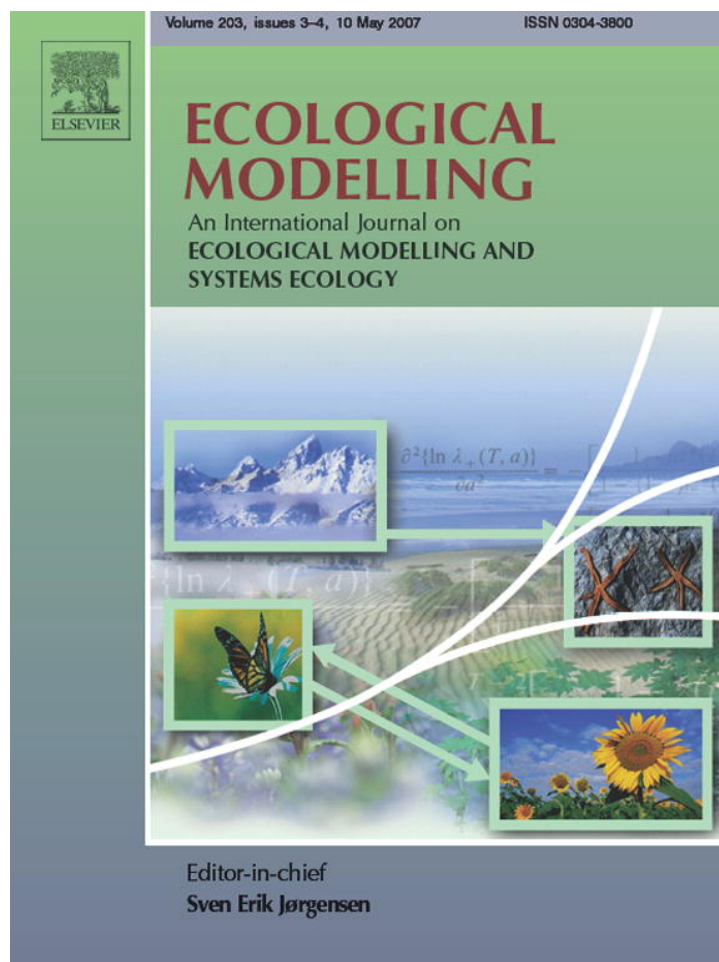


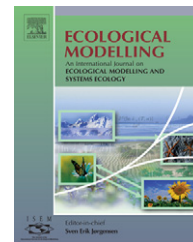
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Modelling seed dispersal to predict seedling recruitment: Recolonization dynamics in a plantation forest

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ABSTRACT

The extent to which seed dispersal influences seedling recruitment is of major importance for forest dynamics. In non-equilibrium situations, seed dispersal might be of even further importance as it is a major determinant of the rate and composition of secondary succession. We modelled primary seed dispersal in a planted pine–spruce stand intensively recolonized by *Abies alba* and *Fagus sylvatica*, an ecological situation commonly found throughout southern Europe. We then evaluated the role of primary seed dispersal in seedling emergence and recruited seedling density. Using a seed trap experiment and inverse modelling methods, we calibrated short- and medium-distance seed dispersal functions. The relationship between the density of dispersed seed, the density of emerging seedlings and microsite characteristics were assessed using generalized linear models. The cumulative distribution function of seedling-to-nearest-adult distances made it possible to test the concordance between seed rain patterns and seedling spatial distributions. Seed production was highly variable between years for *A. alba* and *F. sylvatica*. Seed dispersal was shown to be locally restricted (median dispersal distance of 13.2–19.2 m for *A. alba* depending on the year and 6.49 m for *F. sylvatica*). Model prediction was considerably increased when seed production was directly assessed (and not indirectly estimated using diameter, for example). The number of *A. alba* seedlings that emerged in 1999 was positively correlated with the number of seeds dispersed in 1998 and with the local density of *Picea abies* adults, and negatively correlated with grass cover. The spatial distribution of seedlings was less aggregated around adult trees than expected from seed dispersal models, but significantly different from random beyond 6 m to the nearest adult for *F. sylvatica* and 26 m for *A. alba*. Thus, seed rain patterns are only partially responsible for recruitment dynamics in our model forest. Our study demonstrates that inverse modelling methods are well suited for the study of seed dispersal at the local scale, especially when a direct count of seed production can be made, and are therefore of particularly high interest in forests where several successional stages are present.

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1. Introduction

Predicting the local distribution of new recruits in a plant community has long been a major challenge in ecology. The distribution of seedlings results from several processes: adult fecundity, seed dispersal, spatial distribution of suitable microsites, pre- and post-dispersal seed predation, and intra- and inter-specific competition (e.g. Harper, 1977; Janzen, 1970; Clark et al., 1998; Nathan and Müller-Landau, 2000; Van der Wall et al., 2005). The relative importance of each process might be variable according to ecological requirements and biological traits of species, overall plant community density and composition, successional status within the community, density of seed predator populations and temporal fluctuations in climatic factors (Clark et al., 1999a). The regeneration dynamics of plant communities can thus be considered as a temporal and spatial sequence of different stages, from seed production to recruited seedlings, interacting with biotic and abiotic factors (Clark et al., 1999a; Nathan and Müller-Landau, 2000).

Over the last decades, most experimental studies of seedling recruitment have focused on just one stage (but see Herrera et al., 1994; Jordano and Herrera, 1995; Clark et al., 1998; Uriarte et al., 2005). For example, sowing experiments made it possible to describe microsites suitable for seed germination (De Steven, 1991a) and early seedling survival (De Steven, 1991b). However most of them only provided partial understanding of natural regeneration dynamics, because they assumed that seed rain was unlimited and homogeneous (but see Clark et al., 1998). Likewise, calibrating dispersal functions was not sufficient to measure the existence of recruitment limitations in plant communities, without knowledge of the spatial distribution of safe sites (Jordano and Godoy, 2002) and their saturation threshold (Nathan and Müller-Landau, 2000). Integrated approaches combining information on seed dispersal and seedling establishment are needed to better understand recruitment processes (Schupp, 1995; LePage et al., 2000).

The heterogeneity of seed rains is now considered a major determinant of natural regeneration dynamics (e.g. Nakashizuka, 2001). However, integrated studies were previously limited by difficulties in measuring seed dispersal. In natural uneven-aged forest communities where individual seed shadows overlap and fecundity varies among adult trees, measuring seed dispersal has been considered an impossible task until fairly recently (Ribbens et al., 1994; Clark et al., 1998). Increasingly refined statistical methods (Ribbens et al., 1994; Clark and Ji, 1995; Clark et al., 1998, 1999a), and the development of spatially explicit forest dynamics models (Pacala et al., 1996) now make it possible to quantify seed shadow patterns within forest communities and to measure the role played by seed dispersal in natural regeneration dynamics. Indeed, although several processes might interact simultaneously to shape a spatial pattern and limit the ecological information that can be drawn from spatial statistics, spatial analysis of fully mapped data can help us to better understand the demographic dynamics of plant populations when using clearly identified ecological hypotheses (Barot et al., 1999; Péliissier and Goreaud, 2001).

Most studies of natural regeneration dynamics have focused on closed-canopy, late-successional forests, where competition and microsite distributions were more important than seed dispersal limitation (but see Dalling et al., 2002). In this study, our goal is to investigate the early stages of regeneration dynamics in a forest characterized by several successional stages, where seed dispersal can determine the speed of recolonization as well as the initial composition of the recolonizing forest community (Grubb, 1977; Howe and Smallwood, 1982; Willson, 1993). Natural recolonization of plantation forests and old fields by late-successional forest tree species is currently occurring on a wide scale in many southern European mountainous regions since the middle of the 20th century (Rameau, 1992). We studied seed dispersal and recruitment of new seedlings of silver fir, *Abies alba* (Mill.) and European beech, *Fagus sylvatica* (L.), two shade-tolerant, late-successional species, recolonizing a planted pine (*Pinus uncinata*) and spruce (*Picea abies*) stand on Mont Ventoux, south-eastern France. Calibrating seed dispersal using seedling distribution is not straightforward as seedling distribution is a function of multiple processes, and not just seed dispersal. In this study, we calibrated primary seed dispersal functions for both *A. alba* and *F. sylvatica* using a seed trap experiment and we evaluated the effect of the primary seed rain and microsite characteristics on seedling emergence in *A. alba*. We show that inverse modelling approaches are powerful for calibrating seed dispersal and greatly improved when seed source production potential is thoroughly described.

2. Material and methods

2.1. Study species and study site

A. alba and *F. sylvatica* are two keystone tree species in low to mid-altitude European mountainous forest ecosystems. Both are shade-tolerant late-successional species that form mixed forests over a broad range of ecological conditions from sub-Mediterranean to upper Montane bioclimatic regions. *A. alba* only regenerates from seeds (it is an obligate seeder) and produces winged seeds dispersed by wind. *F. sylvatica* reproduces both by seeds (beech nuts) and by root sprouting. Beech nuts are relatively heavy, highly nutritious and consumed by many vertebrate species. Twenty-six species of birds and 17 species of mammals feeding on beech seeds were recorded by Turcek (1961 and 1967, in Nilsson, 1985). Although beech nuts' primary dispersal is by gravity, their most important dispersal vector is by scatter-hoarding animals.

The study was conducted on Mont Ventoux (44°11'N; 5°17'E), a calcareous mountain located at the southwesternmost tip of the Alps. By 1850, it was almost entirely deforested due to over-grazing by sheep and goat. Mixed *A. alba*-*F. sylvatica* forests were reduced to small forest islands in the most inaccessible parts of the mountain. The decrease of grazing combined with the reforestation efforts undertaken in the early 20th century (using mostly pine and spruce) made it possible for *A. alba* and *F. sylvatica* to gradually recolonize the planted stands.

Field data used in this study were collected from a 1 ha Intensive Study Plot (ISP) on the northern slope of Mont Ventoux at an elevation of 1450 m above sea level. There, average annual precipitation is 1400 mm per year and snow is frequent from December to March. This area was planted approx. 80 years ago with exotic trees, Mountain pine (*P. uncinata*) and Norway spruce (*P. abies*). We selected this ISP for our study because, although pine and spruce adult trees greatly outnumbered naturally occurring adult *A. alba* and *F. sylvatica* trees (we measured that their basal area was 8% that of pine and spruce combined), regeneration was predominantly made of *A. alba* (48% of seedlings) and *F. sylvatica* (23%). *P. uncinata* seedlings were not found and *P. abies* seedlings accounted for less than 4% of all seedlings. Other rare adult tree species that significantly contributed seedlings within the ISP included *Sorbus aria* (17% of all seedlings) and *S. aucuparia* (6%). The few selective cuttings (thinning) performed over the last decades within the ISP only removed the planted pine and spruce trees.

2.2. Mapping of adults and seedlings

All trees over 20 cm in height, growing within the ISP, were individually mapped using a laser telemeter Impulse 200 (Laser Technology Inc., Colorado, USA) during the summer of 1998. All *A. alba* and *F. sylvatica* adult trees located within 100 m of plot edges were also mapped, as they were considered as possible seed contributors to the ISP (Fig. 1). The diameter at breast height (dbh) of adult trees and the diameter of pine and spruce stumps were measured. We called “adult trees” those bearing seeds and we called “recruited seedlings” those immature trees that were between 20 and 50 cm in height (i.e. between 10 and 30 years old).

2.3. Seed production and seed trap design

During the summers of 1998 and 1999, a direct estimation of *A. alba* seed production was made by visually counting the cones

produced by each adult tree. Visual count is possible in *A. alba* because female cones are located on the outer margins of the crown. However, this was not possible for *F. sylvatica*. In the summer of 1998, 37 seed traps were established along a regular grid in the ISP to assess seed rain variability within the entire plot (Fig. 1). This design was meant to assess primary seed dispersal, which was supposed to be the main or only seed dispersal process in *A. alba*. In *F. sylvatica*, it is only the primary dispersal by gravity that can be monitored by a seed trap experiment, although secondary dispersal by vertebrates is extremely important for seedling emergence (Nilsson, 1985). Therefore, we expect to only explain part of the dispersal process in *F. sylvatica*. Traps were made of fine-mesh non-woven bags of 0.25 m² circular collecting surface, stapled to a wire frame (Hughes et al., 1987). They were placed horizontally 30 cm off the ground. Using this design, we did not find any evidence of seed predation in the seed traps (e.g. teeth holes, droppings, partially eaten seeds). All seed traps were mapped and thus, distances between each trap and all mapped adult trees could be calculated.

We also installed 10 seed traps in an additional stand (which we called the “mature” stand), situated in the vicinity of the ISP (Fig. 1). The mature stand is within a mature *A. alba*–*F. sylvatica* mixed forest (over 200 adult *A. alba* trees per hectare and over 60 adult *F. sylvatica* trees per hectare). In this stand, all adult *F. sylvatica* trees had previously been mapped, and we used it as a replicate of the ISP for beech nut dispersal, because beech nut production occurred only once during the 2 years of the experiment. There, we observed that density of young *F. sylvatica* trees (less than 1.30 m high) was 1500 per hectare.

Seed traps were regularly emptied in 1998 (eight times) and in 1999 (five times), from the end of September to early November, and once in the following springs when the snow was melted. *A. alba* and *F. sylvatica* seeds were counted in the laboratory. Filled and empty seed proportions were estimated for each seed trap using X-rays.

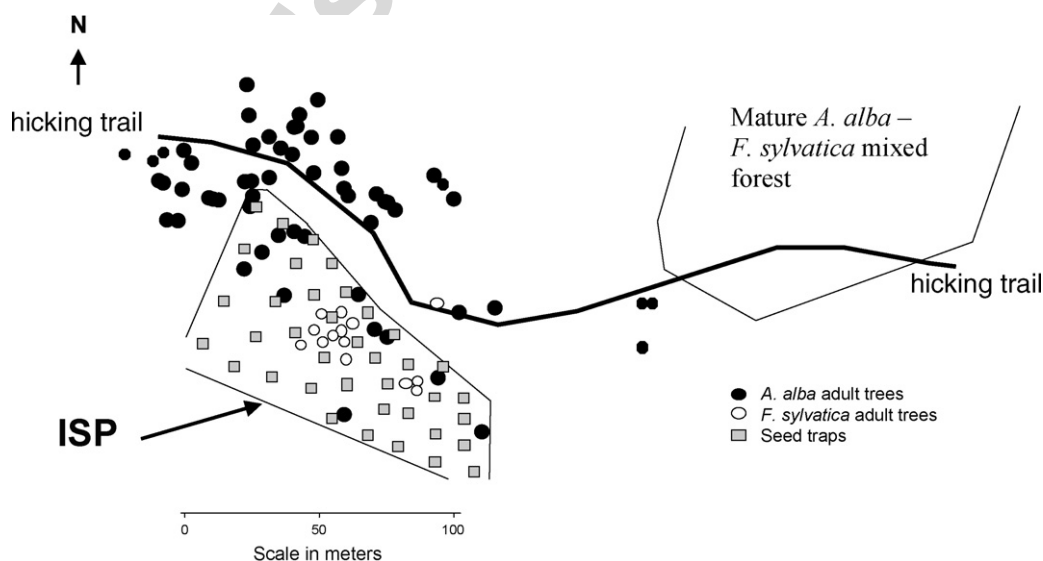


Fig. 1 – Spatial distribution of *F. sylvatica* and *A. alba* adult trees within the Mont Ventoux Intensive Study Plot (ISP). Adult trees found within a 100 m radius from the ISP are also shown. The adult trees within the mature *A. alba*–*F. sylvatica* mixed forest located further than a 100 m from the ISP were not mapped.

2.4. Modelling seed dispersal

We assumed that seed trees located farther away than 100 m from the edge of the ISP were unlikely contributors to the local seed rain, as almost all seeds from wind-dispersed conifers are found near (typically less than 25 m) seed trees (Nathan et al., 2000). In closed-canopy forests wind-dispersal distances are quite short due to slower wind speeds (Nuttle and Haefner, 2005). The density of seeds arriving in one location (x, y) is the summed contribution of seeds dispersed from all conspecific adult trees within the ISP and up to 100 m away from the edges of the plot. We used an inverse modelling method that assumes that each adult's contribution to the seed rain at a location depends only on its individual fecundity and its distance to the location. The approach we followed is an adaptation of that of Ribbens et al. (1994) which models the dispersion of seedlings in a forest stand (but see also Clark et al., 1998). Here, we used seeds and seed traps instead of seedlings.

The number of seeds N_i in a seed trap i is the overall sum over each adult j of the product of its fecundity P_j by the dispersal kernel f which gives the probability that a seed is dispersed at a distance r_{ij} from a tree:

$$N_i = \sum_j P_j f(r_{ij}) \quad (1)$$

We modelled adult fertility and dispersal kernel components, we estimated dispersal parameters and validated our model as follows.

2.4.1. Adult fecundity component

We constructed a fecundity model linking seed production to tree size, similar to that generally used in forest tree species (Ribbens et al., 1994; Clark and Ji, 1995; Clark et al., 1998, 1999a), which we used for *F. sylvatica* for which a direct estimation of seed production was not possible:

$$P_j = \beta A_j \quad (2)$$

where the number of seeds produced by a tree (P_j) is the product of β , the fecundity parameter (in number of seeds per square centimeter of basal area) and A_j , the basal area at breast height (in cm^2) calculated from individual dbh measures.

For *A. alba*, as cone production can be directly estimated, we constructed another fecundity model:

$$P_j = S C_j \quad (3)$$

where the number of seeds produced by a tree (P_j) is the product of the number of cones it bears (C_j) by the mean number of seeds per cone (S).

2.4.2. Dispersal kernel components

We considered the dispersal as isotropic and assumed that the dispersal kernel belonged to the exponential family (Ribbens et al., 1994; Clark et al., 1998). The dispersal kernel f is as follows:

$$f(r) = \frac{1}{n} e^{-Dr^c} \quad (4)$$

In this equation, n is the normalizer, calculated from the model, that constrains the dispersal kernel between 0 and 1 ($n = \int_{r=0}^{r=\infty} e^{-Dr^c}$), D the dispersal parameter that determines the speed of dispersal decrease with distance, c the parameter controlling the shape of the kernel (e.g. exponential: $c = 1$; Gaussian: $c = 2$, etc.) and r the distance between seed trap i and seed tree j (see Eq. (1)).

2.4.3. Parameter estimation

We assumed that the observed number of seeds in a seed trap O_i followed a Poisson distribution as in Ribbens et al. (1994) and Clark et al. (1999b). We used the Poisson likelihood:

$$L(O|\beta, S, D) = \prod_1^{37} \frac{e^{-N_i} N_i^{O_i}}{O_i!} \quad (5)$$

where β or S are the fecundity parameters to estimate from Eq. (2) to Eq. (3) and D and c the dispersal parameters from Eq. (4), O is the vector of the 37 seed trap counts and N_i the expected number of dispersed seeds in a seed trap i calculated from the model. The combination of parameter estimates that maximized the likelihood was retained in seed dispersal models.

2.4.4. Goodness-of-fit and validation

We computed a Pearson correlation coefficient between observed and expected values. To analyze the quantitative difference between observed and predicted seed rain, we performed paired t-tests ($H_0: \mu = 0$). In addition, we analyzed the spatial distribution of residuals with Moran's autocorrelation index (Cliff and Ord, 1981) on the 0–25 m distance lag to verify that our seed dispersal models did not exhibit spatial biases. We compared model predictions and observations and computed correlation coefficients to test the robustness of models.

2.5. Microsite characteristics and germinated seeds (seedling emergence)

We assessed germinated seeds by counting emerged, first year seedlings, which we distinguished from recruited seedlings. Emerged seedlings are closely tied to the seed rain of a given year, whereas recruited seedlings are a composite of many years of seed rains. We designed seedling emergence sampling points around each seed trap within the ISP and at 43 other mapped locations regularly distributed within the ISP. Each sampling point was made of eight 1- m^2 quadrats chosen on a 3 m \times 3 m grid, omitting the centre quadrat. Total sample size was thus 80 sampling points, i.e. approx. 7% of the total ISP size. Emerging seedlings were counted in late spring of 1999 and 2000 and summed over the quadrats. We chose the following variables to describe microsite characteristics: grass cover, bare ground cover, moss cover, shrub layer cover (including saplings up to 5 m in height), litter cover, stone cover, stump cover, and cover by debris resulting from tree cutting. Cover in percent at each sampling point was calculated as the mean cover over the eight quadrats. We also computed, from the adult tree map, the local density (number of stems) of adult pine and adult spruce trees within a 10 m diameter circle centered on the sampling point center. The number of dispersed seeds at each sampling point was estimated using our seed

dispersal model fitted with seed trap data collected in the ISP the previous autumn.

Variables were normalized using angular and log transformations for cover percentages and counts, respectively. A principal component analysis (PCA) was first performed (results not shown) to measure the correlation between microsite variables and to remove those most correlated to avoid information redundancy. The relationship between the number of emerged seedlings and microsite descriptors was then analyzed with a general linear model and the logarithmic link function (McCullagh and Nelder, 1989). The best model was retained after analyses of deviance tables (χ^2 tests).

2.6. Seed dispersal limitation and spatial distribution of recruited seedlings

We used the $F(d)$ function (Hamill and Wright, 1986) to measure the relative distribution of *A. alba* and *F. sylvatica* recruited seedlings (20–50 cm in height) relative to conspecific adults. $F(d)$ is a cumulative distribution function of juvenile-to-nearest-adult distances that represents the proportion of recruited seedlings located within a certain distance to the nearest adult. It is only conditional to plot dimensions and adult locations and offers two advantages over most commonly used spatial statistics such as Ripley's (1981) $K_{12}(d)$ function: it does not need edge corrections and allows adults located outside the plot to be taken into account. We tested two null hypotheses using Monte Carlo procedures:

- Under the “uniform distribution hypothesis (H_0)”, there is spatial independence, and recruited seedling spatial distribution is random relative to adult trees (Poisson distribution). Under this hypothesis, recruited seedling spatial distribution depends solely on the availability of suitable microsites and does not match the seed rain.
- Under the “seed rain hypothesis (H'_0)”, recruited seedling distribution matches the seed rain pattern estimated from seed dispersal models. Recruited seedlings are distributed according to the non-homogeneous Poisson process in which the density of seeds $\lambda(x, y)$ is estimated from the model.

When performing the Monte Carlo procedures, seedlings were distributed randomly over the whole ISP under the “uniform distribution hypothesis (H_0)”. Under the “seed rain hypothesis (H'_0)”, a number of recruited seedlings equivalent to the observed number of recruited seedlings was distributed according to the probability density of the summed seed shadows over the ISP. Rejection limits (5% confidence intervals)

were estimated as the envelopes of 199 simulated seedling distributions, under both the “uniform distribution hypothesis (H_0)” and the “seed rain hypothesis (H'_0)”.

Programs for computations of the seed dispersal models, generalized linear models and spatial analyses were performed using the R statistical environment (<http://www.r-project.org/>).

3. Results

3.1. Seed rain pattern and dispersal

Cone production in *A. alba* was higher in 1998 (64.5 ± 54.5 cones/adult tree) than in 1999 (37.5 ± 46.6). Beech nuts were only produced in 1999 (production data not available). Seed rains were highly heterogeneous within the ISP (Table 1). No silver *A. alba* tree under 14.9 cm in dbh had seed cones during the time of the study. There was a significant linear correlation between the number of cones and tree basal area in 1998 ($r=0.70$, $p<0.001$) and in 1999 ($r=0.62$, $p<0.001$) but the slope coefficients of the regression lines were significantly different (0.089 and 0.050, respectively, $p<0.05$). We found no significant difference for the number of filled versus empty seeds among seed traps. The mean proportion of filled to empty seeds was one third.

The estimated parameters for the seed dispersal models and goodness-of-fit tests are given in Table 2. For *A. alba*, observed data were better fitted by a fat-tailed negative exponential dispersal function ($c < 1$, Fig. 2a) while a Gaussian function ($c = 2$, Fig. 2c) performed better for *F. sylvatica*. Correlation coefficients between observed and predicted seed count values were highly significant (Table 2), and paired t-test for the non-significant difference for all models (data not shown). The fit between observed and expected seed count values (Fig. 2b and d) is expected as the two datasets are not independent. However, it did not reveal over-dispersion and made us consider that our assumption that the observed number of seeds per seed trap followed a Poisson distribution (see Section 2.4.3), was true.

Spatial biases occurred when fecundity was modelled as a function of the adult tree basal area for *A. alba*, since residuals of the models were spatially auto-correlated at short distance (Moran's index > 0 and significant in 1999, Table 2). For *A. alba*, temporal cross-validation of models was possible. The number of seeds observed in 1999 was significantly correlated to the number of 1999 seeds predicted using the 1998 model ($r=0.89$, $p<0.001$), and the number of seeds observed in 1998 was significantly correlated to the number of 1998

Table 1 – Seed rain intensity in 1998 and 1999 in the ISP and the mature reference stand

Species	Year	ISP (37 seed traps)	Mature stand (10 seed traps)
<i>A. alba</i>	1998	42.7 (108%)	59.6 (18%)
	1999	18.9 (132%)	118.8 (30%)
<i>F. sylvatica</i>	1998	0 (–)	0 (–)
	1999	7.78 (348 %)	77.6 (228%)

Mean values of seed density are expressed as number of seeds/m². Coefficients of variation are indicated in parenthesis.

Table 2 – Estimation and goodness-of-fit of dispersal model parameters.

Species	Year	Fecundity ^a	c	D	MDD ^b (m)	r	I _(0-25 m)
<i>A. alba</i>	1998	S = 443	0.594	0.525	19.2	0.92 ^{***}	0.02
		$\beta = 10.0$	0.521	0.778	18.1	0.88 ^{***}	0.13 ^{**}
	1999	S = 480	0.835	0.240	13.2	0.91 ^{***}	0.05
		$\beta = 4.75$	0.414	1.321	19.4	0.69 ^{***}	0.24 ^{**}
<i>F. sylvatica</i>	1999	$\beta = 0.745$	2	0.01648	6.49	0.77 ^{***}	-0.06

S and β are the fecundity parameters, c and D the parameters of the dispersal kernels, r the correlation coefficient between observed and expected number of seeds per seed trap, and Moran's I the spatial autocorrelation of the residuals at short distance (between 0 and 25 m). ^{***}p < 0.001; ^{**}p < 0.01.

^a Fecundity models according to Eq. (2) for β and Eq. (3) for S.

^b MDD is the median dispersal distance, calculated from the dispersal kernel.

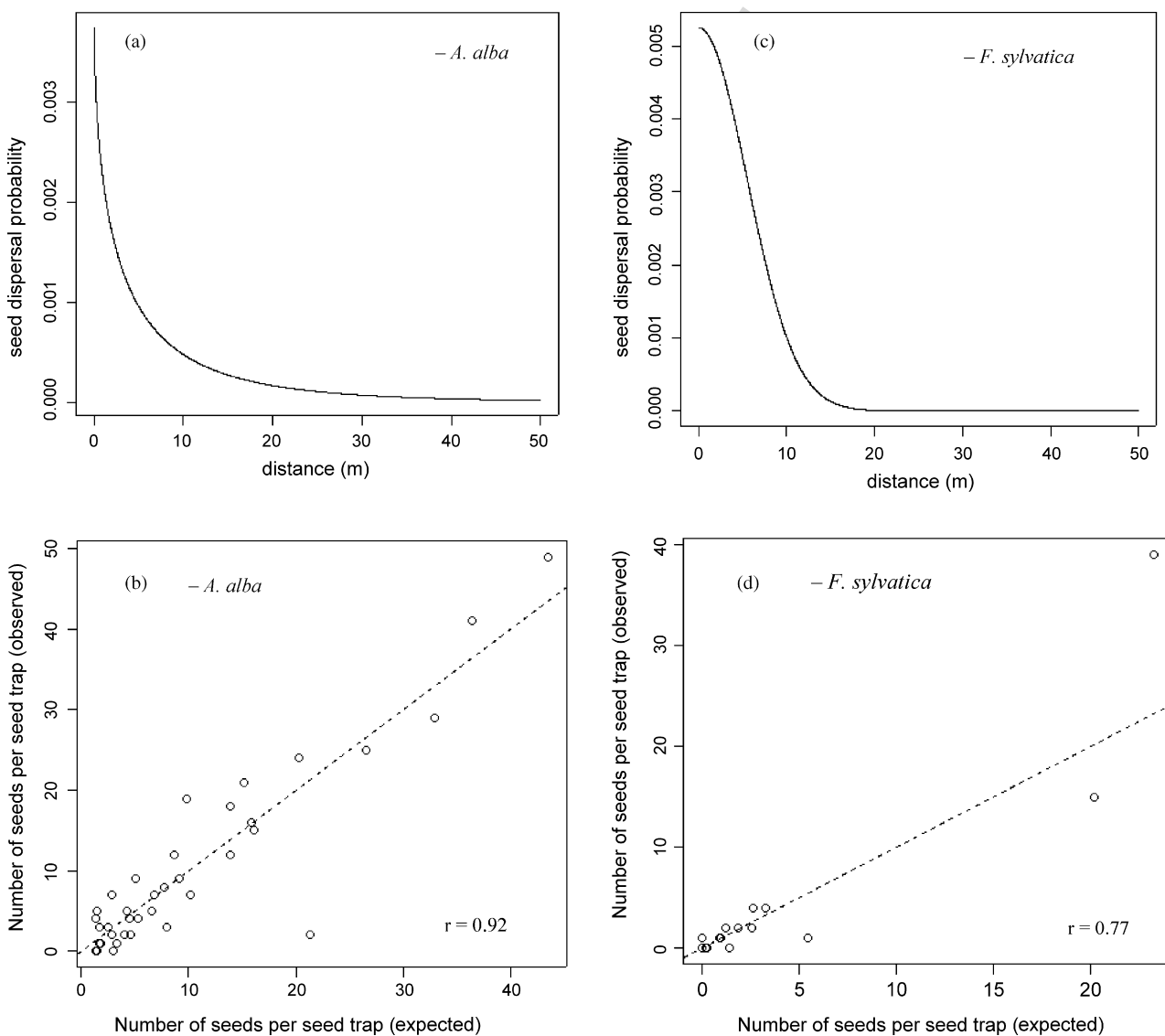


Fig. 2 – Seed dispersal models (a and c) and fit between observed and expected seed numbers (b and d) in the 37 seed traps of the Intensive Study Plot (ISP). In (a) and (c), the seed dispersal probability density is expressed at a given distance (as in Eq. (4)), and r is the correlation coefficient of Table 2. In (a), the fecundity model used is from Eq. (2) in 1998 (see Table 2).

Table 3 – Effect of the number of seeds dispersed in 1998 and microhabitat characteristics on the number of *A. alba* seedlings emerged in June 1999

Variables ^a	df	Regression coefficient	Standard error	Probability
Nseed	1	0.0235	0.0038	4.6×10^{-14}
GRASS	1	-0.9401	0.2501	1.7×10^{-4}
dPicea \times Nseed	1	0.3429	0.1253	6.2×10^{-3}

General linear model coefficients are estimated using the Poisson regression model (link function: log) and $n = 80$ sampling locations. Significance of variables was assessed by an analysis of deviance (χ^2 test). Only those microhabitat characteristics with significant p -values are listed in the table.

^a Variables—Nseed: number of dispersed seeds, estimated from the model; GRASS: percentage of grass cover; dPicea: local density of *P. abies* adult trees located within a 5 m radius centered on the sampling location.

seeds predicted using the 1999 model ($r = 0.91$, $p < 0.001$). For *F. sylvatica*, we validated the model by comparing the 1999 predicted values from the ISP and the observed values in the mature stand ($r = 0.80$, $p < 0.01$). These temporal and spatial cross-correlations provide a rigorous validation of our model as the datasets used are, this time, rather independent.

Primary seed dispersal of *F. sylvatica* (median dispersal distance = 6.49 m) was less than that of *A. alba* (from 13.2 m in 1999 to 19.2 m in 1998 using the direct fecundity estimation model). Predicted seed density was typical of models using decreasing-with-distance functions. It was less than 2 seeds/m² for *A. alba* and almost zero for *F. sylvatica* in those areas of the ISP most distant from adult trees. Using best fitted models (Table 2), the probability of seeds reaching at least 100 m from the seed source was 3.5×10^{-4} for *A. alba* and 10^{-6} for *F. sylvatica*.

3.2. Microsite characteristics and seedling emergence

We did not find any emerged seedlings in the ISP in 2000. In 1999, there were no emerged seedlings of *F. sylvatica* (no seeds were produced in 1998) and seedling emergence in *A. alba* was between 0 and 15/m², i.e. less than 1% of the total seed rain. Grass cover was positively correlated to moss cover, and negatively correlated to bare ground, litter and stone cover. Three variables could explain the observed variance of the 1999 *A. alba* emerged seedling density. The number of emerged seedlings was positively correlated with the number of dispersed seeds and negatively correlated with grass cover (Table 3). There was also an interaction between the number of emerged seedlings and the density of planted spruce. Under the spruce canopy, density of emerged seedlings was strongly and positively correlated with number of seeds dispersed the previous season, but not under the canopy of planted pines. The Spearman's rank correlation between the number of dispersed seeds and emerged seedlings was highly significant when all quadrats were used ($r = 0.71$, $p < 0.001$). However, it became non-significant when only those quadrats with grass cover > 40% were considered ($r = 0.07$, $p > 0.05$), because seedling emergence there was lower than expected from the number of seeds dispersed. Stump, shrub layer and debris cover were not correlated with emerged seedling density.

3.3. Seed dispersal limitations and spatial distribution of recruited seedlings

At short distances from seed trees, the “uniform distribution hypothesis (H_0)” was accepted and the “seed rain hypothesis

(H_0)” rejected for both *A. alba* and *F. sylvatica* (Fig. 3). The spatial distribution of recruited seedlings was found to be random and not correlated to the seed rain pattern at distances from seed trees less than 26 m for *A. alba* and 6 m for *F. sylvatica*.

At greater distances both hypotheses were rejected. The observed $F(d)$ function crossed the upper rejection limit of the random distribution hypothesis for both species (Fig. 3), indicating that recruited seedlings tend to be closer to adult trees (especially for *F. sylvatica*) than would be expected by chance alone. At still greater distances, the observed $F(d)$ function neared the lower rejection limit of the “seed rain hypothesis (H_0)”, especially for *F. sylvatica* (Fig. 3). At these distances, we did not observe any aggregated distribution of suitable microsites within the ISP. Thus, and although the probability to find a recruited seedling is never strictly determined by the probability of finding a dispersed seed at the same location, once a threshold distance from seed trees is reached, seed dispersal becomes a limiting factor which influences the spatial structure of recruited seedlings.

4. Discussion

4.1. Inverse modelling of seed dispersal

Our seed dispersal model only takes into account primary seed dispersal, i.e. by wind for *A. alba* and by gravity for *F. sylvatica*. Secondary dispersal of seeds by wind can move seeds farther from adult trees than primary dispersal, depending on ground surface roughness (Matlack, 1989; Johnson and Fryer, 1992), which is very high in the ISP. Snow can smooth ground surface, but the majority of seeds in the ISP were dispersed before the first snow (e.g. 84.8% in 1998 and 73.7% in 1999 for *A. alba* seeds). However, secondary dispersal by birds and rodents is known to play an important role in *F. sylvatica* (Nilsson, 1985).

The shape of the dispersal kernel differed between the two species: *A. alba* is better described by a fat-tailed model ($c < 1.0$) whereas *F. sylvatica* is better described by a Gaussian model ($c = 2.0$). Both for *A. alba* and *F. sylvatica*, we demonstrated strong goodness-of-fit between observed and expected data using independent temporal and spatial cross-validations. Our estimates are comparable to those obtained in previous studies of forest tree dispersal. Ribbens et al. (1994) estimated mean distances between seed trees and seedlings (which should be higher than the mean seed dispersal distance if both secondary seed dispersal and density-dependent mortality occur) for several North American forest species to be

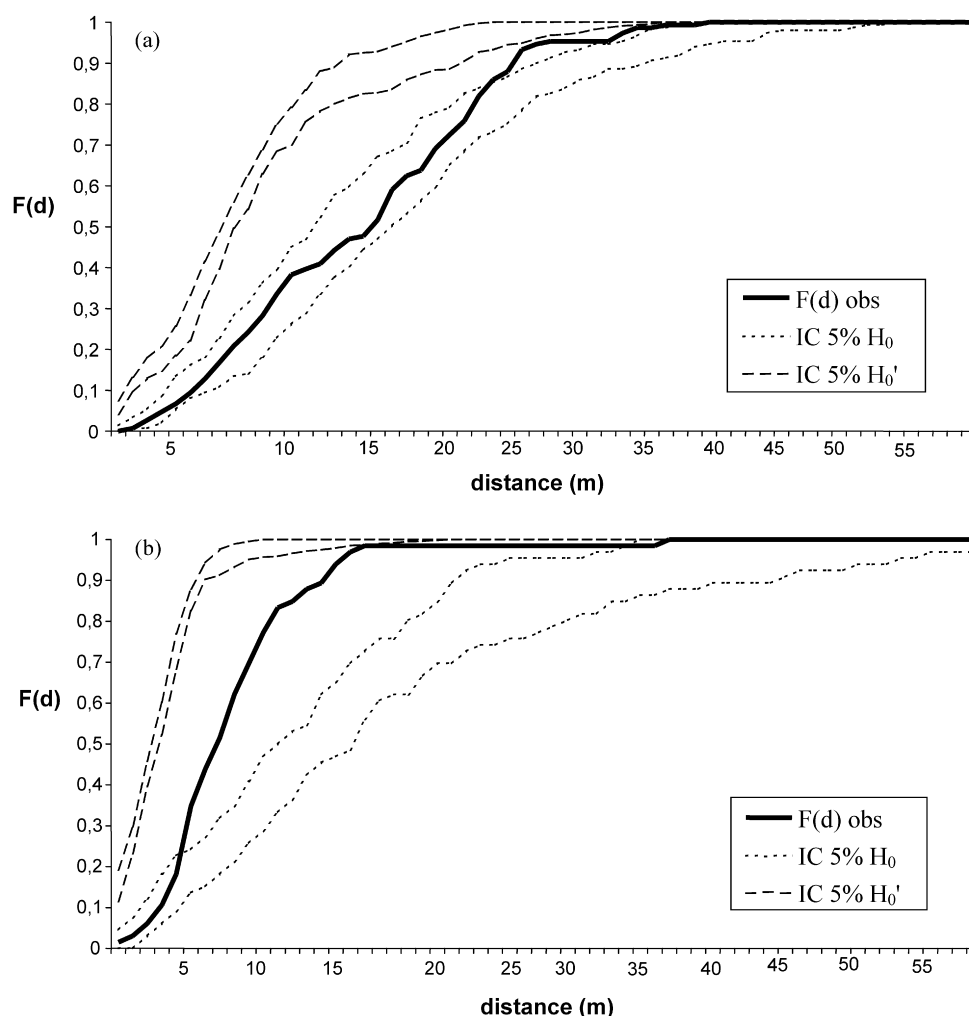


Fig. 3 – Distribution of cumulated distances between each seedling and the nearest adult tree ($F(d)$). H_0 corresponds to the “uniform distribution hypothesis” and H'_0 to the “seed rain hypothesis”. IC 5% H_0 and IC 5% H'_0 represent the 5% confidence envelope of the expected $F(d)$ under the two hypotheses: (a) *A. alba* and (b) *F. sylvatica*. Up to 26 m from the nearest adult tree, *A. alba* seedling spatial distribution is included within the “uniform distribution hypothesis” confidence envelope and is independent from the seed rain pattern (H'_0 hypothesis). The same holds true for *F. sylvatica*, but only up to 6 m from the nearest adult tree.

between 3.5 and 16.3 m. This range encompasses our *A. alba* and *F. sylvatica* seed dispersal estimates. Clark et al. (1998) gave parameter estimations for Gaussian dispersal kernels, also for several species of eastern North American forest trees. Their α' parameter is related to D as: $\alpha' = 1/D^{1/2}$. Hence, our α' for *F. sylvatica* is 7.79, which is in the range of α' reported by Clark et al. (1998) for *Cornus florida* (3.65), *Nyssa sylvatica* (6.02), *Carya glabra* (10.8) and *Quercus* sp. (11.8), which are animal-dispersed species. Willson (1993) found that most coniferous species have dispersal parameters (D) less than 0.05, e.g. 0.01 for *Abies amabilis* and 0.02 for *A. procera*, although the D value we estimated for *Abies* was 0.10–0.12. As *A. alba* seeds are morphologically similar to other *Abies* seeds, this difference may be due to the fact that Willson's (1993) seed dispersal models provide negative exponential coefficients based on simple regressions that do not take into account overlapping of individual seed rains (and thus overestimate dispersal and underestimate D).

While our estimated dispersion parameters (D) were consistent among years for *A. alba*, the fecundity component showed strong annual variations, typical of masting species (Herrera et al., 1994). We observed a 10-fold variation in cone production for some trees between two consecutive years. *F. sylvatica* is also known to have highly variable annual seed crops (Nillson and Wästljung, 1987). Using fecundity estimates (for example, tree size as we did for *F. sylvatica*) instead of direct count can thus be a serious bias for modelling seed rain, and long-term surveys are needed to obtain reliable estimates of fecundity (Clark et al., 1999b). In *A. alba*, spatial autocorrelations of residuals for seed counts in traps were only observed when fecundity was estimated using tree size (and not cone production). When fecundity estimation is supported by direct observation, our model provides consistent seed per cone estimates over the years, an indication of its biological reliability. We were able to estimate the number of seeds per cone in *Abies* to be 443 and 480, in 1998 and 1999, respectively. Direct

count of seed quantity per cone on controlled samples (from 198 to 416 seeds per cone) showed that our modelled values were slightly overestimated, possibly because the number of cones per tree was underestimated when direct counts were made on site.

4.2. Ecological factors affecting seedling emergence after dispersal

Pre- and post-dispersal seed predation is known to have severe demographic consequences, especially for non-buried seeds (Hulme, 1998; Van der Wall et al., 2005). It could explain the absence of emerged seedlings for *F. sylvatica*, as beech nuts are the main diet of several forest rodents (e.g. Jensen, 1985). Seed predation could also explain the absence of *A. alba* seedling emergence in 2000 and the low seedling emergence (only 1% of overall seed rain) of 1999. The genus *Abies* (Franklin, 1974) is also known to have a low percentage of filled seeds which we also observed in our study site (between 55 and 7% filled seed depending on the seed tree), and could be a further cause to low seedling emergence. Seedling emergence is thus strongly dependent on the quantity of seeds produced.

A dense grass layer inhibits *A. alba* seedling emergence, possibly through several mechanisms such as constituting a physical barrier that prevents the penetration of emerging seedling roots into the ground, and direct competition for water and nutrients (De Steven, 1991a). Within the ISP, we observed that those seedlings that were dying, were characterized by yellowing needles, a definite sign of drought stress. The fact that *A. alba* seedling emergence increased with planted spruce density (and thus with increasing bare ground and litter cover), and not planted pine density, can probably also be interpreted in terms of water availability. The canopy of *P. abies* produces more shade than that of *P. uncinata*, and thus better reduces ground surface temperature and the intensity of direct solar radiation, as well as the density of the grass layer. It has been shown that both high temperature and high transpiration rate can lead to the rapid death of young seedlings in shade-tolerant species (De Steven, 1991b). *A. alba* needs sufficient humidity to survive during the first years after germination (Tan and Bruckert, 1992) and it is likely that the dense shade of spruce produces more favorable microsite conditions than does pine. In many late-successional forest species, seedling density is generally greater in small gaps compared to large gaps more exposed to direct solar radiation (Gray and Spies, 1996). Our study is a further demonstration that, although the more seeds are found in a location the more seedlings emerge, it is the interaction of many different ecological processes that shape the spatial distribution of natural regeneration in forest stands (e.g. Clark et al., 1999a; Nathan and Müller-Landau, 2000).

4.3. Spatial distribution of recruited seedlings

At distances from seed trees less than 26 m for *A. alba* and 6 m for *F. sylvatica* (as shown in Fig. 3), recruited seedling spatial distribution is random and does not follow the seed rain pattern. The threshold distance is less for the barochorous (*F.*

sylvatica) than for the anemochorous (*A. alba*) species. This random spatial distribution of seedlings may be explained by a density-dependent mortality of seedlings, which assumes that the high mortality of seeds and seedlings in the neighborhood of adult plants is due to seed predators and seedling herbivores (Howe and Smallwood, 1982). Several herbivorous species that feed on *F. sylvatica* and *A. alba* seedlings, with a preference for the latter species (Ammer, 1996), are present on Mont Ventoux (e.g. mountain goat and deer). Browsing is high during winter, particularly around large adult trees where the snow layer is thinner. Density-dependent seedling mortality has also often been observed in dense tropical forests (Janzen, 1970; Harms et al., 2000) and in a Mediterranean Aleppo pine stand (Nathan et al., 2000).

Seed dispersal limitation starts influencing recruitment dynamics in both *A. alba* and *F. sylvatica* once a certain threshold distance from seed trees is reached. There, recruited seedlings tend to be located closer to seed trees. This pattern may be typical of recolonizing forests or forests where several successional stages are present. Seed dispersal limitation was found to be a highly significant predictor of seedling composition in neotropical pioneer species (Dalling et al., 2002). Concordance between seed rain and recruited seedling spatial patterns are less likely to occur in dense late-successional and old-growth forests, where safe sites are rapidly saturated with seeds and seedlings (e.g. Houle, 1992). In recolonizing forests, safe sites might become saturated at short distances, but because seed trees are less abundant than in dense late-successional forests, safe site availability is not limiting after a certain threshold distance.

The higher seed production and dispersal ability of *A. alba* compared to *F. sylvatica* might have landscape scale consequences. Given an initial advantage in its spread from proximate seed sources when suitable microsites are randomly distributed, it could explain why we observed that *A. alba* spreads faster than *F. sylvatica* in Mont Ventoux.

4.4. Dispersal and recruitment: understanding both local and landscape scale processes

Recolonization can be viewed as a bimodal process: a local wave spreading from nearby seed sources, and founding events due to rare long-distance dispersal of seeds (Cain et al., 2000; Clark et al., 2001; Nathan et al., 2002). As shown by population dynamics studies based on molecular markers and parentage tests, long-distance events are generally underestimated in classical dispersal models (e.g. Godoy and Jordano, 2001). This is especially true of species with animal-mediated seed dispersal (such as *F. sylvatica*), for which such long-distance dispersal events are not rare (Jordano and Godoy, 2002; Hardesty et al., 2006). Long distance seed dispersal by animals cannot be modelled as a decreasing function of distance. It requires direct observation of frugivorous microhabitat preferences and animal scatter-hoarding behaviors (Schupp, 1995; Jordano and Schupp, 2000; Van der Wall et al., 2005). It is also true for wind-dispersed species, where long distance dispersal also occurs and is not realistically estimated by models calibrated at short distances, such as ours. As pointed out by Clark et al. (1999b), extrapolating the tail of dispersal model beyond the data would be “speculative and inappropriate”.

ate". Fitting flexible kernels (2Dt models, Clark et al., 1999b) or mixed dispersal models, which represent a mixture of several kernels (Higgins and Richardson, 1999), might yield more realistic behaviors at intermediate scales. At the landscape scale, using seeds to model long distance dispersal is virtually impossible as they cannot be captured with reasonable probability at great distances from sources (Nathan, 2006), and other approaches must be used. Mechanistic approaches (Katul et al., 2005) and methods relying on genetic analyses (Godoy and Jordano, 2001) hold good promises for the study of long distance dispersal. However, it seems that only methods relying on both seed dispersal models and environmental constraints on seedlings can fully help measure and understand the role of long distance dispersal in population structure and evolution under different constraints (Pennanen et al., 2004; Bohrer et al., 2005; Nathan, 2006).

Still, dispersal processes at all scales must currently be better understood, e.g. to predict species dynamics under climate change (Neilson et al., 2005). Our study is a further demonstration (e.g. Dalling et al., 2002) that inverse modelling methods are a valuable conceptual tool to characterize local seed rain patterns. They only require a small amount of information, such as the adult tree spatial distribution, an estimate of their seed production, and a limited sampling of seed rain density. Their power is greatly improved when a direct measure (rather than a regressed estimate) of seed production is available. Mechanistic dispersal models, that constitute an alternative approach (e.g. Nathan et al., 2001) are based on accurate measures of the dispersal vector (wind speed and direction) which are often difficult to collect within forest stands.

Inverse modelling methods are therefore broadly applicable to the study of forest communities at the local scale (Clark et al., 1998), and are of particular interest in recolonizing forests. Here, we addressed the local scale process, and identified how primary seed dispersal occurs and how it influences seedling emergence and recruitment. Our study demonstrates the role played by seed dispersal limitations in the recruitment dynamics of recolonizing forests and forests where several successional stages are present. It supports the idea that, indeed, "seed dispersal matters" (Howe and Miriti, 2000), but only up to a certain point where recruitment becomes strongly limited by the availability of suitable microsites and density-dependent mortality.

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