

Density-dependent dispersal and spatial population dynamics

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The synchronization of the dynamics of spatially subdivided populations is of both fundamental and applied interest in population biology. Based on theoretical studies, dispersal movements have been inferred to be one of the most general causes of population synchrony, yet no empirical study has mapped distance-dependent estimates of movement rates on the actual pattern of synchrony in species that are known to exhibit population synchrony. Northern vole and lemming species are particularly well-known for their spatially synchronized population dynamics. Here, we use results from an experimental study to demonstrate that tundra vole dispersal movements did not act to synchronize population dynamics in fragmented habitats. In contrast to the constant dispersal rate assumed in earlier theoretical studies, the tundra vole, and many other species, exhibit negative density-dependent dispersal. Simulations of a simple mathematical model, parametrized on the basis of our experimental data, verify the empirical results, namely that the observed negative density-dependent dispersal did not have a significant synchronizing effect.

Keywords: habitat fragmentation; metapopulation; population synchrony; population cycles; tundra voles

1. INTRODUCTION

To what extent do biological populations exhibit spatially synchronous dynamics, and what is the synchronizing mechanism that is currently subject to intensive research (e.g. Grenfell *et al.* 1998; Blasius *et al.* 1999; Post & Forchhammer 2002; Schwartz *et al.* 2002)? Studies of population synchrony provide a valuable approach to the most fundamental question in population biology: by which mechanisms are populations regulated? From a more applied point of view, the degree of population synchrony determines the extinction risk of fragmented populations (Earn *et al.* 2000) and the opportunities for control of pests and diseases (Earn *et al.* 1998). A distinguished body of theory suggests that dispersal movement is a powerful synchronizing mechanism (Ranta *et al.* 1995, 1997; Blasius *et al.* 1999; Lande *et al.* 1999; Bjørnstad & Bolker 2000; Kendall *et al.* 2000; Sherratt *et al.* 2000). Indeed, among three main causes of population synchrony that have been identified largely based on theoretical studies (Bjørnstad *et al.* 1999a); i.e. dispersal movements, regionalized disturbances (the so-called Moran effect) and trophic interactions (e.g. predator–prey interactions), dispersal movements have been claimed to be the most parsimonious (Schwartz *et al.* 2002). Theoretical studies have demonstrated that even spatially restricted dispersal movements can account for large-scale synchrony under certain circumstances (Ranta *et al.* 1997; Bjørnstad & Bolker 2000; Kendall *et al.* 2000). Moreover, dispersal-induced population synchrony is compatible with the pattern of decaying synchrony with distance that is commonly observed in population survey data (Ranta *et al.* 1995; Sutcliffe *et al.* 1996; Lambin *et al.* 1998; Paradis *et al.* 1999; Cattadori

et al. 2000), yet dispersal is generally the most poorly known demographic parameter. It is notoriously difficult to measure in the field and, in most cases, estimates of dispersal rate have to be derived from indirect methods that are associated with large uncertainties and potential biases (Ims & Yoccoz 1997). To the best of our knowledge, no previous study has been able to map independent estimates of distance-dependent dispersal rates on equivalent estimates of population synchrony.

In this study, we use an experimental setting to examine the relationship between dispersal and population synchrony. Experimental studies conducted on small spatial and temporal scales (so-called experimental model systems) have proved to be instrumental in population biology, especially for facilitating a better dialogue between theory and data (Ims & Stenseth 1989; Wiens *et al.* 1993; Lawton 1995). For instance, such experiments have been used to verify the theoretical conjecture that dispersal can promote metapopulation persistence and species coexistence (Burkey 1997; Gonzales *et al.* 1998). Although the issue of population synchrony typically concerns large-scale and long-term phenomena beyond the realm of controlled experiments, we justify our relatively small-scale study on the following grounds: in order to be a powerful agent of region-wide synchrony, dispersal must at least be able to exert its synchronizing effect on a more local scale (Bjørnstad, Ims & Lambin 1999). As has been carried out successfully in conjunction with model system experiments previously (Ellner *et al.* 2001), we use mathematical modelling as a tool for evaluating the consistency of our experimental results.

2. MATERIAL AND METHODS

Data on dispersal movements and population synchrony was obtained from a study of 14 experimentally fragmented

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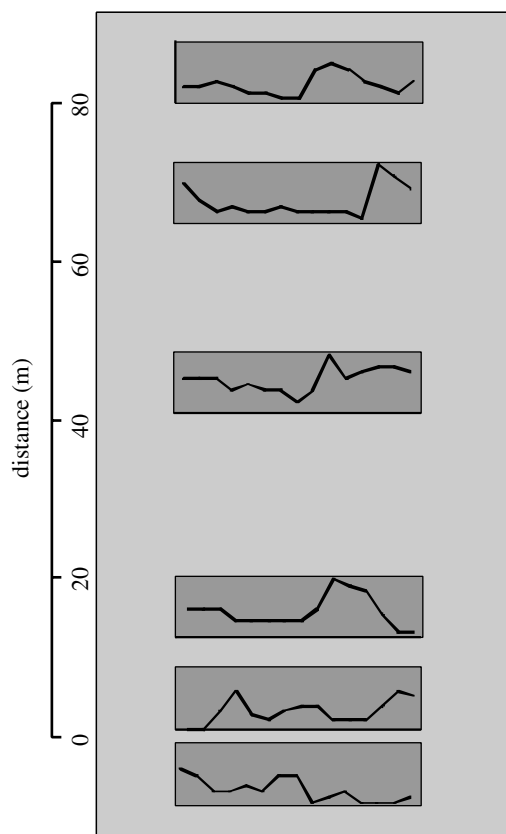


Figure 1. The spatial arrangement of the six habitat fragments (=subpopulations) within 1 of the 14 replicates of fragmented populations that were studied. Dark grey rectangles are the habitat patches, embedded in a matrix area (light grey), which were uninhabitable for voles. Subpopulation density trajectories over the 3.5 month breeding season for one arbitrarily chosen replicate are superimposed on the habitat fragments.

populations of tundra voles, *Microtus oeconomus*, at Evenstad Landscape Ecological Field Station in southern Norway (Johannesen *et al.* 2003). Voles and lemmings are among the best-known species with large-scale population synchrony (Krebs & Myers 1974; Ranta & Kaitala 1997; Lambin *et al.* 1998; Ims & Andreassen 2000). Each of the experimental populations was studied in $50 \times 100 \text{ m}^2$ enclosed plots with six meadow patches arranged according to a gradient of inter-patch distances (range: 1.5–80 m) in a non-habitat matrix (figure 1). The habitat patches were large enough (225 m^2) to harbour small subpopulations of voles similar to size of natural tundra vole patches in boreal and arctic landscapes (Lambin *et al.* 1992).

For each of the years 1992 and 1993, seven experimental, fragmented populations were initiated by releasing five laboratory-raised mothers with weaned litters into separate enclosures (figure 1). Population dynamics and dispersal movements between patches/subpopulations were monitored on a weekly basis with 2 days of trapping and six trap checks per week from early July (week 26) until mid October (week 42). The 3.5 month monitoring period per year encompassed three vole generations (Johannesen *et al.* 2003). In total, 1407 individuals were captured 16 519 times. We recorded dispersal movements according to whether an individual had changed patch from one week to the next. If an individual was captured in more than one patch in a week, the home patch was assigned as the patch in which it had been captured most in that week.

In the few cases where a living animal was not captured in one week it was assigned its previous week's home patch. Animals captured equally in two patches were assigned the previous week's home patch, as this was always one of the two. In total, we recorded 553 weekly dispersal movements by 351 individuals. Potential aberrant effect of frustrated movements beyond the enclosures was avoided by removing animals frequently trapped in particular fence traps (Johannesen *et al.* 2003). Removed animals did not make up more than 5.6% of the total number of individuals in any population, and the removals did not affect demography (Johannesen *et al.* 2003).

The vegetation was burned and fertilized every spring prior to the introduction of voles to standardize habitat productivity among patches and populations. The spatial habitat configuration with a gradient of inter-patch distances (figure 1) was already set at the start of the experimental period for half of the 14 experimental populations, while it was created by fragmenting one initial large habitat block after six weeks for the other half. The latter manipulation was carried out as a part of a study of the effect of habitat destruction on local demography (Johannesen *et al.* 2003). Only data from the period after habitat fragmentation was used for the latter seven populations. The matrix between the patches was maintained uninhabitable for voles by frequently mowing the vegetation.

3. RESULTS

(a) Experiment

The intensive live-trapping programme allowed us to accurately monitor dispersal movements and population dynamics on a weekly basis through the 3.5 month breeding season (early July to late October) in 2 years. The size of the 84 subpopulations varied from 0 to 49 individuals/patch over the season. A Gompertz-type model fitted the population time-series adequately (see Lebreton 1991 for model fitting procedure) and there was clear evidence for density-dependent regulation (test for log-linear negative density-dependence: $F = 66.9$, $p < 0.001$, estimated model parameters are given below).

Weekly dispersal rate between pairs of patches (e.g. exchange rate) was quantified as the proportion of the animals in a patch/subpopulation that had dispersed to another patch/subpopulation during a week. The dispersal rate was highest between the closest subpopulations and it dropped steeply with increasing distance (figure 2a). Synchrony in the weekly growth rates among subpopulations was quantified by the cross-correlation coefficient equivalent to Kendall's tau proposed by Buonaccorsi *et al.* (2001). This measure of population synchrony (which focuses on short-term, week-to-week dynamics) was generally statistically indistinguishable from zero, and there was no trend that could be ascribed to distance (figure 2b). In order to test whether there was any cumulative effect of dispersal that acted to spatially homogenize subpopulation sizes on the time-scale of a full breeding season, we also computed the spatial autocorrelation (Cliff & Ord 1973) in subpopulation sizes at the end of the experimental period (i.e. week 42). However, not even this measure of population synchrony was significant at any inter-patch distance (figure 2c). These results imply that dispersal had no synchronizing effects either on a short (a week) or on a longer time-scale (a 3.5 month breeding season = three vole generations).

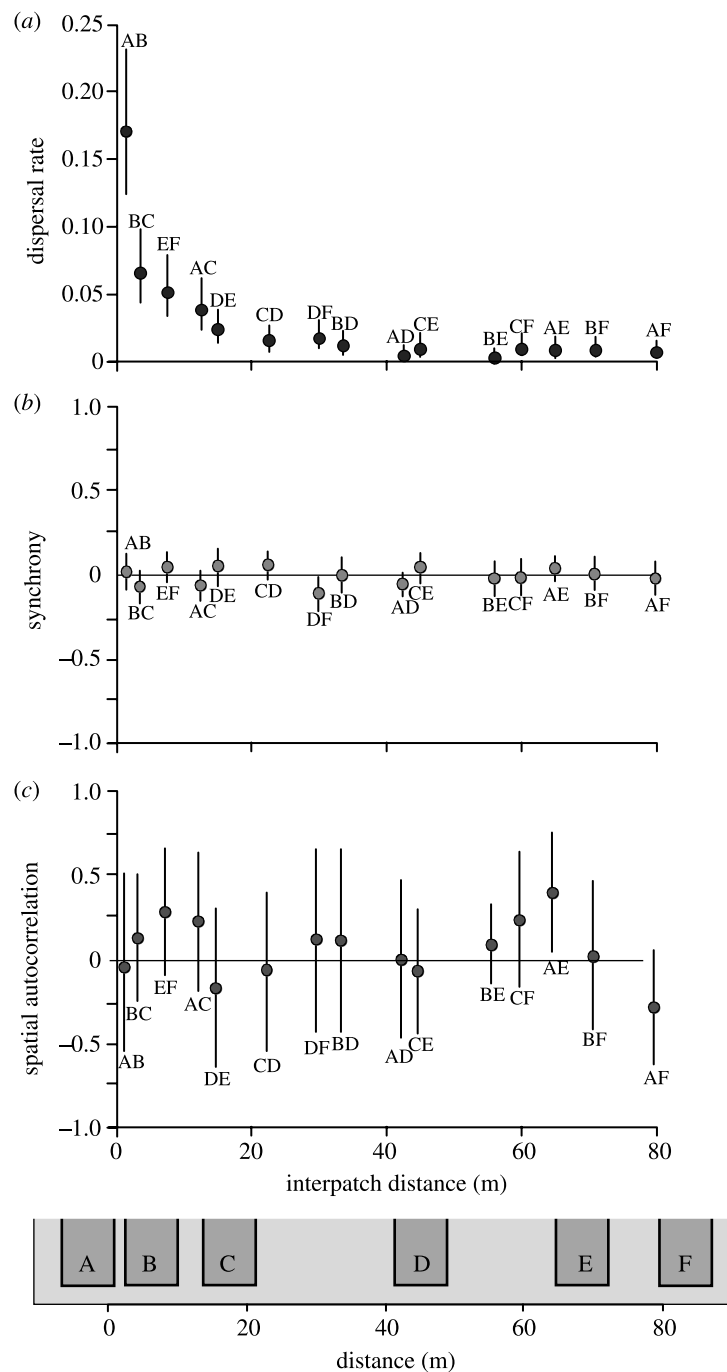


Figure 2. Dispersal rate and degree of synchrony between subpopulations as a function of inter-patch distance. (a) weekly dispersal rate among subpopulations. (b) The degree of synchrony quantified as cross-correlations between weekly growth rates among subpopulations. (c) spatial autocorrelation in subpopulation sizes at the end of the breeding season. All estimates are given with 95% confidence intervals based on the 14 replicates of the fragmented populations.

Most theoretical studies demonstrating that dispersal movements can act as a powerful synchronizing mechanism, assume an arbitrary, constant (i.e. density-independent) dispersal rate. However, density-dependent dispersal is common in nature (Ims & Hjermann 2001; Clobert *et al.* 2004). We tested for density-dependent dispersal applying a mixed logistic-binomial model (SAS GLIMMIX macro; Littell *et al.* 1996) with proportion dispersers as a response variable. In addition to subpopulation density, we included week in season as a fixed predictor variable to control for possible season effects, and subpopulation identity as a random effect to control for non-independence between the repeated measurements of dispersal within

subpopulations. We rejected the assumption of a constant dispersal rate in favour of a negative density-dependent dispersal rate ($F=21.79$, $p<0.001$; figure 3a, the estimated parameter for the density-dependence is given below). A negative density-dependent movement rate may imply that the demographic importance of dispersal relative to survival and mortality will decrease with increasing population density. Indeed, this was evident in our data (figure 3b,c), although most clearly for growing subpopulations (figure 3b).

(b) Mathematical modelling

We used a simple stochastic difference equation model to evaluate the consequences of the observed

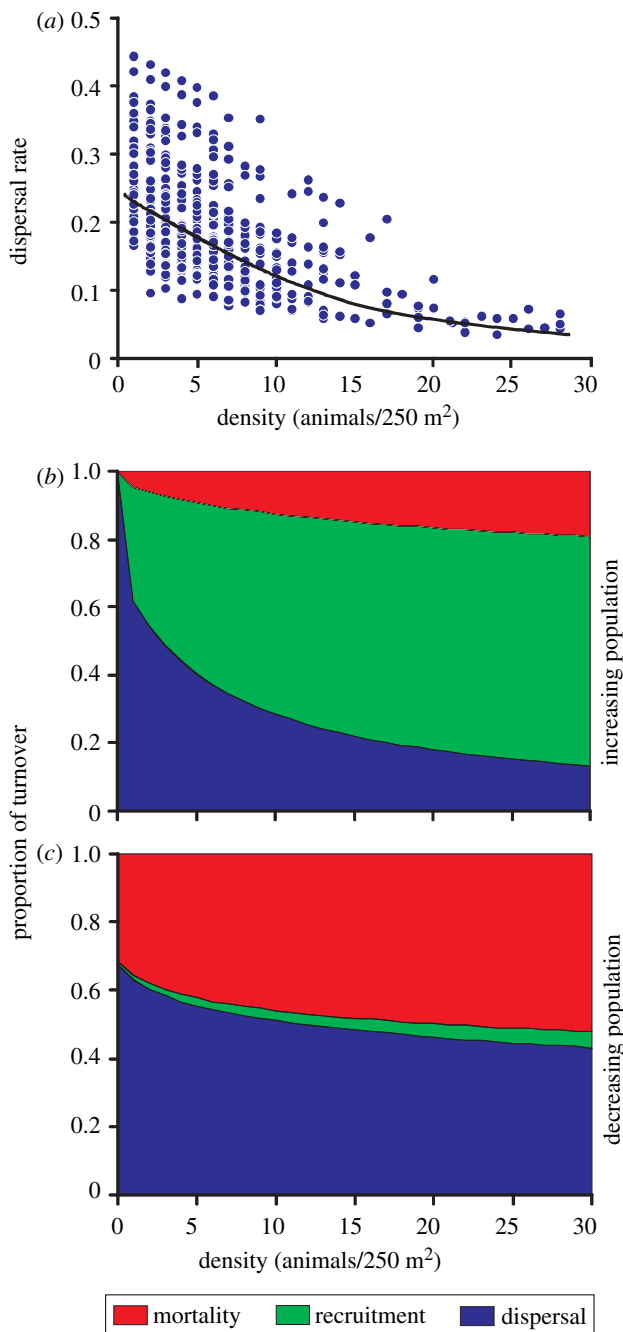


Figure 3. Negative density-dependent dispersal and its proportionate effect on the dynamics of the subpopulation. (a) Density-dependent dispersal rate function fitted by logistic-biomodal modelling. (b) and (c) Density-dependent proportionate contribution of dispersal (emigration and immigration), mortality and recruitment to total turnover of increasing (b) and decreasing (c) subpopulations. Total turnover is defined as the sum of individuals recruited, immigrating, dying and emigrating to/from a subpopulation during a week. The density-dependent functions are obtained from a repeated measures logistic regression with subpopulation identity as the subject-level random effect and the demographic parameter (dispersal, mortality and recruitment) as the within-subject, repeated effect (cf. [Andreassen & Ims 2001](#)).

density-dependent dispersal rate on population synchrony. The model was formulated and parametrized so as to mimic the main features of the observed dynamics of our experimental subpopulations; i.e. density-dependent

subpopulation growth and dispersal rates. However, to simplify the analysis we modelled a system consisting of two patches only. This simplification is justified by the fact that most of the movements in our experimental systems took place between the two closest subpopulations/patches ([figure 2a](#)).

The dynamics in the system consisting of the two patches/subpopulations i and j was modelled as

$$\begin{aligned} N_{t+1,i} &= \lambda(N_{t,i})N_{t,i} - \varphi(N_{t,i})N_{t,i} + \varphi(N_{t,j})N_{t,j} + \varepsilon_{t,i}, \\ N_{t+1,j} &= \lambda(N_{t,j})N_{t,j} - \varphi(N_{t,j})N_{t,j} + \varphi(N_{t,i})N_{t,i} + \varepsilon_{t,j}, \end{aligned} \quad (3.1)$$

where $\lambda(N_{t,i})$ is the density-dependent per capita growth rate owing to patch-specific survival and reproduction, $\varphi(N_{t,i})$ is the density-dependent dispersal rate (the proportion of animals dispersing from one patch to the other during a week) and $\varepsilon_{t,j}$ is a noise term owing to stochastic patch-specific sources of variability. A Gompertz-type model described the density-dependence in the weekly subpopulation growth:

$$\lambda(N_{t,i}) = \exp(0.43 - 0.30 \log[N_{t,i}]). \quad (3.2)$$

The parameters in this growth model were estimated from population time-series for which all individuals immigrating onto, or emigration from, subpopulations were excluded to highlight subpopulation dynamics without dispersal.

The density-dependent dispersal was estimated by the logistic function

$$\varphi(N_{t,i}) = \frac{\exp(-1.09 - 0.08N_{t,i})}{1 + \exp(-1.09 - 0.08N_{t,i})}. \quad (3.3)$$

The standard deviation of the residuals from (3.2) was used as an estimate of additive local white noise operating on each subpopulation ($e = \text{s.d.} = 0.75$). Thus, in the simulations, independent values for ε were drawn from a normal distribution with mean = 0 and s.d. = 0.75 and added to the weekly growth rate of each population. Each simulation was run for 100 time-steps and the degree of synchrony in population growth between the patches was quantified for the last 50 time-steps, employing the same cross-correlation coefficient used to estimate growth rate synchrony in our experimental data ([Buonaccorsi *et al.* 2001](#)). Mean \pm 95% confidence intervals for this coefficient were obtained from 1000 independent simulations. To contrast the synchronizing effect of negative density-dependent dispersal with that of constant dispersal, we also ran simulations assuming a constant dispersal rate. The constant rate was set to the average dispersal rate obtained in the density-dependent simulations ($\varphi = 0.18$).

Simulating the model with the observed negative density-dependent dispersal rate was not able to produce statistically significant synchrony (mean cross-correlation coefficient: 0.14 ± 0.15), even in a tightly coupled two-patch system. On the other hand, equivalent simulations with the same amount of constant (density-independent) dispersal yielded a significant synchronizing effect of dispersal (0.27 ± 0.13).

4. DISCUSSION

According to current theory (e.g. [Haydon & Steen 1997](#); [Lande *et al.* 1999](#)) the degree of synchrony in fragmented populations is determined by a tension between local

synchrony-disrupting factors, such as demographic stochasticity, and large-scale synchrony-inducing factors, such as dispersal and regional disturbances. Despite the fact that the dispersal rate was high in our experimental study, especially among the closest subpopulations, dispersal was not able to counteract the influence of the variance in local growth rates. Our model analysis showed that this was not because the average dispersal rate was not sufficiently high. Indeed, a constant dispersal rate of the same magnitude as the average of the density-dependent rate yielded significant population synchrony against the background of the observed local variance in subpopulation growth. Hence, it was the negative density-dependent nature of dispersal rather than its average magnitude that precluded its synchronizing effect. Also a recent purely theoretical analysis, using Richer-type local dynamics, many subpopulations and other dispersal functions, has hinted that the synchronizing power of dispersal is likely to be conditional on the specific dispersal rule implemented in models (Ylikarjula *et al.* 2000).

Emerging empirical evidence indicates that negative density-dependent dispersal is prevalent in voles (Andreassen & Ims 2001; Lin & Batzli 2001) and in several other taxa as well (Hanski 1999; Ims & Hjermann 2001). Negative density-dependent dispersal may be expected on different biologically justifiable grounds (Hanski 1999). For example, both scarcity of mates and inbreeding avoidance may result in enhanced dispersal at low population density. Moreover, reduced dispersal at high densities may result from suppressed sexual maturation in species such as voles where natal dispersal is induced at puberty (Clobert *et al.* 2004).

As noted above, cyclic vole and lemming populations are among the best-known cases of large-scale population synchrony. Recent analyses of large-scale survey data and some experimental results have indicated that mobile predators (Norrdahl & Korpimäki 1996; Ims & Andreassen 2000) or climate (Krebs *et al.* 2002; Sundell *et al.* 2003) are the main synchronizing factors. The relative unimportance of dispersal in this context has been inferred from two sources of information: (i) The extent of the synchrony domain is usually much larger than would be expected based on the assumed dispersal range of voles (Bjørnstad *et al.* 1999b; Sundell *et al.* 2003); (ii) Population synchrony has in some cases been found to be unaffected by dispersal barriers (Heikkilä *et al.* 1994; Aars *et al.* 1999). In this study, we have provided more direct evidence for the lacking effect of dispersal on population synchrony than any previous study. Moreover, based on our combined experimental and theoretical analyses, we can now explain why dispersal, at least under these circumstances, does not act to synchronize population dynamics by elucidating the role of negative density-dependence.

Our findings are so far restricted to dispersal during the breeding season and do not incorporate the multi-annual dynamics of cyclic vole populations. Indeed, dispersal rate and its density-dependence may depend on season and phases of the cycle, but it is not known whether such dependencies exist and what their effects could be on spatial population dynamics. Clearly, a new perspective in the study of role dispersal in population dynamics is warranted by including its dynamic interaction with

population density and other time-dependent processes (Andreassen & Ims 2001; Haydon *et al.* 2003).

5. CONCLUSION

Our results challenge the common generalization that dispersal is a parsimonious cause of population synchrony (e.g. Schwartz *et al.* 2002), and that the synchronizing power of dispersal only depends on its average rate and distance in combination with other synchronizing and de-synchronizing factors (Bjørnstad *et al.* 1999a; Koenig 1999). As shown in this study, whether dispersal is density-dependent also matters. Specifically, the synchronizing effect of dispersal in a metapopulation context becomes significantly diminished when dispersal is negatively density-dependent. Recent reviews have testified for the richness of conditional responses to both internal and external drivers of dispersal in animal and plant populations (e.g. Ims & Hjermann 2001; Clobert *et al.* 2004). Population biologists, therefore, need to take into account the fact that dispersal is a more dynamic and complex factor than they conventionally have assumed when posing applied and fundamental problems in spatial population dynamics.

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