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Abstract
The paper presents a simulation and parameter-estimation approach for evaluating stochastic patterns of population growth and spread of an annual forest herb, *Melampyrum pratense* (Orobanchaceae). The survival of a species during large-scale changes in land use and climate will depend, to a considerable extent, on its dispersal and colonisation abilities. Predictions on species migration need a combination of field studies and modelling efforts. Our study on the ability of *M. pratense* to disperse into so far unoccupied areas was based on experiments in secondary woodland in NE Germany. Experiments started in 1997 at three sites where the species was not yet present, with 300 seeds sown within one square meter. Population development was then recorded until 2001 by mapping of individuals with a resolution of 5 cm. Additional observations considered density dependence of seed production. We designed a spatially explicit individual-based computer simulation model to explain the spatial patterns of population development and to predict future population spread. Besides primary drop of seeds (barochory) it assumed secondary seed transport by ants (myrmecochory) with an exponentially decreasing dispersal tail. An important feature of population-pattern explanation was the simultaneous estimation of both population-growth and dispersal parameters from consistent spatio-temporal data sets. As the simulation model produced stochastic time series and random spatially discrete distributions of individuals we estimated parameters by minimising the expectation of weighted sums of squares. These sums-of-squares criteria considered population sizes, radial population distributions around the area of origin and distributions of individuals within squares of 25*25 cm, the range of density action. Optimal parameter values, together with the precision of the estimates, were obtained from calculating sums of squares in regular grids of parameter values. Our modelling results showed that transport of fractions of seeds by ants over distances of 1…2 m was indispensable for explaining the observed population spread that led to distances of at most 8 m from population origin within 3 years. Projections of population development over 4 additional years gave a diffusion-like increase of population area without any "outposts". This prediction generated by the simulation model gave a hypothesis which should be revised by additional field observations. Some structural deviations between observations and model output already indicated that for full understanding of population spread the set of dispersal mechanisms assumed in the model may have to be extended by additional features of plant-animal mutualism.

Introduction

In recent years it has been widely recognized that phytodiversity is not only dependent on habitat conditions such as climate, soil and land use, but also on the accessibility of the habitats for plants (e.g. Ehrlén und Eriksson, 2000). As site conditions are rapidly altered by changing land use, pollution, and climate change, the fate of a species under these conditions will depend, to a considerable extent, on its dispersal and colonisation abilities (e.g. Higgins and Richardson, 1999; Higgins et al., 2003a). Moreover, dispersal mediates the spread of invasive plant species (e.g. Shigesada and Kawasaki, 1997; Deckers et al., 2005). Dispersal limitation can be observed for many vascular plants of northern temperate woodlands (Europe, NE America): forest patches, newly created on former arable land, are only slowly colonized (Hermy et al., 1999; Flynn and Vellend, 2005). While the majority of woodland herbs do not have morphological adaptations for dispersal by wind, adhesion, or ingestion (Bierzychudek, 1982), ant-plant mutualisms represent one of the most common modes of seed dispersal in these forests (e.g. Handel et al., 1981). Ants move seeds on a strictly local scale, and dispersal patterns of several myrmecochorous seed species are well documented (e.g. Higashi et al., 1989; Gibson, 1993; Kalisz et al., 1999).

Up to now, few studies have attempted to quantify ant-mediated spread rates and patterns of herbaceous forest plants. These investigations were done in second-growth stands of known age adjacent to ancient forests (Matlack, 1994; Brunet and Oheimb, 1998; Bossuyt et al., 1999; Dzwonko, 2001). Because spread patterns cannot solely be attributed to dispersal, but are also influenced by life-cycle processes and by environmental factors as, e.g., canopy development and different soil properties (Brunet et al., 2000), such studies should be supplemented with direct observations of population development and spread of plants from known release points in homogenous woodland stands.

Heinken (2004) used a seed-sowing approach to examine colonization patterns of *Melampyrum pratense* (Orobanchaceae), an annual myrmecochorous (ant-dispersed) woodland herb, in a recent woodland in Germany. From general knowledge this woodland should be suitable for the species but lacked a natural population of it. As a consequence, dispersal processes could be clearly separated from local turnover of already established parts of a population. The advantage of using an annual as a bioassay of plant migration ability is that plants reproduce and die in one growing season, so that several generations can be studied quickly. Additionally the population biology of the species was well known (e.g. Masselink, 1980). The study gave detailed empirical data of colonization patterns for 3 populations over 4 years for an area of approximately 200 m² and with a spatial resolution of 5 cm.

For the explanation of the observed population patterns, i.e. for their reduction to basic mechanisms, for estimation of parameters, for predictions in more general situations, and for pointing out limits in our knowledge a combination of field studies and modelling efforts was needed. Modelling of dispersal processes and of their impact on population spread and invasion processes was a topic of several reviews (e.g., Levin et al., 2003; Hastings et al., 2005; Pyšek and Hulme, 2005; Buckley et al., 2006). Up to now, many studies focused on detailed evaluation of pure dispersal patterns (e.g., Clark, 1998; Nathan et al., 2003; Higgins et al, 2003b; Skarpaas et al., 2005). Anderson, 1988, and Gorb et al., 1999, offered examples for the simulation of ant-mediated dispersal. When dispersal was linked with full life cycle sometimes general theoretical problems were in the foreground (Kot et al., 1996; Cain et al., 1998; Frantzen et al, 2000; Pakeman, 2001). Case studies used data from different experiments or sources (e.g., Neubert and Caswell, 2000; Wadsworth et al. 2000; Higgins et al., 2001; Clark et al., 2003), or spread was parameterized using the asymptotic velocity by which an invasion front is moving (e.g., Hastings et al. 2005, Dwyer et al. 2006). We now were able to fill this gap by designing a model that integrates population biology and seed dispersal of a species, and which was largely based on the data of one complex, but coherent experiment covering the initial spread phase of a population.

For modelling of initial population spread over several years on the basis of the distribution patterns of individuals a spatially explicit individual-based model (SEIB model) was the method of choice (Grimm and Railsback, 2005). A systematic comparison between model-generated and field patterns as well as an estimation of parameter values had to consider the stochastic nature of simulation-model results. In the process of parameter estimation

such stochastic features were, up to now, only occasionally taken into account by modellers in ecology (Berk et al., 2002; Waller et al., 2003; Wiegand et al., 2004). Therefore we had to design appropriate objective functions for the evaluation of parameters of stochastic plant spread.

In the present study we first present the general design of a stochastic SEIB model for the spread of an annual plant species, *Melampyrum pratense*. We then give parameter estimation on the basis of the empirical data in order to explain the spatio-temporal data patterns as functions of population life cycle and of dispersal mechanisms. These results will allow elucidating the role of myrmecochory, both for observed population increase and spread. Finally, further population spread is projected over several years giving patterns that can be considered as testable hypotheses on population development in the future and on the impact of dispersal mechanisms.

Material and methods
The species
The study was carried out with Common Cow-wheat, *Melampyrum pratense* L. (Orobanchaceae), a widespread species in mixed oak and pine forests on acidic soils in northern Germany. It is an annual hemiparasite, which apparently requires woody plants like *Betula* spp., *Quercus* spp. and *Pinus sylvestris* L. as hosts (e.g. Masselink, 1980; Salonen et al., 2000). Cotyledons and green shoots emerge in spring. *M. pratense* flowers during the whole summer and fruits until autumn. Most solitary plants have long, horizontal lateral branches; while in dense populations branches are fewer and much shorter (see density effects). Seeds are found in capsules most of which are strung on the horizontal branches. The seeds are large, with a mean dry weight of 3.95 mg (Heinken, 2004), and their number per plant is low (Masselink, 1980: 40-75; own data (cf. Fig. 1): 2-227, mean 59).

As *Melampyrum pratense* seeds are heavy, have no features supporting wind dispersal and their exposition height is low they fall within a very small distance from the parental plant, i.e. they simply drop from the capsules (primary dispersal, "barochory"). Because of an elaiosome seeds are attractive to ants (e.g. *Formica rufa* L. and *Myrmica ruginodis* Nyl.) and thus are readily taken and dispersed by them after being released (secondary dispersal, myrmecochory). Thompson et al. (1997) rate *M. pratense* as forming only a transient seed bank. However, a portion of the seeds is dormant for at least the first season and may account for the presence of a substantial short-term persistent seed bank (Masselink, 1980; Heinken, 2004).

Field study
The field study (Heinken, 2004) was carried out in the woodland area of the "Glauer Berge" in north-eastern Germany (lat 52°15', long 13°08'-13°11'), an isolated mixed Scots pine forest stand with dry acidic sands within an agricultural landscape. Natural populations of *M. pratense* are lacking, due to dispersal limitation because the forest was established not until the 19th century. Heinken chose three sites with varying topographies which appeared to be suitable to host populations of *M. pratense* in terms of environment because their substrate and vegetation was similar to habitats of natural populations. Various seed-dispersing ant species occurred at all three sites (see Heinken, 2004).

To establish the experimental populations, seeds of *M. pratense* with regional provenance were introduced to the three sites in autumn 1997. A set of each 300 seeds was sown in a 1*1 m plot. Development of population size and colonization patterns following artificial introduction were investigated by mapping the position of adult, flowering plants in July/August from 1998 through 2001 with a resolution of 5 cm.

Population sizes $X(t)$ increased exponentially (with only some modifications due to unfavourable weather conditions in 1999) and reached 500…1000 individuals after 4 years. Also population areas increased steadily from 1 m² in 1998 up to 35…40 m² in 2001. After 3 years of dispersal (2001) the farthest individuals were 7.6 m apart from the centre of the starting plot. A wider area (d = 50 m) was checked for *M. pratense* individuals, but without any suc-

cess. Maps of increasing population areas were shown by Heinken (2004), and details for one site are discussed below.

For visualisation and comparison with simulation, plants within squares of 5*5 cm or 25*25 cm were summed up, and the plant number per cell expressed in maps by colour or grey-tones. From the spatial records the number $x(t, r_i)$ of individuals in circular rings with mean radius

$$r_i = \frac{\delta}{2}(2i - 1) \qquad (1)$$

(with i = 1, 2, … and ring width δ = 10cm) were determined per year t. From these values two radial distributions were calculated for comparison with simulation results:

1) Individual density distribution (density of adult plants in rings of 10 cm width with mean radius r_i):

$$d(t,r_i) = x(t,r_i)/A(r_i) \qquad (2)$$

with circular ring area

$$A(r_i) = \pi \, \delta^2 (2i - 1) \qquad (3)$$

2) Radial population distribution (distribution of the population over circular rings):

$$p(t, r_i) = x(t,r_i) / X(t) \qquad (4)$$

Additionally, occupancy distributions were determined, which describe the distribution of individuals on 25* 25 cm cells that include j = 1, 2, 3, … individuals:

$$b(t,j) = j \, z(t,j) / X(t), \qquad (5)$$

where $z(j,t)$ denotes the number of cells containing j individuals in year t.
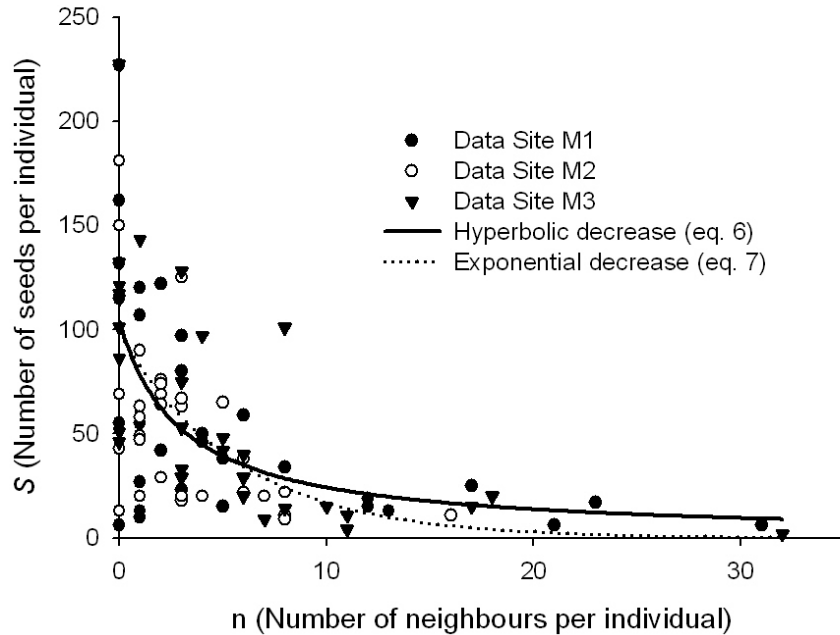

Fig. 1 – Empirical data for the density dependence of seed production *S* per individual. Abscissa *n* denotes the number of *Melampyrum pratense* neighbours around a focal individual in test plots of 25cm×25 cm. Within 30 plots at each site (M1–M3) the number of individuals and the number of seeds of a randomly chosen individual within the plot were recorded. Data of all populations are summarized, because there were no significant differences. Correlations with both functions were significant (*r* = 0.62 (Eq. (6)) and *r* = 0.61 (Eq. (7))).

Density effects

We performed additional field studies at all sites in order to check the density dependence of seed production per individual: In September 2004, i.e. towards the end of the fruiting period, we randomly chose 30 plots (25*25 cm) per population. Within each plot the number of individuals and the number of seeds of a randomly chosen individual within the plot were determined. As seeds are shed over a long period (see above) we estimated seed number per individual by counting the number of capsules, and the number of seeds of all closed cap-

sules (which still contained all seeds). The mean number of seeds per capsule was then extrapolated to the total number of capsules. Fig. 1 gives data on seed production per focal individual in dependence on number n of neighbours in the test plots from the three sites. These data were fitted by either a hyperbolic function:

$$S = S_0 \frac{b+1}{b+1+n} \qquad \text{(Beverton-Holt function)} \qquad (6)$$

or an exponential function

$$S = S_0 e^{-bn} \qquad \text{(Ricker function)} \qquad (7)$$

Fits with the two functions gave almost the same correlation coefficient (r = 0.61). In our simulations we used the hyperbolic function as the standard version. The exponential version which may give rise to more complicated dynamics (Caswell, 2001) was only used for comparison. The coefficients S_0 (average seed production of an isolated individual) and the density coefficients b are given in Table 1.

Table 1 Model parameters, their standard values, and model output. Bold figures indicate parameters that were estimated by the Least-Squares procedure. Other values were fixed (see text). Spatial parameters are given in cell units of 5 cm.

		Standard values for sites:		
Parameters		M_1	M_2	M_3
p_e	Juvenile establishment probability	**0.13**	**0.06**	**0.095**
p_g	Germination probability		1	
m_S	Seed mortality		0	
$S_{0\,H}$	Parameters density control Eq. 6		100	
b_H	(hyperbolic function)		2.1	
$S_{0\,E}$	Parameters density control Eq. 7		100	
b_E	(exponential function)		0.18	
Φ	Reduction factor N_{S0} in "bad" years	**0.02**	**0.70**	**0.50**
a_B, s_B	Barochory distances: mean $\pm$ SD (Dispersal 1)		3.0 $\pm$ 1.0 (15cm $\pm$ 5 cm)	
a_M	Myrmecochory distances: mean = SD (Dispersal 2)	**20** **(100 cm)**	**15** **(75 cm)**	**20** **(100 cm)**
f_M	Fraction of Myrmecochorous dispersal	**0.50**	**0.50**	**0.10**
$w(t)$	Weather indices (1998…2004)		0 -1 0 0 0 -1 0	
Model output				
$X(t)$	Population size			
$d(t,r_i)$	Individual density distribution Eq. 2			
$p(t,r_i)$	Radial population distribution Eq. 4			
$b(t,j)$	Cell occupancy distribution Eq. 5			

Dispersal patterns

The distribution of barochorous dispersal distances was determined by an experiment with adhesive cardboard (Heinken, 2004). Primary dispersal distances followed a Gaussian distribution. A robust individual with long lateral branches exhibited a mean barochorous dispersal distance of approximately 15 cm, and distances larger than 25 cm were extremely unlikely. There are hints for a reduction of average distances from 15 cm in locally dense stands. We did not consider this effect in simulations as it was negligible in relation to a species distribution of 10…100 m².

Secondary, myrmecochorous dispersal distances follow, beyond very small distances, an exponential distribution, giving a long tail of the dispersal shadow (e.g. Higashi et al., 1989; Kalisz et al., 1999). For the vicarious species *Melampyrum lineare*, Gibson (1993) found a mean ant-mediated dispersal distance of 110 cm, and the longest transport distance was

4.45 m. These data served as a reference for our own parameter estimation. We can assume that mostly medium-sized ant species (*Formica fusca* L., *Myrmica ruginoidis* Nyl., *M. rubra* L.) with high nest densities and small foraging territories and hence short dispersal distances are responsible for seed dispersal in our context (see discussion in Heinken, 2004).

Climatic conditions

Field data from 1998-2001 (Heinken, 2004) revealed that extraordinarily dry climatic conditions during the vegetation period (April – September) had negative effects on individual number of *M. pratense* in the following year, at least on the driest site (population M1). We assumed a lower seed production due to reduced fitness of individuals, because both the climate of north-eastern Germany and the sandy soils are relatively dry compared with many other habitats within the natural range of the species. We described climatic conditions for each year by a humidity index (HI), the quotient of the precipitation [mm] and the mean temperature [°C], both from April – September. Climatic data were provided by the Potsdam weather station 15 km NNW of the study site. Here the mean HI for 1961-2004 is 21.9. While for most years from 1998-2004 HI were not lower than 19.9, 1999 and 2003 turned out to be extraordinarily dry years (HI 11.8 and 12.2, respectively).

Simulation model

Our approach combined simulation of plant population dynamics on a grid base with continuous dispersal modelling. The grid structure facilitated the consideration of density effects. Model parameters are listed in Table 1.

"Space" was presented by a non-toroidal array of 800*800 cells of 5*5 cm, giving an area of 40*40 m. Each cell could host more than one individual. For calculating dispersal distances all individuals of a cell were assumed to be located in its centre.

Dynamics were modelled in time steps of one year including a sequence of flowering plus density-dependent seed production, dispersal and seed deposition in a (transient) seed bank, mortality, seedling emergence, and establishment of new adults. All individual demographic events included demographic stochasticity (random decisions, or Poisson-distributed number of seeds).

All adult individuals flowered and produced seeds in summer. Seed set s per individual plant was Poisson-distributed and density-dependent. The number of neighbours n in a square of 25*25 cm around the target individual determined the parameter S of a Poisson distribution by either Eq. 6 (hyperbolic dependence) or Eq. 7 (exponential dependence). The counting of individuals in a square instead of a circle of 12.5 cm somewhat overestimated density action, but as the range of density effects was only approximated this error was of minor importance.

Seeds were dispersed sequentially in two different ways. First, all seeds underlay barochorous dispersal, starting from the centre of the cell of seed production. Individual barochorous distances were drawn, following the adhesive-cardboard experiment (Heinken, 2004), from a truncated (a_B, s_B) normal distribution, and dispersal angles were drawn at random. The deposition points, given in relative polar coordinates, were discretized by shifting them to the centre of the deposition cells.

Starting from the new positions a fraction f_M of seeds (individual random decision) was further transported to cells some distance away (secondary transport by myrmecochory). Myrmecochorous distances followed an exponential distribution with parameter a_M (following Gibson, 1993), and dispersal angles were again determined at random. Finally, the deposition points were discretized. As we did not assume torus geometry any seeds falling beyond the boundaries of the simulation area were lost.

After barochorous and possibly myrmecochorous dispersal seeds were deposited in the local seed bank of the deposition cell. In winter all adults died, and seeds in the seed bank were subject to a seed-bank mortality m_S.

In the following year seeds germinated with germination probability p_g and gave rise to new adults with establishment probability p_e. We had only scarce hints for density dependence of establishment (see Heinken, 2004); hence all density control in the model was incorporated in the regulation of seed production. We also had no sufficient support to assume a perma-

nent seed bank. Hence, for an annual plant density-independent seed productivity S_0, seed-bank parameters m_S and p_g, and juvenile establishment probability p_e, could be coupled, giving together the intrinsic rate of population increase

$$\lambda = S_0\,(1 - m_S)\,p_g\,p_e \qquad\qquad (8)$$

This rate λ basically determined population increase from one year to the next, excluding density and dispersal effects. As S_0 was given separately, a product of three parameters remained. We set $m_S = 0$ and $p_g = 1$ and hence condensed the fate of seeds between seed production and establishment of a new seed-producing adult into juvenile establishment probability p_e. This parameter also included the effect of seed losses due to consumption by rodents or disappearance in ant nests, any loss of plants before seed-setting, but also potential enhancement or reduction of germination after removal by ants because of elaiosome consumption (e.g. Ohkawara 2005, Imbert 2006) or seed deposition on favourable microsites (cf. Gibson 1993 for *Melampyrum lineare*). As we had no data for unequal germination and establishment of *M. pratense* seeds affected versus unaffected by ants we did not distinguish here between these seeds which were mixed in the area of distribution.

Climate was assumed to affect seed production. Following the humidity index we divided "weather" into two classes: normal years (class index $w = 0$) and negative years (class index $w = 1$). The sequence of class indices $w(t)$ derived for the years 1998-2004 is shown in Table 1. If $w(t) = -1$, seed-production parameter S was reduced by multiplication with a factor $\varphi < 1$. The model output was designed to match the results of the empirical study. All adult individuals were counted to give population size $X(t)$. The calculation of radial distributions $d(t,r_i)$ and $p(t,r_i)$ according to Eqs. 2 and 4 had to consider the discreteness of plant positions in the model plane where all individuals were located in the centre of their cell. This gave some inaccuracies for small radii, but as we were dealing with expanding populations we could neglect such effects. Cell occupancy distribution $b(t,j)$ followed the evaluation of experimental data. For visualisation mapping of individual distribution (coloured or in grey tones) was possible on a 5*5 or 25*25 grid scale.

Simulations

Simulations were initialised by attributing to each cell in a central area of 20*20 cells (1*1m) a Poisson-distributed number of seeds (with parameter $S = 0.75$). This corresponded with a distribution of 300 seeds on an average, as in the experiments. Simulation area was 15*15 m for parameter estimation and 40*40 m for projections of population development.

Parameter estimation

Non-linear least squares procedures for parameter estimation (Draper and Smith, 1998) are appropriate when the structure of the model and the number of parameters to be estimated is known. As we had to consider stochastic time series and random spatially discrete distribution of individuals we worked with $n_{sim} = 100$ stochastic simulation runs per parameter combination and selected parameter combinations that minimised the expectation of weighted Sum of Squares. We had three different sets of results: temporal series of population sizes $X(t)$, radial population distribution $p(t,r_i)$ and cell occupancy distribution $b(t,j)$. Hence we used three different Sums of Squares (*SS*) as objective functions to be minimized:

$$SS_1 = \frac{1}{n_{sim}} \sum_{k=1}^{n_{sim}} \sum_{l=1}^{4} W_l (X(t_l) - \xi(t_l,k))^2 \qquad\qquad (9a)$$

$$SS_2 = \frac{1}{n_{sim}} \sum_{k=1}^{n_{sim}} \sum_{l=1}^{4} \sum_{i} (p(t_l,i) - \pi(t_l,i,k))^2 \qquad\qquad (9b)$$

$$SS_3 = \frac{1}{n_{sim}} \sum_{k=1}^{n_{sim}} \sum_{l=1}^{4} \sum_{j} (b(t_l,j) - \beta(t_l,j,k))^2 \qquad\qquad (9c)$$

In this context, Latin letters denote experimental values, whereas Greek letters denote stochastic simulation values. The first criterion was weighted by $W_l = 1/X(t_l)$ (assuming Poisson-distributed population sizes), whereas for the other two criteria we set $W = 1$. The time index ran from 1 to 4 (years 1998-2001). The criteria were judged separately, as we did not find a

sufficient basis to link the objective functions. Population density distribution p was preferred against individual density distribution d to express spatial distribution (averaged over all angles) as it was decoupled from population size X.

Criteria values were calculated in regular grids of parameter values. The SS-surfaces created by these systematic calculations allowed for determining optimum parameter combinations (with minimal SS), sensitivities and correlations by visual evaluation of the plots. If necessary, a compromise between the outcomes of different criteria had to be found. In general, we ranked the criteria according to the sequence population size (temporal pattern), radial distribution (spatial pattern), and cell occupancy.

Results

Parameter estimation: fitting temporal and spatial patterns

The simulation model as applied for an annual species without permanent seed bank contained 8 parameters for each site (S_0, b, φ, p_e, a_B, s_B, f_M, a_M; see Table 1). Seed productivity S_0 was determined from Fig. 1. For density control of seed production we usually assumed hyperbolic regulation with factor b_H from Fig. 1. Results of model fitting or prognosis with exponential control could not be separated along the data from the standard, hyperbolic cases. Barochory parameters a_B and s_B were fixed according to the adhesive cardboard experiment of Heinken (2004) neglecting density effect on a_B (see above). Simulations showed that the objective function somewhat increased with $a_B < 15$ cm, ruling out this parameter region, and an increase of a_B to values $a_B > 20$ had scarcely any additional positive effect on all least-squares criteria.

Parameter estimation thus had to focus on p_e and φ, mainly responsible for the time series, and a_M and f_M, which described the main aspect of the study, the effect of ant-mediated dispersal on population spread. The sequence of calculations was as follows:

First, we screened over large ranges the effect of the parameters on the objective functions Eqs. 9. Then we selected pairs of parameters in order to visualise and discuss results by contour plots of the objective functions. We present some details for site M3 in order to demonstrate the course of analysis; sites M1 and M2 did not give, in general, qualitative deviations from these results.

With predetermined value for a_M (100 cm) Fig. 2 shows contour plots for site M3 of the three objective function Eq. 9 in dependence of parameters p_e (juvenile establishment probability) and f_M (fraction of myrmecochorous dispersal). The estimates of both parameters were correlated. For SS_1 we got a banana-like contour plot, a typical result for many nonlinear least-squares problems (Draper and Smith, 1998). Clearly, very low and very high f_M-values can be ruled out, also from the SS_2- and SS_3-plots. A compromise between the three plots had to
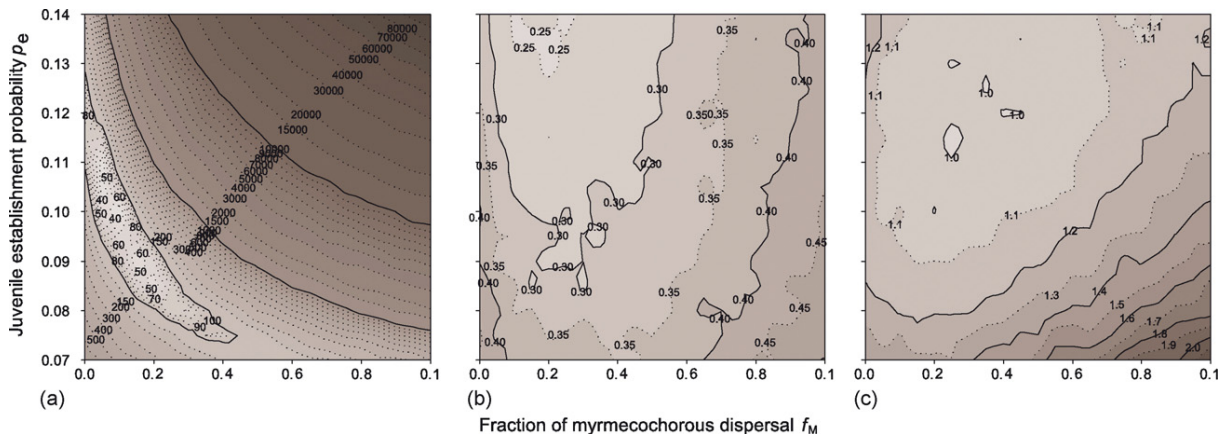

Fig. 2 – Sum of squares contour plots (Eq. (9)) for site M3 in dependence on the fraction of myrmecochorous dispersal f_M and juvenile establishment probability pe. Empirical data and simulation results were compared for (a) population size (Eq. (9)), (b) population-density distribution (Eq. (9)), and (c) cell occupancy distribution (Eq. (9)). Sum of squares for each parameter combination were averaged over 100 runs.

be found for p_e because minima of both SS_2 and SS_3 tended to higher p_e-values than criterion SS_1 (see Table 1). Qualitatively, the plots for sites M1 and M2 showed the same behaviour.

Especially population development $X(t)$ is also affected by the climate parameter φ, giving the reduction of seed production under unfavourable weather conditions. When plotting sums of squares in dependence of parameters p_e and φ (with $f_M = 0.10$, as determined from Fig. 2, and again $a_M = 100$ cm), the estimate of p_e turned out to be little correlated with that of φ (plots not shown). This held also for site M2, but not for site M1, a rather unusual case because of the large population reduction in year 2000 (see Fig. 5 below).

Fig. 3 shows the joint effect of changes in mean myrmecochorous dispersal distance a_M and juvenile establishment probability p_e on the three criteria of Eq. 9. Small a_M-values can be ruled out from all criteria: there is a minimum average distance for myrmecochorous dispersal of at least 50 cm. Because of the low fraction of myrmecochorous dispersal at site M3 criterion SS_1 is almost independent of a_M for higher a_M-values, and also the other two criteria gave almost no effect. At the other sites, with higher f_M, criterion 3 sharply increased with increasing a_M, thus setting an upper limit.
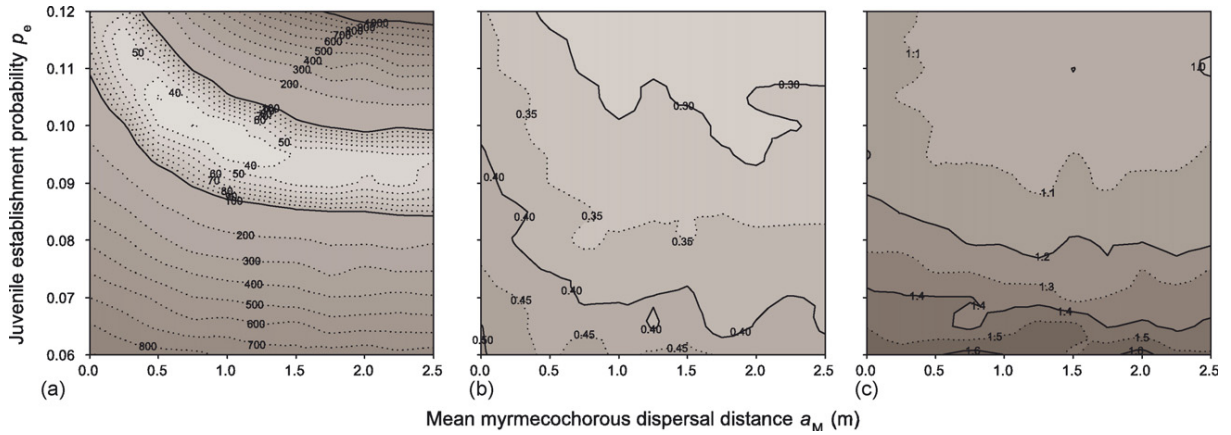

Fig. 3 – Sum of squares contour plots (Eq. (9)) for site M3 in dependence on mean myrmecochorous dispersal distance a_M and juvenile establishment probability p_e. For details see legend to Fig. 2.
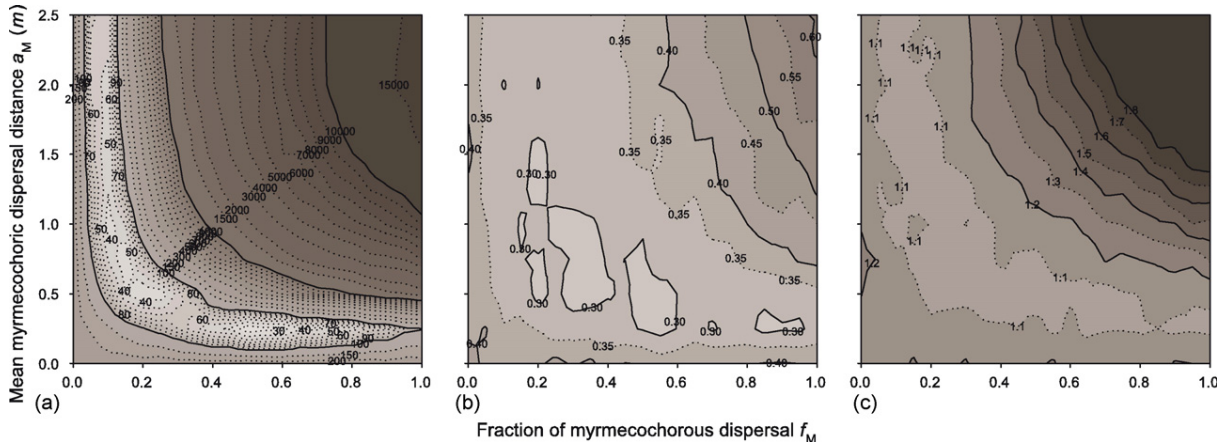

Fig. 4 – Sum of squares contour plots (Eq. (9)) for site M3 in dependence on the fraction of myrmecochorous dispersal f_M and mean myrmecochorous dispersal distance a_M. For details see legend to Fig. 2.

This dispersal parameter a_M was also included in the plots of Fig. 4, varied together with the fraction of myrmecochorous dispersal f_M. We have two sharply separated regions in plot SS_1. Very small and high values of f_M can again be ruled out, as from Fig. 2. At small values of f_M all criteria were, above some threshold, almost independent of a_M (see also Fig. 3). At higher f_M-values, a_M was almost fixed. Hence the data allow for either small f_M values together with rather large a_M values or vice versa. Taking figures 2, 3, and 4 together, at site M3 f_M-values

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being small but distinctly larger than zero were best suited to explain the patterns. For sites M1 and M2 this fraction was higher, with the same qualitative features (details not shown). Parameter estimates that best corresponded to all contour plots for the three sites are listed in Table 1. Estimates of f_M and a_M were already discussed above. Establishment probability p_e was determined rather precisely from SS_1 (± 0.01), whereas φ was more uncertain (± 0.20 for sites M2 and M3, and ± 0.02 for site M1). It was surprising that criterion 1, based on population size, was rather selective against all parameters, even against the "spatial" parameters a_M and f_M. This is because population development is linked with dispersal due to the existence of density control.

Fig. 5 shows the best model fits (average model simulations with standard deviations) of temporal series and spatial distributions from the field data. Time series giving the development of population sizes $X(t)$ were well fitted, with the exception of one point for site M1. The fit of radial distributions gave some deviations from the data at sites M1 and M2 for radii below 300 cm. But the tails of the distributions, comprising the extreme dispersal cases, were well fitted in all three cases.
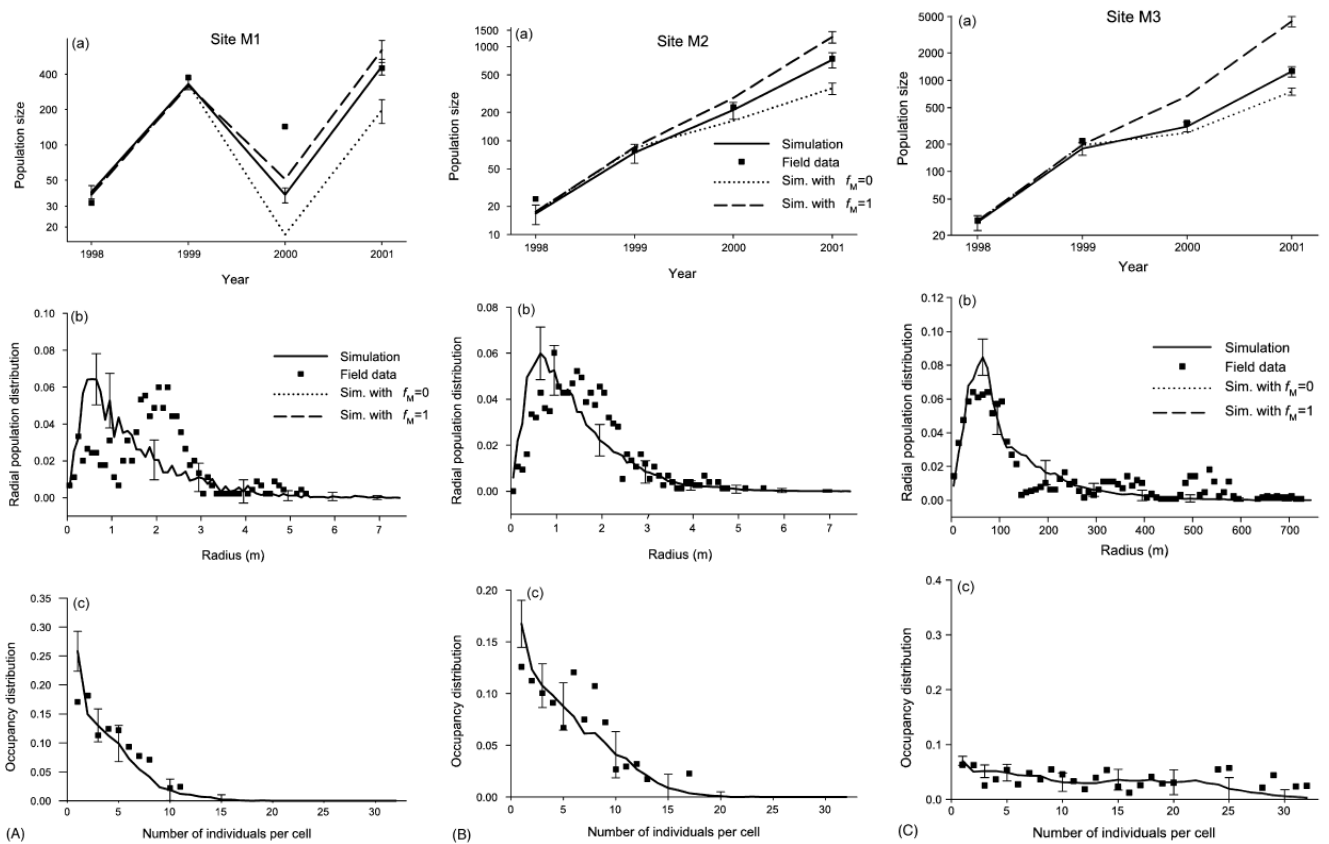

Fig. 5 – Comparison of empirical data for sites M1–M3 (A–C) with simulation results (averages over 100 simulation runs, with standard deviations) obtained with the optimal parameter values of Table 1: (a) Population size $X(t)$, together with simulation results with $f_M = 0$ (no myrmecochory) and $f_M = 1$ (all seeds underlying myrmecochory), (b) radial population distribution $p(t, r)$, and (c) cell occupancy distribution $b(t, j)$. Plots (b) and (c) for years 1998–2000 were omitted, but these results entered into the construction of the surface plots of Figs. 2–4.

There was almost no dispersal beyond the boundaries of a 15*15 m area: on average 6.7 seeds per simulation (giving rise to approximately 0.6 individuals). This "export" was only into the vicinity, as no seeds crossed the boundaries of a 40*40 m area after 3 years of dispersal. Fig. 6 gives the maps of plant distribution at site M3 in the last year of the study (2001) in the field, i.e. after 3 years of dispersal, and a typical simulation snapshot of the same situation. Especially, both maps agree in the maximum distance of individuals from the centre (appr. 7…8 m). Hints for some structural model deficiencies arising from the distributions of Fig. 5 and the mapping of Fig. 6 are discussed below.
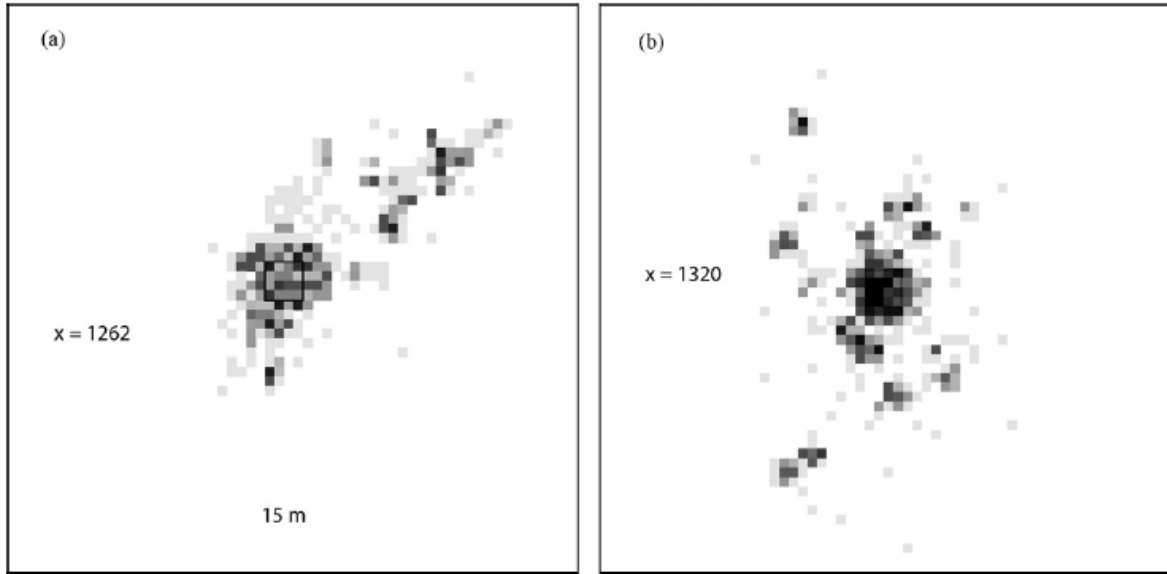
Fig. 6 – Spatial distribution patterns for site M3 in year 2001: Mapping of empirical data (a) and one simulation snapshot (b). Area of one cell: 25cm×25 cm, total area 15m×15 m. The grey tones correspond to the number of individuals in a cell (light grey: 1 or 2 individuals, darker tones up to 32 individuals per cell). The spread of the population was initiated by seed sowing in year 1997 in a square of 4×4 cells in the centre of the area.

Impact of myrmecochory: Parameter sensitivity

In addition to the insights on the precision of parameter estimates (Figs. 2-4) simulation results of radial distributions with different fractions of myrmecochorous dispersal f_M were plotted against experimental values (Fig. 7, only for site M3) in order to elucidate the impact of myrmecochory. Also from these plots extreme values of fraction f_M could clearly be ruled out.
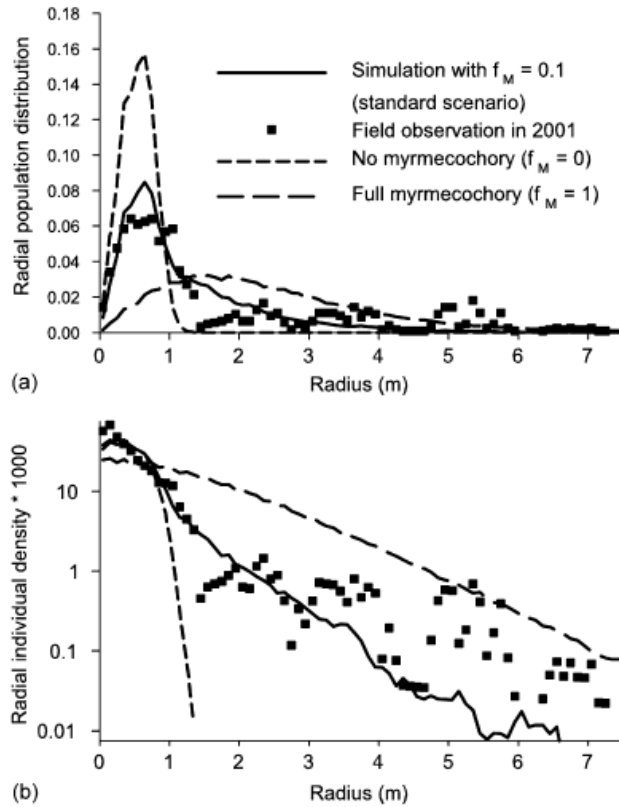

Fig. 7 – Simulation results for (a) radial population distribution (Eq. (4)) and (b) individual density distribution (Eq. (2)) for site M3 in year 2001 for different fractions of myrmecochorous dispersal *f*M in comparison with field data.

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Without myrmecochory ($f_M = 0$), there would be almost no spread of individuals beyond the central 1m²-square, even after 3 years of dispersal. If all seeds were carried away by ants ($f_M = 1$) there would be a much more averaged distribution over some area, but even then maximum migration distance would not increase substantially compared to that at $f_M = 0.10$. Nevertheless, the spread outside the 15*15 m-area would be higher: 1.860 of 250.400 dispersed seeds (0.7 %), all of them settling within a 40*40 m square. The impact of extreme values of myrmecochory ($f_M = 0$ or $= 1$) is visualized by the spatial distribution snapshots of Fig. 8. Obviously, the empirical data of Fig. 6a did not resemble either Fig. 8a or 8b. Extreme degrees of myrmecochory would also strongly influence individual numbers of populations: after 3 years of dispersal simulated population sizes $X(t)$ clearly deviated from the empirical values (see Figs. 6b and 8 for site M3, Fig. 5a for all sites).
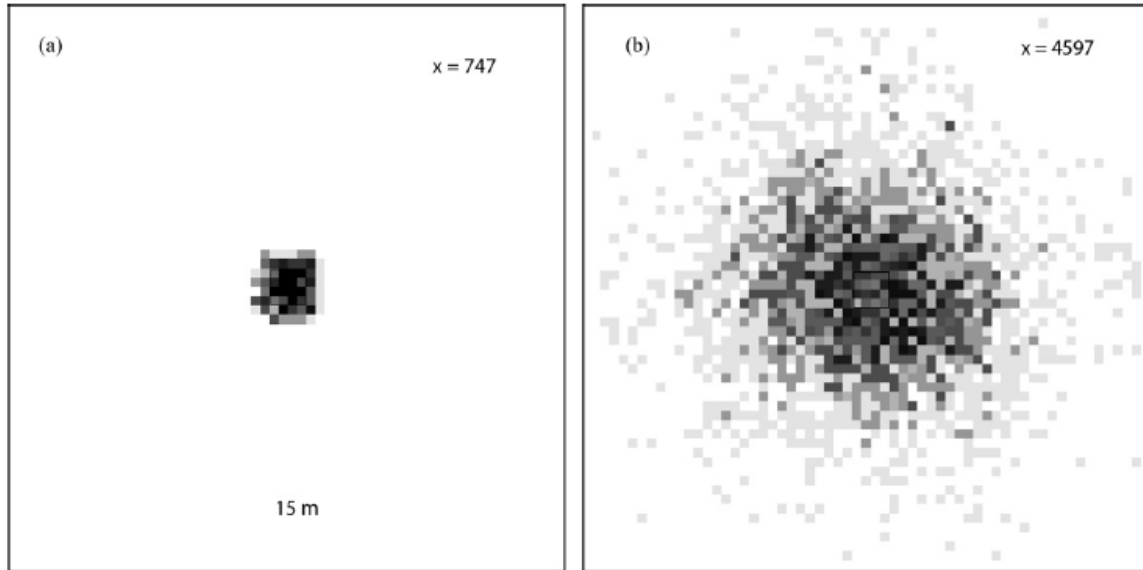

Fig. 8 – Simulated spatial distribution patterns (snapshots) in year 2001 for site M3 under the assumption of (a) no myrmecochory ($f_M = 0$) and (b) full myrmecochory ($f_M = 1$). The standard case of $f_M = 0.1$ is given in Fig. 6b for comparison. For details see legend of Fig. 6.

Projection of population development

With the simulation model parameterized along the field data 1997-2001 we projected population development and spread into the present year 2005. Climate indices were assumed as given in Table 1. The presentation of results which further reveals the role of myrmecochory is focused on site M3.

Figs. 9 and 10 (radial distributions and spatial mappings) predicted only a moderate spread since the last survey of 2001. Maximum distance from the centre should be 10 … 15 m, and the main bulk of individuals should be still in the range of less than 10 metres. In 100 simulation runs no seeds were dispersed beyond the 40*40 m square. Population sizes were predicted to increase up to 30.000 individuals ($X = 22.980 \pm 2.700$). If all seeds would be subject to myrmecochory ($f_M = 1$) plants would densely fill a circle of approximately 10 m radius (Fig. 11a) with population size $X = 147.000 \pm 9.000$. In this case there would be also some dispersal beyond the 40*40 m square: 900 seeds of 5.500.00 dispersed seeds (0.02 %). Only a significant increase in mean dispersal distance a_M would lead to a more extended spread, even with the low standard degree of myrmecochory (Fig. 11b with $a_M = 200$ cm and $f_M = 0.1$; see Fig. 10b for comparison), giving a population size of $X = 53.200 \pm 7.200$. Here, distribution would be more clumped: isolated outposts would give rise to new aggregates which would expand by barochory and short-distance myrmecochory. It is remarkable that even with an average dispersal distance of 200 cm the overwhelming amount of seeds would not cross the boundaries of the 40*40 m square.
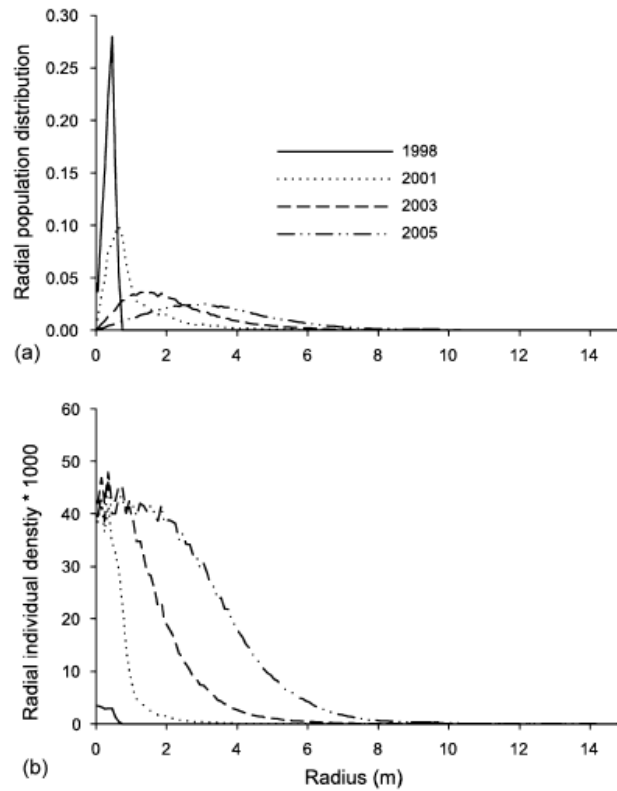
Fig. 9 – Simulated development of (a) radial population distribution (Eq. (4)) and (b) individual density distribution (Eq. (2)) (averages over 100 runs) for site M3 from year 1998 until 2005 (prognosis) with standard parameters from Table 1.
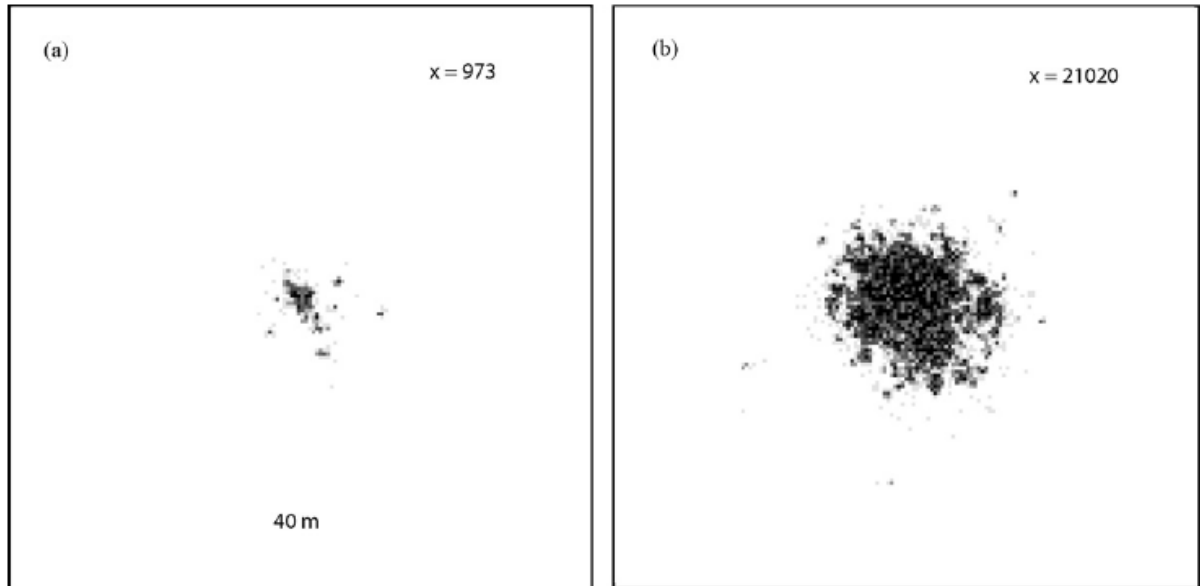

Fig. 10 – Simulated spatial distribution patterns (snapshots) after 4 years (a) and 8 years (b) of population development, i.e., 3 and 7 years of population spread (2001 and 2005) for site M3 (prognosis) with standard parameters. For year 2001 see another snapshot in Fig. 6b. Area of a cell: 25cm×25 cm, total area 40m×40 m.
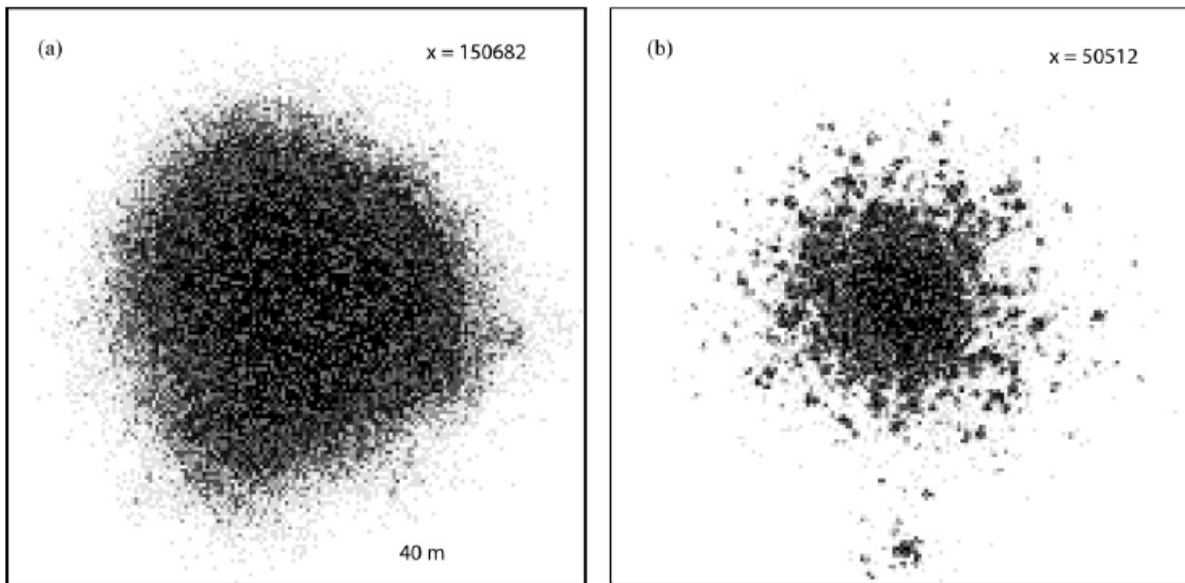
Fig. 11 – Simulated spatial distribution patterns (snapshots) after 7 years of population spread (year 2005) for site M3 (prognosis) under alternative conditions for myrmecochory: (a) all seeds underlying myrmecochory ($f_M = 1$ and $a_M = 100$ cm) and (b) extended dispersal range ($f_M = 0.1$ and $a_M = 200$ cm). For details see legend to Fig. 10.

Discussion

We used a spatially explicit individual-based stochastic model to simulate population increase and spatial spread of the annual hemiparasitic plant species *Melampyrum pratense* following experimental establishment of small populations. Because of its particular ecological niche and the ubiquitous availability of suitable hosts in the studied environment the species in question is scarcely affected by competition from other plant species justifying its treatment by a one-species model.

We could base our modelling on consistent data sets from observations over 4 years (1998-2001) from an area of about 200 m². Only two small additional records on density action and on barochorous dispersal, also raised from the experimental plots, had to be included into the analysis. The common method for parameterisation of population-spread models uses separate experiments to determine model parameters. The study of Cain et al. (1998) on population spread of *Asarum canadense* exemplifies this approach. It estimated local growth rate via matrix modelling of a patch population, and seed-dispersal distribution parameters via observation of a number of seeds transported by ants. Such a characterisation of frequency distributions of distances travelled by seeds was often described (e.g., Higgins and Richardson, 1999). As the coherence of different experiments used for parameter determination may sometimes be questionable, the foundation of modelling on a coherent data set, consisting of a time sequence of spatial point patterns, is a salient feature of our approach. It allowed combined determination of parameters of population dynamics (including local density control) and of dispersal (as a stratified process).

Our model provided different temporal and spatial criteria of population development which were reasonably fitted against observations: time series, radial distributions and distributions of occupancy of small space units. Thus it allowed extracting parameters for population increase, barochorous and myrmecochorous dispersal of seeds. Parameter estimation had to take into account the stochastic nature of model simulation results by averaging over objective functions. Precision of these estimates and correlations between estimates of the main parameters were studied by contour plots of the objective functions. This joint evaluation of parameters gave an advantage to pure sensitivity analyses proposed, e.g., by Wiegand et al. (2004). As the procedure aims at optimal fit any remaining inconsistencies can be well recognized and hence give hints for model improvement. Especially an individual-based model approach is open for including new insights into relevant processes.

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Model validation was aided by comparison of parameters with values from the literature. Our results for juvenile establishment probability p_e (0.06…0.13) were somewhat higher than those communicated by Masselink (1980). Habitats may be different in their quality, and Masselink additionally included some deposition of seeds in a permanent seed bank and thus a delayed germination. Results for myrmecochorous distances well fitted to the findings by Gibson (1993): average distances 75…100 cm vs. 110 cm. The ability for long-distance dispersal can be quantified by the 99-percentile distance of the dispersal density function applied in the model (Soons and Ozinga, 2005). In our case 99 % of all seeds will be dispersed within a radius of only 350 or 460 cm: For *Melampyrum lineare* Gibson (1993) did not find any seeds dispersed beyond 450 cm. This value can also be validated by the negative outcome of an empirical check of the study area for any individuals established in 2001 beyond the population radius of appr. 10 m.

The results suggest that our model was constructed using biologically realistic assumptions and that it should yield insights into the dynamic and spatial behaviour of spreading populations over some years. An explanation of data patterns always needs some decisions which features can be neglected and which need further specification. Our main assumptions were:

- Differences in habitat quality were only expressed by individual random establishment decisions; any heterogeneity on different spatial scales is neglected, but may be present in the field. The same holds for differences in ant-nest density and ant activity, which also were neglected. A hint for the existence of such differences is given by the different myrmecochory fractions f_M estimated for the three sites.

- Any general differences in juvenile establishment and seed production between years were neglected, with the exception of climate impact. We know of herbivory – presumably by deer – which is generally included into parameter p_e, and herbivory varies between years and populations (Heinken, 2004). However, quantitative data were not available.

- Spread directions were also treated as being purely stochastic. This can be justified by the facts that ants transported seeds only over small distances, that ant nests were small and randomly distributed with high density. A search for below-ground nest localities in the population area of M1 in September 2006 resulted in a nest density of 13.6 ant nests of seed dispersing species (*Formica fusca* and *Myrmica ruginodis*) per 100 m^2 with a more or less regular distribution pattern. This coincides with the generally high nest densities of seed dispersing ant species in temperate woodlands (approximately 10-50 nests per 100 m^2; Higashi et al. 1989, Ohkawara and Higashi 1994, Kalisz et al. 1999). Moreover, relocations of nests among years (e.g. Kalisz et al. 1999) and even within one growing season (Banschbach and Herbers, 1999) are common. Thus, in our study sites effects of directed seed dispersal to ant nests, and density effects of seed dispersing ants are usually in dimensions of at most few square metres and may be equalized by ant nest shifts over some years. We assume that they are not important for prediction of population spread patterns over a study period of a few years.

With respect to the complex interaction of ants and plants our model should be considered as a null model. Some lacks in the fitting of available plant distribution data may give hints to structural deficiencies and thus for model improvement:

- The field data showed higher clumping of individuals outside the population centre than found in simulations (see Fig. 5b), and there even were aggregates in regions where no individuals occurred in all preceding years (details not given). This may be due to habitat heterogeneities, but, in contrast to our null-model assumption, also due to directed seed transport to ant nests. Both features may act together.

- The model overestimated the fraction of cells with only 1 individual (see Fig. 5c). Again, the degree of clumping in the data is obviously somewhat higher than reproduced by the model.

- The comparison of field data and model snapshot for site M3 (Fig. 6) suggests that there is, in contrast to the other sites (patterns not shown), some directionality in population development in the field that is beyond pure randomness in dispersal angle.

We assume that all these features together require investigating and considering ant behaviour in more detail. A re-examination of the sites and their comparison with model predictions may be a useful approach. We projected population development over 4 years (2002…2005)

on the basis of the dispersal mechanisms included in our present model. These simulations showed a diffusion-like increase in area covered by *M. pratense*. There was almost no creation of "outposts", of new, small subpopulations outside the core area of the population. This outcome is due to the "exponential-tail" rule: the population front is advancing in a closed form if the seed dispersal curve is declining exponentially (as in our case) or even faster (Kot et al., 1996; Wallinga et al., 2002). Just this qualitative outcome of the present model projections is to be compared with new empirical findings which may give additional evidence whether our present set of dispersal mechanisms is sufficient to explain real spread patterns after several years of population development.

Irrespective of any future extensions our model emphasizes the effect of plant-animal mutualism for population development and spread rate: Myrmecochory per se does not only facilitate a considerable spread of the *M. pratense* populations, but also leads to substantially higher progeny of colonizing populations via reduced population density in the proximity of the mother plant. Our model results clearly show that the abundance and species composition of dispersal vectors (here: ants) have to be considered predicting population development of initial colonizers and migration processes. Actually, presence and diversity of seed-dispersing ants varies in temperate woodlands, for example due to patch size and historical land use (Mitchell et al., 2002). Thus, efficiency of myrmecochory in forests depends on site characteristics and is highly variable (Guitian et al., 2003). Probably because ants were largely absent in their study forest, Petersen and Philipp (2001) found very low rates of increase of individual number and spread of myrmecochorous woodland herbs following implantation in previously unoccupied habitats during ten years.

Our study presents modelling of growth and stochastic spread of plant populations that is fully linked to consistent data sets from field work. We were able to explain migration patterns generated by the activity of ants and could demonstrate that even small fractions of seed carried away by ants are a very important factor to provide an expansion of populations. The role of occasional long-distance seed transport by ants or any other vector remains to be studied by additional field work and, if necessary, model extension. Our pattern-oriented model design (Wiegand et al., 2003) included estimation of parameters of a stochastic model, and we argue that it will also be applicable to more complicated habitat structures, life histories, and other dispersal mechanisms. Such studies will also shed light on mechanisms that are responsible for the spread of invasive species, for the creation of new populations, and for species migration in landscapes of a changing world (Pyšek and Hulme, 2005).

References
Anderson, A.N., 1988. Dispersal distance as a benefit of myrmecochory. Oecologia, 75: 507-511.
Banschbach, V.S. and Herbers, J.M., 1999. Nest movements and population spatial structure of the forest ant *Myrmica punctiventris* (*Hymenoptera: Formicidae*). Ann. Entomol. Soc. Am., 92: 414-423.
Berk, A.R., Bickel, P., Campbell, K., Fovell, R., Keller-McNulty, S., Kelly, E., Linn, R., Park, B., Perelson, A., Rouphail, N., Sacks, J. and Schoenberg, F., 2002. Workshop on statistical approaches fort he evaluation of complex computer models. Statist. Sci., 17: 173-192.
Bierzychudek, P., 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. New Phytol., 90: 757-776.
Bossuyt, B., Hermy, M. and Deckers, J., 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. J. Ecol., 87: 628-638.
Brunet, J. and Oheimb, G. von, 1998. Migration of vascular plants to secondary woodlands in southern Sweden. J. Ecol., 86: 429-438.
Brunet, J., von Oheimb, G. and Diekmann, M., 2000. Factors influencing vegetation gradients across ancient-recent woodland borderlines in southern Sweden. J. Veg. Sci., 11: 515-524.

Buckley Y.M., Anderson, S., Catterall, C.P., Corlett, R.T., Engel, T., Gosper, C.R., Nathan, R., Richardson, D.M., Setter, M., Spegel, O., Vivian-Smith, G., Voigt, F.A., Weir, J.E., and Westcott, E.S., 2006. Management of plant invasions mediated by frugivore interactions. 43: 848-857.

Cain, M., Damman H. and Muir, A., 1998. Seed dispersal and the Holocene migration of woodland herbs. Ecol. Monographs, 68: 325-347.

Caswell, H., 2001. Matrix population models. 2nd ed. Sinauer, Sunderland, Mass., 722 pp.

Clark, J.S., 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleo-record. Am. Nat., 152: 204-224.

Clark, J.S., Lewis, M., McLachlan, J.S. and HilleRisLambers, J., 2003. Estimating population spread: What can we forecast and how well? Ecology, 84: 1979-1988.

Deckers, B., Verheyen, K., Hermy, M. and Muys, B., 2005. Effects of landscape structure on the invasive spread of black cherry *Prunus serotina* in an agricultural landscape in Flanders, Belgium. Ecography, 28: 99-109.

Draper, N., Smith, H., 1998. Applied regression analysis. 3rd ed. Wiley, New York, 706 pp.

Dwyer, G. and Morris, W.F., 2006. Resource-dependent dispersal and the speed of biological invasions. Am. Nat., 167: 165-176.

Dzwonko, Z., 2001. Migration of vascular plant species to a recent wood adjoining ancient woodland. Acta Societas Botanicorum Poloniae, 70: 71-77.

Ehrlén, J. and Eriksson, O., 2000. Dispersal limitation and patch occupancy in forest herbs. Ecology, 81: 1667-1674.

Flynn, K.M. and Vellend, M., 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers Ecol. Environment, 3: 243-250.

Frantzen, J. and van den Bosch, F., 2000. Spread of organisms: can travelling and dispersive waves be distinguished? Basic Appl. Ecol., 1: 83-91.

Gibson, W., 1993. Selective advantages to hemiparasitic annuals, genus *Melampyrum*, of a seed-dispersal mutualism involving ants I: Favourable nest sites. Oikos, 67: 334-344.

Guitian, P., Medrano, M. and Guitian, J., 2003. Seed dispersal in *Erythronium dens-canis* L. (Liliaceae): variation among habitats in a myrmecochorous plant. Plant Ecology, 169: 171-177.

Gorb, S.N. and Gorb, E.V., 1999. Dropping rates of elaiosome-bearing seeds during transport by ants (*Formica polyctena* Foerst.): Implications for distance dispersal. Acta Oecologia, 20: 509-518.

Grimm, V. and Railsback, S., 2005. Individual-based modelling and ecology. Princeton University Press, Princeton, New Jersey, 428 pp.

Handel, S.N., Fisch, S.B. and Schatz, G.E., 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. Bulletin of the Torrey Botanical Club, 108: 430-437.

Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C. and Thomson, D., 2005. The spatial spread of invasions: new developments in theory and evidence. Ecology Letters, 8: 91-101.

Heinken, T., 2004. Migration of an annual myrmecochore: a four-year-experiment with *Melampyrum pratense* L. Plant Ecol., 170: 55-72.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C. and Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biol. Conservation, 91: 9-22.

Higashi, S., Tsuyuzaki, S., Ohara, M. and Ito, F., 1989. Adaptive advantages of ant-dispersed seeds in the myrmecochorous plant *Trillium tschoskii* (Liliaceae). Oikos, 54: 389-394.

Higgins, S.I. and Richardson, D.M., 1999. Predicting plant migration rates in a changing world: The role of long-distance dispersal. Amer. Nat., 153: 464-475.

Higgins, S.I., Richardson, D.M. and Cowling, R.M., 2001. Validation of a spatial simulation model of a spreading alien plant population. J. Appl. Ecol. 38: 571-584.

Higgins, S.I., Clark, J.S., Nathan, R., Hovestadt, T., Schurr, F., Fragoso, J.M.V., Aguiar, M.R., Ribbens, E. and Lavorel, S., 2003a. Forecasting plant migration rates: managing uncertainty for risk assessment. J. Ecol., 91: 341-347.

Higgins, S.I., Nathan, R. and Cain, M.L., 2003b. Are long-distance dispersal events in plants usually caused by non-standard means of dispersal? Ecology, 85: 1945-1956.

Imbert, E., 2006. Dispersal by ants in *Centaurea corymbosa* (Asteraceae): What is the elaiosome for? Plant Species Biology, 21:109-117.

Kalisz, S., Hanzawa, F.M., Tonsor, S.J., Thiede, D.A. and Voigt, S., 1999. Ant-mediated seed dispersal alters pattern of relatedness in a population of *Trillium grandiflorum*. Ecology, 80: 2620-2634.

Kot, M., Lewis, M.A. and van den Driesche, P., 1996. Dispersal data and the spread of invading organisms. Ecology, 77: 2027-2042.

Levin, S.A., Muller-Landau, H.C., Nathan, R. and Chave, J., 2003. The ecology and evolution of seed dispersal: a theoretical perspective. Ann. Rev. Ecol. Evol. Syst., 34: 575-604.

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Mitchell, C.E., Turner, M.C. and Pearson S.M., 2002. Effects of historical land use and forest patch size on myrmecochores and ant communities. Ecol. Appl., 12: 1364-1377.

Masselink, A.K., 1980. Germination and seed population dynamics in *Melampyrum pratense* L. Acta Bot. Neerl., 29: 451-468.

Matlack, G.R., 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology, 75: 1491-1502.

Nathan, R., Perry, G., Cronin, J.T., Strand, A.E. and Cain, M.L., 2003. Methods for estimating long-distance dispersal. Oikos 103: 261-273.

Neubert, M.G. and Caswell, H., 2000. Demography and dispersal-calculation and sensitivity analysis of invasion speed for structured populations. Ecology 81: 1613-1628.

Ohkawara, K., 2005. Effect of timing of elaiosome removal on seed germination in the ant-dispersed plant, *Erythronium japonicum* (Liliaceae). Plant Species Biology, 20: 145-148.

Ohkawara, K. and Higashi, S., 1994. Relative importance of ballistic and ant dispersal in two diplo-chorous *Viola* species (Violaceae). Oecologia, 100: 135-140.

Pakeman, R.J., 2001. Plant migration rates and seed dispersal mechanisms. J. Biogeography, 28: 795-800.

Petersen, P.M. and Philipp, M., 2001. Implantation of forest plants in a wood on former arable land: a ten year experiment. Flora, 196: 286-291.

Pyšek, P. and Hulme, P., 2005. Spatio-temporal dynamics of plant invasions: Linking pattern to process. Écoscience, 12: 302-315.

Salonen, V., Setala, H. and Puustinen, S., 2000. The interplay between *Pinus sylvestris*, its root hemi-parasite, *Melampyrum pratense*, and ectomycorrhizal fungi: Influences on plant growth and repro-duction. Écoscience, 7:195-200.

Shigesada, N. and Kawasaki, K., 1997. Biological invasions: theory and practice. Oxford University Press, Oxford.

Skarpaas, O., Shea, K. and Bullock, J.M., 2005. Optimizing dispersal study design by Monte Carlo simulation. J. Appl. Ecol., 42: 731-739.

Soons, M.B. and Ozinga, W.A., 2005. How important is long-distance seed dispersal for the regional survival of plant species? Diversity Distrib., 11: 165-172.

Thompson, K., Bakker, J.P. and Bekker, R.M., 1997. The soil seed banks of North West Europe: Methodology, density and longevity. Cambridge University Press, Cambridge.

Wadsworth, R.A., Collingham, Y.C., Willis, S.G., Huntley, B. and Hulme, P.E., 2000. Simulating the spread and management of alien riparian weeds: are they out of control? J. Appl. Ecol., 37(Suppl. 1): 28-38.

Waller, L.A., Smith, D., Childs, J.E. and Real, L.A., 2003. Monte Carlo assessments of goodness-of-fit for ecological simulation models. Ecol. Modelling, 164: 49-63.

Wallinga, J., Kropff, M.J. and Rew, L.J., 2002. Patterns of spread of annual weeds. Basic Appl. Ecol., 3: 31-38.

Wiegand, T., Jeltsch, F., Hanski, I. and Grimm, V., 2003. Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. Oikos, 100: 209-222

Wiegand, T., Revilla, E. and Knauer, F., 2004. Dealing with uncertainty in spatially explicit population models. Biol. Conservation, 13: 53-78.