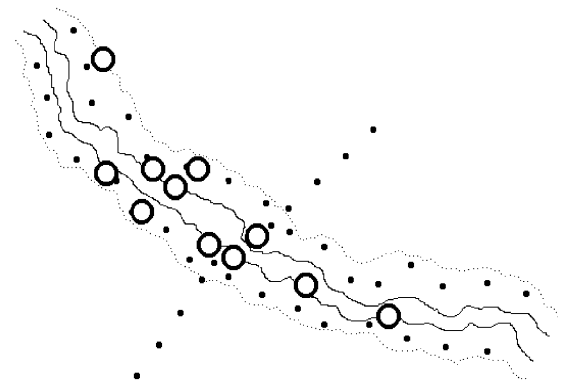
**Fig. 1** *Frangula alnus* seeds (left) and seed mimics made of coloured polyethylene (right) that were used for experiments on secondary dispersal by water.

hereafter termed Puerto Oscuro and Aljibe) located in gorges in the Aljibe Mountains about 40 km NNW of Gibraltar (36°30' N, 5°35' W; Cádiz Province, Spain). The two study sites are *c.* 5 km apart and separated by a major watershed. They are situated at 420–510 m (Aljibe) and 620–690 m (Puerto Oscuro) above sea level. Mean annual temperature of the area is about 16.7 °C, and rainfall averages 880 mm year<sup>-1</sup> (704 mm, 1380 mm, 634 mm and 1047 mm in the study years), with almost all precipitation falling between October and April. The winters maintained the same ranking when maximum rainfall within 24 h, 48 h or 1 week was considered instead of total precipitation (Picacho meteorological station, 3–4 km from the study areas; 'Los Alcornocales' Natural Park, unpublished data). The streams flow throughout the year, but discharge varies markedly between seasons, rising dramatically within a few hours of heavy winter rains. Accordingly, the area affected by peak winter discharges (hereafter termed winter riverbed) is considerably wider than the channel of continuous water flow. The intensity and frequency of peak discharges may differ considerably between winters. The riparian forests of the two gorges are similar, and *F. alnus* is common in the dense woody vegetation dominated by *Alnus glutinosa* (L.) Gaertn., *Rhododendron ponticum* ssp. *baeticum* (Boiss. & Reuter) Hand.-Mazz., *Nerium oleander* L., *Arbutus unedo* L., *Viburnum tinus* L. and *Quercus canariensis* Willd. Herbaceous vegetation is scarce, probably as a consequence of the violent winter water currents. Each *F. alnus* population contains between 1000 and 1500 adult trees and they are thus among the largest known populations of the subspecies. *F. alnus* trees grow exclusively within the winter riverbed, probably because the water table remains close to the surface even during the summer, preventing drought from inhibiting any establishment.

## Methods

### MONITORING OF FRUIT PRODUCTION, SEEDFALL AND SEEDLING EMERGENCE

Three seed cohorts (2000–02) and four seedling cohorts (2000–03) were sampled; thus, combined seed and seedling data were obtained for the 2000/01, 2001/02 and 2002/03 recruitment cycles. Seedfall and seedling emergence were monitored along permanent transects. Four replicate transects, separated by 80–100 m, were established within each population, with each replicate made up of three line transects (see Fig. 2). Two of them were 60 m long and ran along the winter riverbed on each side of the permanent stream, consisting of 16 sampling points, at 4-m intervals. (Exact positions were determined by drawing the shortest line between the



**Fig. 2** Design of a transect replicate used for sampling of seedfall and seedlings. Continuous lines indicate the permanent stream, dotted lines the winter riverbed. Small black circles denote the permanent sampling points (16 along each of the two longitudinal transects, 10 along the perpendicular transect), large open circles show the location of fruiting *Frangula alnus* canopies.

watercourse and the margin of the winter riverbed and placing a point at a distance selected using a randomization procedure). The third transect crossed the centres of the two longitudinal transects and consisted of points halfway between the water and the edge of the riparian vegetation, under the vegetation edge and 4, 8 and 12 m from the edge on each side of the creek. All sampling points were mapped and georeferenced for later analyses with GIS methods. At each sampling point, an area with a visually homogeneous surface was permanently marked in March 2000 and left unaltered for recording seedling emergence (see below). Every year in early spring I examined whether points had been flooded during the previous winter: distances to the margin of the winter riverbed and distances to and heights above the minimum permanent watercourse were measured on 10 September 2003.

All adult *F. alnus* trees within the transect areas were individually marked and mapped at the onset of the study, and the sizes of their fruit crops were estimated by direct count with binoculars at the start of the ripening seasons in 2000, 2001 and 2002. The single-layered crown, relatively sparse leaf cover and fruit display at branch tips exposed to direct sunlight allows reasonably accurate fruit crop estimates (Hampe & Arroyo 2002). In order to assess the sampling error, I additionally determined the crop sizes of 50 randomly chosen trees from the two populations on four consecutive days at the beginning of the fruiting period in 2002. The sequential estimates achieved a reasonably low *CV* of  $5.6 \pm 15.1\%$  (mean  $\pm 1$  SD).

Seedfall was recorded in three of the four transect replicates per population ( $n = 252$  sampling points). Two seed traps, consisting of aluminium dishes ( $30 \times 20 \times 5$  cm) with holes to allow drainage and covered with a resistant mesh wire (mesh size 12 mm) to prevent seed predation by mice, were placed at each point before the ripening seasons in 2000, 2001 and 2002. Seed traps were censused fortnightly throughout the fruiting season; all propagules were recorded and classified as unripe fruits, ripe fruits (with the number of filled and empty seeds being recorded), filled seeds, or empty seeds. Seedlings in the permanently marked areas were counted weekly or biweekly from the emergence of the first plants until no more individuals appeared. Recently germinated seedlings were marked with small bamboo sticks to prevent confusions between new and disappeared individuals. The total area sampled for seedlings was  $55.6 \text{ m}^2$  in the Puerto Oscuro and  $47.6 \text{ m}^2$  in the Aljibe population.

#### EXPERIMENTS ON SECONDARY SEED DISPERSAL

Two experiments were carried out to examine the secondary mobilization and delivery of dispersed seeds, already on the ground, by winter floods. Small pieces of brightly coloured polyethylene were used to mimic

*F. alnus* seeds (see Fig. 1). These seed mimics have a similar size and form to the original seeds, and their weight does not differ significantly ( $t = -1.3$ ,  $n = 200$ ,  $P = 0.20$ ; test with separate variance estimates). Seeds and mimics are both able to float. The first experiment was designed to examine the degree of seed removal. I placed 20 mimics at each of 35 randomly chosen sampling points per population on 25 October 2000. These were searched again after the first heavy autumn rain ( $54 \text{ L m}^{-1}$  rainfall in one day), i.e. on 18 November 2000, also recording if the sampling point had been flooded or not.

The second experiment analysed the dispersal distances achieved during the sequential flooding events of winter 2001/02. On 1 September 2001, c. 80 000 seed mimics per population were carefully spread across the winter riverbed at the uphill limit of the transect replicates in the two populations. On 29 September, 26 October, 24 November, 13 January 2002, 11 March and 19 May, the riverbeds were searched thoroughly for mimics from the release points to 250 m downstream and retrieved mimics were classified as dispersed 5–20, 20–50, 50–100, 100–150, 150–200 or 200–250 m (mimic dispersal  $< 5$  m was not considered).

#### STATISTICAL ANALYSES

Measures of seed dispersal distributions are often spatially autocorrelated (e.g. Houle 1998; Nathan *et al.* 2000; Tomita *et al.* 2002) and statistical non-independence then needs to be taken into account (Legendre *et al.* 2002). I therefore examined seedfall and seedling data for the existence of spatial autocorrelation before proceeding with further analyses on spatial patterns. After having tried different distance classes to optimize the spatial information in the data, I chose classes of 4.0 m to perform spatial correlation analyses on seedfall and seedling data along the transect replicates. Twelve distance classes were considered that contained  $> 50$  point pairs. Analyses of spatial autocorrelation were performed using the Quantitative Traits module of the program SGS (Degen *et al.* 2001). This software is able to incorporate multiple data sets into the analysis; thus, seedfall and seedling emergence data could be examined for each year separately as well as pooled across years. SGS calculates a simple city-block distance measure ( $D$ ) which is equivalent to the commonly used Moran's  $I$  except for the fact that it calculates spatial autocorrelation for parametric instead of categorical data (see Degen *et al.* 2001 for further details). Confidence intervals for  $D$  were calculated using 5000 permutations.

Further statistical analyses were carried out over two spatial scales: single sampling points and entire transect replicates. As no spatial autocorrelation was detected, comparisons were done with commonly used parametric statistics, or with their non-parametric equivalents when data could not be transformed to meet assumptions of parametric tests. This happened

mostly with analyses based on single sampling points, because a high fraction of 'empty' points without seeds or seedlings precluded normalization of data. The abundances of fruits, seedfall and seedlings were compared across years with repeated-measures ANOVA on log-transformed values. ANOVA models included the site identity as between-group factor in order to account for possible differences between populations. Different correlation coefficients were used to assess the spatial consistency of seedfall and the corresponding seedling emergence, as well as the congruence between the seedfall of one year and the seedling emergence of the following year. Comparisons at the sampling point level were done with Spearman rank correlations on raw data. When entire transect replicates were the unit of comparison, different years' data were regressed against the replicate means and Pearson coefficients were calculated on the residuals in order to remove variation that arose from differences between replicates.

Multiple linear regressions were carried out to compare the densities of filled seedfall and seedling emergence (i) as a function of the distance of sampling points from the nearest fruiting *F. alnus* tree (DT), as well as its fruit crop size (CS), and (ii) in relation to the position of sampling points within the winter riverbed, i.e. their distance from (DW) and height above (HW) the permanent watercourse, and their distance to the margin of the winter riverbed (DM). Data from both populations were pooled for the analysis. Seed and seedling data of each sampling point were averaged across years and log-transformed before the analyses. The two independent variables of the first regression model were likewise log-transformed. This procedure was based on the assumption that, close to source trees, seed and seedling densities decrease exponentially with distance from the tree (Willson & Traveset 2000; but see also Clark *et al.* 1999b). The second analysis considered only sampling points located within the non-permanent winter riverbed. A previous analysis of collinearity showed that both regression models had tolerances higher than 0.6; i.e. each independent variable contained more than 60% of variation that was not explained by the other variables. All statistical analyses were done with Statistica version 5.1 (StatSoft Inc. 1997).

## Results

### YEARLY VARIATION IN FRUIT, SEED AND SEEDLING ABUNDANCE

All three parameters varied considerably between years in both populations, although in different ways (see Table 1). Fruit and seedfall abundance were highest in 2002 in the Aljibe population but highest in 2000 in the Puerto Oscuro population, with maximum values around twice as high as minima. Seedling abundance was much higher in both populations in 2000 and 2003

**Table 1** Yearly abundances of fruit production, seedfall and seedlings in the two study populations. Data represent population means with SD in parentheses unless stated otherwise

	Puerto Oscuro										Source of variations§				
	2000	2001	2002	2003	CV†	n‡	2000	2001	2002	2003	CV	n	Population	Year	Year interaction
Individual fruit crop size¶	350 (480)	300 (650)	700 (1520)		38.2	39	250 (750)	150 (590)	180 (575)		40.2	67	NS	***	**
Total fruit production	39435	31830	65100				43600	25950	30745						
Total seedfall m <sup>-2</sup>	104 (239)	70 (216)	191 (616)		64.3	126	60 (187)	31 (97)	34 (129)		65.2	126	**	***	NS
Filled seedfall m <sup>-2</sup>	85 (200)	55 (174)	164 (522)		64.6	126	50 (150)	23 (72)	28 (102)		65.5	126	*	***	***
Seedling density m <sup>-2</sup>	3.5 (10.7)	0.9 (3.7)	0.6 (1.7)	5.6 (18.7)	85.5	168	11.9 (48.2)	1.3 (5.0)	0.5 (2.6)	5.2 (26.1)	82.0	168	NS	***	NS
Seedlings:filled seeds (%)††		1.1	1.1	3.4		126			2.6	2.2	18.6	126			

†Mean relative coefficient of variation among years (in percent).

‡Sample sizes refer either to the number of trees growing within the study areas or to sampling points along transects.

§According to repeated-measures ANOVA (between-group effect: population, repeated-measures effect: year; \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , NS = not significant).

¶Median with quartile range in parentheses.

††Overall seedling density, expressed as percentage of the overall filled-seed rain density of the previous year.

than in the other two years, and the highest values were between nine-fold (Aljibe) and more than twenty-fold (Puerto Oscuro) greater than the lowest abundances. Accordingly, the coefficients of variation among years increased from fruit production through seedfall to seedling emergence (Table 1). Fruit abundance and seedfall density of transect replicates were positively and highly correlated across years ( $r = 0.94$ ,  $n = 18$ ,  $P < 0.0001$ ; data pooled over all years and both populations, and corrected for differences between replicates). Seedling abundance was not related to any other variable.

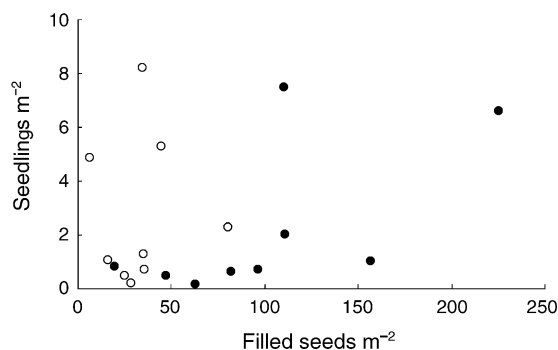
#### SPATIAL CONSISTENCY OF SEEDFALL AND SEEDLING EMERGENCE AMONG YEARS

Spatial autocorrelation was virtually absent. A few weak and inconsistent signals appeared when different years were tested separately, but the global analysis including all years simultaneously did not detect any significant autocorrelation.

Both seedfall and seedling emergence showed a remarkable spatial consistency over time (Table 2). A comparison of the significant Spearman coefficients revealed that the seedfall was spatially less variable than the seedling emergence at Aljibe ( $t = 4.6$ , d.f. = 6,  $P = 0.004$ ), but not in the Puerto Oscuro population ( $t = 0.43$ , d.f. = 7,  $P = 0.68$ ). Comparison of the two populations showed, moreover, that seed rain was more variable in Puerto Oscuro than in Aljibe ( $t = 3.6$ , d.f. = 4,  $P = 0.02$ ). Between-year consistency of seedling distributions could be assessed separately for flooded and non-flooded points for the years 2001, 2002 and 2003. The consistency was similar or higher at flooded points in five out of six comparisons (detailed results not shown).

#### SPATIAL CONCORDANCE BETWEEN SEEDFALL AND SEEDLING EMERGENCE

In contrast to the high between-year consistency of the spatial patterns of seedfall and of seedling emergence, no spatial concordance existed between the seedfall in a given year and the resulting seedling emergence in the following year (Table 2). At the scale of entire transect replicates, the density of filled seeds and the seedling density in the following year were likewise not correlated (Fig. 3;  $r = 0.11$ ,  $P = 0.67$ ,  $n = 18$ ; data from both populations and all years pooled). In other words, the spatial uncoupling of the two stages was not limited to only a few metres but spanned at least 60 m (the replicate size). Seedfall density at a given sampling point was largely explained by the distance to the nearest tree and its crop size (Table 3), whereas seedling density was only related to the distance to the nearest tree and the model explained very little variation ( $R^2 = 0.06$ ).



**Fig. 3** Relation between the densities of seedfall and of the resulting seedling cohort. Data are shown separately for all transect replicates and years. Filled circles refer to the Aljibe population, open circles to the Puerto Oscuro population.

**Table 2** Spearman rank correlations between the spatial patterns of seedfall and seedling abundance in different study years in the two populations. Significant  $r_s$  values are shown in boldface type

	Seedfall density			Seedling density		
	2000	2001	2002	2000	2001	2002
<b>Aljibe</b>						
Seedfall density						
2001		<b>0.58***</b>				
2002		<b>0.65***</b>	<b>0.58***</b>			
Seedling cohort abundance						
2001		-0.14		<b>0.48***</b>		
2002		0.14		0.12	<b>0.22*</b>	
2003			0.05	<b>0.25**</b>	<b>0.30***</b>	<b>0.24**</b>
<b>Puerto Oscuro</b>						
Seedfall density						
2001		<b>0.37***</b>				
2002		<b>0.51***</b>	<b>0.40***</b>			
Seedling density						
2001		0.07		<b>0.42***</b>		
2002		0.08		<b>0.28***</b>	<b>0.32***</b>	
2003			-0.06	<b>0.52***</b>	<b>0.41***</b>	<b>0.46***</b>

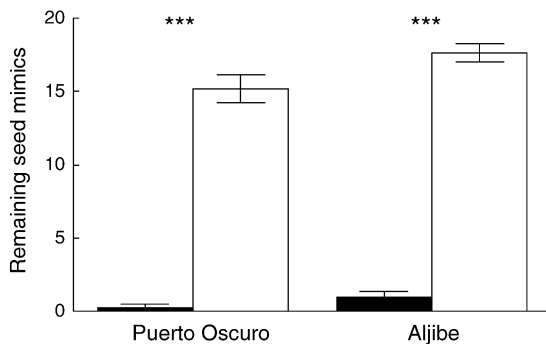
\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ; critical alpha levels have been Bonferroni-adjusted for multiple tests;  $n = 168$  sampling points for seedling–seedling comparisons,  $n = 126$  for seedfall–seedling or seedfall–seedfall comparisons.

**Table 3** Linear regression models for observed densities of filled seedfall and seedlings in relation to fruiting *Frangula alnus* trees and sampling point position within the non-permanent winter riverbed

Independent variables†	Dependent variable	Adj. $R^2$	$F$	$P$	Significant predictors‡
DT, CS	Filled seedfall density	0.53	43.5	< 0.001	DT*** (-0.66) CS*** (0.26)
	Seedling density	0.06	3.4	0.04	DT* (-0.29)
DW, HW, DM	Filled seedfall density	-0.01	0.5	0.7	
	Seedling density	0.16	5.14	0.001	DM** (0.20) DW* (0.14)

†Independent variables: distance to (DT) and crop size of (CS) the nearest fruiting tree, distance to (DW) and height above (HW) the permanent water course, distance to the margin of the non-permanent winter riverbed (DM).

‡Significant predictors (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ) are given with the standardized regression coefficients in parentheses.

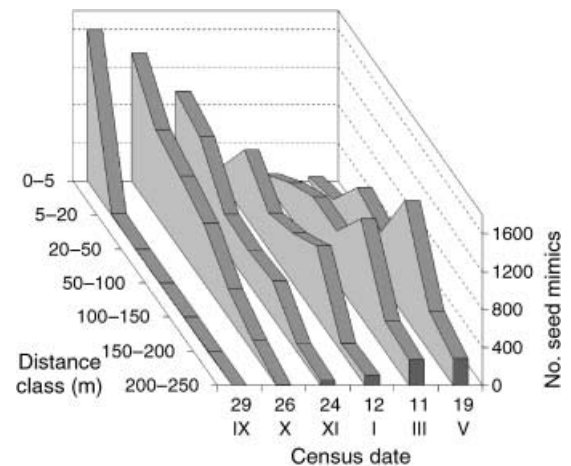


**Fig. 4** Secondary dispersal of *Frangula alnus* seeds by stream flow. Columns indicate how many of the original 20 seed mimics remained at sampling points after a major discharge event. Black columns refer to sampling points that had been flooded in the interval between release and retrieval; white columns refer to non-flooded points. Means  $\pm$  1 SE are shown.

Seedfall density decreased much more rapidly with increasing distance ( $\beta = -0.66$ ) than did seedling density ( $\beta = -0.29$ ;  $t$ -test:  $t = 5.36$ , d.f. = 144,  $P < 0.0001$ ). The second regression analysis indicated that more seedlings emerged at points that were located further from both the permanent watercourse and from the margin of the winter riverbed; in other words, seedling density was highest along reaches with the widest winter riverbed.

#### EXPERIMENTS ON SECONDARY SEED DISPERSAL

The seed removal experiment showed that even a single major flooding event may result in the displacement of most seeds to other parts of the riverbed (Fig. 4; Mann-Whitney  $U$ -test:  $Z_{\text{Puerto Oscuro}} = -4.8$ ,  $Z_{\text{Aljibe}} = 5.0$ ;  $n = 35$ ,  $P < 0.0001$  for both populations). Moreover, a relatively large fraction of the seed mimics was dispersed over several scores of metres over consecutive peaks in discharge (Fig. 5). At the first monitoring, most seed mimics were found in the neighbourhood of the experimental release points. The distance to the source increased as the season progressed and successive water discharges occurred, fattening the tail of the distance distribution.



**Fig. 5** Secondary dispersal of *Frangula alnus* seeds by sequential water flow peaks (pooled data from the two study populations). The distance class 0–5 m included the release point of the c. 160 000 seed mimics, and the number of mimics recorded in this class, which exceeded by far those in the other distance classes, was divided by 100 to improve visibility. The census date axis denotes months (September–May) as roman ciphers.

#### Discussion

It is a common, if not universal, feature of temperate plant populations that their patterns of seedfall and seedling recruitment vary greatly from year to year as a consequence of changes in plant fecundity and environmental conditions (Schupp & Fuentes 1995; Nathan & Muller-Landau 2000). The present study dissects this variation for the first time in the context of a complex seed dispersal system that regularly includes primary and secondary seed transport by very different dispersal vectors.

#### BETWEEN-YEAR VARIATION OF FRUIT, DISPERSED SEED AND SEEDLING ABUNDANCE

All examined variables varied significantly among years, and between-year variation increased through the successive recruitment stages. At the sample point

scale, seedling density was about twice as variable as fruit crop sizes, but the difference was much greater at the replicate scale (up to almost one order of magnitude in the Puerto Oscuro population). Houle (1998) likewise reported that variability increased with recruitment stage in a *Betula alleghanensis* population and suggested that it might be related to stage-specific microsite suitability. Shibata & Nakashizuka (1995), however, observed an opposite trend in four *Carpinus* species, because persistent seed banks smoothed a strong between-year variation in fruiting. In the present case, water-mediated secondary seed dispersal appears to be the most important cause for the increasing variability in abundance of recruits at the late demographic stages studied.

Seedling density varied independently of both local fruit production and seedfall density. Fruit abundance was not synchronized between populations, while seedling density showed some degree of synchrony (see Table 1). The observed patterns suggest that abundance patterns of the two demographic stages are determined by different environmental cues, and neither of them appears to respond directly to the amount of precipitation during the previous winter. Moreover, post-dispersal processes clearly overwhelmed potential effects of seed supply on the density of the resulting seedling cohort, such as any due to heavy and spatially variable post-dispersal seed mortality and/or long-distance seed exchanges between the study plots and neighbouring stream tracks as a result of secondary dispersal by water. Seedling abundance was generally much lower than seedfall abundance (< 5%), except at Aljibe in 2003, where seedling density reached 18.6% of the previous year's seedfall density. Seed losses may be due largely to heavy post-dispersal seed predation by rodents (Hampe & Arroyo 2002).

#### BETWEEN-YEAR VARIATION OF SPATIAL PATTERNS

Contrary to patterns of abundance, the spatial distributions of both seedfall and seedling emergence varied little among years. To my knowledge, no comparable studies exist for animal-dispersed species, while studies on wind-dispersed species have reported only weak spatial relationships between patterns of either seedfall or seedlings in different years (Houle 1998; Nathan *et al.* 2000; see also Clark *et al.* 1999a). For seedfall, this remarkable consistency may be explained by its highly aggregated distribution. Most seeds were found beneath or very near fruiting *F. alnus* canopies, while 133 out of 252 sampling points received, on average, less than one seed per year. Wind-dispersed species usually have less clumped seed shadows and variability among years tends therefore to be higher (Clark *et al.* 1998, 1999b). Moreover, frugivore movements are usually determined by landscape features that do not change significantly within a few years (e.g. Jordano & Schupp 2000), while dominant wind directions may vary greatly from year to year (Nathan *et al.* 2000).

Seedfall generated by a relatively stable frugivore community might be expected to be spatially more consistent among years than seedling emergence shaped by water flow plus other post-dispersal processes. This hypothesis found strong support in the Aljibe population. No significant difference was detected, however, in the Puerto Oscuro population, where both seedfall density and its between-year consistency were markedly lower than in the Aljibe population. In both populations 2001 had the smallest fruit crops and the highest proportion of bird-processed seeds. The (relatively) elevated activity of frugivorous dispersers may therefore have reduced seedfall clumping beneath fruiting trees and the consistency of the seedfall pattern with those in 2000 and 2002.

Seedling distributions were markedly more stable among years than expected given the variable rainfall throughout the study period. Precipitation differed markedly through the four winters, and one might have expected to see this variation reflected in the seedling yearly distributions. Among-year consistency was moreover similar, or even higher, at flooded sampling points than at non-flooded points in five of six cases. Hence, the deposition of secondarily dispersed seeds appears to depend more on relatively permanent microsite characteristics (e.g. position relative to the main current, surface substrate and roughness, presence of rocks, tree stems, roots and other retaining structures, etc.) than on the variable surface and strength of the water flow. In an elegant experimental study on hydrochorous dispersal of *Betula fontinalis* seeds, Merritt & Wohl (2002) demonstrated how hydraulic regime and channel structure interact in determining spatial patterns of seed deposition. Seed delivery is dominated, particularly at high discharges, by so-called 'macro-scale hydraulic features', such as eddies or expansions produced by physical obstacles to water flow. Once these have drawn seeds from the main current into calm stream parts, channel microtopography (or 'microscale hydraulic features') can determine the fine-scale pattern of seed deposition. Importantly, macroscale hydrological features appear to be determined mostly by relatively stable channel characteristics and relatively little by variable water flow dynamics. The torrential nature of the flow regime in the study area suggests that macro-scale features may be primarily responsible for seed deposition patterns of *F. alnus* at the spatial scales investigated, and this is corroborated by the high observed year-to-year consistency of seedling emergence. In other words, the combination of both high flow intensity and a very heterogeneous riverbed structure (containing abundant rocks, tree stems, etc.) appears to contribute much to the observed consistency of seedling emergence and subsequent recruitment patterns. A better understanding of the role of macro-scale physical obstacles would therefore be useful for habitat management aimed at supporting the regeneration of *F. alnus* and other threatened riparian plant species of the area (cf. Merritt & Wohl 2002).

SPATIAL UNCOUPLING OF REGENERATION  
STAGES DUE TO SECONDARY DISPERSAL BY  
WATER

The spatial distributions of seedfall and seedling emergence in the following year were almost completely uncoupled at both spatial scales studied, and the experiments indicated that extensive secondary seed dispersal might be the major reason. Previous studies have reported results that range from high concordance to strong discordance between seedfall and seedling emergence patterns (Streng *et al.* 1989; Houle 1992, 1998; Herrera *et al.* 1994; Rey & Alcántara 2000; Tomita *et al.* 2002). Seed bank dynamics, changing distributions of suitable microsites, spatially variable post-dispersal seed mortality or spatially differential germination rates have also been suggested to explain the 'missing' spatial coupling (see also Schupp & Fuentes 1995). In the case of *F. alnus*, however, seed bank dynamics do not exist and changes in microsite distributions are negligible given the high between-year consistency of both seedfall and seedling patterns. Although post-dispersal seed predation by rodents is indeed severe (Hampe & Arroyo 2002), it could not create a spatial discordance between seedfall and seedling patterns, while simultaneously maintaining their observed strong between-year consistency, unless it maintained exactly the same patterns of spatial variability from year to year. This seems, however, extremely unlikely (Crawley 2000). The seed germination rate of *F. alnus* is generally high and differs more in time than in space because the fraction of seeds destroyed by the water current varies from year to year (A. Hampe, unpublished data), so differential germination cannot explain the observed patterns. Although further studies are required to rule other factors definitively out, substantial secondary seed dispersal is therefore the process that best accounts for the observed spatial discordance between seedfall and resulting seedling distributions.

IMPORTANCE AND CONSEQUENCES OF THE  
TWO DISPERSAL MODES

Few studies have quantitatively compared seed shadows generated by different dispersal modes within the same population (Levey & Byrne 1993; Böhning-Gaese *et al.* 1999; Vander Wall 2002). Even less is known about how temporal variation in dispersal agents may alter seed distributions and resulting patterns of seedling recruitment (Willson & Traveset 2000; but see Merritt & Wohl 2002). To my knowledge, only Vander Wall (2002 and cited references) has reported detailed distance distributions of seed dispersal for a plant species with a regular two-step dispersal system that incorporates different transport vectors. In the present study, bird-mediated primary dispersal and hydrochorous secondary dispersal produced very different distributions; the first can be described relatively well with a negative exponential function, while the second changed

through the duration of the experiment from a negative exponential towards an extended Poisson distribution. The multiple regression model, despite its unrealistic assumption that all seeds and seedlings came from the nearest fruiting tree, indicated a strong difference between initial and final seed distributions. The seed mimic experiment, however, probably more accurately reflects the actual secondary dispersal process (see also Nilsson *et al.* 1991; Andersson *et al.* 2000). The two dispersal modes should have very different consequences for the spatiotemporal patterns of recruitment, the demography and the genetic population structure of *F. alnus* populations.

All major frugivorous dispersers of *F. alnus* move preferentially within the narrow riparian forest galleries (Hampe 2001), so most seeds are delivered within the winter riverbed. Seedlings that recruit outside the stream riverbed are invariably killed by summer drought. It is therefore probable that almost all seeds are moved at least once by water flow before they germinate and produce an established plant. Other *F. alnus* populations are primarily ornithochorous, but those studied have apparently switched to hydrochorous seed dispersal as the secondary dispersal component acquired predominance, at least in terms of the local demographic dynamics. (Although some secondary dispersal by seed caching rodents cannot completely be ruled out, its importance for recruitment patterns is certainly very limited.) This dispersal system is a direct consequence of the particular habitat that provides a climatic refugium for these relict populations, whereas frugivorous birds are the principal seed dispersers in other parts of the species' distribution range (Hampe & Bairlein 2000b and references therein). The case provides an example of the ecological differentiation of populations inhabiting range peripheries, which may ultimately result in evolutionary divergence (Hampe & Bairlein 2000a).

Nevertheless, bird-mediated seed transport certainly plays a more important role than this study suggests at first sight: the influence of water dispersal decreases upstream, and birds remain the most reliable dispersal agents in the uppermost reaches. They are also indispensable for any seed dispersal upstream or between different streams. Their service is therefore crucial for the establishment of new *F. alnus* populations and seed-mediated gene flow between existing stands, as well as for altitudinal distribution shifts of populations induced by modern climate change. Long-distance dispersal by birds followed by successful plant establishment is, however, likely to be extremely rare (Hampe *et al.* 2003).

On the other hand, the regular, directional long-distance seed dispersal mediated by water flow might largely shape within-population genetic patterns producing altitudinal trends from clear genetic structuring in the highest stream tracks towards a weak genetic structure and an elevated genetic diversity in the lowermost parts of the populations (Lundquist & Andersson 2001). Moreover, secondary seed dispersal has also

diverse delayed effects on population recruitment and demography; for instance, it determines microhabitats of seed deposition and mediates levels of seed germination and seedling survival (Hampe & Arroyo 2002; A. Hampe, unpublished data).

### Conclusions

Riparian forests are among the most vulnerable habitats in southern Spain and the Mediterranean Basin in general. Many of their plant species are threatened and most are restricted to relatively undisturbed stream tracks near the headwaters. The reported results indicate that hydrochory is an important determinant of spatiotemporal patterns of regeneration in these plant communities and corroborate observations from other geographical regions (Jones *et al.* 1994; Barat-Segretain 1996; Merritt & Wohl 2002; Nilsson *et al.* 2002; Shafroth *et al.* 2002). Populations of *F. alnus* and co-occurring species are restricted to relatively short stream tracks, and many seeds are probably removed each year from suitable growing places and thus lost for regeneration. Conservation management might presumably reduce this loss and increase the reproductive potential of populations by (i) maintaining or, if necessary, restoring the extremely heterogeneous surface structure of natural riverbeds, and (ii) reducing the impact of vegetation slashing in creek surroundings on erosion and amplitudes of peak water discharges (see also Hampe & Arroyo 2002). Both measures might be achieved with considerably less financial effort than used in ongoing plantation for population reinforcement (F. Oliveros, Director of 'Los Alcornocales' Natural Park, personal communication).

More generally, the dynamics of streams in Mediterranean-climate regions are underlain by strong variation in precipitation, whose between-season predictability contrasts with their interannual unpredictability (Gasith & Resh 1999). This study is one of the first to shed light on how this meteorological regime affects spatiotemporal patterns of initial recruitment in riparian plant species. However, more and broader long-term studies are clearly needed to understand how the interaction between channel character and hydrological regime in Mediterranean climate streams shapes the demography and regeneration of plant populations, as well as the community structure and diversity of riparian forests (Naiman & Décamps 1997; Gasith & Resh 1999).

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