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DISPERSAL SPECIAL FEATURE

Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation

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Summary

1. Plant fecundity and seed dispersal often depend on environmental variables that vary in space. Hence, plant ecologists need to quantify spatial environmental effects on fecundity and dispersal.
2. We present an approach to estimate and model two types of spatial environmental effects: *source effects* cause fecundity and dispersal to vary as a function of a source's local environment, whereas *path effects* depend on all environments a seed encounters during dispersal. Path effects are described by first transforming physical space so that areas of low seed permeability are enlarged relative to others, and then evaluating dispersal kernels in this transformed 'movement space'.
3. Models for source and path effects are embedded into the established inverse modelling (IM) framework. This enables the statistical estimation of environmental effects from easily available data on the spatial distribution of seeds, seed sources and environmental covariates.
4. The presented method is applied to data from a well-studied population of the wind-dispersed Aleppo pine (*Pinus halepensis*). We use local tree density as an environmental covariate, model fecundity as a function of a tree's basal area, and consider four dispersal kernels: WALD (a closed-form mechanistic model for seed dispersal by wind), log-normal, exponential power and 2Dt.
5. The inclusion of source and path effects of tree density markedly improves IM performance. IM analyses and independent data agree in the parameter range of the mechanistic WALD kernel and in suggesting weak negative density-dependence of fecundity. Of 64 IMs considered, the best four involve the WALD kernel and negative source effects on its shape parameter. The best IM predicts that increasing tree density at the source shortens median dispersal distance while enhancing long-distance dispersal (LDD). Additionally, path effects lead to lower seed permeability of high density areas. These results shed light on the mechanisms by which environmental variation affects fecundity and dispersal of *P. halepensis*. Moreover, the predicted density-dependent dispersal causes a pronounced lag-phase in simulations of population spread.
6. *Synthesis*. The presented method can quantify environmental effects on fecundity and dispersal in a wide range of study systems. The movement space concept may furthermore promote a unified understanding of how various organisms move through spatially heterogeneous environments.

Key-words: density-dependence, dispersal kernel, inverse modelling, local interactions, mechanistic model for seed dispersal by wind, movement space, path effect, plant fecundity, population migration, source effect

Introduction

Sessile plants live in spatially heterogeneous environments where seed production and dispersal determine the number of individuals dispersing between habitat types. This number in turn affects the regional dynamics of a species (e.g. Freckleton & Watkinson 2002), its ability to track environmental changes in space and time (Higgins *et al.* 2003), and its potential for local adaptation to environmental conditions (Kawecki & Ebert 2004).

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Due to the importance of seed production and dispersal, plant ecologists need to know how many seeds a plant produces and how far these seeds are dispersed. In many systems, these simple questions are difficult to answer (e.g. Clark *et al.* 1998, 1999b; Nathan & Muller-Landau 2000): pre-dispersal seed numbers are often difficult to quantify and tend to overestimate the number of successfully dispersed seeds. Alternatively, one can infer fecundity from post-dispersal seed densities. However, this requires knowledge about the mother plants from which the seeds originate, which is difficult to obtain because dispersing seeds typically cannot be tracked and seed shadows of neighbouring plants typically overlap.

A powerful and elegant solution to the problem of estimating plant fecundity and seed dispersal is the so-called 'inverse modelling (IM)' approach (Ribbens *et al.* 1994; Clark *et al.* 1998; see also Higgins *et al.* 2008; Muller-Landau *et al.* 2008; Jones & Muller-Landau 2008). IM simultaneously estimate fecundity and seed dispersal from the spatial distribution and size of mother plants, and the spatial distribution of seeds. They do not require the identification of each seed's mother plant, but instead infer fecundity and seed dispersal by searching for the fecundity and dispersal models that are most likely to generate the observed seed distribution from the observed adult distribution. IMs are also commonly used on seedling data (e.g. Ribbens *et al.* 1994), but this practice implicitly incorporates post-dispersal processes. Hence, special care must be taken when inferring seed dispersal processes from kernels fitted to seedling distributions.

The original application of IM in the context of plant dispersal and recruitment (Ribbens *et al.* 1994) has been extended in various directions to accommodate alternative dispersal kernels (Clark *et al.* 1999a), complex random effects and fecundity schedules (Clark *et al.* 2004) and genetic data (Jones & Muller-Landau, 2008). However, existing IM methods cannot simply be used to estimate effects of spatially varying environments on fecundity and dispersal. The study of such environmental effects seems particularly important for understanding and predicting how plants perform in heterogeneous environments and how they will respond to environmental change.

To examine how spatial variation in the environment affects fecundity and dispersal, a basic distinction should be made among two types of environmental effects introduced here as *source effects* and *path effects*. *Source effects* arise from the fact that seed sources located in different environments may differ in fecundity and dispersal. Hence, source effects are a function of the environment in which the seed source is located. *Path effects* arise from the fact that environmental heterogeneity along the dispersal path may affect the movement and deposition of seeds. Hence, path effects are a function of all environments a seed encounters along its dispersal path.

There is ample empirical evidence for both source and path effects on fecundity and dispersal. For instance, it is obvious that the local environment experienced by a plant can affect its seed production and can thus have a source effect on fecundity (e.g. Crawley 1997). Examples of source effects on seed dispersal involve cases of animal-dispersed seeds where local conditions at the seed source may affect the composition of the seed disperser coterie and the amount of seeds removed (Sargent 1990; Herrera *et al.* 1994; Jordano & Schupp 2000; Carlo & Morales 2008). In wind-dispersed seeds, turbulence conditions and wind velocities at the source affect a seed's probability to be uplifted above the canopy, which is a prerequisite for long-distance dispersal (LDD) by wind (Nathan *et al.* 2002; Bohrer *et al.* 2008; Soons & Bullock 2008). Path effects on seed dispersal are evident for animal-dispersed seeds, where habitat preferences of seed-dispersing animals cause seed deposition to peak in certain environments (e.g. Herrera *et al.* 1994; Wenny & Levey 1998; Jordano & Schupp 2000; Wenny 2001; Russo *et al.* 2006). Path effects on wind dispersal can result from spatial variation in wind conditions (Tackenberg 2003) as well as from collisions of the moving seed with obstacles. These processes affect both airborne seed movement (Thiede & Augspurger 1996; Pounden *et al.* 2008) and secondary seed dispersal along the ground (Schurr *et al.* 2005). In the case of water-dispersed seeds, spatial variation in the geomorphology of streams can greatly affect rates of seed deposition (Merritt & Wohl 2002), thus causing a path effect on dispersal.

The wealth of empirical evidence for environmental effects on plant fecundity and seed dispersal contrasts with a lack of quantitative tools for describing and modelling these effects. In this paper, we introduce a new approach capable of quantifying source and path effects on fecundity and dispersal. Integral to this approach is the idea of measuring space in units of '*movement space*' that are relevant to the dispersing seed, rather than in units of physical space. We embed this approach into the IM method, and use it to analyse how an environmental variable (local tree density) affects fecundity and dispersal of Aleppo pine (*Pinus halepensis*, Miller). Based on this analysis, we then explore the mechanisms underlying these environmental effects, and examine their consequences for the dynamics of population spread. Finally, we discuss how the concept of movement space may be extended beyond seed dispersal to study the movement of a wide range of organisms.

Methods

In this section, we first describe the standard IM framework, extend it to incorporate source and path effects on fecundity and dispersal, and show that the extended method can estimate such environmental effects from simulated data. We then use the extended IMs to quantify source and path effects in the recruitment of a *P. halepensis* population. To permit independent assessments of IM estimates, we conclude the Methods section by summarizing the available information on the fecundity and dispersal of this population.

INVERSE MODELS OF FECUNDITY AND DISPERSAL

IMs predict seed arrival at a given location by summing the seed shadows of all individual seed sources at this location. The seed shadow of an individual plant s is modelled as the product of the plant's fecundity Q and a dispersal kernel f (Ribbens *et al.* 1994; Clark *et al.* 1998). The expected seed number in a seed trap t of area A_t is thus

$$\hat{S}_t(G, r_t, A_t; \beta) = \sum_s Q_s(G_s; \beta_{\text{fec}}) f(r_{st;}\ \beta_{\text{disp}}) A_t \qquad \text{eqn 1}$$

where β is a vector of model parameters containing both fecundity parameters β_{fec} and dispersal parameters β_{disp}, r_t is a vector containing all distances r_{st} from a given trap t to all seed sources s, and G is a vector of size measurements G_s that are used to predict the fecundity of the seed sources s. We follow Clark *et al.* (1999a), in using a tree's basal area as this 'size variable' G and modelling fecundity Q as

$$Q_s(G_s) = bG_s \qquad \text{eqn 2}$$

so that $\beta_{\text{fec}} = [b]$. Alternative allometric fecundity models did not improve the fit of IMs to data for *P. halepensis* (F. Schurr, unpublished data, see also Clark *et al.* 1999b).

We consider four alternative dispersal kernels, each of which describes a two-dimensional probability density as a function of dispersal distance r with scale parameter u and shape parameter p (hence $\beta_{\text{disp}} = [u, p]$). Following the recommendation of Canham & Uriarte (2006), we use both flexible phenomenological and mechanistic models. The considered dispersal models are the exponential power kernel (Ribbens *et al.* 1994; Clark *et al.* 1998, 1999a)

$$f(r) = \frac{p}{2\pi u^2 \Gamma(2/p)} \exp\left[-\left(\frac{r}{u}\right)^p\right], \qquad \text{eqn 3}$$

the 2Dt distribution (Clark *et al.* 1999a)

$$f(r) = \frac{p}{\pi u \left(1 + \dfrac{r^2}{u}\right)^{p+1}}, \qquad \text{eqn 4}$$

and a bivariate log-normal kernel (Stoyan & Wagner 2001)

$$f(r) = \frac{1}{(2\pi)^{3/2} p r^2} \exp\left[-\frac{(\ln r - \mu)^2}{2p^2}\right], \qquad \text{eqn 5}$$

where we model the log-scale mean μ as a function of the log-scale standard deviation p and the mean dispersal distance u, so that $\mu = \ln(u) - (p/2)^2$. This parameterization of the log-normal distribution ensures that $u > 0$ and $p > 0$ as for the other kernels.

Finally, we consider the WALD kernel, a closed-form simplification of a mechanistic model for seed dispersal by wind (Katul *et al.* 2005)

$$f(r) = \left(\frac{p}{8\pi^3 r^5}\right)^{1/2} \exp\left[-\frac{p(r-u)^2}{2u^2 r}\right]. \qquad \text{eqn 6}$$

Formulas to calculate the mean, variance and higher moments of these kernels can be found in Klein *et al.* (2006) for the 2Dt and exponential power, and in Stoyan & Wagner (2001) for the log-normal. For details on WALD, see Katul *et al.* (2005); note that their eqn 5b is a one-dimensional kernel that denotes u and p as μ' and λ', respectively.

SOURCE EFFECTS ON FECUNDITY AND DISPERSAL

In agreement with the approach typically taken in geographical information systems, we assume that information about the spatial variation of environmental conditions can be represented in a spatially discrete grid E. To account for source effects, we model the fecundity and/or the dispersal parameters of each seed source s as a function of the local environment, E_s, in the source's grid cell. We ensure that b, u and p are positive by using an approach borrowed from link functions in generalized linear models (McCullagh & Nelder 1989)

$$b_s = \exp(\beta_{b0} + \beta_{b1}E_s),\ u_s = \exp(\beta_{u0} + \beta_{u1}E_s), \text{ and}$$
$$p_s = \exp(\beta_{p0} + \beta_{p1}E_s). \qquad \text{eqn 7}$$

For $E_s = 0$, b_s, u_s and p_s, are thus defined by the 'intercepts' β_{b0}, β_{u0} and β_{p0}, respectively, whereas the 'slopes' β_{b1}, β_{u1} and β_{p1} describe how b_s, u_s and p_s change with E_s. For $\beta_{b1} = \beta_{u1} = \beta_{p1} = 0$, the model reduces to a 'standard' IM without source effects.

PATH EFFECTS ON DISPERSAL

While the standard IM approach can easily be extended to describe source effects, the incorporation of path effects is more challenging, because these effects depend not only on the environmental conditions at the source but on *all* environments a seed encounters between source and deposition. For the sake of simplicity, we assume that path effects depend only on the environments crossed by the straight line extending from the source to the deposition site.

We describe these path effects by evaluating the dispersal kernel around a seed source in '*movement space*' rather than physical space. Movement space is obtained by projecting physical space so that distances through environments with low seed permeability are enlarged relative to distances in other environments (Fig. 1a). We emphasize that the concept of 'movement space' is widely used in everyday life: for instance, distances along hiking trails are typically expressed in units of movement space ('walking hours') rather than in units of physical space ('kilometres'). For a hiker, units of movement space are more informative because the probability of arrival at a certain point in a certain time (e.g. before sunset) does not only depend on the physical distance to that point but also on the roughness of the terrain crossed along the path.

Formally, we express the projection of physical space onto movement space as an inhomogeneous central dilation with origin at the source (Fig. 1a). In polar coordinates, a point P at distance r and angle θ from the source is projected according to

$$P(\theta, r) \rightarrow P'(\theta', r') \quad \text{with} \quad \theta' = \theta \quad \text{and} \quad r' = \sum_c d_c w_c, \qquad \text{eqn 8}$$

where c denotes all cells intersected by a straight line between the source and the trap, d_c is the length of the line segment in each cell $(\sum_c d_c = r)$, and w_c is a 'resistance' factor that reflects the cell's environment. The lower the seed permeability of an environment, the larger its resistance factor w_c. Setting $w_c > 0$ ensures that for any angle θ, an increase in physical distance from the source, r, also increases the distance in movement space, r'. Consequently, the projection is bijective so that any point in physical space has a unique equivalent in movement space, and vice versa. To describe the relationship between a cell's resistance factor w_c and its environmental value E_c, we again use a log-link

$$w_c = \exp(\beta_{w1}E_c). \qquad \text{eqn 9}$$

The omission of an 'intercept' in eqn 9 sets $w_c = 1$ for the 'reference environment' $E_c = 0$ An intercept is redundant because it would mean that all w_c are multiplied with the same constant factor. The resulting projected grid would then simply be a rescaled version of the grid obtained without an intercept. Note that for $\beta_{w1} = 0$, the model reduces to an IM without path effects.

The single parameter β_{w1} thus governs the projection of physical space onto movement space and provides a simple way of describing path effects on seed dispersal. Depending on the environment and the choice of β_{w1}, a simple isotropic kernel in movement space can

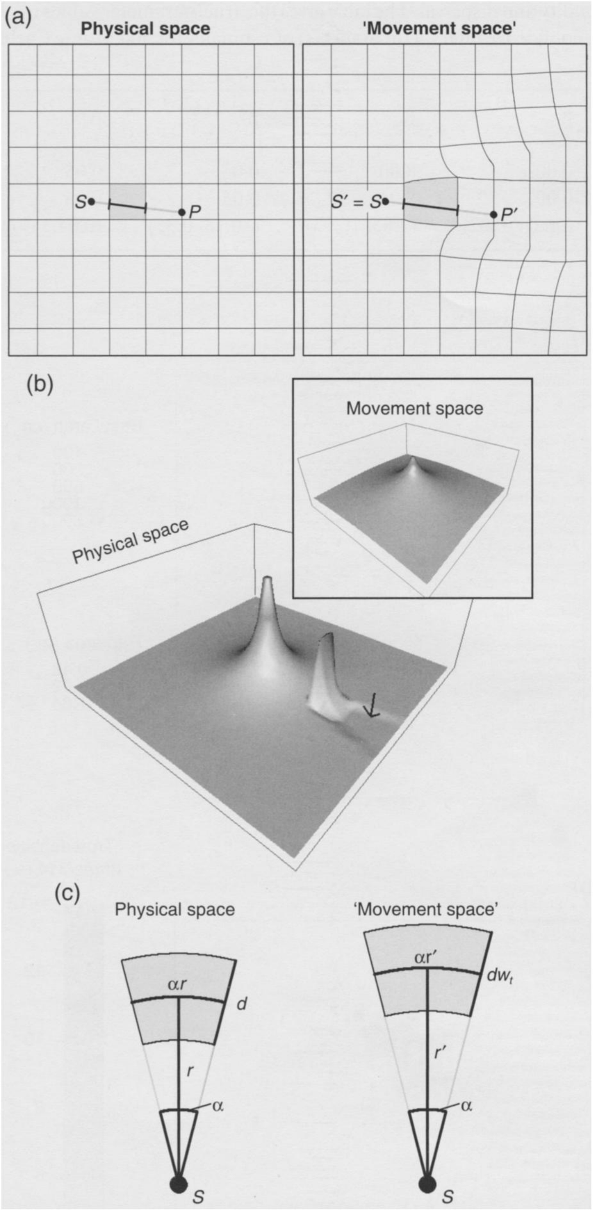

Fig. 1. (a) Path effects on seed dispersal are modelled by projecting the physical space around a seed source *S* onto 'movement space' so that *S'* = *S*. The projection enlarges distances in environments with low permeability for moving seeds (grey cell) relative to distances in other environments (white cells). Consequently, areas of low permeability are enlarged and locations 'shaded' by these areas (point *P* in physical space) are projected to be further away from the source (point *P'* in movement space). (b) A simple isotropic kernel in movement space (small insert) can describe anisotropic and discontinuous seed dispersal in physical space (large graph). The large graph shows two-dimensional seed densities in physical space predicted by an exponential power kernel in movement space. The minor peak indicates an area with low seed permeability that receives more seeds because it is enlarged relative to other areas. The arrow indicates an area behind this secondary peak that receives fewer seeds due to 'shading effects' (see Fig. 1a). (c) To efficiently project trap areas from physical space to movement space, we assume that traps have the shape of a ring sector. In physical space, this sector has length *d* and width $\alpha\, r$ (the product of apex angle α, and the distance *r* between the trap centre and the seed source *S*). In movement space, trap length is $d\, w_t$ (where w_t is the resistance factor of the trap's local environment), and trap width is $\alpha\, r'$ (where r' is the trap-source distance in movement space).

describe anisotropic and discontinuous seed dispersal in physical space (Fig. 1b): environments with low permeability for moving seeds (i) receive more seeds because they are enlarged relative to others; and (ii) reduce seed deposition in the areas behind them by increasing the movement distance between these 'shaded' areas and the seed source. Hence, by invoking the concept of movement space it is possible to describe a number of phenomena that cannot be incorporated into standard IMs.

To embed the concept of movement space into IMs, it is necessary to project both the distances between sources and seed traps, and the areas of the seed traps (if only distances were transformed, the dispersal kernel would not integrate to 1 in physical space). For traps of arbitrary shape, the calculation of projected trap areas is computer intensive. Hence, we approximate trap shapes as sectors of rings centred at the source (Fig. 1c). In physical space, such a ring sector has area *A* defined as

$$A = \alpha r d$$

where *r* is the distance between the source and the trap centre, *d* is the length of the trap in this direction, and α (in radians) is an apex angle that defines the width of the trap, $\alpha\, r$ (Fig. 1c). In movement space, the projection of this ring sector has area

$$A' = \alpha r' d w_t = A \frac{r'}{r} w_t \qquad \text{eqn 10}$$

where w_t is the resistance factor of the environment in which the trap is situated (Fig. 1c).

The projection of physical space onto movement space depends on the source's position in a heterogeneous environment *E* (Fig. 1). To calculate the contribution of each seed source *s* to all traps, it is thus necessary to separately project the physical space for each source and then evaluate the dispersal kernel for this projection. As in standard IMs (eqn 1), the predicted seed number in trap *t* is then calculated as the sum of the contributions of all seed sources.

$$\hat{S}_t(G, r_t, A_t, E; \beta) = \sum_s Q_s(G_s; \beta_{\text{fec}}) f(r'_{st}; \beta_{\text{disp}}) A'_{st}, \qquad \text{eqn 11}$$

MODEL FITTING AND PARAMETER ESTIMATION

To fit the IMs (eqns 1 and 11) to seed trap data, we calculate the likelihood of the data under a model with parameter vector β. Under the assumption that errors are Poisson distributed, the likelihood is a product of Poisson densities (Clark *et al.* 1999a)

$$L(s \mid \beta) = \textstyle\prod_n \text{Poisson}(\hat{S}_t(\beta)) \qquad \text{eqn 12}$$

where *S* is a vector of seed counts from *n* seed traps, and the mean of the Poisson distribution is given by $\hat{S}_t(\beta)$, the seed number predicted according to eqn 1 or 11. To obtain maximum-likelihood estimates of the parameters β, we minimized the negative log-likelihood (–ln *L*) using the simplex algorithm (Nelder & Mead 1965) with several overdispersed starting points. All numerical calculations were done in R 2.4.1 (R Development Core Team 2006) and R code for fitting IMs with source and path effects is given in Appendix S1 in Supplementary material. Since a main emphasis of this study is on the comparison of alternative models, we use a frequentist framework, where there is more agreement on methods of model selection than in a Bayesian framework (Carlin *et al.* 2006). We emphasize, however, that the IMs discussed here can also be embedded into a Hierarchical Bayesian framework (see Clark *et al.* 2004).

Table 1. Test of an inverse model with a path effect and source effects on fecundity and dispersal. The table gives the 'true' parameter values used to predict mean seed arrival at a seed trap, as well as the median and the 95% confidence interval (in brackets) of estimates for 500 Monte Carlo combinations of fractal landscapes, source and trap configurations

	β_{u0}	β_{u1}	β_{p0}	β_{p1}	β_{b0}	β_{b1}	β_{w1}
'True' value	2.00	0.05	1.00	0.00	8.00	0.05	0.05
Parameter estimate	2.03	0.05	1.02	0.00	8.01	0.05	0.05
	(–5.36, 8.40)	(–0.34, 0.33)	(0.37, 1.62)	(–0.04, 0.02)	(2.85, 16.93)	(–0.18, 0.35)	(0.04, 0.07)

To test the proposed method, we generated 500 Monte Carlo realizations of landscape, source and trap configurations. The landscapes were grids of 100 × 100 cells with each cell having a value of an environmental variable that ranged from 0 to 50 (in arbitrary units). Two-dimensional fractal distributions of this environmental variable were generated using the midpoint displacement algorithm (Saupe 1988) with a Hurst factor of 0.8, causing positive spatial autocorrelation. Five hundred seed sources were placed completely spatially random (CSR) within the central area of 60 × 60 cells, and were assigned a size drawn from a uniform random distribution between 0 and 1000 (in arbitrary units). One hundred seed traps of 1 m^2 were distributed randomly (CSR) across the entire landscape. Fecundity was modelled according to eqn 2 with $\beta_{b0} = 8$ and $\beta_{b1} = 0.05$. Moreover, we simulated a source effect on the scale of a log-normal dispersal kernel ($\beta_{u0} = 2$ and $\beta_{u1} = 0.05$), but not on kernel shape ($\beta_{p0} = 1$; $\beta_{p1} = 0$). Path effects were included by setting $\beta_{w1} = 0.05$. For each trap we then obtained a random number of trapped seeds by drawing from a Poisson distribution with mean given by eqn 11.

We analysed the simulated data sets by fitting a model with a path effect and source effects on the parameters of a log-normal dispersal kernel. Median parameter estimates from the Monte Carlo simulations were virtually identical to the 'true' values, despite considerable variation between simulations (Table 1). This demonstrates that the proposed method can produce unbiased estimates of source and path effects on fecundity and dispersal.

EXAMPLE: ENVIRONMENTAL EFFECTS ON FECUNDITY AND DISPERSAL OF PINUS HALEPENSIS

We use the presented method to analyse environmental effects on the fecundity and seed dispersal of Aleppo pine (*Pinus halepensis*, Miller). *Pinus halepensis* is a native Mediterranean tree that has been widely introduced throughout the world (Barbéro *et al.* 1998). Aleppo pines are monoecious, semi-serotinous (having serotinous and non-serotinous cones on the same tree simultaneously) and produce large amounts of seeds annually (Nathan *et al.* 1999; Thanos & Daskalakou 2000; Goubitz *et al.* 2004). Seed release is stimulated by fire and by Sharav events – dry and hot spells characteristic of the eastern Mediterranean, which occur in the spring and fall (Nathan *et al.* 1999). The seeds are samara-like structures typical of wind-dispersed pines, with a single asymmetric wing loosely attached to the seed, which autorotates while falling (Nathan *et al.* 2001).

The study site is an area of 60 ha (Fig. 2a) at Mount Pithulim, Israel (31°45′N, 35°04′E, 628 m altitude). Mean annual rainfall is 600 mm, and mean monthly temperature ranges from 25 °C (August) to 12 °C (January). The vegetation in the study site is a mixture of maquis (scrubland) and batha (shrubland). *Pinus halepensis* is the only tree species taller than *c.* 5 m and is thus a major determinant of vegetation structure (for a detailed description of the study site see Nathan *et al.* 1999). The large and presumably native Aleppo pine population that currently occupies the site has expanded from five individuals at the beginning of the 20th century to 1576 *P. halepensis* individuals larger than 20 cm^2 basal area in 2006.

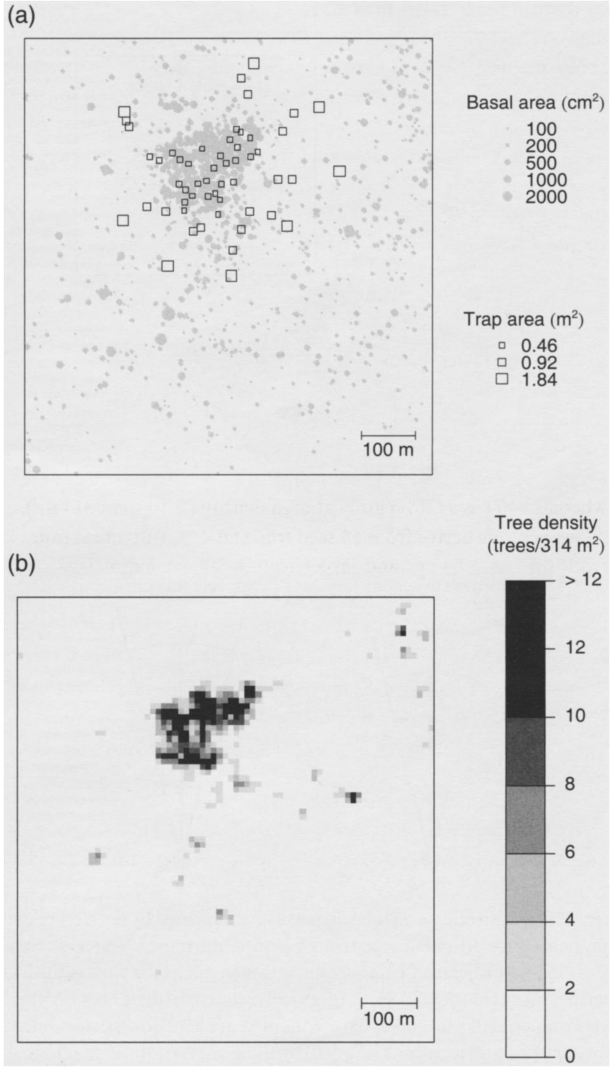

Fig. 2. (a) Map of the study site at Mount Pithulim, Israel, showing the location and basal area of 1576 *Pinus halepensis* trees (grey dots) as well as the location and area of 54 seed traps (squares). Note that symbol sizes are enlarged relative to the actual size of trees and traps. (b) Local tree density in circles of 10 m radius around the centre of 10 × 10 m cells. Tree density is indicated by different shades of grey (see legend).

Between 2003 and 2006 the location of these trees was mapped by tachymeter combined with differential GPS, and their basal area was calculated by measuring the d.b.h. (137 cm). For this study, we only considered trees larger than 20 cm^2 basal area, because trees below this threshold are rarely reproductive (R. Nathan, personal observation). The basal area of the studied trees ranges from 20 to 3867 cm^2 with a median of 177 cm^2 and a mean of 278 cm^2.

Local tree density is highly variable (Fig. 2a) and can be expected to affect both fecundity and seed dispersal of *P. halepensis*. Our re-analysis of data available from previous work in the site (Goubitz *et al.* 2004) reveals that seed production and seed release are affected by the number of conspecific trees in a 10-m radius (see Independent data on fecundity and dispersal of *Pinus halepensis*). Although different zones of effects were not tested, it appears that tree density in a circle of 10 m radius can reasonably be selected as the environmental covariate for our study. This variable could in principle be evaluated in a spatially continuous fashion by calculating the number of trees in 10 m radius for any tree location and for any point between each tree and each trap. However, in concordance with the spatially discrete framework formulated above (Fig. 1), we evaluated tree density on a grid of 10×10 m cells by calculating the number of trees within 10m distance from each cell centre (Fig. 2b). We chose this spatial resolution because it is computationally feasible and corresponds with the scale of large tree canopies: in a sample of 60 pine trees of the Mount Pithulim population, the maximum canopy radius was 5.8 m, which is roughly equivalent to a canopy area of 100 m^2. According to the obtained grid of tree densities (Fig. 2b), 581 trees (37%) grow in low density neighbourhoods (< 3 trees/314 m^2), whereas 446 trees (28%) grow at high density (> 10 trees/314 m^2).

Seed counts derive from 54 seed trap stations, with areas ranging from 0.46 to 1.84 m^2, and larger trap areas located at larger distances from the closed stand (Fig. 2a). Twenty-six trap stations (48%) were located in low density areas (< 3 trees/314 m^2), whereas 11 trap stations (20%) were located in high density areas (> 10 trees/314 m^2). At all trap stations, a total of 1255 seeds were trapped between 14 April 2003 and 17 May 2006. As the focus of this study was on spatial rather than temporal variation, we summed seed counts over the entire study period for each trap station. Fecundity estimates are thus sums of 3 years.

To analyse effects of tree density on fecundity and dispersal of *P. halepensis*, we considered IMs with four alternative dispersal kernels (eqns 3–6), with or without a source effect on fecundity, scale and/or shape of the dispersal kernel, and with or without a path effect, yielding a total of 64 alternative models. If the error variance of seed counts was well described by a Poisson distribution, these alternative models could be compared using Akaike's Information Criterion (AIC, Burnham & Anderson 1998). However, since seed counts proved to be overdispersed, we instead compared models based on their Quasi Akaike Information Criterion (QAIC). The QAIC value for each model was determined using the variance inflation factor estimated from the model with the lowest negative log-likelihood (Burnham & Anderson 1998).

INDEPENDENT DATA ON FECUNDITY AND DISPERSAL OF *PINUS HALEPENSIS*

Independent assessments of fecundity and dispersal are essential to build confidence in fitted parameters, but difficult to obtain. In fact, we are not aware of any IM study which contrasted the fitted parameters with independent empirical data. Taking advantage of previous work on tree density effects in this population (Goubitz *et al.* 2004), and the fact that WALD parameters have a clear mechanistic interpretation (Katul *et al.* 2005), we can independently evaluate several parameters fitted by IM.

Goubitz et al. (2004) sampled *P. halepensis* populations in 10 sites across Israel to examine how serotiny (the phenomenon that cones remain closed on the canopy, forming a canopy seed bank) depends on stand history, tree size and tree density. Among the 60 trees they sampled in our study site, 50 trees met the criterion of basal area > 20 cm^2 we set for the current study. We re-analysed these data to examine the relationship between tree density (measured in a radius of 10 m around the focal tree) and the following components of tree fecundity: (i) the annual seed crop per tree, calculated as the mean cone production in the previous 2 years multiplied by 72, the mean number of seeds per cone (Nathan *et al.* 1999); (ii) the proportion of open cones; and (iii) the mean annual seed rain, which is the product of (i) and (ii), and our best estimate for tree fecundity. We standardized seed crop and seed rain by the basal area of the focal tree, and used linear and generalized linear models (McCullagh & Nelder 1989) to quantify the relationships of seed crop, proportion of open cones and seed rain to tree density.

The scale and shape parameters of WALD correspond to a set of biological and atmospheric parameters (Katul *et al.* 2005) that can be measured independent of IM fitting. Most of these parameters were measured at the study site in 1996–98 by Nathan *et al.* (2001). However, two points need to be considered when relating these independent measurements to IM estimates of WALD parameters: (i) the independent measurements did not consider tree density as a covariate and thus cannot be used to independently evaluate density effects on seed dispersal; (ii) the mechanistic derivation of the WALD parameters depends on the mean horizontal wind speed and the turbulence experienced by a seed that flies mostly within the canopy and beneath the height of release (Katul *et al.* 2005). These quantities are most likely overestimated by Nathan *et al.*'s (2001) wind measurements which were taken at the top of Mount Pithulim, outside the main pine stand, and higher (10 m) than the typical flight height of seeds in the study site. Hence, we use the data of Nathan *et al.* (2001) to derive *upper* limits for the scale and shape of a WALD kernel fitted by a standard IM without environmental covariates.

For WALD's scale parameter $u = Uh_r/v_t$, h_r is the mean height of seed release (5.16 m), U the mean horizontal wind speed experienced by moving seeds (assumed to be < 5.46 $m\ s^{-1}$, the mean horizontal wind speed measured at 10 m height), and v_t the mean terminal fall velocity of seeds in still air (0.81 $m\ s^{-1}$). For WALD's shape parameter $p = h_r^2\ U/2k\ H\ \sigma_w$, H is the mean canopy top (8.5 m), and σ_w the standard deviation of the vertical wind speed experienced by moving seeds (assumed to be < 0.35 $m\ s^{-1}$, the standard deviation of vertical wind speed at 10 m height). The coefficient k is a 'black box' entity that is difficult to quantify empirically, but typically varies between 0.3 for very dense and 0.4 for very sparse forests (Katul *et al.* 2005). Based on independent information, we thus expect that a standard IM estimates WALD to have $u < 34.6$ m, and $p < 81.8$ m.

Results

COMPARISON OF ALTERNATIVE INVERSE MODELS

IM analyses detect both source and path effects of local tree density on the recruitment of *P. halepensis* (Table 2). As a basis for the exploration of these effects, we first consider standard IMs without environmental effects (eqn 1). When fitting these standard models with each of the four alternative

Table 2. Comparison of alternative inverse models for fecundity and seed dispersal of *Pinus halepensis*. For the best model in each of four model categories (models without environmental effects, with only source or only path effects, with both source and path effects), the table gives the dispersal kernel, the included source and path effects, the number of parameters (N_{par}), the negative log-likelihood ($-\ln L$), the deviance and the QAIC

Best model	Dispersal kernel	Source effect on *b*	Source effect on *u*	Source effect on *p*	Path effect	N_{par}	$-\ln L$	Deviance	QAIC
Including source and path effects	WALD	–	x	x	x	6	285.4	355.2	87.5
Including only source effects	WALD	–	x	x	–	5	298.4	381.3	89.0
Including only path effects	2Dt	–	–	–	x	4	336.3	457.1	97.0
Without environmental effects	2Dt	–	–	–	–	3	337.4	459.2	95.3

Table 3. Parameter estimates, number of parameters and QAIC of alternative WALD models describing effects of tree density on fecundity and dispersal of *Pinus halepensis*. Models describe source and/or path effects of tree density and are ordered according to increasing QAIC values. The table furthermore gives QAIC weighted averages of model parameters that are based on all models including the respective parameter

Source effects *b*	Source effects *u*	Source effects *p*	Path effect	Parameter estimates† β_{b0}	β_{b1}	β_{u0}	β_{u1}	β_{p0}	β_{p1}	β_{w1}	N_{par}	QAIC
–	x	x	x	2.4	–	2.3	48.4	6.1	–91.6	22.1	6	87.5
–	x	x	–	2.3	–	2.3	28.1	5.7	–98.3	–	5	89.0
–	–	x	–	2.3	–	2.6	–	5.5	–89.7	–	4	89.4
x	x	x	x	2.4	–0.5	2.3	48.3	6.1	–91.1	22.2	7	89.5
x	–	x	–	2.5	–8.0	2.6	–	5.4	–86.6	–	5	90.2
x	x	x	–	2.4	–3.0	2.4	26.4	5.6	–95.8	–	6	90.7
–	–	x	x	2.3	–	2.6	–	5.5	–88.1	2.5	5	91.3
x	–	x	x	2.5	–7.8	2.6	–	5.4	–85.6	1.2	6	92.2
x	–	–	–	2.6	–15.4	2.6	–	4.7	–	–	4	94.2
x	–	–	x	2.6	–15.3	2.7	–	4.8	–	3.5	5	95.5
x	x	–	–	2.6	–16.8	2.6	–4.3	4.8	–	–	5	95.7
–	x	–	x	2.3	–	2.3	39.3	5.2	–	20.5	5	95.8
–	–	–	–	2.2	–	2.7	–	4.4	–	–	3	96.5
x	x	–	x	2.6	–15.9	2.7	–1.8	4.8	–	2.7	6	97.4
–	x	–	–	2.2	–	2.6	7.9	4.3	–	–	4	97.9
–	–	–	x	2.1	–	2.7	–	4.6	–	3.2	4	98.1
Averaged parameters				2.4	–4.8	2.4	40.8	5.8	–91.9	18.8	–	–

†β_{b0} has units of ln [seeds cm^{-2}]; β_{b1} has units of m^2/tree ln [seeds cm^{-2}], β_{u0} and β_{p0} have units of ln[m]; β_{u1} and β_{p1} have units of m^2/tree ln[m], and β_{w1} has units of m^2/tree.

dispersal kernels (eqns 3–6), we find that the 2Dt kernel provides the best fit (deviance = 459.2, QAIC = 95.3; Table 2), whereas the mechanistic WALD kernel performs worst (deviance = 468.3, QAIC = 96.5).

The inclusion of source effects markedly lowers the deviance and improves the performance of IMs compared to the standard approach (Table 2). In remarkable contrast to the standard models, the best source-effect model involves the mechanistic WALD kernel and describes source effects on the shape and scale of dispersal (Table 2). The addition of a path effect to source effect models leads to a further marked decrease in model deviance, while the simple inclusion of a path effect without source effects did not improve model performance (Table 2). The overall best model has a path effect, source effects on shape and scale of the WALD kernel, but no source effect on fecundity (Table 2). Compared to the best standard IM, this model fits the observed seed trap counts better and has a more homogenous distribution of residuals (Fig. 3). Model bias, measured as the mean difference between model prediction and observation, was 15.4 seeds for the best standard IM, but only 0.002 seeds for the best IM with source and path effects.

In the full set of 64 models, the WALD kernel performs best: the four models with lowest QAIC all involve the WALD kernel and a negative source effect on kernel shape *p* (Table 3). The best non-WALD model (a log-normal kernel with a path effect and source effects on kernel scale and shape, deviance 373.4, QAIC 89.9) is clearly inferior to the best WALD model (deviance 355.2, QAIC 87.5).

INVERSE MODELS VS. INDEPENDENT INFORMATION

Re-analysis of the independent data available from Goubitz *et al.* (2004) reveals a negative effect of tree density on annual seed crop (regression for log-transformed seed crop, $F_{1,48}$ = 22.7, $P < 0.001$; Fig. 4a), implying that trees in dense forest

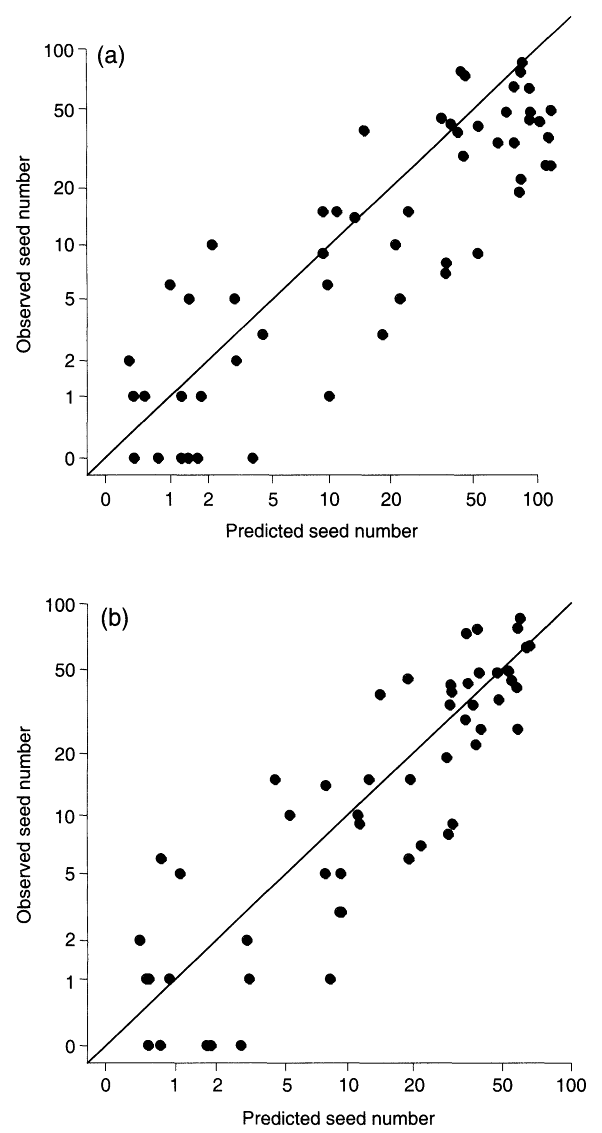

Fig. 3. Number of *Pinus halepensis* seeds collected from 2003 to 2006 in 54 seed traps at Mount Pithulim, Israel, vs. predictions of two inverse models. (a) The predictions of the best standard inverse model with a 2Dt dispersal kernel. (b) The predictions for the overall best model that describes source and path effects on a WALD dispersal kernel. Note that observed and predicted seed numbers are plotted on a quasi-logarithmic scale (seed number + 1 is plotted logarithmically). Lines indicate the 1 : 1 identity.

produce fewer seeds per unit basal area each year than trees in sparser locations. Opposed to this is a positive effect of tree density on the proportion of open cones (generalized linear model with quasibinomial family, $F_{1,48} = 22.9$, $P < 0.001$; Fig. 4b), implying that a larger proportion of cones are opened (and release seeds) in trees located in denser locations. We found that the former effect overrides the latter, so that the combined effect – the mean annual seed rain – shows a weak negative relationship to tree density (regression for log-transformed seed rain, $F_{1,48} = 4.1$, $P = 0.05$; Fig. 4c). This implies that trees in dense forest disseminate fewer seeds per year per unit basal area than trees in sparser locations. We emphasize that this third quantity – clearly the one most relevant to seed trap counts – has the weakest relationship to tree density (Fig. 4c).

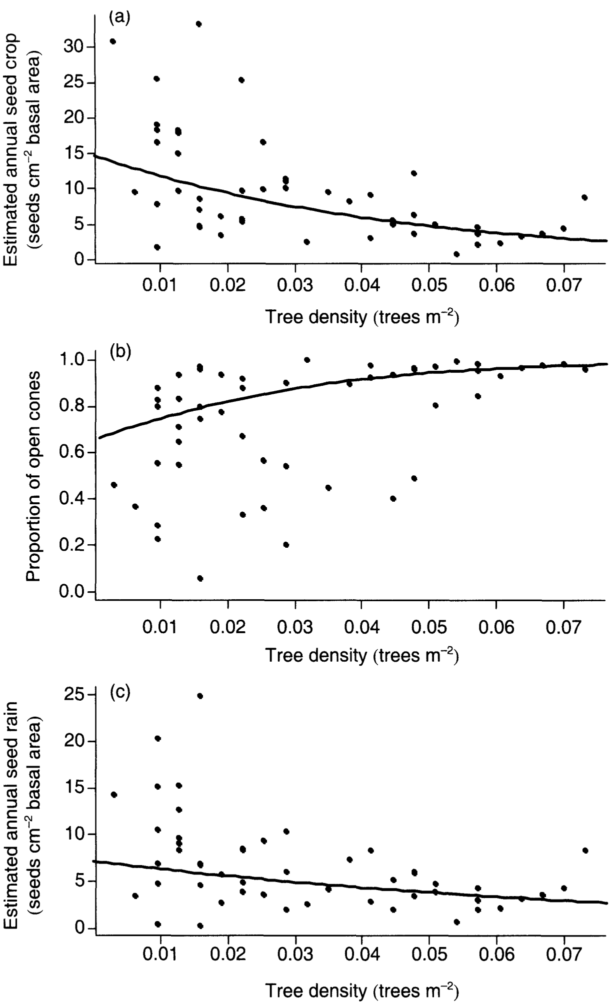

Fig. 4. The relationship between local tree density in 10-m radius circles and fecundity components based on a sample of 50 *Pinus halepensis* trees at Mount Pithulim. Local tree density is (a) negatively related to the mean annual seed crop estimated by counting the easily distinguishable green (second year) and brown (third year) cones in each tree, standardized by the tree basal area, (b) positively related to the proportion of open cones, defined as the proportion of open brown and grey cones out of all brown and grey cones counted in each tree, and (c) negatively related to the mean annual seed rain calculated as the product of (a) and (b). The lines in (a) and (c) are fits of linear models with log-transformed response variables ($P < 0.001$ and $P = 0.05$ for tree density effects, respectively); the line in (b) shows the fit of a generalized linear model with quasibinomial family ($P < 0.001$ for the tree density effect). Data are obtained from previous work of Goubitz *et al.* (2004).

IM analyses agree with this independent information in that they also indicate a weak source effect of tree density on fecundity. While such an effect is not included in the best three IMs, it is described by several other highly ranked IMs (see Table 3 for IMs involving WALD). In agreement with the relationship shown in Fig. 4c, all 32 IMs including a source effect on fecundity estimate this effect to be negative. Moreover, for all but one of these 32 IMs, this estimate falls within the 95% confidence interval of the regression slope depicted in Fig. 4c (–24.8 to –0.02 m^2/tree ln [seeds cm^{-2}]).

To compare IM estimates of dispersal parameters to independent information, we fitted a standard IM with a WALD kernel, and generated 999 bootstrap replicates by jointly resampling seed traps, their distances to the seed sources and the associated seed counts (see Clark *et al.* 1999a). Eight hundred and eighty-five of these replicates (89%) resulted in a scale parameter $u < 34.6$ m that is consistent with average biological and atmospheric parameters measured at the study site (Nathan *et al.* 2001). Similarly, 817 replicates (82%) yielded an estimate of $p < 81.8$ m, as predicted from this independent information.

SOURCE AND PATH EFFECTS ON SEED DISPERSAL

As shown in Table 3, the source and path effects on dispersal estimated by the best model are very similar to the respective parameter estimates obtained by averaging all relevant WALD models using QAIC weights (Burnham & Anderson 1998). In the following, we thus focus on the parameter estimates of the best performing model.

According to this best model (Table 3), increasing tree density at the source increases the scale parameter u and decreases the shape parameter p of a WALD kernel. The path effect of tree density furthermore acts to increase resistance to dispersal (resistance factor w). To assess how well these parameter estimates are supported by the data, we generated 999 bootstrap replicates. For all parameters, the distribution of bootstrap estimates has a well-defined mode close to the maximum-likelihood estimate (Fig. 5), suggesting that the estimated effects are at the least qualitatively robust. Nevertheless, overdispersion in seed counts results in these distributions being relatively broad. Hence, 0 is just included in the 95% confidence intervals for two of the three ‘slope parameters’ (95% confidence intervals: β_{u1}: 9.3–127.0 m^2/tree ln[m]; β_{p1}: −154.7 to 8.2 m^2/trees ln[m]; β_{w1}: −1.5 to 54.3 m^2/tree). Inspection of the relationship between bootstrap estimates of different parameters revealed the expected negative correlation between associated intercepts and slopes (Spearman’s ρ was −0.79 for β_{u0} and β_{u1}, and −0.82 for β_{p0} and β_{p1}). Apart from this, there was no strong correlation between parameter estimates (for all other parameter combinations, Spearman’s ρ ranged from −0.27 to 0.32), indicating that all parameters are well identifiable from the data.

We used the parameter estimates of the best model to explore how source and path effects of tree density affect the seed dispersal of *P. halepensis*. A comparison of kernels predicted for trees growing in homogeneous areas of low density (0.003 trees m^{-2}) vs. high density (0.03 trees m^{-2}) reveals clear differences between these environments: at high tree density, the dispersal kernel has a shorter median and a fatter tail (Fig. 6a). Comparison of these kernels with the kernel predicted by the best model without environmental effects furthermore suggests that such standard models provide a poor description of dispersal both in areas of low and high density (Fig. 6a). Based on the parameter estimates of the best model, we systematically explored how predictions for different quantiles of dispersal distance vary with tree density in spatially homogeneous stands. In this analysis, we find that the predicted median dispersal distance is largely constant at tree densities between 0 and 0.03 trees m^{-2} and drops steeply thereafter (Fig. 6b). Predictions for higher quantiles of dispersal distance show a pronounced unimodal relationship to tree density: the 95% quantile, for instance, is predicted to peak at around 0.05 trees m^{-2} (Fig. 6b). Source effects thus cause

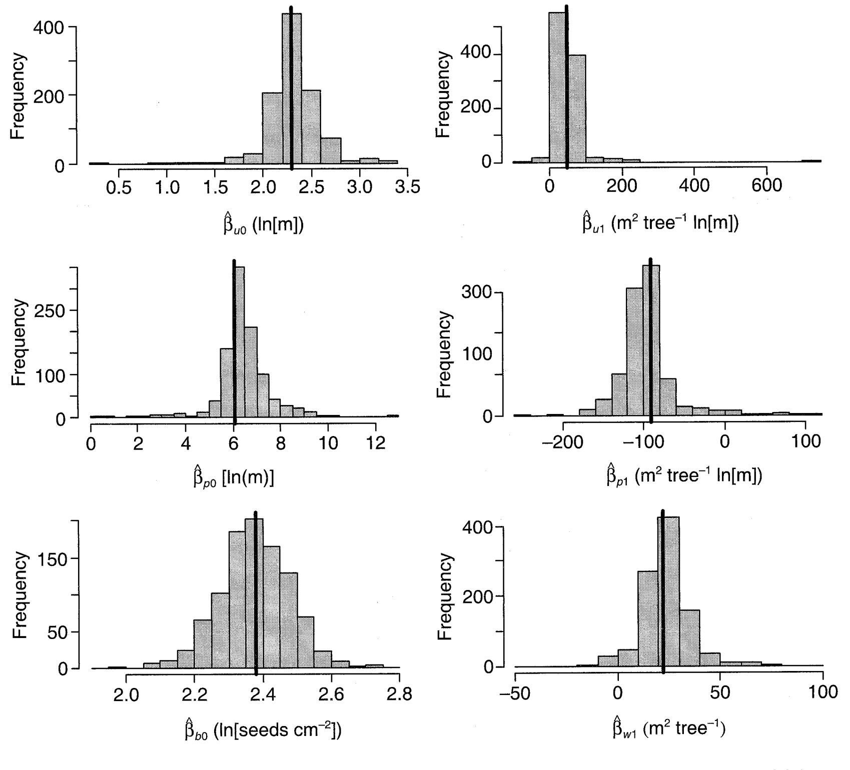

Fig. 5. Distribution of 999 bootstrapped parameter estimates for the selected inverse model that includes fecundity parameter β_{b0}, source effects on the shape and scale of a WALD dispersal kernel (described by intercepts β_{u0} and β_{p0}, and slopes β_{u1} and β_{p1}), and a path effect (parameter β_{w1}). The bold lines indicate maximum-likelihood parameter estimates.

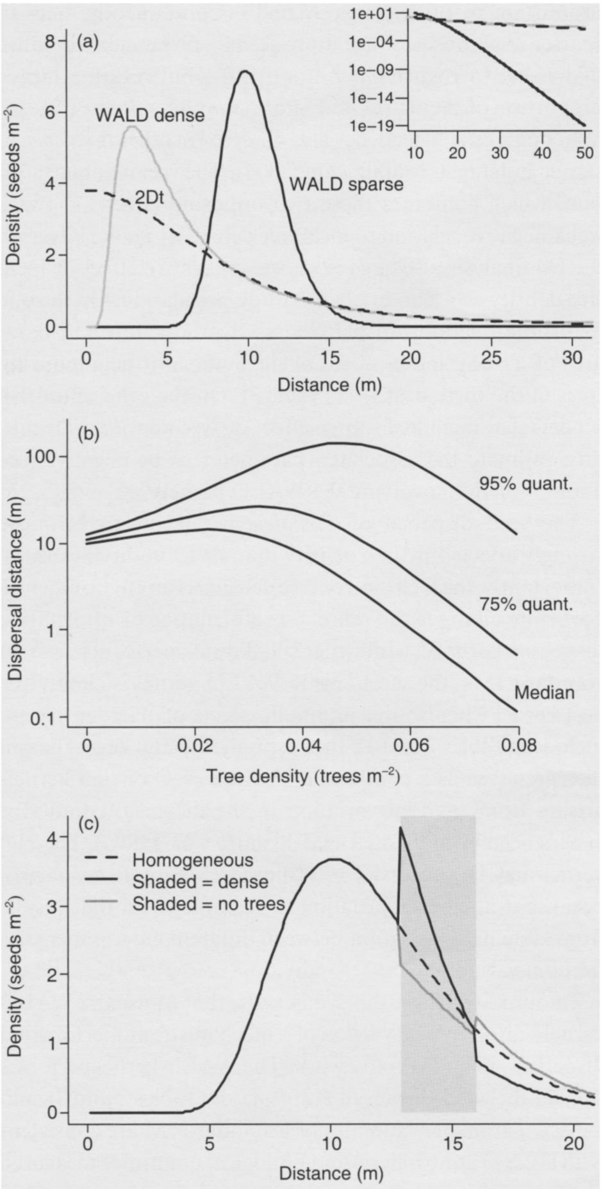

Fig. 6. Source and path effects on the seed dispersal of *Pinus halepensis* as predicted by the selected model. (a) Source effects on seed dispersal are apparent from a comparison of WALD dispersal kernels for trees growing in homogeneous environments of high tree density (0.03 trees m^{-2}; grey line) vs. low tree density (0.003 trees m^{-2}; black line). For comparison, the hatched line shows the kernel predicted by the best standard model without environmental effects (2Dt). The insert depicts the tails of the three kernels in a semi-log plot. (b) Predicted quantiles of dispersal distance (median, 75% and 95 quantile) in environments of different homogeneous tree density. (c) Predicted path effects on the seed dispersal of a tree that grows in a matrix of intermediate tree density (0.01 trees m^{-2}). The shaded area either has high tree density (0.03 trees m^{-2}; black line) or no trees (dark grey line). The hatched line shows predictions for dispersal in a homogeneous environment (0.01 trees m^{-2} throughout). Seed densities in (a) and (c) are based on the predicted fecundity of a tree with 200 cm^2 basal area.

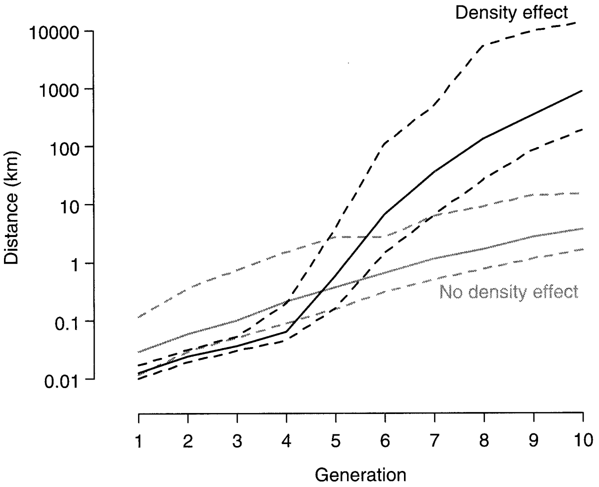

Fig. 7. Comparison of population spread resulting from density-dependent dispersal as predicted by the overall best inverse model (black), and from density-independent dispersal as predicted by the best standard model (grey). For 99 replicate simulations, the graphs indicate the medians (solid lines) and 95% confidence intervals (hatched lines) of the distance between the origin of spread and the furthest forward individual. Note that distances are plotted on a log-scale.

seeds released from dense stands to have both a short modal dispersal distance and a relatively high probability of travelling long distances (see Fig. 6a).

In spatially heterogeneous environments, path effects are apparent (Fig. 6c). Note, however, that the above predictions for spatially homogenous environments also depend on the path effect parameter β_{wl}. The estimated value of β_{wl} = 22.1 m^2/tree means that a distance in an area of 0.03 trees m^{-2} provides about twice the resistance to seed movement as the same distance in an area without trees (exp (22.1 m^2/tree × 0.03 trees m^{-2}) ≈ 2). Consequently, a dense patch of trees in a matrix of intermediate tree density is predicted to intercept a substantial amount of seeds and to 'shade' the areas behind it (Fig. 6c). On the other hand, a clearing in an area of intermediate tree density is predicted to receive fewer seeds, which leads to higher seed deposition in the areas behind the clearing (Fig. 6c).

CONSEQUENCES FOR POPULATION SPREAD

To explore the consequences of source and path effects for population spread, we constructed a spatially explicit simulation model of an expanding population with seed dispersal given either by the best model with environmental covariates (WALD) or by the best standard model (2Dt). For each dispersal kernel, we conducted 99 replicate simulations that started with a single individual, assumed a constant reproductive rate $R_0 = 3$, and followed population spread over 10 generations. To keep local density within realistic bounds, we used lottery competition to limit the number of individuals co-occurring in a 10 × 10 m cell to eight (272 of 281 occupied cells at Mount Pithulim contained ≤ 8 trees). As shown in Fig. 7, the inclusion of environmental effects has pronounced effects on the simulated spread of the population front (measured as the location of the furthest forward individual, Clark *et al.* 2001). Source and path effects of local tree density caused the population to initially spread more slowly but then expand rapidly after a lag-phase of five generations. After 10 generations, spread predictions of a model with environmental effects on dispersal by far exceeded that of a model without environmental effects.

Discussion

Spatial variation in the environment has pervasive effects on plant fecundity and seed dispersal. These effects can be partitioned into source effects (which depend on the local environment of a seed source) and path effects (which depend on the environments encountered along the dispersal path). We introduced source and path effects into the established IM framework (Ribbens *et al.* 1994; Clark *et al.* 1998), which enables the estimation of these effects from easily available data. Source effects are incorporated by linking the fecundity and dispersal parameters of a seed source to its local environment with functions borrowed from generalized linear models (McCullagh & Nelder 1989). Path effects are incorporated by projecting the physical space around a source onto movement space and then evaluating the dispersal kernel in this movement space (Fig. 1).

The introduced method is capable of simultaneously estimating path effects on dispersal as well as source effects on fecundity and dispersal (Table 1). For the *P. halepensis* 3-year data set (Fig. 2), IMs with source and path effects provide a better fit and a more parsimonious explanation of seed trap data than standard IMs without environmental covariates (Fig. 3, Table 2). Parameter estimates conform with independent data on fecundity and seed dispersal of *P. halepensis* at the study site (Nathan *et al.* 2001; Goubitz *et al.* 2004), and estimates averaged across all WALD models are close to the estimates of the best model with lowest QAIC (Table 3). Despite considerable variation in seed trap data that even the best model cannot explain, bootstrap resampling shows that the parameter estimates of the selected model are reasonably well defined (Fig. 5) and that all parameters are identifiable from the data.

The unexplained variation may be due to random effects which can be estimated by fitting IMs in a Hierarchical Bayesian framework (Clark *et al.* 2004). It should be noted, however, that the fixed source and path effects considered here explain a considerable amount of variation that would be attributed to random effects in a standard IM approach. We nevertheless emphasize that the likelihood formulation of the presented models enables their incorporation into a Hierarchical Bayesian framework, so that fixed and random effects can be estimated simultaneously, if deemed necessary. The focus of the present study is, however, on the fixed effects of environmental covariates. In the following, we will thus examine how the consideration of local tree density improves our understanding of fecundity and seed dispersal in *P. halepensis*.

EFFECTS OF TREE DENSITY ON FECUNDITY AND DISPERSAL OF *PINUS HALEPENSIS*

Local tree density in the study population is negatively related to seed production (Fig. 4a) and positively related to the proportion of open cones (Fig. 4b). Consequently, trees in sparser locations produce more seeds – presumably because of weaker intraspecific competition – but retain a larger proportion of them in closed serotinous cones on the canopy, reflecting a general tendency also observed in other *P. halepensis* stands in Israel (Goubitz *et al.* 2004). The mean annual seed rain, which combines these two opposing effects, shows a weak negative relation to local tree density (Fig. 4c). Overall, the IM analysis also suggests a weak negative effect of local tree density on fecundity in the study population. On the one hand, the relationship between seed production and basal area of a tree is independent of the number of neighbouring trees in the three best IMs (Table 3). On the other hand, all models that include a source effect of tree density on fecundity, estimate the associated parameter to be negative (see Table 3 for IMs involving the WALD kernel).

The seed dispersal of *P. halepensis* seems to be more strongly affected by tree density than its fecundity (Table 3). Importantly, the inclusion of tree density as an environmental covariate changes the relative performance of alternative dispersal kernels: while the 2Dt kernel performs best in standard IMs, the mechanistic WALD kernel is clearly the best kernel when source and path effects of tree density are included (Tables 2 and 3). Interestingly, the 2Dt kernel has an interpretation as a continuous mixture of Gaussian kernels arising from random variation in the dispersal conditions experienced by individual seeds (Clark *et al.* 1999a). The 2Dt kernel may be successful in standard IMs for *P. halepensis*, because it attributes variation in seed dispersal that results from systematic variation between different environments to random variation between individual seeds.

To our knowledge, this study is the first to use the WALD kernel – an analytical version of a mechanistic model for wind dispersal – in an IM framework. The WALD kernel performs well for the wind-dispersed *P. halepensis* (Tables 2 and 3), and WALD parameter estimates of a standard IM are consistent with average atmospheric and biological quantities measured at the study site (Nathan *et al.* 2001). While previous studies (Katul *et al.* 2005; Skarpaas & Shea 2007) have shown the benefits of using WALD as a mechanistic analytical wind dispersal model parameterized independently of observed dispersal data, our study suggests that this kernel should also be used more widely in IM studies of species with predominantly wind-dispersed seeds. However, this study also shows that the superior performance of the WALD kernel may only be visible once environmental effects on dispersal are included. An advantage of mechanistic dispersal kernels over phenomenological kernels is that their parameters can be interpreted in terms of the processes driving dispersal. In the following, we will thus interpret the estimated environmental effects on dispersal in terms of underlying mechanisms.

According to the best WALD model (Table 3), increasing tree density at the source leads to stronger skewness of the two-dimensional dispersal kernel (Fig. 6a,b) and causes divergence between the median and the mean of predicted dispersal distances. Source and path effects interact in this model to the effect that *starting in* an area of high tree density increases mean dispersal distance (Fig. 6a,b), whereas *moving through* an area of high tree density decreases dispersal distance (Fig. 6c).

The estimated increase of WALD's mean seed dispersal distance u with tree density could result from an increase in the release height of seeds, an increase in the horizontal wind speed they experience, or a decrease in their terminal velocity (Katul *et al.* 2005). Amongst these potential mechanisms, it seems most likely that release height increases with tree density because trees in dense stands may be taller and/or have their cones concentrated towards the canopy top. Since horizontal winds speed up with height above the ground surface (Monteith & Unsworth 1990), an increase in release height might furthermore increase the horizontal wind velocity experienced by seeds, even if the ambient wind velocity at a reference height decreases with tree density. The estimated decrease of WALD's shape parameter p with tree density (and the associated increase of the variance of dispersal distance u^3/p) could theoretically result from a decrease in release height or mean wind velocity experienced by seeds, or from increases in canopy height or turbulence (Katul *et al.* 2005). Amongst these potential mechanisms, an increase in canopy height and turbulence seems the most likely explanation for the source effect of tree density on kernel shape.

The finding that seeds released from a dense forest have a longer mean dispersal distance compared to seeds released from a sparse forest apparently contradicts the conclusions of Nathan & Katul (2005) of higher frequency and magnitude of LDD for seeds released from sparse vs. dense canopies. In fact, there is no real contradiction here: Nathan & Katul (2005) assumed release height to be independent of canopy density, whereas release height is likely to increase with density at our study site as trees in dense stands tend to be taller and have their cones concentrated towards the canopy top (O. Steinitz, personal observation). Moreover, Nathan & Katul (2005) specifically studied the uplifting of seeds above the canopy, a process acting at low frequencies (3% at most, usually much lower) and over large spatial scales (hundreds of metres) for which seed trap data are unlikely to contain much information.

The strong path effects detected by the IM approach correspond well with the wind regimes described by Nathan & Katul (2005) for sparse and dense canopies, and with their likely effect on the flight of non-uplifted seeds. Dense canopies slow down the movement of non-uplifted seeds by lowering the horizontal wind velocity within the canopy (Monteith & Unsworth 1990; Nathan & Katul 2005). When moving through high density areas, these seeds may additionally be intercepted by trees (Greene *et al.* 2004; Pounden *et al.* 2008). Both of these effects make areas of high tree density less permeable for moving seeds, as estimated by all WALD models including path effects (Table 3). Clearly, the estimated source and path effects of tree density do not permit direct conclusions about the underlying mechanisms. However, they allow us to formulate hypotheses that can be tested by measuring seed release heights and wind conditions in areas of different tree density. Such measurements are currently underway at the study site.

Source and path effects of tree density affect not only seed dispersal, but can also qualitatively alter the dynamics of population spread (Fig. 7). When comparing spread predictions of the best density-dependent dispersal model (WALD) with predictions of the best standard model (2Dt), we find that the WALD model exhibits a lag-phase behaviour with initial slow spread being followed by a rapid advance of the population front (Fig. 7). This can be explained by the fact that the density-dependent dispersal model predicts a lower LDD probability if tree density at the source is low (Fig. 6a,b). As tree density builds up in the core of the population, the seeds produced in core cells have an increasing probability of LDD. This causes the population to expand rapidly after a lag-phase of several generations. Hence, density-dependent dispersal may contribute to the time-lag often observed in the spread of exotic organisms (Hastings *et al.* 2005). This consequence of density-dependent dispersal has not yet been acknowledged, whereas it is well known that Allee effects (an effect of density on fecundity) can markedly alter rates of population spread (Kot *et al.* 1996). To predict population spread, it thus is necessary to test for density effects on both fecundity and dispersal.

GENERALIZATION OF THE PRESENTED METHOD

In this study, we have applied IMs with environmental covariates to the specific example of *P. halepensis*. However, the presented framework can easily be used to quantify environmental effects on fecundity and dispersal in a wide range of other systems. In part, this is because the toolbox of linear predictors and link functions which we borrowed from Generalized Linear Models (GLMs, McCullagh & Nelder 1989) provides an extremely flexible description of source and path effects: (i) Submodels for source and path effects can describe the action of one or several environmental variables that may be continuous (as in this study) or categorical (e.g. habitat type). (ii) Different sets of environmental variables can be used to model different source and path effects. (iii) Quadratic terms for environmental variables can be added to describe, for instance, intraspecific facilitation of fecundity at low densities and intraspecific competition at high densities. (iv) Alternative link functions can be used to describe how the environment affects fecundity and dispersal parameters. Despite its flexibility, however, the GLM toolbox is not the only way of describing source and path effects. Alternatively, these effects can be modelled based on mechanistic considerations (e.g. of how vegetation alters mean wind speed and turbulence; Bohrer *et al.* 2008). Moreover, the formulation of path effects can easily be extended to cases where seed permeability depends on the direction of movement. For instance, the effect of topography on wind dispersal or the effect of water currents on hydrochory can be described by shortening movement space downslopes or downstream. Clearly, most of these possible extensions come at the cost of increased model complexity, and model selection is necessary to avoid overfitting.

The presented framework is thus flexible both with respect to the nature of environmental covariates and with respect to their functional link to fecundity and dispersal. This flexibility means that IMs with environmental covariates can be used as a simple yet powerful exploration tool into the mechanisms underlying fecundity and dispersal. The mechanistic flavour of the presented approach also facilitates comparisons of IM parameter estimates with independent empirical data, a confidence-building practice that, to our knowledge, is applied here for the first time. These merits imply that the framework can be tested and applied to a wide range of environmental effects on fecundity and dispersal. Furthermore, the general description of source and path effects is not limited to species dispersed by primary wind dispersal (such as *P. halepensis*), but can also be used for species with seeds dispersed by secondary wind dispersal (Schurr *et al.* 2005), animals (e.g. Spiegel & Nathan 2007) or water (Merritt & Wohl 2002). Finally, source and path effects may also prove useful for examining environmental effects on pollen dispersal (e.g. Steffan-Dewenter *et al.* 2001; Klein *et al.* 2003).

Application of the presented method to a broader range of study systems will show whether the incorporation of environmental covariates can help detect commonalities in fecundity and dispersal across environments and species. Currently, the potential for such generalizations across environments and species seems limited (Clark *et al.* 1999b, 2005; Muller-Landau *et al.* 2008). Through the explicit consideration of source and path effects, it becomes possible to test (i) whether populations of the same species occurring in different environments show similar environmental effects on fecundity and dispersal as well as similar movement space kernels; and (ii) whether species with similar traits respond to environmental variation in a similar way and have similar movement space kernels.

THE CONCEPT OF MOVEMENT SPACE

Conceptually, movement space may be regarded as a representation of the energetic costs involved in the movement of individuals through a spatially heterogeneous environment. While source effects determine the potential energy initially available for reproduction and dispersal, path effects represent the loss of energy during movement. In this general formulation, the concept of movement space may prove useful not only for quantifying the dispersal of seeds and pollen, but also for studying the movement of mobile organisms such as animals. This is because movement space quantifies how local environmental conditions alter the scale at which a moving organism perceives distance. It thus fits into the broader concept of Levin (1992), according to which each organism observes the environment and its variability at specific scales. By measuring space in units relevant to the moving organism, the concept of 'movement space' may facilitate generalizations of movement patterns across environments and taxa. This may in turn contribute to the development of a general 'movement ecology' (Holden 2006).

Conclusions

We have formulated and tested a method for modelling and estimating environmental effects on plant fecundity and seed dispersal. This method can be widely used to study the effects of environmental heterogeneity on fecundity and dispersal, and its results have consequences for predictions of population spread. The concept of movement space introduced here may furthermore enhance a unified understanding of how various kinds of organisms move through spatially heterogeneous environments.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 R code for fitting inverse models that describe source and path effects of environmental heterogeneity.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2008.01371.x
(This link will take you to the article abstract).