

Shuffling the offspring: Uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal¹

Pedro JORDANO & Carlos M. HERRERA, Estación Biológica de Doñana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain, e-mail: jordano@cica.es or herrera@cica.es

Abstract: Recruitment of vertebrate-dispersed plants may be divided into a series of sequential stages including fruit removal by frugivores, seed delivery to the ground, post-dispersal seed survival, seedling emergence, and seedling establishment. The particular processes operating at different stages may be independent of each other ("uncoupled"), and peculiarities in the configuration of the interrelationships between stages (sign and magnitude of uncoupling) may lead to high site-specificity of the eventual outcome ("spatial discordance"). This conceptual framework is illustrated in this paper using recruitment data for the bird-dispersed tree *Phillyrea latifolia* (Oleaceae) from two southeastern Spanish localities (forest and scrubland habitats). Between-habitat differences in *P. latifolia* recruitment are best understood by considering that patterns of uncoupling among recruitment stages depend strongly on local conditions, particularly on the thoroughness of fruit crop removal by frugivorous birds. The interaction of *P. latifolia* with frugivores has implications at every subsequent stage in recruitment, and proper understanding of the constraints operating on recruitment requires recognition of the multiplicity of stages involved. Uncoupling of stages was found to originate fine-scale discordances in patterns of regeneration in the two habitats studied. We use a structural equation model to quantify the direct and indirect effects of the various recruitment stages on spatial variation in number of 2nd-year seedlings recruited. Variation among microhabitats in recruitment was due to variation in seed rain intensity and seed survivorship in scrubland, while post-germination events limiting seedling emergence played a major role in forest recruitment. Results of this study highlight the need of considering the multi-staged nature of recruitment in vertebrate-dispersed plants.

Keywords: Mediterranean habitats, population recruitment, seed dispersal by vertebrates, seed and seedling survival, seedling recruitment, spatial variation.

Résumé: Le processus de recrutement chez les plantes qui assurent la dissémination de leurs diaspores grâce à des vertébrés peut être subdivisé en une série d'étapes séquentielles incluant le détachement du fruit du plant-mère par les animaux frugivores, la libération des graines et leur étalement à la surface du sol, la survie des graines après dissémination, l'émergence des plantules et la survie de ces dernières. Les différents processus qui opèrent à chacune des étapes peuvent être indépendants les uns des autres. Le degré d'association qui existe entre les processus de chaque étape peut faire en sorte que le recrutement soit caractérisé par une spécificité élevée pour un site donné, créant ainsi des phénomènes de discordance spatiale. Ce cadre conceptuel est illustré dans cet article grâce à une étude sur le recrutement d'une espèce arborescente (*Phillyrea latifolia*; Oleaceae) dont les graines sont disséminées par les oiseaux. Les données ont été collectées dans deux localités du sud-est de l'Espagne, soit dans un habitat forestier et un habitat arbustif. On comprend mieux les différences qui existent entre les habitats au niveau du recrutement de *P. latifolia* si l'on tient compte du fait que le degré d'association entre les différents processus dépend fortement des conditions locales du milieu, et plus particulièrement de la minutie avec laquelle les oiseaux s'emploient à décortiquer les fruits. Les interactions qui existent entre *P. latifolia* et les oiseaux frugivores ont des conséquences à toutes les étapes du recrutement de cette espèce arborescente. Une compréhension des contraintes agissant sur le recrutement nécessite une connaissance de la multiplicité des étapes impliquées. La non-association qui peut exister entre certaines étapes du recrutement est à l'origine des discordances spatiales que l'on trouve entre les deux habitats étudiés lorsque l'on travaille à une échelle de résolution assez fine. Nous avons utilisé un modèle d'équations structurelles pour quantifier les conséquences directes et indirectes des différentes étapes du recrutement sur le patron spatial des plantules âgées de deux ans. Les différences de recrutement entre les habitats résultent soit d'une pluie de graine et d'un taux de survie des graines variables dans le cas de l'habitat arbustif, soit de facteurs limitant l'émergence des plantules dans le cas de l'habitat forestier. Les résultats de cette étude mettent en évidence l'utilité de considérer dans leur ensemble les multiples étapes du recrutement chez les plantes qui assurent la dissémination de leurs diaspores par des vertébrés.

Mots-clés: habitats méditerranéens, recrutement, dissémination des graines par les vertébrés, survie des graines et des plantules, recrutement des plantules, variation spatiale.

Introduction

The interaction with frugivorous animals which disperse seeds, takes place at the final stage of the reproductive cycle of many higher plants and sets a continuity bridge between generations in their natural regeneration cycle. Rephrasing the vivid description by Harper (1977: 29), dispersal is the stage at which seeds start to make more seeds. Frugivore activity not only influences the realized reproductive output

of female parent plants, but also has lasting consequences for the eventual survival and establishment prospects of seeds and seedlings (Herrera *et al.*, 1994; Howe, 1990; Howe, Schupp & Westley, 1985; Reid, 1989; Schupp, 1993; Schupp *et al.*, 1989). The pervasiveness of interactions with frugivores becomes most evident if one considers plant population recruitment as the result of a series of concatenated events, including fruit removal by dispersal agents, seed dissemination, seed germination and seedling establishment.

¹Rec. 1994-11-21; acc. 1995-04-19.

The main stages in the recruitment phase of vertebrate-dispersed plants, and the major processes operating at each individual stage, are summarized in Table I. The two processes directly effected by frugivorous animals are fruit removal and seed delivery to the ground, but their consequences cascade through the whole recruitment phase. First of all, by selecting among maternal fruit crops to forage, frugivores determine the relative success of maternal phenotypes. Secondly, by selecting among fruits within individual crops, they may determine which seed phenotypes are successfully dispersed. And thirdly, the precise location where seeds are delivered influences the future prospects of propagules, as the landscape is heterogeneous in quality for seed and seedling survival and early establishment (Schupp, 1995).

We might expect these juxtaposed processes to originate two rather general phenomena: independence among processes operating at different stages of recruitment (designated as “uncoupling” in this paper) and also, in most instances, high site-specificity of the eventual outcome (termed “spatial discordance” here), due to peculiarities in the configuration of the interrelationships between stages (sign and magnitude of uncoupling). Uncoupling may lead, for example, to later-acting processes either obscuring or enhancing previously-acting ones (Herrera, 1991; Jordano, 1989), and this effect has been more or less explicitly recognized previously (Andersen, 1989; Harper, 1977; Gill & Marks, 1991; Grubb, 1988; Houle, 1994). Its demographic and evolutionary consequences, however, have begun to be analyzed only recently (Herrera *et al.*, 1994; Horvitz & Schemske, 1994; Howe, 1990; Schupp, 1995). In this paper, the conceptual framework depicted in Table I will be used for a particular case study, using data for the bird-dispersed tree, *Phillyrea latifolia* L. (Oleaceae), in two different habitats. Our specific objectives here include (1): showing that patterns of recruitment are very site-specific in *P. latifolia*,

due to the local uniqueness of the interrelationships between the different recruitment stages; (2) identifying the stages where uncoupled recruitment occurs in this species; and (3) examining the potential consequences of uncoupled effects in the recruitment phase and spatial discordances in recruitment at both the between- and within-habitat spatial scales. Our general objective is to show that analyzing the ripe fruit-established seedling phase into its elemental components provides a powerful tool for understanding the causes of observed spatio-temporal variation in plant recruitment, among and within species.

Methods

An extensive account of the recruitment ecology of *Phillyrea latifolia* has been presented elsewhere (Herrera *et al.*, 1994), and the reader should refer to that publication for information on the species' natural history and seed dispersal ecology, and details on study methods. Only a concise summary is presented in this section.

We studied the seed dispersal ecology of *P. latifolia* during 1989-1992 at two study sites in the Sierra de Cazorla (Jaén province, southeastern Spain). The Agracea site (“forest site” hereafter), at an elevation of 1 200 m, is a tall (height 5-18 m) evergreen forest dominated by *Quercus rotundifolia* Lam., *P. latifolia*, and *Arbutus unedo* L. The Hoyos de Muñoz site (“scrubland site” hereafter) is 2 km away, at an elevation of 1 150 m, and the vegetation is a species-rich, dense sclerophyllous scrub up to 4.5 m in height.

Ripe fruits of *P. latifolia* are single-seeded drupes. They are eaten by several species of small- and medium-sized frugivorous passerine birds, which disperse the seeds. To quantify the probabilities for elemental transitions between the following consecutive stages (Table I) we evaluated: (1) seed rain in different microhabitats during the

TABLE I. Summary of stages leading to recruitment of a vertebrate-dispersed plant, and processes influencing their outcomes. Shown are also the stage-specific and stagewise cumulative recruitment probabilities obtained for *Phillyrea latifolia* in two southeastern Spanish habitats (forest and scrubland) and the key variables measured to characterize each process

Stage	Process (Key variable)	Stage-specific probability		Stage wise, cumulative probability	
		Forest	Scrubland	Forest	Scrubland
Fruit removal	Removal by frugivores and frugivore activity (proportion of fruits consumed ¹)	0.3282 ± 0.0498 N = 32	0.7747 ± 0.0478 N = 20	0.3282	0.7747
Seed dissemination	Seed fall and post-dispersal seed survival (proportion of seeds surviving post-dispersal seed predation ²)	0.6052 ± 0.0010 N = 960	0.4580 ± 0.0015 N = 1 000	0.1986	0.3548
Seed establishment	Germination and seed bank dynamics (proportion of seeds germinated ²)	0.2421 ± 0.0022 N = 822	0.2299 ± 0.0118 N = 548	0.0481	0.0816
Seedling emergence	Underground seedling survival and emergence (proportion of seedlings emerged ²)	0.1716 ± 0.1227 N = 161	... ³	8.25E-3	1.39E-2 ⁴
Early seedling establishment	Survival 1st year (proportion of seedlings surviving to 1st autumn ²)	0.1507 ± 0.0050 N = 2 097	0.1526 ± 0.0040 N = 1 206	1.24E-3	2.14E-3
	Survival 2nd year (proportion of seedlings surviving to 2nd autumn ²)	0.0796 ± 0.0050 N = 316	0.0761 ± 0.0011 N = 184	9.89E-5	1.63E-4
Sapling establishment	Growth, medium-term survival ³
Young reproductive establishment	Growth, survival to reproduction, competition ³

¹ mean ± 1 SE; N, number of trees.

² confidence intervals (95%) based on the binomial distribution. N = number of propagules.

³ no data available.

⁴ computed using the early survival estimate obtained for forest. See text.

seed dispersal period (September 1989–April 1990); (2) associated probabilities of germination and post-dispersal seed survival; (3) seedling emergence; and (4) seedling survival during the first 2 years after emergence. Transitions among these stages were evaluated in the same habitat patches, so that the probability for individual propagules in one stage to survive to successive stages could be quantified for specific sampling points. Ten microhabitat categories were recognized in scrubland based on the identity of overlying tree and shrub species or lack thereof (“open ground”). Similar, distinct microhabitat categories were not discernible in the forest site, so we set up four 120 m-long linear transects with 24 sampling stations per transect. In both sites, most observations and experiments were performed at permanently marked stations.

Seed-collecting traps were used to study patterns of seed rain in different microhabitats. Traps were spread among microhabitat types (scrubland site; 300 traps distributed among 10 microhabitat categories with two traps placed at each of 150 sampling stations) or along transects (forest site; 288 traps, one triplet of traps at each of 96 stations distributed along four transects), and were checked at monthly intervals for *P. latifolia* seeds. All traps were numbered individually and separate records were kept of individual traps. Post-dispersal seed survival was investigated using groups of seeds glued to a piece of plastic mesh and nailing the mesh to the ground. We had no evidence that this protocol would alter handling and accessibility of seeds to rodents. Experimental groups (each consisting of 10 pairs of seeds) were distributed among microhabitat types (scrubland site, $N = 50$ groups totaling 1 000 seeds) and along transects (forest site, $N = 48$ groups totaling 960 seeds). Seed groups were set up in February 1990, at the same sampling stations used for monitoring seed rain, and checked periodically for missing and/or destroyed seeds until February 1991. Seed germination was investigated in an outdoor experiment, carried out in the Agraceña site, using seeds from plants from the two study sites (Herrera *et al.*, 1994). Seeds were sown in January 1990, and we recorded emergent seedlings and checked the viability and status of ungerminated seeds by the end of the experiment (May 1991). All *P. latifolia* seedlings emerging in the permanent sampling stations (within 1.5-m² areas) were tagged individually in the springs of 1991 and 1992, and their survival recorded over an interval of 540 days after marking. We will use here only the survival data corresponding to the 1991 seedling cohort ($N = 3\,303$ seedlings), the one for which survival probabilities could be established for two consecutive growing seasons.

We analyzed how the proportion of surviving seedlings which a specific patch of habitat (sampling station in our design) supports, relative to all the seedlings surviving in the population, is influenced by the combination of recruitment probabilities that are distinct to that patch. Our model (see below and Figure 2) incorporates both the direct influence of each consecutive stage and the influence of every previous stage independently of the correlated effects of other stages. Thus, seed rain might limit seedling emergence both “directly”, by setting the maximum number of seedlings which can emerge in a given patch, and

“indirectly”, through correlated influences on post-dispersal seed survival (*e.g.* higher seed predation risk in patches with more seed fall). Indirect effects were estimated by the product of the structural equation coefficients (actually partial regression coefficients) in the intervening paths between a predictor and its target variable (see Pedhazur, 1982; Mitchell, 1992). Structural equation coefficients, path coefficients, and direct and indirect effects were estimated with SAS procedure CALIS (SAS, 1988) using the maximum likelihood option.

Results

UNCOUPLING OF STAGES AND BETWEEN-HABITAT VARIATION

Three main elements determine the net influence of a given stage in Table I on recruitment: (1) the *absolute number of propagules* entering the stage; (2) the *stage-specific probability* of recruitment, *i.e.* the probability that a propagule entering the stage will pass it successfully; and (3) the *cumulative probability* of recruitment up to and including the stage in question, *i.e.* the product of elemental transition probabilities (component 2 above) computed over all preceding stages. Component 3, when computed for the last stage in recruitment, yields an estimate of the probability for a seed in a ripe fruit to become an early-established seedling (Gill & Marks, 1991; Herrera *et al.*, 1994). Between-habitat differences in recruitment are best understood by considering these three components.

Stage-specific and cumulative stagewise probabilities of recruitment for *P. latifolia* at the two study sites are summarized in Table I. There was an important difference between forest and scrubland in fruit removal rates. Fruit removal was extensive in scrubland, where most plants dispersed > 60% of seed crops, while it was rather poor in forest, where most plants dispersed < 40% of seeds. There was thus a large starting difference between sites in the probability of seed dissemination. Greater dispersal effectiveness in scrubland compensated for the lower average fecundity of trees at this site. Despite smaller fruit crops, scrubland plants dispersed more seeds than forest plants (682 ± 742 versus 387 ± 557 seeds, mean \pm SD; $F_{1,50} = 4.08$, $P = 0.04$). This difference, however, did not translate into differential seed rain intensity, as the greater *P. latifolia* cover in forest (29.8%) led to greater overall seed rain in this habitat (31.2 ± 10.2 seeds/m²; mean \pm 1SD, averaged for different microsites) relative to scrubland (18.2% cover; 12.4 ± 8.3 seeds/m²). Compensatory effects involving plant fecundity (forest > scrubland) and fruit removal effectiveness (scrubland > forest) were thus insufficient to offset between-habitat differences in *P. latifolia* relative cover: input of dispersed seed to the soil was greater at the forest site despite poorer realized seed dispersal of individual plants.

Post-dispersal seed survival was significantly greater in forest than in scrubland (Table I). This difference, however, was not sufficient to translate into greater cumulative probability of recruitment in forest up to the end of that stage. The probability of a ripe fruit recruiting a seed in the soil ready to germinate was 0.1986 in forest, compared to 0.3548 in scrubland. The higher survival prospects for dispersed seeds in the forest thus did not compensate for the

higher seed losses during the fruit removal stage in that habitat (largely due to fruit removal failure and subsequent desiccation). Mean seed germination rate did not differ between sites ($\chi^2 = 0.27$, $df = 1$, $P = 0.23$) and the overall recruitment probability by the end of the germination stage in scrubland nearly doubled the corresponding forest value (Table I), thus mirroring the starting difference between sites in recruitment expectancies at the initial fruit removal stage.

The probability of seedling emergence could not be reliably estimated for the scrubland site, as seed rain, survivorship, and germination data were not available for exactly the same sampling stations. In forest, emerging seedlings represented, on average, 17.2% of the recorded seed rain per station (Table I). As germination rates were similar between sites, as noted earlier, there were no reasons to expect differences between sites in the per-seed probability of seedling emergence.

Seedling densities differed between sites. Forest stations averaged 10.7 (1991) and 22.9 (1992) seedlings/m², while those in scrubland had a density of only 4.5 seedlings/m² (1991). This difference was attributable to the additive effects of smaller seed rain and greater seed losses to post-dispersal seed predators in scrubland (Table I). Probabilities of early seedling establishment were computed using data for the 1991 seedling cohort. Survivorship of seedlings through their first and second years of life did not differ between sites (Table I).

The probability that a seed in a ripe fruit would be recruited as a second-year seedling was computed as the product of all stage-specific transition probabilities. Although it was very low in the two sites (9.89E-5 and 1.63E-4 in forest and scrubland, respectively; Table I), the scrubland had a 1.6-fold advantage over forest. However, the resulting mean densities of surviving, established seedlings were greater in forest (6.3 ± 1.8 seedlings/m²) than in scrubland (1.3 ± 1.4 seedlings/m²).

WITHIN-HABITAT DISCORDANCES IN RECRUITMENT: PATTERNS

Differences among the success of different stages at different microsites imply that it will generally be difficult to predict the abundance of propagules entering a given stage without information on preceding stages (Houle, 1994). Furthermore, if different microhabitat types in a given habitat differ in suitability for seed survival, germination, and seedling establishment, then spatial discordances in these probabilities are also to be expected.

Spatial discordances in the recruitment expectancies of *P. latifolia* propagules are best illustrated using data from the scrubland site, as different (on the basis of plant cover composition) microhabitat types were readily distinguished there. For each microhabitat and recruitment stage, we computed the percentage of propagules recruited relative to the total number of propagules recruited, summed across microhabitats. These values thus illustrate the relative importance of the different microhabitats as 'reservoirs' of propagules in the different stages. Figure 1 shows the marked spatial discordances existing among microhabitats in their relative contributions to the various recruitment stages. Variation among microhabitats in final, 2nd-year

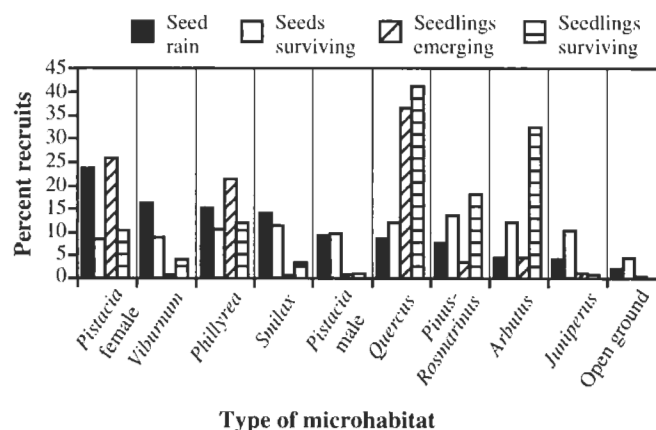


FIGURE 1. Relative abundance of recruits of *P. latifolia* over a range of microhabitat types (defined by dominant vegetative cover) in four stages of the recruitment phase in the scrubland site. For each microhabitat type, we estimated the number of recruited propagules (fallen seeds, surviving seeds after the first year, number of emerged seedlings, and number of seedlings surviving after 1.5 yr) relative to the total number of propagules recruited in each of the four stages. Microhabitats are sorted from left to right by decreasing intensity of seed rain: *Pistacia* = *Pistacia lentiscus*; *Viburnum* = *Viburnum tinus*; *Phillyrea* = *Phillyrea latifolia*; *Smilax* = *Smilax aspera*; *Quercus* = *Quercus rotundifolia*; *Pinus-Rosmarinus* = *Pinus pinaster* + *Rosmarinus officinalis*; *Arbutus* = *Arbutus unedo*; *Juniperus* = *Juniperus oxycedrus*.

seedling recruitment was unrelated to differences in seed rain intensity ($r_s = 0.188$, $P = 0.573$). Seed rain was most intense beneath individuals of fleshy-fruited species (*Pistacia lentiscus* females, *Viburnum tinus*, *Smilax aspera* females, and *Phillyrea latifolia* itself), yet nearly half of the surviving 2nd-year seedlings were found beneath non-fleshy fruited species that received only a light seed rain (*Quercus rotundifolia*, *Pinus pinaster*, *Rosmarinus officinalis*). Across microhabitats, the relative numbers of surviving 2nd-year seedlings were positively correlated with relative numbers of dispersed seeds that survived ($r_s = 0.721$, $P = 0.03$) and seedlings that emerged ($r_s = 0.709$, $P = 0.03$). Similar patterns occurred in the forest site (Herrera *et al.*, 1994): across stations, seed rain and seedling establishment were spatially discordant despite concordance between other stages. More seeds survived where seed rain had been greater, and more seedlings became established where emergence had been greater, but the number of seedlings eventually emerging at a given sampling station was unrelated to the number of surviving seeds.

WITHIN-HABITAT DISCORDANCES IN RECRUITMENT: CAUSES

Understanding the factors responsible for differences among microsites in recruitment probabilities requires explicitly accounting for both the direct effects of each stage on final recruitment and the indirect effects mediated through lagged correlations on intermediate, subsequent stages (see Table I). One structural equation model was fitted to data for each of the two study sites to estimate both direct and indirect causal influences explaining variation among microsites (sampling stations) in the proportion of 2nd-year seedlings recruited relative to the total number of recruits (Figure 2). For each path, total covariation with recruitment can be dissected into causal (both direct and indirect) and non-causal components (Pedhazur, 1982). The contrasting patterns of influences between the two sites were largely

caused by differences in the relative magnitudes of direct and indirect effects of seed rain and post-dispersal seed survival on later stages. Seed rain had a small effect on recruitment in both sites, and > 50% of its total effect on recruitment was accounted for by the indirect causal component (Figure 2). In the forest site, seed rain negatively influenced both post-dispersal seed survival and seedling emergence, while in scrubland it showed a large positive effect only on seedling emergence. Post-dispersal seed survival showed non-significant effects on later stages in the forest, largely (99.6%) due to non-causal correlations. In scrubland, however, most (98.7%) of the total effect of seed survival on recruitment was causal, but only 54.2% was attributable to its direct influence. Spatial variation in seedling emergence thus had a large, causal direct effect

(98.7% of its total effect) on final recruitment in the forest, but a smaller, non-significant effect in scrubland (only 74.4% of its total effect being direct and causal). To sum-up results in Figure 2, among-microhabitat variation of recruitment in scrubland was mainly due to variation in seed rain intensity and seed survivorship, which limited recruitment indirectly through cascading indirect effects on seedling emergence. These pre-germination stages had little direct impact on recruitment in the forest, which was apparently limited by events reducing seedling emergence.

Discussion

Different stages along the ripe fruit-established seedling transition cause variable reductions in the expectancy of

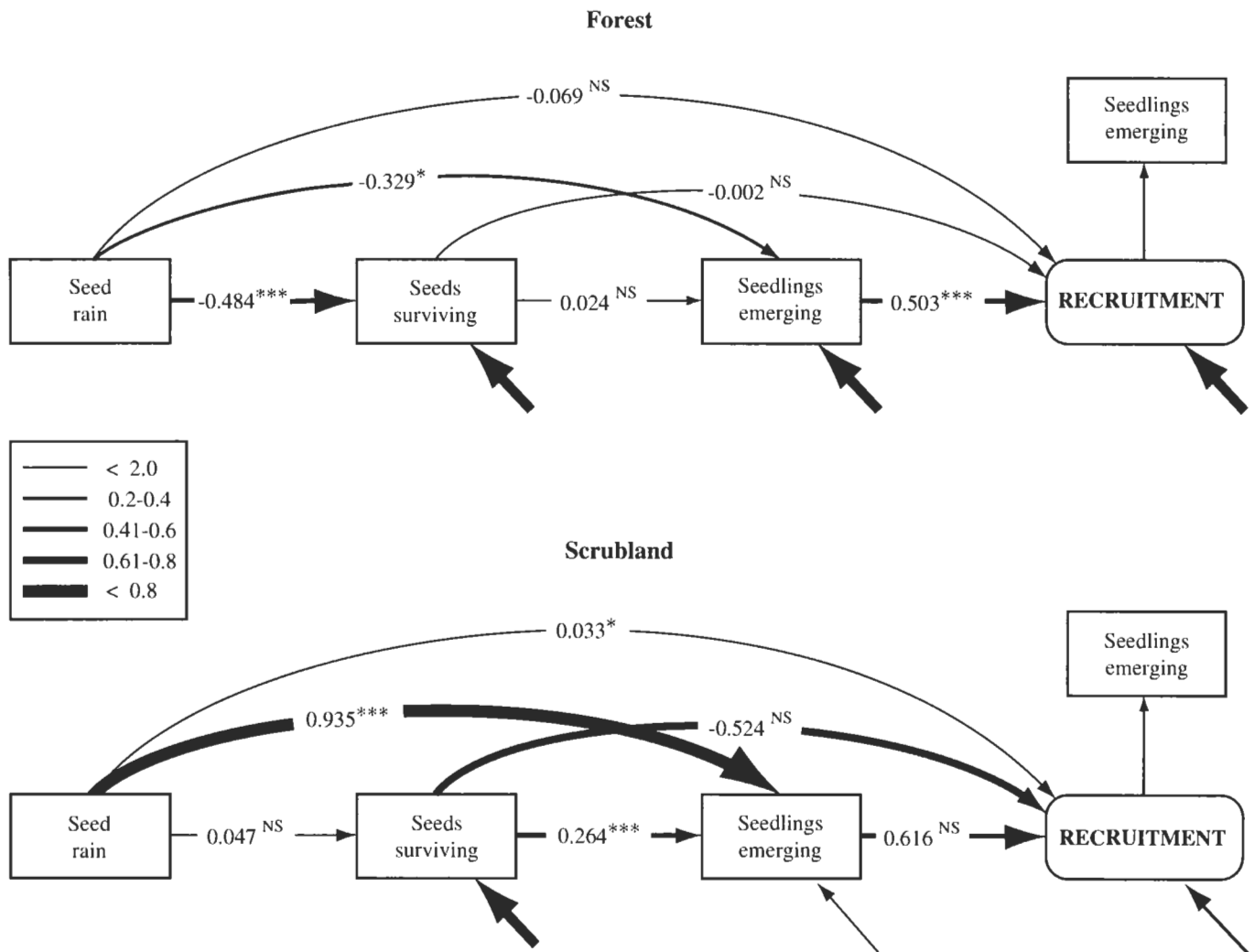


FIGURE 2. Structural equation models for the sequential effects on population recruitment of different stages in the seed dispersal phase of *P. latifolia*. We determined the proportion of recruited 2nd-yr seedlings for each microsite (sampling stations in forest, microhabitats in scrubland) relative to the total number of seedlings recruited (labelled "seedlings surviving" in graph). This was the indicator variable used to scale "Recruitment", the unobserved, latent, endogenous variable of interest. For each particular microsite we determined: proportion of seeds sampled relative to the total seeds collected in seed traps ("seed rain" in graph); proportion of seeds surviving postdispersal seed predation relative to the total surviving seeds ("seeds surviving"); and proportion of seedlings emerged at the microsite relative to the total number of seedlings emerged ("seedlings emerged"). Models depict causal patterns as a series of arrows, labelled with the values of the standardized path coefficients (line widths coded according to the symbol key), and indicate how changing a predictor variable by one standard deviation would directly change the target variable in standard deviation units, holding all other factors constant. The correlations of target variables with unexamined background factors and experimental error are depicted by unlabelled short arrows pointing to measured variables. Models were fitted with procedure CALIS (SAS, 1988) on the covariance matrix, using maximum likelihood estimation. *** $P < 0.001$; * $P < 0.05$; NS = not significant.

establishment of propagules, thus contributing differentially to the overall loss of recruits. We have explicitly adopted this sequential view and applied methods to evaluate the cascading effects of processes influencing early recruitment. Two main effects, which probably apply to other vertebrate-dispersed species as well, emerged in the case of *P. latifolia*. First, the net effect of a particular stage (estimated as the step-specific decay value in the probability of establishment) not only depends on the three basic components of recruitment (absolute number of propagules entering the stage; stage-specific probability of recruitment; and cumulative probability of recruitment up to and including the stage), but also on the interaction, or lack thereof, with the preceding stages. Second, within-habitat spatial discordances in recruitment (see also Gill & Marks, 1991; Herrera *et al.*, 1994; Houle, 1994; Morris *et al.*, 1986) are largely the result of the above process operating among microhabitat patches.

Uncoupling between pairs of consecutive stages has been demonstrated in a number of previous studies (see Schupp, 1995, for a detailed review), but multiple sequential stages have been examined infrequently (Andersen, 1989; Gill & Marks, 1991; Herrera *et al.*, 1994; Kitajima & Augspurger, 1989). Our study demonstrates that the consequences of interactions with frugivores may have implications at every subsequent stage in regeneration and that multiple stages should be considered for a proper understanding of the constraints operating on recruitment in patchy habitats. Uncoupling occurs when the processes influencing a particular demographic stage offset or obscure the effects of previously-acting ones. Between-site differences in *P. latifolia* recruitment are best understood by considering that patterns of uncoupling among demographic stages are site-specific (*i.e.* strongly dependent on local environmental settings). The probability for a ripe fruit of *P. latifolia* to be recruited as a second-year seedling was reduced by > 90% during the pre-germination stages (fruit removal through seed germination). Post-germination stages (seedling emergence through the second growing season) accounted for a further reduction of < 10%. Plants in the scrubland site experienced thorough fruit removal, while frugivore activity limited removal success for the forest plants; this process thus had enduring consequences for the recruitment probabilities in the two sites. The stagewise, cumulative probabilities of recruitment were smaller in forest than in scrubland for every subsequent post-removal stage, despite greater stage-specific probabilities in the forest. Thus, later processes did not offset the initial 2.4-fold advantage of the scrubland site in recruitment expectancies originating through differences in frugivore activity. Rather unexpectedly, the large difference in recruitment probability between forest and scrubland was insufficient to obscure the difference in absolute number of seeds removed by frugivores, which was much greater in the forest site, thus yielding a greater density of recruited seedlings in this habitat.

Previous studies have shown that the spatial distribution of seed rain, seed bank, and seedling abundance may happen to differ if differences in microsite quality for a particular stage are offset by the differences in a subsequent stage of the regeneration phase (De Steven, 1991a; Gill & Marks,

1991; Herrera, 1984; Herrera *et al.*, 1994; Houle, 1994; Morris *et al.*, 1986; see review in Schupp, 1995). Results of the present study indicate that uncoupling of stages in recruitment leads to spatially discordant patterns of regeneration if habitat patches differ in both the stage-specific recruitment probabilities and the degree of uncoupling among sequential stages. In other words, spatial discordances are expected whenever the shapes of decaying cumulative probability curves differ among patches. Results for *P. latifolia* in the scrubland site illustrate these effects well. First, seed rain was unevenly distributed among microhabitats and uncorrelated with the relative abundance (cover) of these in the site ($r_s = 0.367$, $P = 0.299$). Patches beneath fleshy-fruited species received a greater proportion of dispersed *P. latifolia* seeds than patches beneath other types of cover or beneath fleshy-fruited species that did not produce good fruit crops in the study year (*A. unedo*, *J. oxycedrus*, and male plants of *P. lentiscus* and *S. aspera*). Restriction of foraging movements of frugivorous birds to sites with greater fruit availability could explain this pattern (Debussche & Isenmann, 1994; Hoppes, 1988; Izhaki, Walton & Safriel, 1991; Katusic-Malmborg & Willson, 1988; Masaki, Komirami & Nakashizuka, 1994). Despite relatively homogeneous levels of post-dispersal seed survival across patches, differences in seed rain did not translate into concordant recruitment of emerged seedlings. Differences in seedling emergence, most likely associated with microhabitat-specific suitability for seed survival in the soil, offset variation in seed rain. Finally, seedling survival was particularly high in microhabitats where the probability of recruitment in the preceding stages was very low. Although differences among habitat patches in seed rain, post-dispersal seed survivorship, germination, and early seedling survival have been frequently documented (Bazzaz, 1991; Harper, 1977; and references therein), they are rarely integrated to obtain a dynamic view of recruitment for a particular species and environmental settings. Ideally, the suitability of a given patch for propagule establishment should be estimated as a function of the elemental transition probabilities derived from all stages of recruitment; estimations based on one or two consecutive stages, may lead to erroneous conclusions. This key point has been recently stressed by Schupp (1995), who reviewed the available evidence for discordances of patch suitability for seeds and seedlings and found seed-seedling conflicts to be taxonomically, ecologically, and geographically widespread.

Modeling the regeneration phase as a series of steps connected by transition probabilities is not only useful as an heuristic description, but also to obtain empirical estimates of direct and indirect influences on recruitment. Structural equation models, and specifically path analysis, have been used previously in ecological research (Kingsolver & Schemske, 1991; Mitchell, 1992; Schemske & Horvitz, 1988), and are particularly useful when applied to multi-staged processes such as developmental or demographical sequences (see Maddox & Antonovics, 1983, and references therein). Both direct and indirect effects of processes acting during recruitment were important in determining the final proportion of *P. latifolia* seedlings established in different microhabitats. In particular, unevenness of seed rain had an

important indirect causal effect on final recruitment in the two sites, largely mediated by its influence on seed survivorship and seedling emergence. If these cascading influences of seed rain on recruitment occur commonly in nature, their relative importance would be difficult to assess without designs explicitly accounting for indirect effects among stages (Eriksson & Ehrlén, 1992). It is not surprising that seed rain variation (among habitats, microhabitats, or reproductive seasons) often obscures variation in other demographic processes (De Steven, 1991a,b; Gill & Marks, 1991; Herrera *et al.*, 1994; Hett, 1971; Houle, 1992, 1994; Streng, Glitzenstein & Harcombe, 1989), because spatial variance in the influx of seeds tends to be very large. Seed rain limitation on recruitment can be established whenever additional seed input results in increased final seedling recruitment (Crawley, 1990). This was not the case in the forest site, where patches with increased seed rain yielded lower survivorship values for seeds and seedlings. Whether the seeds fail to germinate because of inadequate microenvironmental conditions, underground seed mortality, or early mortality of seedlings prior to emergence, would be difficult to evaluate in the field but may determine a strong uncoupling between pre- and post-germination stages (De Steven, 1991b; Herrera *et al.*, 1994; Horvitz & Schemske, 1994). Data for the scrubland site contrasted markedly with those of the forest, and indicate that seedling emergence was primarily limited by the activity of frugivorous birds, which resulted in differential seed delivery beneath fruit-bearing cover. Whether microsite quality or seed availability constrains recruitment in populations of fleshy-fruited species is a complex question (Crawley, 1990). A combination of these two effects will most likely influence recruitment depending on the spatial and temporal scale considered (Eriksson & Ehrlén, 1992). The major demographic consequence of animal dispersal for zoochorous species is whether the resulting seed delivery is limiting for recruitment or not, and the *P. latifolia* data reveal that this consequence might offset later-acting processes. Most variance in among-habitat seedling recruitment was explained by both indirect and direct effects of seed rain in the - seed limited - scrubland site. In contrast, frugivores did not limit seed rain among patches on the forest site, recruitment variation being largely explained by post-germination processes. Frugivore activity first limits the absolute number of seeds delivered, then their dissemination over a complex landscape of microenvironments that differ in survivorship expectancies for propagules (Schupp, 1993); thus, limitation of recruitment shows up as a result of the interaction of these two processes.

Plant regeneration strategies' have been often interpreted as adaptive responses to the combination of selective pressures from multiple filters during the regeneration phase, resulting in integrated, predictable combinations of traits related to germination, dormancy, timing of seedling emergence, and seedling growth patterns (Denslow, 1980; Ellison *et al.*, 1993; Grubb, 1977). In the presence of strong uncoupling of regeneration stages, as shown here for *P. latifolia*, it would be extremely difficult to predict how the 'strategies' specific to particular stages 'add up' to a regeneration strategy, as the net result of each stage is so

context-specific. Future studies explicitly addressing the multi-staged nature of recruitment in sets of coexisting species and/or under variable environmental settings should therefore contribute in significant ways to improve our understanding of this critical phase in plant demography.

Acknowledgements

We appreciate the collaboration of J. A. Amat, M. Carrión, and L. López-Soria during the field work that provided the basis for this paper. E. W. Schupp kindly sent us reprints of his work. Funding was provided by grants PB87-0452 and PB91-0114 from the Dirección General de Investigación Científica y Técnica, Ministerio de Educación y Ciencia.

Literature cited

- Andersen, A. N., 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia*, 81: 310-315.
- Bazzaz, F. A., 1991. Habitat selection in plants. *American Naturalist*, 137: S116-S130.
- Crawley, M. J., 1990. The population dynamics of plants. *Philosophical Transactions of the Royal Society of London, Series B*, 330: 125-140.
- De Steven, D., 1991a. Experiments on mechanisms of tree establishment in old-field succession: Seedling emergence. *Ecology*, 72: 1066-1075.
- De Steven, D., 1991b. Experiments on mechanisms of tree establishment in old-field succession: Seedling survival and growth. *Ecology*, 72: 1076-1088.
- Debussche, M. & P. Isenmann, 1994. Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos*, 69: 414-426.
- Denslow, J. S., 1980. Gap partitioning among tropical rainforest trees. *Biotropica*, 12: 47-55.
- Ellison, A. M., J. S. Denslow, B. A. Loiselle & M. D. Brenes, 1993. Seed and seedling ecology of neotropical Melastomataceae. *Ecology*, 74: 1733-1749.
- Eriksson, O. & J. Ehrlén, 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia*, 91: 360-364.
- Gill, D. S. & P. L. Marks, 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecological Monographs*, 61: 183-206.
- Grubb, P. J., 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Quarterly Review of Biology*, 52: 107-145.
- Grubb, P. J., 1988. The uncoupling of disturbance and recruitment, two kinds of seed bank, and persistence of plant populations at the regional and local scales. *Annales Zoologici Fennici*, 25: 23-36.
- Harper, J. L., 1977. *Population Biology of Plants*. Academic Press, London.
- Herrera, C. M., 1984. Seed dispersal and fitness determinants in wild rose: Combined effects of hawthorn, birds, mice, and browsing ungulates. *Oecologia*, 63: 386-393.
- Herrera, C. M., 1991. Dissecting factors responsible for individual variation in plant fecundity. *Ecology*, 72: 1436-1448.
- Herrera, C. M., P. Jordano, L. López Soria & J. A. Amat, 1994. Recruitment of a mast-fruiting, bird-dispersed tree: Bridging frugivore activity and seedling establishment. *Ecological Monographs*, 64: 315-344.

- Hett, J. M., 1971. A dynamic analysis of age in sugar maple seedlings. *Ecology*, 52: 1071-1074.
- Hoppes, W. G., 1988. Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology*, 69: 320-329.
- Horvitz, C. C. & D. W. Schemske, 1994. Dormancy and seedling emergence of an ant-dispersed tropical herb, *Calathea ovan-densis*. *Ecology*, 75: 1949-1958.
- Houle, G., 1992. Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of north-eastern North America. *Journal of Ecology*, 80: 99-108.
- Houle, G., 1994. Spatiotemporal patterns in the components of regeneration of four sympatric tree species: *Acer rubrum*, *A. saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*. *Journal of Ecology*, 82: 39-53.
- Howe, H. F., 1989. Scatter- and clump-dispersal and seedling demography: Hypothesis and implications. *Oecologia*, 79: 417-426.
- Howe, H. F., 1990. Seed dispersal by birds and mammals: Implications for seedling demography. Pages 191-218 in K. S. Bawa & M. Hadley (ed.). *Reproductive Ecology of Tropical Forest Plants*. Man and the Biosphere Series Vol. 7. UNESCO & Parthenon Publ. Group, Paris.
- Howe, H. F., E. W. Schupp & L. C. Westley, 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology*, 66: 781-791.
- Izhaki, I., P. B. Walton & U. N. Safriel, 1991. Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *Journal of Ecology*, 79: 575-590.
- Jordano, P., 1989. Pre-dispersal biology of *Pistacia lentiscus* (Anacardiaceae): Cumulative effects on seed removal by birds. *Oikos*, 55: 375-386.
- Katusic-Malmborg, P. & M. F. Willson, 1988. Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois woodlot. *Condor*, 90: 173-186.
- Kingsolver, J. G. & D. W. Schemske, 1991. Path analyses of selection. *Trends in Ecology and Evolution*, 6: 276-280.
- Kitajima, K. & C. K. Augspurger, 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor*. *Ecology*, 73: 153-169.
- Maddox, G. D. & J. Antonovovics, 1983. Experimental ecological genetics in *Plantago*: A structural equation approach to fitness components in *P. aristata* and *P. patagonica*. *Ecology*, 64: 1092-1099.
- Masaki, T., Y. Kominami & T. Nakashizuka, 1994. Spatial and seasonal patterns of seed dissemination of *Cornus controversa* in a temperate forest. *Ecology*, 75: 1903-1910.
- Mitchell, R. J., 1992. Testing evolutionary and ecological hypotheses using path analysis and structural equation modelling. *Functional Ecology*, 6: 123-129.
- Morris, W. F., P. L. Marks, C. L. Mohler, N. R. Rappaport, F. R. Wesley & M. A. Moran, 1986. Seed dispersal and seedling emergence in an oldfield community in central New York (USA). *Oecologia*, 70: 92-99.
- Pedhazur, E. J., 1982. *Multiple Regression in Behavioral Research*. Holt, Rinehart and Winston, New York.
- Reid, N., 1989. Dispersal of mistletoes by honeyeaters and flower-peckers: Components of seed dispersal quality. *Ecology*, 70: 137-145.
- SAS, 1988. *SAS/STAT User's Guide*, Release 6.03 edition. SAS Institute, Inc., Cary, North Carolina.
- Schemske, D. W. & C. C. Horvitz, 1988. Plant-animal interactions and fruit production in a neotropical herb: A path analysis. *Ecology*, 69: 1128-1137.
- Schupp, E. W., 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. Pages 15-29 in T. H. Fleming & A. Estrada (ed.). *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects*. Kluwer Academic Publishers, Dordrecht.
- Schupp, E. W., 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, 82: 399-409.
- Schupp, E. W., H. F. Howe, C. K. Augspurger & D. J. Levey, 1989. Arrival and survival in tropical treefall gaps. *Ecology*, 70: 562-564.
- Streng, D. R., J. S. Glitzenstein & P. A. Harcombe, 1989. Woody seedling dynamics in an east Texas floodplain forest. *Ecological Monographs*, 59: 177-204.