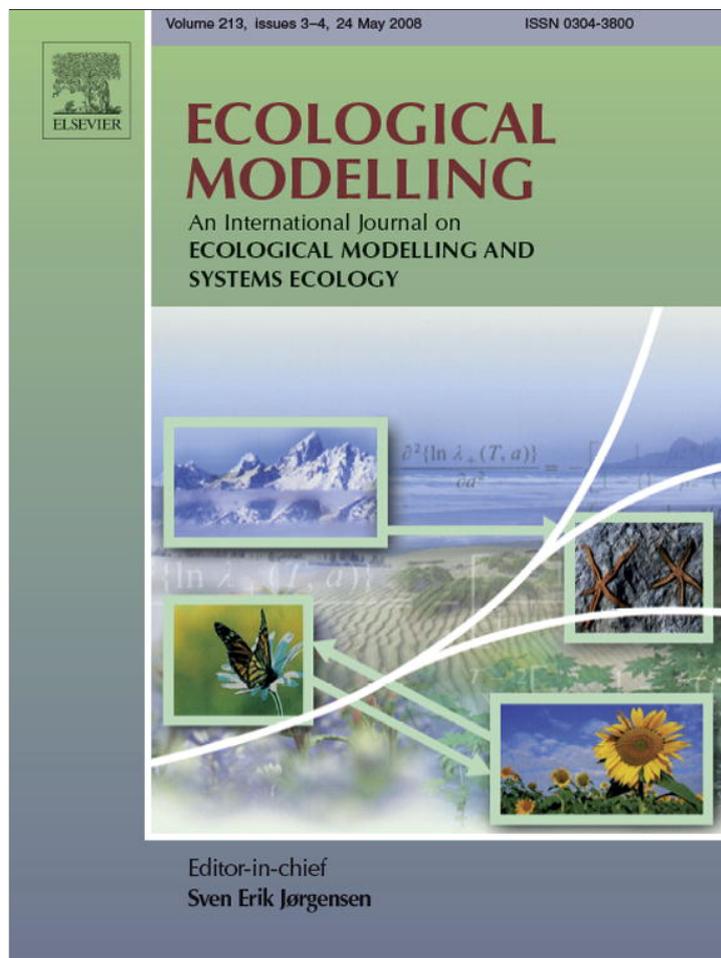


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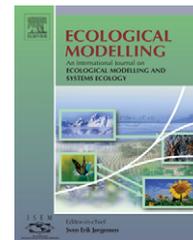
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Dispersal leads to spatial autocorrelation in species distributions: A simulation model

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ARTICLE INFO

Article history:

Received 22 February 2007

Received in revised form

11 December 2007

Accepted 12 December 2007

Published on line 1 February 2008

Keywords:

Species distributions

Spatial autocorrelation

Dispersal

Distribution modelling

Carrying capacity

Growth rate

Population dynamics

Source-sink populations

Spatial patterns

Environmental autocorrelation

ABSTRACT

Compared to population growth regulated by local conditions, dispersal has been underappreciated as a central process shaping the spatial distribution of populations. This paper asks: (a) which conditions increase the importance of dispersers relative to local recruits in determining population sizes? and (b) how does dispersal influence the spatial distribution patterns of abundances among connected populations? We approached these questions with a simulation model of populations on a coupled lattice with cells of continuously varying habitat quality expressed as carrying capacities. Each cell contained a population with the basic dynamics of density-regulated growth, and was connected to other populations by immigration and emigration. The degree to which dispersal influenced the distribution of population sizes depended most strongly on the absolute amount of dispersal, and then on the potential population growth rate. Dispersal decaying in intensity with distance left close neighbours more alike in population size than distant populations, leading to an increase in spatial autocorrelation. The spatial distribution of species with low potential growth rates is more dependent on dispersal than that of species with high growth rates; therefore, distribution modelling for species with low growth rates requires particular attention to autocorrelation, and conservation management of these species requires attention to factors curtailing dispersal, such as fragmentation and dispersal barriers.

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1. Introduction

Local population dynamics are determined by birth, death, immigration, and emigration. A crucial, yet unanswered question is: what is the relative importance of local recruitment (birth and death) versus recruitment from elsewhere (immigration and emigration, or dispersal) to population size locally and distribution patterns over the whole range? The significance of this question stems from its direct relation to a central goal of ecology. Andrewartha and Birch (1954), and Krebs (1972)

defined ecology as the study of the distribution and abundance of organisms. Most attempts at explaining the distribution and abundance of organisms have focused on the environmental conditions that define the fundamental niche and the biotic interactions that define the realized niche (Guisan and Zimmermann, 2000). In terms of population dynamics, such approaches focus solely on the birth and death components of local population dynamics. The immigration and emigration, or dispersal part of the dynamics equation has received much less attention (Bullock et al., 2002), which might be explained

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✕ Deceased fall 2005.

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doi:10.1016/j.ecolmodel.2007.12.005

by the difficulty of quantifying dispersal in the field (Stenseth and Lidicker, 1992).

Dispersal connects populations across space and time, influencing persistence, size and dynamics of local populations. In a niche model, the predicted local abundance of an organism depends exclusively on the local conditions. In a spatially explicit model that includes dispersal, the predicted local abundance depends on the local conditions and the population sizes and conditions of neighbouring sites because these neighbouring sites supply immigrants and receive emigrants from the local population. This paper determines the conditions under which neglecting dispersal in distribution models results in misleading conclusions.

This question is of particular importance when distribution models are used to predict into new areas or into new conditions such as those expected under climate change. The success of such extrapolation hinges on environmental conditions being a dominant and consistent determinant of species distributions (Araujo and Luoto, 2007). If spatial population dynamics linked by dispersal and dependent on the spatial configuration of habitat played an important role in the distribution of population abundances, environmental distribution models alone would not predict well into new situations.

The effect of dispersal on the distribution of organisms is at the core of some important ecological theories and related research, namely metapopulation ecology (Hanski, 1999), island biogeography (MacArthur and Wilson, 1967), and spatial synchrony or spatio-temporal autocorrelation research (e.g., Bjørnstad et al., 1999; Blasius et al., 1999; Koenig, 1999; Engen et al., 2002a). However, the present study differs fundamentally from these fields of research by focusing on a single species, using abundance rather than presence/absence, using a spatially explicit approach, and analyzing the long-term effects of dispersal on distribution, rather than the resulting dynamic synchrony among populations.

The model presented here combines a landscape with a continuous distribution of habitat qualities and the simulation of abundance of populations distributed across this landscape to answer two specific questions. First, which population characteristics increase the importance of dispersers relative to local recruits in determining population sizes? Second, how

does dispersal influence the spatial distribution patterns of abundances among connected populations?

2. Methods

We used a simulation model to investigate the effects of dispersal on population dynamics and abundances in connected populations. The simulation model consisted of 900 cells in a regular 30×30 grid, each containing a population (Fig. 1a). The 900 populations experienced deterministic density-dependent growth, immigration and emigration in discrete time steps. Each population was operating with identical base rates in growth and emigration, and differed only in carrying capacity (K). The change in population size per time step was modelled with a logistic growth equation (Begon and Mortimer, 1986) expanded by immigration and emigration:

$$\Delta N = N_t \left(\frac{R}{(1 + (R - 1) \times N_t/K)} - 1 \right) + I - E;$$

where N_t = population size at time t , R = potential population growth rate (birth minus death rate not adjusted for density-dependent effects), K = carrying capacity (maximum number of individuals supported at the location before the growth rate falls to 1), I = immigration (number of individuals entering the population), and E = emigration (number of individuals leaving the population).

The potential net growth rate R is the multiplier by which the population would grow in each time step if no density-dependent effects were present. R combines birth and death rates in one value (Begon and Mortimer, 1986). The realized net growth rate is R divided by $(1 + (R - 1) \times N_t/K)$, a term that approaches R when the population size N_t approaches the carrying capacity K . Thus, the realized growth rate equals one when K is reached. We covered values of R from one to five in our research. As an exemplary relation to R values found in empirical data, this range encompasses the range of maximum possible R -values (1.32–5.23) for passeriform and piciform birds in Saether and Bakke (2000). These maxima were derived from fecundity values assuming absence of adult or juvenile mortality and onset of reproduction within the first time step after birth.

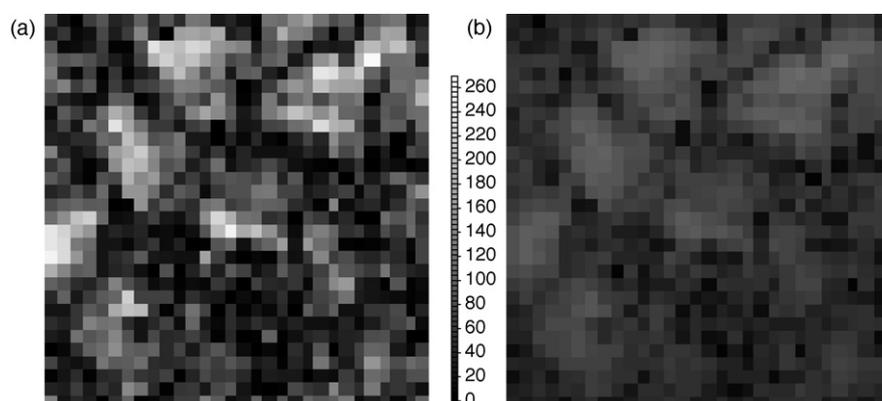


Fig. 1 – Distribution of population sizes before (a) and after (b) dispersal in a 30×30 matrix. Before dispersal, population size equals the carrying capacity (K) of the patch. K is positively autocorrelated in space up to a range of 8 cells. The population growth rate R was 1.05 and the dispersal rate in (b) was 10% of the population per time step.

The carrying capacity (K) symbolized habitat quality analogous to how patch size symbolizes habitat quality and environmental conditions in metapopulation models (Hanski, 2001). The concept of carrying capacity used here did not impose a hard ceiling on the population size but only adjusted the realized growth rate to one when K was reached and below one when the population size was larger than K . Consequently, it was possible that a population persisted at a size larger than K , fed by higher immigration than emigration. We chose to model K as a continuous variable because the reduction of the landscape into a binary view of habitat and matrix may hamper the understanding of demographic processes (Wiegand et al., 1999). K -values were selected at random for every cell from a normal distribution with a mean of zero and a standard deviation of 100. However, we used the absolute values of these random values so that no negative K -values were present.

To introduce autocorrelation into the landscape, as is typically found in the environment (Legendre and Fortin, 1989), we used the function `rfsim` in `S-PLUS` (Kaluzny et al., 1996, pp. 117–119). It first calculated a covariance matrix based on a spherical function of distance, which we gave a maximum distance of eight cells. Then the random vector of K -values was multiplied with the Cholesky decomposition of this matrix. The resulting distribution of K -values over the 30×30 matrix was spatially positively autocorrelated up to a distance of eight with similarities among neighbours decaying with distance according to a spherical function. Finally, we took the absolute values of the generated K -values, resulting in a distribution with many low carrying capacities and few large ones. A distribution of abundances with most locations having small populations and few locations having large populations is to be expected in many organisms (Brown et al., 1995; McGill and Collins, 2003).

In our default approach (but see alternative approaches tested below), Emigration (E) was set as a fixed proportion of the cell population in each time step. We used 10, 20, 30, and 40% dispersal rates in our trials with 10% being the default value used in most simulation runs. The emigrants from each population were distributed to the other cells in proportion to their distance to the power of minus two, leading to a dispersal function that declined rapidly with distance. The number of immigrants for a given population in a time step was the sum of all emigrants coming from other populations. Note that the approach to modelling dispersal in this model is deterministic and allows fractions of individuals.

Dispersal typically comes at a cost, which, among other factors, depends on the distance travelled and the local resistance encountered. In the model presented here, distance implicitly signifies total costs, including resistance. Thus, a distance in the model signifies the total difficulty for an individual to move between two points, where a long geographic distance with low resistance could be equivalent to a short geographic distance with high resistance. Note that costs only influenced the distribution of dispersal distances among emigrants. No mortality was associated with dispersal. While this simplification is unrealistic, systematic dispersal mortality would be equivalent to a lower dispersal rate combined with a higher local mortality, which are parameter variations covered in our approach. Therefore, our experiments indirectly covered death associated with dispersal.

We used two different measures to describe the effect of dispersal on the distribution of population sizes in our model. The first was based on the change in distribution patterns brought about by dispersal. In the absence of dispersal, the carrying capacities (K -values) completely explain the population sizes resulting from the simulation because the simulation model is deterministic. Therefore, the change in pattern brought about by dispersal can be directly quantified as a disruption in this perfect relationship between K -values and population size. We quantified this disruption in the relationship as the R^2 of a linear regression of the population sizes on the K -values. This measure can be seen as an indicator of the relative importance of local versus immigrant recruits. In the absence of dispersal, all population dynamics are determined by local recruitment and the R^2 is one. With the introduction of dispersal, differential immigration over-rides local recruitment, which is measured as the deviation of the R^2 from one because these effects are not explained in the K -values. In addition, the deviation of the R^2 from one gives an indication of the amount of variation in population size that would be missed in a distribution model based on habitat characteristics and linear regression.

The second measure relates to the expected effect of dispersal on the spatial distribution of population sizes—a correlation in population sizes among neighbouring populations that decays with distance. Such a correlation is called positive spatial autocorrelation and can be measured with Moran's I . We used a standardized version of Moran's I (Haining, 1990) for cell pairs one to eight cell distances apart as a measure of the effect of dispersal on autocorrelation in distributional patterns. Note that the underlying K -values were autocorrelated up to a range of eight cells as part of the landscape design, and population sizes were correspondingly autocorrelated in the absence of dispersal. We therefore measured Moran's I first in the absence of dispersal and then with the dispersal being investigated. The increase of Moran's I with dispersal is then an indication of changes in distribution patterns and increasing importance of dispersers versus local recruits.

We tested the model for sensitivity to assumptions and approaches by modifying its structure, running the model on 100 randomly generated landscapes for each parameter set, and averaging the results. The default model was on an autocorrelated landscape as described above (Table 1, on models 1–8). First, we ran the model on landscapes without spatial autocorrelation (Table 1, models 9 and 10). Second, we tested for edge effects by implementing the 30×30 matrix as a torus, which means that edges are eliminated by connecting them to the opposite edges (Table 1, models 7 and 8). While real ranges have edges this test was useful for finding out whether the range edges played a part in the observed effects or whether similar effects could be observed within the range of a species far away from range edges. Third, we investigated the influence of our original dispersal function (Type I, models 2, 8, and 10) on the simulation results by implementing four alternative functions: (1) uniform dispersal to the nearest eight neighbours only (Type II, model 3), (2) uniform dispersal to the nearest 24 neighbours only (Type III, model 4), (3) dispersal with a spherical decay in intensity up to a maximum distance of eight cells in distance (Type IV, model 5) and (4) density-dependent dispersal (Type V, model 6). Finally, we provided

Table 1 – Comparison of 10 different model structures

Model	Landscape type	Dispersal	Edge correction	Moran's I	R ²
1	Correlated	None	No	0.29 ± 0.10	1.00 ± 0.00
2	Correlated	Type I ^a	No	0.44 ± 0.12	0.84 ± 0.02
3	Correlated	Type II ^b	No	0.44 ± 0.12	0.83 ± 0.02
4	Correlated	Type III ^c	No	0.52 ± 0.11	0.78 ± 0.03
5	Correlated	Type IV ^d	No	0.55 ± 0.11	0.76 ± 0.03
6	Correlated	Type V ^e	No	0.33 ± 0.11	0.98 ± 0.00
7	Correlated	None	Yes	0.22 ± 0.09	1.00 ± 0.00
8	Correlated	Type I	Yes	0.33 ± 0.10	0.88 ± 0.01
9	Uncorrelated	None	No	0.07 ± 0.04	1.00 ± 0.00
10	Uncorrelated	Type I	No	0.23 ± 0.05	0.73 ± 0.01

Means ± standard deviations of Moran's I are given from runs on 100 randomly generated landscapes (see Section 2) with potential population growth rate $R = 1.05$, and dispersal rate = 10%. See Section 2 for landscape generation, dispersal types, Moran's I, and R^2 calculations.

^a Dispersal decays in intensity proportional to $1/\text{distance}^2$ without a maximum dispersal limit.

^b Dispersal is uniform and only to the eight closest neighbours.

^c Dispersal is uniform and only to the 24 closest neighbours.

^d Dispersal decays with distance following a spherical function up to a maximum distance of eight cells.

^e Density-dependent dispersal.

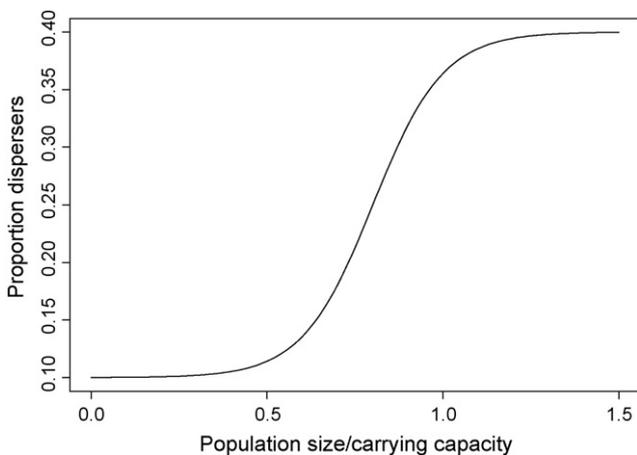


Fig. 2 – Dependence of dispersal on the ratio between population size and carrying capacity in model 6 (density-dependent dispersal Type V). The exact functional form is given in Section 2.

statistics for correlated and uncorrelated landscapes without dispersal for comparison (Table 1, models 1, 6, and 8). Table 1 gives an overview of the investigated model structures.

We modelled density-dependent dispersal with a logistic function that varied the proportion of dispersers from 10 to 40% depending on the ratio of population size to carrying capacity (N_t/K). The equation was

$$\text{Percent dispersers} = \frac{0.1 + 0.0001 \times \exp(10 \times (N_t/K))}{(1 + \exp(10 \times (N_t/K)))/3000}$$

leading to the distribution of disperser proportions shown in Fig. 2.

Simulations were run until an equilibrium was reached, defined as a change from one time step to the next smaller than 0.01 in the sum of all populations. Therefore, all results presented here are based on the final balance between growth and dispersal that the populations moved into, and not dynamics or changes in populations between the start of the

simulation and the final equilibrium. The analyses varying the model parameters R , and the proportion of dispersal were based on a single typical random landscape. All simulations and statistics were programmed in S-PLUS 6.2 (Insightful, 2003) (use of this product does not imply endorsement).

3. Results

Introducing dispersal in the population simulation model led to a systematic deviation of population sizes from their underlying carrying capacities (K) (Figs. 1, 3 and 4) and an increase in positive spatial autocorrelation (Fig. 5 and Table 1, model 1 and 2). Populations with below average K -values tended to exceed K and turned into sinks, while cells with above average K -

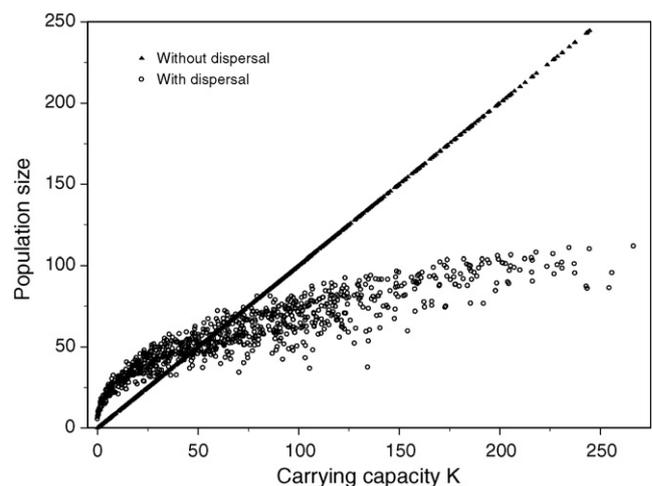


Fig. 3 – Deviation of population size from underlying carrying capacity (K) with and without dispersal. Without dispersal population sizes are identical to K -values. With dispersal populations with small K -value are larger than expected, while populations with large K -value are smaller than expected. The population growth rate R was 1.05 and the dispersal rate was 10% of the population per time step.

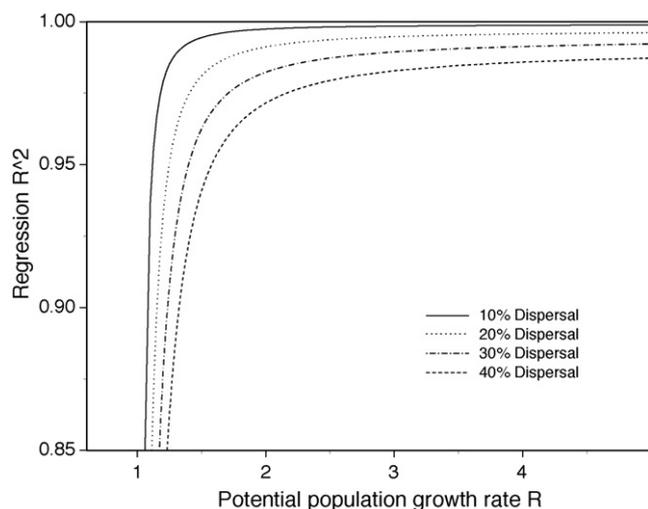


Fig. 4 – Effect of potential population growth rate R on distribution patterns under a range of dispersal rates. The regression R^2 is the coefficient of determination of a linear regression of the vector of 900 populations at equilibrium after dispersal against the vector of carrying capacities (K) underlying the populations. This coefficient is an expression of how strongly local population sizes are controlled by local carrying capacity rather than by immigration and emigration. R is the potential population growth rate or the factor by which the population can maximally grow in each time step before adjustment for density dependence.

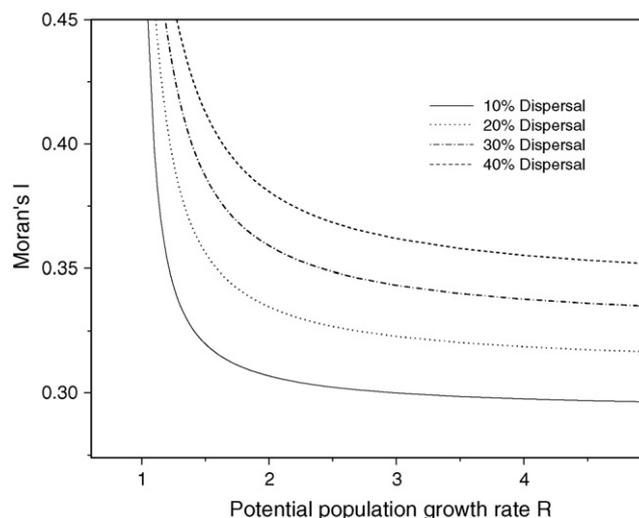


Fig. 5 – Effect of potential population growth rate R on autocorrelation in distribution patterns under a range of dispersal rates. Moran's I is a measure of autocorrelation based on all cell pairs with a maximum distance of eight cells. This measure is an expression of the similarity among population sizes within an eight-cell distance, above and beyond the overall similarity among population sizes in the whole range. Note that the lower bottom of the graph is at the value of Moran's I for the population size distribution without dispersal. R is the potential population growth rate or the factor by which the population can maximally grow in each time step before adjustment for density dependence.

values attained population sizes below K and acted as sources (sensu Pulliam, 1988). Thus, dispersal led to a reduction in the range and variance of population sizes (Figs. 1 and 3) and a stronger correlation in population sizes among neighbours, decaying with distance. With the default parameter values (net potential local growth rate $R=1.05$ and proportion of dispersers = 10%), Moran's I increased by 0.15 ± 0.01 (SE) or 50% when dispersal was introduced, while K -values lost $16.4 \pm 2.0\%$ (SE) of their explanatory power (as measured by reduction in R^2 from models 1 to 2) in the distribution of population sizes.

The magnitude of these effects depended on the potential population growth rate R and the proportion of dispersers (Figs. 4 and 5) but was not strongly influenced by the underlying model structure (Table 1). The influence of the potential population growth rate R on the changes in distribution patterns under dispersal is shown in Figs. 4 and 5. With a dispersal rate at 10%, only low values of R allowed for strong influences of immigrants on the deviation of dispersal patterns from underlying K -values. When R was 1.3 or above, 10% dispersal changed distribution patterns by less than 1%. However, the increase in autocorrelation was not as dependent on low R -values as the deviation in patterns from underlying K -values (Fig. 5). Moran's I increased by 23% with $R=1.3$ and dispersal rate at 10%. Higher dispersal rates caused a larger deviation in the distribution of population sizes from the pattern of underlying K -values (Fig. 4) and delayed the decrease in deviation with higher R -values: the distribution pattern was changed

by 6% and autocorrelation was increased by 34% with 40% dispersal and $R=1.5$.

Tests of the sensitivity of the model to its structure confirmed its adequacy. First, the variance in results introduced through the random selection of K -values during landscape creation was low (Table 1, see low standard deviations). Very few generated landscapes led to extreme results, except when all cells with high K -values were clumped around the edges of the matrix. Second, the results were sensitive to the introduction of spatial autocorrelation in the landscape. Dispersal led to a lower R^2 and a larger increase in autocorrelation in uncorrelated landscapes than in correlated landscapes (Table 1, compare change from models 1 to 2 vs. change from models 9 to 10). However, the total autocorrelation in the distribution of population sizes was still higher in correlated landscapes than in uncorrelated landscapes after dispersal. Third, edge effects were observable in the simulation. When we implemented the 30×30 matrix as a torus, the observed effects of dispersal on the distribution of abundances decreased (Table 1, model 2 vs. model 8). However, autocorrelation in the distribution of K -values was also lower in the toroidal landscape (Table 1, model 1 vs. model 7), indicating that the edge effects were not solely due to dispersal anomalies at the edges but also computational differences in the analyses of the dispersal patterns. The main effect of the toroidal correction was to reduce outlying population sizes due to edge effects and thus reduce the variance in population sizes. It did not change

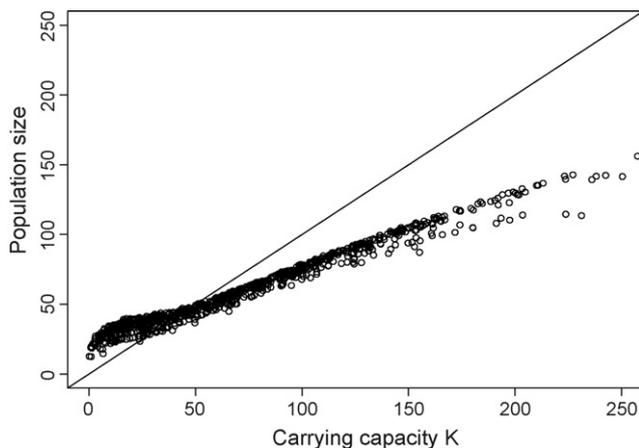


Fig. 6 – Deviation of population size from underlying carrying capacity (K) with density-dependent dispersal. The population growth rate R was 1.05 and the dispersal rate varied between 10 and 40% of the population per time step. The dispersal rate was dependent on the ratio between population size and carrying capacity as shown in Fig. 2.

the main observed effect of dispersal in changing distribution patterns. Fourth, the three alternate dispersal functions (Type II–IV) led to minor quantitative differences in the overall results (Table 1, models 3–5), but did not influence the qualitative insights gained, so that a more detailed investigation or a more complicated model were not justified.

The only alternate scenario that led to a substantial change in results was the introduction of density dependence in dispersal (Table 1, model 6 and Fig. 5). Density dependence in dispersal reduced the maximum deviation of populations from their carrying capacity and thus led to a much straighter distribution of abundances (Fig. 6) and thus a higher R^2 (Table 1, model 6). Morin's I decreased but was still substantially higher than in no-dispersal scenarios.

4. Discussion

The approach presented here takes a process-based rather than habitat-centred view of spatial distributions (Thomas and Kunin, 1999) by incorporating immigration and emigration into the population dynamics. The core insight of the model is that dispersal is less important for shaping the distribution of abundances in species with a large potential population growth rate than those with a small potential growth rate. In other words, the population dynamics of species that have the potential to grow quickly are dominated by local recruitment. Immigrants cannot contribute much to the local abundances of such species. In contrast, in species with low potential population growth rates, migrants can play a very important role in the distribution of abundances. Typical species falling in this category have low numbers of offspring and a high parental investment, such as large mammals and many large birds. This result is consistent with Söndgerath and Schröder (2002), who, with a different goal and methodology, concluded that increasing the connectivity of a landscape has a notewor-

thy effect on spatial spread only when reproductive rates are low.

How low must the reproductive rate of a species be for dispersal to have an important influence on distribution? Due to the necessary omission of some ecological complexities, the results of this model should not be taken as numerical predictions for the parameter combinations under which dispersal has ecologically significant effects on distribution patterns. However, the model could give a rough indication for which species dispersal effects could be important. For example, Thompson (1987) gives estimates of intrinsic rate of natural increase (r_m) for 42 mammals. When translated into the discrete time R used here, the average rate of increase for large mammals (over 5 kg, $N=25$) was 1.61 ± 0.06 (SE). Such a rate would allow for significant dispersal-caused deviations in the distributions of these species from what would be expected if environment was the only determinant (Figs. 3 and 4). It is also important to note that Thompson's estimates assume zero mortality until after the physical maximal reproductive age is reached, which makes this type of r_m estimate an absolute maximum estimate similar to the estimate of bird R -values given in Section 2 (1.32–5.23 for passeriform and piciform birds). In reality maximum attained intrinsic rates of increase could be considerably lower than those presented above and thus dispersal could be considerably more important to species' distributions than the above figures suggest.

Several complications influence our results, not all of which we were able to address in the presented model. We did not include local extinctions or environmental and demographic stochasticity. Both effects would likely increase the importance of migrants to overall population distribution because migrants would assume more pivotal roles by recolonising locally extinct populations, by rescuing populations on the brink of extinction, and by spreading the risk of extinction by local environmental fluctuations (Engen et al., 2002b). In contrast, the presented effects of dispersal may be weakened slightly by introducing dispersal mortality into the model, which could decrease the connection among populations. Thus, the combinations of growth and dispersal rate would have to be more extreme to come to the same effects on distribution patterns as without dispersal mortality. Another simplification of the model is the assumption of reaching an equilibrium in population dynamics (Pickett et al., 1994; Guisan and Zimmermann, 2000). The simulation model presented here works on the assumption that an equilibrium is reached through logistic growth. We contend that the introduction of stochastic, non-equilibrium elements would not have changed the fundamental insights gained by this model and would thus have been an unnecessary complication. As long as the system is not continuously growing or shrinking, the population dynamics would have averaged out over the simulation duration of several 100 time steps and would not change the fundamental effects of dispersal on spatial distribution patterns posed as the core question of this research.

Introducing density-dependent dispersal as a complication to the model reduced the effects of dispersal substantially. Under this scenario, sources that fall well below carrying capacity because of emigration experience lower rates of

emigration than sinks, which are above carrying capacity. This density dependence of dispersal weakens the source-sink pattern arising from dispersal and brings populations closer to the expected abundance equalling carrying capacity (Fig. 6). In particular, extreme deviations from carrying capacity (above or below) were prevented in this scenario. We could not find data on density dependence of dispersal that would have allowed us to gauge how important this effect could be in natural populations.

Other complications not considered in this model were directional bias in dispersal towards good habitat (e.g., Schooley and Wiens, 2003), and differential mortality associated with movement through different quality habitats (e.g., Amarasekare, 1998). These complications have the potential to influence the presented results but are beyond the scope of this investigation.

In contrast to other studies (e.g., Pulliam, 2000; Keitt, 2003), we did not designate source and sink populations *a priori*. Instead, we specified carrying capacities. A fixed percentage of dispersal led to a source-sink structure because the populations in cells with high K-values supplied more dispersers and the cells with low K-values accepted more dispersers. Under this scenario the logistic growth function led to higher realized population growth rates in the source cells and lower or zero growth in the poorer habitats because the population size was closer to or even at or above K in the latter populations, although the fundamental potential population growth rates were identical. Given the fixed death rate, the cells with positive net immigration then turned into functional sinks and the ones with negative net immigration turned into sources.

The simulation approach presented here differs from the approach taken by several other ecological theories that are centred on the effects of dispersal. Island biogeography uses dispersal for colonisation rates and subsequently to predict biodiversity but does not deal with abundances of individual species (MacArthur and Wilson, 1967). In addition, it requires an unchanging mainland population supplying a constant stream of immigrants, which is not a model applicable to many terrestrial situations (Hanski, 2001). Metapopulation ecology uses dispersal as a connection between populations for recolonisations and rescue effects, but does not analyze the spatial consequences of dispersal on the distribution of abundances. Such an approach is appropriate for discrete habitat patches such as islands or highly fragmented landscapes but is of questionable value for a landscape of continuous habitats (Hanski, 1999, 2001). The study of synchrony in population dynamics of neighbouring populations, brought about by environmental synchrony (the Moran effect) or by dispersal, investigates the spatio-temporal consequences of dispersal but not how these consequences change distributions over many generations (e.g., Bjørnstad et al., 1999).

The results presented here are important for the fields of distribution modelling and conservation management. Many authors assert that spatial models are a significant advance in distribution modelling and should be used whenever possible and appropriate (e.g., Legendre, 1993; Thomson et al., 1996; Keitt et al., 2002; Lichstein et al., 2002; Segurado et al., 2006). However, it is important to understand the source of spatial structure in distributions to properly apply spatial models (Austin, 2002). If the only source of a spatial pattern

in the form of positive spatial autocorrelation stems from the autocorrelation in the underlying environmental gradients, a model including all gradients will implicitly model the spatial structure, and more explicit spatial modelling will be an unnecessary complication (Diniz-Filho et al., 2003). If, however, another process, such as dispersal, causes spatial patterns, it is important to understand under which conditions this process may be influential enough to warrant inclusion in a distribution model.

Our results show that species with low to moderate potential population growth rates and density-independent dispersal are most likely to exhibit ecologically significant spatial autocorrelation above and beyond the spatial autocorrelation caused by environmental gradients. These species are the most likely candidates to require spatially explicit models, whether all environmental gradients are included or not. In addition, these species will be least successfully modelled with climate envelope models and the predictions of their future distributions under climate change will likely be unreliable.

The spatial patterns in the distribution of species and the relative importance of dispersal to these patterns are also important to the field of conservation biology. Species with a high potential population growth rate are less dependent on dispersal than species with a low rate. Therefore, conservation efforts for species with low growth rates will likely require more connectivity in the landscape and larger conservation areas than efforts for species with high growth rates.

Acknowledgements

We are indebted to the following people for advice, interesting discussions, reviews and editorial support: Brian McGill, Brian Ripley, David Hiebeler, Deanna Newsom, Frederic Beaudry, Genevieve Nesslage, Spencer Graves, William Halteman, Steven Campbell, and Walter Koenig. This project was funded by the U.S. Geological Survey's (USGS) Gap Analysis Program, and is a contribution of the Maine Cooperative Fish and Wildlife Research Unit (USGS, University of Maine, Maine Department of Inland Fisheries and Wildlife, and Wildlife Management Institute, cooperating). This is publication number 2986 of the Maine Agriculture and Forest Experiment Station.

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