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On the evolution of conditional dispersal under environmental and demographic stochasticity

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ABSTRACT

Questions: How will density-dependent and costly dispersal evolve in populations subject to local density regulation and environmental stochasticity? What type of density response will evolve, a strong threshold type response or a soft response gradually increasing dispersal?

Method: An individual-based model including density dependence, environmental fluctuations, and population variation was used to simulate evolution of dispersal behaviour.

Key assumptions and variables: Individuals can assess the instantaneous difference between habitat densities and base their dispersal behaviour thereon. However, future density and thus future quality of a chosen habitat patch remain uncertain due to behavioural variation and density fluctuations. Local density regulation was given by the Beverton-Holt map, affected by stochastic environmental forcing. An individual's dispersal decision is a sigmoid function of the density ratio between patch densities. The half-saturation point and steepness of the dispersal reaction norm were allowed to evolve.

Conclusions: Conditional dispersal evolves from a state of random behaviour, yet we do not observe threshold dispersal as the evolutionary endpoint (as found in previous models). Among a heterogeneous set of dispersal strategies, the most successful respond softly to density differences but require a large density advantage to trigger emigration. Although threshold dispersal might be evolutionarily stable, we propose that such an endpoint may not be attainable if the evolutionary trajectory becomes less affected by selection and more by drift. The variability in dispersal behaviour within populations leads to unpredictability in the potential benefit of dispersal and hence may select for conservative emigration criteria. Other evolving life-history traits, such as phenological traits, subject to density- and frequency-dependent effects may show similar evolutionary patterns.

Keywords: conditional dispersal, density dependence, environmental noise, evolutionary trajectory, individual-based, stochasticity.

INTRODUCTION

There are evolutionary advantages if individuals move occasionally to adjacent or distant habitats (Gadgil, 1971; van Valen, 1971). Temporal fluctuations in local conditions promote dispersal regardless of whether the causes are intrinsic (demographic stochasticity) or

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extrinsic (environmental stochasticity) (Comins *et al.*, 1980; Levin *et al.*, 1984; McPeek and Holt, 1992; Olivieri *et al.*, 1995; Cadet *et al.*, 2003). Similarly, avoidance of inbreeding depression (Bengtsson, 1978; Gandon, 1999; Perrin and Mazalov, 1999; Gandon and Michalakis, 2001; Perrin and Goudet, 2001; Guillaume and Perrin, 2006) and avoidance of kin competition (Hamilton and May, 1977; Taylor, 1988; Motro, 1991; Gandon and Michalakis, 1999; Bach *et al.*, 2006) have also been shown theoretically to promote dispersal. However, few models have considered conditional dispersal, while empirical results support the existence of such a behavioural plasticity (Albrectsen and Nachman, 2001; Ims and Hjermann, 2001). The limited number of models allowing for conditional dispersal can be explained by the many possibilities to represent individuals' responses to local conditions and with what degree of certainty individuals can access the appropriate information or proxies thereof (but see Ezoe and Iwasa, 1997; Travis *et al.*, 1999; Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002; Clobert *et al.*, 2004; Ronce *et al.*, 2005; Kun and Scheuring, 2006). Future studies could therefore provide suggestions about the specific mechanisms behind conditional behaviour – that is, the factors affecting dispersal and the sensitivity towards them.

The local conditions experienced by individuals provide an obvious starting point in the decision of whether to emigrate or not. If information about conditions in the potential destination habitat is accessible this should also be taken into account, as moving from bad to worse conditions could be fatal. In fact, the difference between the two habitats determines the potential advantage (or disadvantage) of relocating and, ideally, the gradient in local conditions should directly drive the propensity to disperse. Since local conditions are affected by the local density of individuals, it is not merely the density or the externally inflicted spatiotemporally fluctuations that influence the fitness consequences of emigration, but also the timing of decisions of conspecifics (or even heterospecifics).

Here we investigate if conditionality evolves from unconditional dispersal and how abruptly or gradually the evolved dispersal behaviour reacts to density. The frequent presumption that populations have settled at the evolutionary equilibrium implies that *all* individuals already behave accordingly. Here the dispersal function corresponds to the behavioural reaction norm and when allowed to evolve it can disclose the adaptive trajectories of conditionality while taking stochastic processes, individual variability, and cost into account. Previous models of conditional dispersal have often assumed simultaneous dispersal based exclusively on local density (Travis *et al.*, 1999; Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002; Kun and Scheuring, 2006). In contrast, we let dispersal be sequential and dependent on differences in patch density.

THE MODEL

Two locally density-regulated populations are linked by dispersal of individuals with different degrees of density dependence. The success of an individual's matching rule, which assesses the potential advantage of dispersal, depends on the net fitness gain of emigration. Through differential survival and proliferation in our individual-based model, the dispersal response to density gradients is allowed to evolve in the face of dispersal mortality and hence disclose the evolutionary dynamics of the reaction norm of dispersal.

The dispersal decision function

The sigmoid dispersal function P_1 maps the instantaneous density gradient onto the probability of emigration from patch 1:

$$P_1 = a + \frac{(1-2a)}{1+e^{(z^*(g-d))}}, \tag{1}$$

where $d = (N_1/K_1)/(N_2/K_2)$ is the ratio of focal density N_1/K_1 to the density in the destination patch N_2/K_2, with N_i and K_i being the population size and carrying capacity of patch i. z controls density-dependent sensitivity through the steepness of the sigmoid dispersal function (i.e. level of conditionality), and g determines the half-saturation point ($P = 0.5$) (see Fig. 1). Note that P_2 is defined analogously to P_1. Due to initial variation and variance introduced by reproductive recombination of the parameters z and g, individuals in the population express diverse dispersal reaction norms. The parameter a controls the upper and lower bounds (compare $a = 0$ and $a = 0.2$ in Fig. 1B). When $a = 0$, dispersal probability ranges from zero to unity and this is used throughout unless otherwise specified.

Individuals are initialized with behaviours corresponding to unconditional or very vague responses to an increasing density gradient between the patches. As previous studies suggested the existence of threshold dispersal (e.g. Crespi and Taylor, 1990; Metz and Gyllenberg, 2001), we also conducted simulations with fixed and strong conditionality – that is, high z-values corresponding to a threshold response, but with varying location of g.

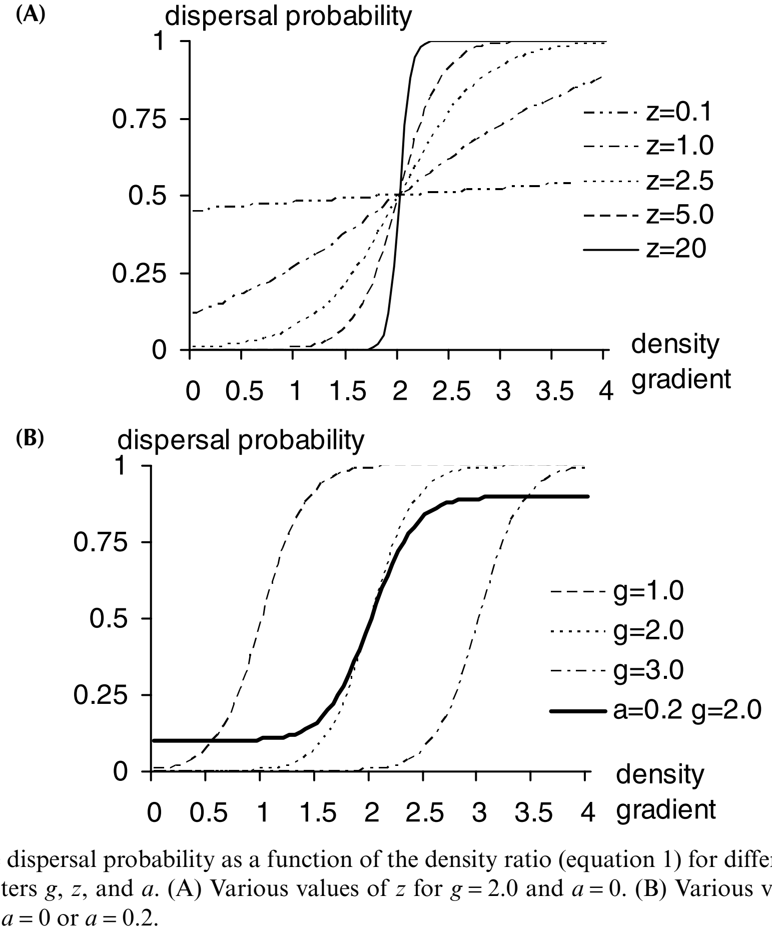

Fig. 1. The dispersal probability as a function of the density ratio (equation 1) for different values of the parameters g, z, and a. (A) Various values of z for $g = 2.0$ and $a = 0$. (B) Various values of g for $z = 5.0$ and $a = 0$ or $a = 0.2$.

Individuals disperse sequentially such that each individual is given a chance to move exactly once per generation. When an individual moves from one population to the other, the density gradient is updated instantaneously, which decouples the fast time scale of patch exploration and dispersal from that of population renewal. The stochastic decision process presumes that the individuals have non-complete information or, alternatively, behave somewhat imperfectly. Another interpretation is that a probabilistic behaviour has evolved, in the sense of 'adaptive coin flipping' (Cooper and Kaplan, 1982; Kaplan and Cooper, 1984), as a response to an unpredictable, stochastic environment.

Evolving dispersal parameters

The g and z parameters control the shape of the dispersal function and are held by individuals as decimal values (genotypes) and inherited to their offspring as a normally distributed value with the mid-parent average as the mean and standard deviation 0.05. This approximates the infinitesimal additive genetic model of inheritance and the variation is maintained through recombination of the parental genes (Lynch and Walsh, 1997). Negative values of z imply negative density dependence and therefore set to zero.

Population dynamics

As a basis for individual-based population renewal, we use the discrete Beverton-Holt map and, in addition to the individual-level demographic stochasticity, the dynamics is also affected by environmental noise through a population-wide, log-normally distributed random factor (Yodzis, 1989). This gives the expected population growth,

$$E(N_{t+1}|N_t, k_t) = \lambda N_t(1 + \alpha N_t)^{-1} \cdot e^{k_t}, \tag{2}$$

where $\alpha = (\lambda - 1)/K$, N_t is the local population size at time t, and λ is the growth rate. The individual fecundity is drawn from a Poisson distribution with mean $\lambda(1 + \alpha N_t)^{-1}$ and the environmental noise enters each time-step by k_t, which is drawn from a normal distribution with zero mean and variance v. The population cycle consists of dispersal and local growth, with post-dispersal densities entering equation (2).

RESULTS

Evolving conditionality and emigration threshold

As shown in Fig. 2, when parameters g and z were allowed to co-evolve dispersal evolved from almost unconditional to being conditional on the density difference. The steepness was initialized with mean $z_{\text{average}} = 1.0$ uniformly from [0.0–2.0], resulting in negligible density dependence. The g-values in the population were initialized to give $g_{\text{average}} = 1.0$ by drawing uniformly from [0.9–1.1] (see Fig. 1). For high z-values, $g_{\text{average}} = 1.0$ corresponds to sharply increased dispersal when $(N_1/K_1)/(N_2/K_2) > 1$; however, for small z, the reaction norm becomes flat and thus g becomes inconsequential for the dispersal behaviour.

Figure 2 shows the evolution of z_{average} and g_{average} based on 20,000 generations in a fluctuating environment with the dispersal cost corresponding to a mortality probability of either 0.0 or 0.33. The evolutionary trajectories of the parameters in Fig. 2A show that

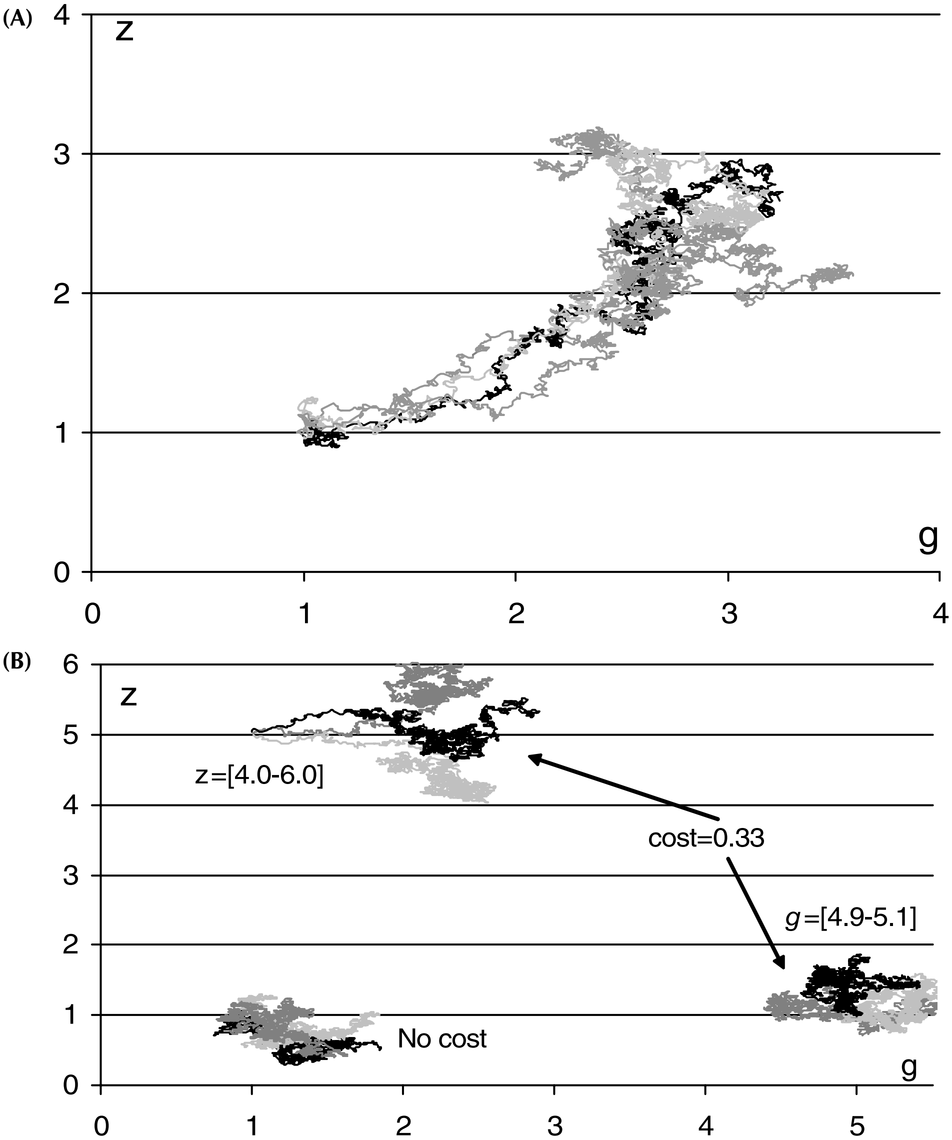

Fig. 2. Examples of evolutionary trajectories in the parameter space of the dispersal parameters, initially $g_{\text{average}} = 1.0$ uniformly from [0.9–1.1] and $z_{\text{average}} = 1.0$ uniformly from [0.0–2.0]. Population sizes are $K_1 = K_2 = 200$ and results are shown for 20,000 generations. Growth rate was $\lambda = 2$ and environmental noise $v = 0.3$. (A) Four realizations with dispersal mortality 0.33. (B) Three examples without any cost of dispersal and six examples with cost = 0.33, three initiated with ($g_{\text{average}} = 5$, [4.9–5.1]; $z_{\text{average}} = 1$, [4.0–6.0]) and three initiated with ($g_{\text{average}} = 1$, $z_{\text{average}} = 5$).

when dispersal is costly and initialized with ($g_{\text{average}} = 1$, $z_{\text{average}} = 1$), conditional dispersal behaviour takes over the initial population of nearly unconditional dispersers, although no threshold dispersal evolves as values increase no further than $z_{\text{average}} \approx 2.5$. However,

g evolves to $g_{\text{average}} \approx 3$, which corresponds to a right-shift of the onset of dispersal towards high-density gradients (Fig. 2A). After the population averages converge to ($g_{\text{average}} \approx 3$, $z_{\text{average}} \approx 2.5$), the trajectories tend to remain in this domain while resembling a random walk (see Fig. 2A). As seen in Fig. 2B, starting from the same initial conditions ($g_{\text{average}} = 1$, $z_{\text{average}} = 1$) as in Fig. 2A but without a dispersal cost, a random walk-like pattern emerges without prior evolution towards conditionality. With equal carrying capacity and no cost, unconditional dispersal with $P = 0.5$ on average in the initial population tends to equalize densities. Sustained equal densities will obviously tend to remove any incentive to evolve density dependence. However, obliterating this symmetry with costly dispersal (Fig. 2A and the cost = 0.33 scenarios in Fig. 2B) or by introducing unequal carrying capacities (not shown) suffice for conditionality to evolve.

When initializing either g or z with higher values, ($g_{\text{average}} = 5$, $z_{\text{average}} = 1$) or ($g_{\text{average}} = 1$, $z_{\text{average}} = 5$), there was no downward evolution from the higher parameter values (see Fig. 2B). This suggests that the region of convergence observed in Fig. 2A cannot be attributed to the selection gradient changing sign. The lack of downward evolution suggests that there is no convergence towards an evolutionarily stable strategy (ESS) but rather that selection gradually tapers off and hence drift begins to govern the evolutionary trajectory. If the evolutionary outcome in Fig. 2A (i.e. $g = 3$, $z = 2.5$) had been an ESS, then starting from higher values should show downward convergence to these values. Together with the lack of a further increase and random walk-like dynamics of z, this suggests that the fitness surface has levelled off (whether or not an underlying ESS exists for higher values of z).

With ($g_{\text{average}} = 5$, $z_{\text{average}} = 1$), only the left tail of the function will be relevant for emigration due to the high g-value and thus right-shifted position. It follows that for the emigrants the dispersal function will be relatively flat regardless of z. This causes different z- and g-values to be feebly distinguishable and thus prone to drift. With ($g_{\text{average}} = 1$, $z_{\text{average}} = 5$), the dispersal function is now steep and dispersal behaviour becomes highly sensitive to the location of the inflexion point (g) and hence subject to selection. Therefore, we observe some directional movement towards higher g-values as opposed to the random drift observed in the z-dimension.

By affecting the same phenotype, the two evolving parameters are not entirely independent and from Fig. 2A it appears that only after g increases somewhat above unity can selection become effective on z. There are also indications in Fig. 2A (and simulations not shown) that at the endpoints, higher g_{average} is associated consistently with lower z_{average} and vice versa (resembling a Pareto frontier). Finally, allowing dispersal to evolve within less extreme bounds by letting $a = 0.2$ did not alter the evolved reaction norms (results not shown) compared with those based on $a = 0$, which was therefore used throughout.

Evolving the position of the emigration threshold (fixed *z*)

To represent threshold emigration as found in previous models, we fixed $z = 20$. Two scenarios of environmental noise ($v = 0.0$ and $v = 0.3$) and two different growth rates ($\lambda = 2$ and $\lambda = 20$) were investigated with respect to the evolution of g_{average} in the threshold model. As anticipated, the emigration threshold increased as a function of cost since the individuals gained from remaining in their natal patch when costs became high relative to the density gradient (Fig. 3). A comparison of stable environments ($v = 0.0$) and fluctuating environments ($v = 0.3$) suggests that environmental fluctuation can select for higher g_{average}.

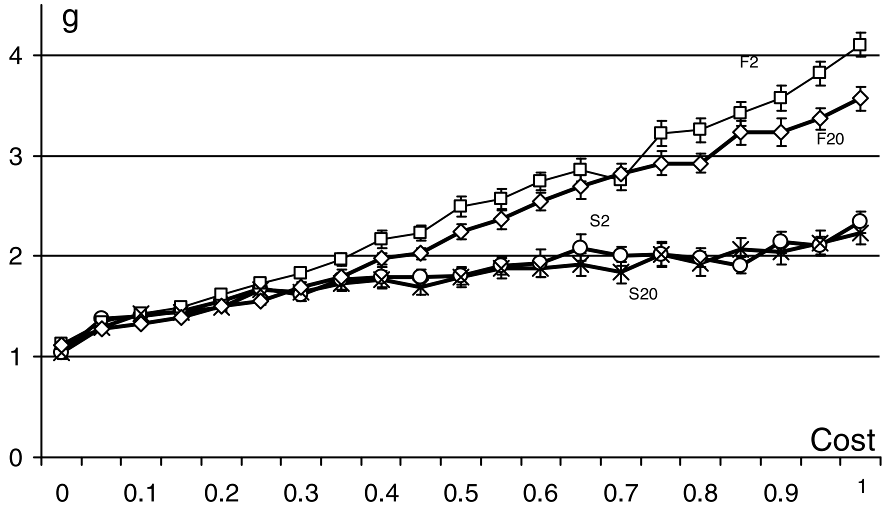

Fig. 3. Average evolved g-values for varying dispersal cost after 20,000 generations. Initially $g_{\text{average}} = 1$ drawn uniformly from [0.9–1.1] and $z = 20$ for all individuals. Population sizes were $K_1 = K_2 = 200$. For each scenario, the confidence intervals (95%) of 40 replications are shown. Four scenarios are shown: S2 is a stable environment with low growth ($v = 0.0$ and $\lambda = 2$); S20 is a stable environment with high growth ($v = 0.0$ and $\lambda = 20$); F2 is a fluctuating environment with low growth ($v = 0.3$ and $\lambda = 2$); and F20 is a fluctuating environment with high growth ($v = 0.3$ and $\lambda = 20$).

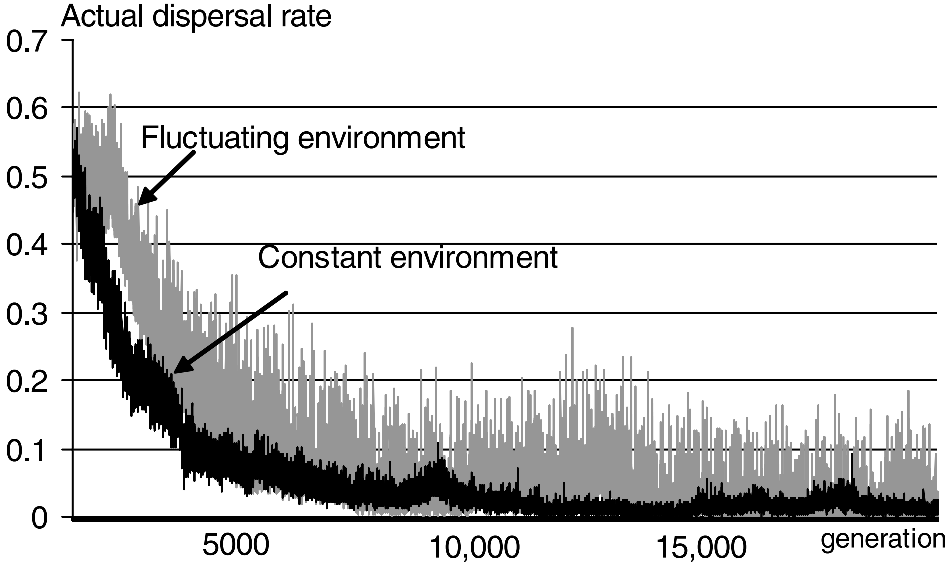

Fig. 4. The actual dispersal rates of two simulations depicted in Fig. 2A except one is without environmental noise.

However, as evident from Fig. 4 the *de facto* flow of individuals, or emergent dispersal, still remains substantially higher in the environmentally noisy scenario in spite of a markedly higher emigration threshold.

DISCUSSION

Co-evolution of the two parameters revealed evolutionary trajectories characterizing a change from almost no density dependence to moderate density dependence (Fig. 2A). The function evolves towards a reaction norm where dispersal increases only moderately with increasing density difference and where the position (*g*) is right-shifted. The evolution of conditional dispersal is not surprising *per se*, as it has been predicted previously under synchronized dispersal. This was shown for a linear relation between density and dispersal (Travis *et al.*, 1999) and non-linear relations (Poethke and Hovestadt, 2002; Kun and Scheuring, 2006), which assumed synchronous dispersal and a large number of patches (see also Metz and Gyllenberg, 2001).

The evolutionary trajectories in Fig. 2A show pronounced directionality in the region of low g_{average} and z_{average}, indicating a strong selection gradient. Subsequently, when parameters converge at ($g_{\text{average}} \approx 3$, $z_{\text{average}} \approx 2.5$), they begin to drift. Furthermore, as seen from Fig. 2B initializing as ($g_{\text{average}} = 5$, $z_{\text{average}} = 1$), random drift prevails from the very beginning. Similarly, ($g_{\text{average}} = 1$, $z_{\text{average}} = 5$) results in an increase in *g* but *z* moves randomly rather than showing directional selection to lower values. Hence the region of convergence ($g \approx 3$, $z \approx 2.5$), as seen in Fig. 2A, does not correspond to an ESS but rather to a weakening of the selection pressure. In spite of the fact that we fail to find the footprint of an ESS (i.e. no change of sign in the selection gradient), there may indeed still be an underlying ESS at high *z* corresponding to threshold dispersal as suggested by earlier models. Nevertheless, when the fitness landscape levels off, such an EES may be difficult for populations to attain and therefore perhaps less relevant.

Assuming an emigration threshold by conducting simulations with fixed *z* gives an idea about the location of such an emigration threshold. The extent of spatial heterogeneity in density-dependent reproduction is reflected in *g*, as elevated values imply larger differences in density before emigration is triggered. Under synchronous dispersal based on local density, Kun and Scheuring (2006) recently showed that wider density distributions can indeed result from higher costs. Heterogeneity in density may, however, still be characterized as a state where no individual can increase its fitness by emigrating given the concomitant cost. In other words, total fitness may be higher when remaining sedentary even if reproductive fitness is higher in the other patch because it would cost too much to move there.

In line with previous studies (Poethke and Hovestadt, 2002; Kun and Scheuring, 2006), Fig. 3 shows that as dispersal cost increased, the overall dispersal seemed to be limited by a higher emigration threshold, in terms of the density difference required. The scenario with environmental noise shows higher emigration thresholds compared with the zero-noise scenarios because selection on dispersal necessitates the frequent occurrence of the conditions that require emigration. The critical phenotypes have to be exposed to selection to change the underlying genotypes. Without environmental stochasticity, strong density gradients rarely occur, which in turn makes selection ineffective, in particular with respect to high emigration thresholds. With increasing cost the discrepancy between the two scenarios increases, as higher cost requires even stronger density gradients (i.e. wilder fluctuations) to warrant dispersal. In other words, drift becomes more likely to govern the evolutionary dynamics of a trait that is rarely tested in terms of its fitness consequences.

In spite of the elevated dispersal criterion (higher *g*) that evolves under noisy scenarios, the actual flow of individuals remains distinctly higher under environmental fluctuation (Fig. 4). This illustrates how the emigration criterion is fulfilled more frequently in a fluctuating environment (despite higher thresholds) than in stable environments. With fluctuations, selection is allowed to drive the evolution of emigration contrary to the environmentally stable scenarios where the emigration trait is less exposed to selection. In Fig. 3, this is manifested as higher evolved values of g for the fluctuating scenarios compared with the environmentally stable scenarios. Higher emergent dispersal rates under environmental noise is in line with results from unconditional models of dispersal indicating that increased temporal variability selects for higher dispersal rates due to minimization of temporal fitness variation and bet-hedging effects (Comins *et al.*, 1980; Levin *et al.*, 1984; McPeek and Holt, 1992; Olivieri *et al.*, 1995).

In simulations, individuals sequentially decide on emigration based on instantaneous conditions, which means that even if the focal individual apparently makes the (instantaneously) most optimal decision, it may be discounted by subsequent decisions of other individuals (except for the very last individual in a given iteration). As the variation among individuals in the emigration behaviour influences what constitutes the most optimal behaviour, the variation can itself affect the evolution of dispersal. The variation may undermine the individual's basis for forecasting the dispersal pattern in the population and hence the consequence of its emigration behaviour. In this model, the variation stems from two sources. First, unless z is extremely high the dispersal function is sigmoid with more or less heavy tails, which means that occasionally individuals emigrate either earlier or later relative to the average midpoint. Second, due to recombination there is a sustained residual of genetic variation, which generates variation around the average dispersal behaviour of the population. The risk of the subsequent demographic density cost eventually could select for a more sedentary strategy making sure that there is a margin in the density gradient mitigating the effects of variability. Future research should attempt to show if the bias towards risk aversion is generic in the sense that other life-history related reaction norms, which imply a cost, evolve in a similar manner. Models of frequency- and density-dependent behaviour may additionally help us to understand if the sequential and synchronous decision processes have different evolutionary dynamics and are affected differently by individual-level variation.

Few studies have addressed what takes place during the process of evolution to the state of convergence (or equilibrium), something which normally lies beyond the explanatory scope of evolutionary equilibrium state theories. Although threshold dispersal can be shown to be an ESS, it need not be reachable in very flat fitness landscapes where drift begins to prevail as the principal evolutionary agent. Consequently, we suggest a combination of ESS analyses and investigations allowing for other aspects of the evolutionary dynamics such as drift.

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