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Reply

Models of Dispersal Evolution Highlight Several Important Issues in Evolutionary and Ecological Modeling

(A Reply to Poethke et al.)

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abstract: Previous results showing that lack of information on local population density leads to higher emigration probabilities in unpredictable environments but to lower emigration probabilities in constant or highly predictable scenarios have recently been challenged by Poethke et al. By reimplementing both our model and that of Poethke and colleagues, we demonstrate that our original results indeed hold to the presented critiques and do not contradict previous findings. The comment by Poethke and colleagues does, however, present potentially intriguing results suggesting that negative density-dependent dispersal evolves under white noise for some model formulations. Here, through intermodel comparison, we seek to better understand the source of the differences in results obtained in our study and theirs. We conclude that the apparent negative density dependence reported by Poethke et al. is effectively density independence and that the shape of the reaction norm they obtain is a model artefact. Further, this response provides an opportunity to elaborate on some important issues in evolutionary and ecological modeling regarding (i) the importance of carefully considering different models' assumptions in comparisons among models, (ii) the need to consider the role of stochasticity and uncertainty when presenting and interpreting results from stochastic individual-based models, (iii) the adequate choice of the underlying ecological model that creates the selective pressures determining the evolution of behavioral reaction norms, and (iv) the appropriate choice of mutation models.

Keywords: informed dispersal, reaction norm evolution, intermodel comparison, mutation model.

Introduction

Poethke et al. (2016) recently commented on our article (Bocedi et al. 2012) investigating the role of information acquisition and information uncertainty in the evolution of density-dependent emigration. In their comment, Poethke and colleagues argue that there is a risk that all our results are obscured by important "deficits" in our choice of methods, and, in particular, they challenge our finding that, in some cases, lack of information leads to lower emigration probabilities compared to when some information about population density is available to individuals. The authors present new results that they attest falsify those we presented, showing that full knowledge on population density leads to emigration probabilities that are comparable to or lower than noninformed emigration probabilities. They argue that these differences are due to "(i) a misleading use of the term 'population density,' (ii) a misconception concerning the true informative value of different decision criteria used, and (iii) arbitrary constraints imposed on the evolution of the dispersal function" (Poethke et al. 2016, p. 136). These represent quite major challenges to both the conceptual and the technical robustness of our work. We welcome the opportunity to provide some clarity and hope that our response will inform a debate on appropriate model design and especially on best practice in comparisons among models; this is a debate that has relevance for theory development well beyond the topic of dispersal evolution.

First, we want to emphasize that we believe part of the disagreement results from Poethke et al. (2016) misinterpreting our results. From the abstract of our study (Bocedi et al. 2012), we read, "Lack of information led to higher emigration probabilities in more unpredictable environments but to lower emigration probabilities in constant or highly predictable scenarios" (p. 606). Hence, as also shown in that article's figure 3, in more unpredictable environments or white noise (i.e., when fluctuations in habitat quality are temporally uncorrelated), we found that noninformed individuals have higher emigration probabilities and not lower, as claimed by Poethke et al. (2016). These results are in agreement with previous studies that considered only white noise (Enfjäll and Leimar 2009;

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Poethke et al. 2011). In contrast, when fluctuations in the environment are positively correlated (i.e., red noise) or when the environment is stable, we found that noninformed individuals evolve lower emigration probabilities than informed ones, which is also in agreement with previous studies that considered these scenarios (Schjørring 2002; Armsworth 2009).

Second, we wish to defend the way in which we use the term "population density." We do not believe our usage to be incorrect or misleading. Strictly speaking, population density is defined as the number of individuals per unit area. This is clearly different from population size, which is simply the number of individuals N in a population, unless the area is held constant. However, the ecological significance of area for a species might not coincide with the simple spatial meaning. In fact, the number of individuals that can stably coexist in a given area will depend on the amount of resources present in that area. Space may sometimes be the single limiting resource, but there are typically other factors, such as food or mates, for example. In our study, we considered fluctuation in habitat quality (K); it therefore makes ecological sense to consider individuals responding to population density, where the "area" is not just space but resources and, hence, is varying with habitat quality. A small or large N will typically not mean much to the individual if N is not in relation to how many individuals a given area can support (K). Furthermore, we find it rather confusing that Poethke et al. (2016) refer to N both as population size and population density interchangeably. However, we do agree that under a white noise environment, as opposed to a more predictable environment (red noise), current N/K holds very little information on the fitness of individuals in the next generation, a point we had already amply discussed in Bocedi et al. (2012). In this case, N has somewhat more informative value because even if K changes unpredictably, given the type of population dynamics implemented, N will respond more gradually to these changes. However, as Poethke et al. showed and we confirm below, under white noise, the correlation between N and next-generation fitness is still rather low, making informed dispersal decisions basically equivalent to noninformed ones.

Third, we here demonstrate that our results hold and argue that there are no misconceptions in our original study. Poethke et al. challenge our finding by "replicating" our model. "Replicate" is an interesting choice of word given that the authors changed almost every component and parameter of our original model (table A1, available online). It is therefore not possible, from their model, to judge from where the differences in results stem. To shed light on this issue, we have replicated exactly the model by Poethke et al. (2016), as far as it is possible from the presented description, and compared it with our original model (Bocedi et al. 2012). We show that both models in fact confirm the key qualitative results that we previously presented.

Beyond the specific results, this debate give us the opportunity to comment on some important issues in evolutionary, as well as in ecological, modeling. These are (i) the importance of carefully considering models' assumptions when evaluating their results and especially in comparisons among models, (ii) the need to consider the role of stochasticity and uncertainty when presenting and interpreting results from stochastic individual-based models, (iii) the adequate choice of the underlying ecological model that creates the selective pressures determining the evolution of behavioral reaction norms, and (iv) the appropriate choice of the mutation model.

Model Reimplementation or a New Different Model?

We reimplemented both models exactly as described in Bocedi et al. (2012) and Poethke et al. (2016) and repeated all the simulation scenarios performed by Poethke et al. (2016). As in our model, there is no equivalent of Poethke and colleagues' N_{ran} for the individual's estimate of population size; for our model, we substitute that scenario with low information precision, where population density is estimated by sampling from a negative binomial distribution with mean equal to the real population size and dispersion factor $\lambda = 1$. However, it should be noted that these two estimates are not the same. While the latter contains some information, the first (N_{ran}) is equivalent to no information. For both models, we used the same initialization distributions and the same distributions of mutational effects (but not the same rates) used by Poethke et al. (table A1). We ran both models on a grid of 20×20 cells. Otherwise, all the model components and parameters are equivalent to their respective original versions (table A1). Simulations were replicated either 20 or 40 times.

The type of information had no significant effect on the evolved mean emigration probability when modeled with either our model or our reimplementation of Poethke et al.'s model (fig. 1). This is in agreement with our previous finding (cf. fig. 3*D* in Bocedi et al. 2012), and it is explained by the fact that under white noise, estimates of current population density or size have little value as they poorly correlate with the next year's population density or size. This result was also previously corroborated by the finding that individuals invest much fewer resources in acquiring information under white noise than stable or red noise environments (fig. 4 in Bocedi et al. 2012). In our model, individuals evolved much lower emigration probabilities compared to those evolved in our reimplementation of Poethke et al.'s model. This is likely due to the difference in environmental stochasticity and population dynamics between the two models (table A1). Poethke et al. (2016) modeled a much

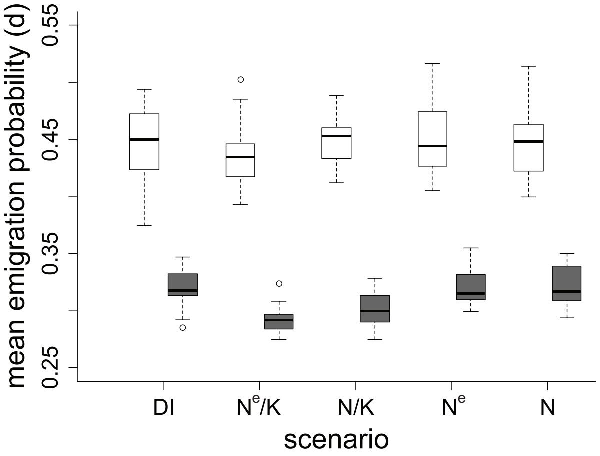

Figure 1: Effect of the type of information used on the evolution of emigration probabilities: comparison between results obtained by reimplementing exactly Poethke et al.'s (2016) and Bocedi et al.'s (2012) models (white and gray boxes, respectively). The value N^e corresponds to N_{ran} in the case of Poethke et al.'s (2016) model and to a value sampled from a negative binomial distribution with mean equal to N and $\lambda = 1$ in the case of Bocedi et al.'s (2012) model. Mean individual emigration probabilities (d) at generation 7,000 are presented as medians (solid bands), first and third quartiles (box limits), and approximately twice the standard deviation (whiskers) over 20 replicate simulations.

more variable environment than ours, with higher variance in K (fig. 2*A*); hence, it is to be expected that higher emigration probabilities evolve (Travis 2001; Poethke and Hovestadt 2002; Kun and Scheuring 2006; Bach et al. 2007). Notably, the combination of different models for environmental stochasticity and population dynamics led our model to have both higher mean and higher variance in population size (fig. 2*B*) compared to the distribution of N obtained from Poethke et al.'s model. As we will show below, this is very important for the evolution of emigration probabilities and especially reaction norms to density, as it changes the range of densities in which the trait (emigration probability) is under stronger selection (figs. 3, 4).

The mean emigration probabilities obtained with our reimplementation of Poethke et al.'s model (fig. 1) are higher than those reported by the authors (fig. 1), and we did not find the same differences among different types of information. We do not have an explanation for this discrepancy. However, the emigration probabilities given by the reaction norms reported in Poethke et al. (2016; fig. 2) at realized population densities are much higher than those reported by the authors (fig. 1) and are closer to our results.

Poethke et al. showed that negative density-dependent emigration probability evolves when individuals base their decision on N_{ran}/K or on N/K (fig. 2*A* in Poethke et al. 2016). We argue that what they show is not the evolution of negative density dependence but rather the evolution of density-independent emigration. By replicating their model, what apparently evolves is a range of reaction norms from positive to negative density dependence (fig. 3*A*, 3*B*). In fact, due to the distribution of population density values (fig. 3*A*, 3*B*, histograms), the range of densities experienced by individuals is very limited; hence, selection effectively acts over this very narrow range of densities. This causes all the curves to converge around the median population density and evolve the same value as density-independent emigration. The shape the curve assumed over the rest of the density space is then largely irrelevant, as selection is weak or absent and, thus, the overall shape of the curve is highly variable.

In contrast, in our model, individuals experience a much broader range of population densities, extending the region in which emigration probability is effectively under selection (fig. 4*A*, 4*B*). In this situation, a reaction norm evolves that is clearly positively density dependent. Note, however, that because of the low value of information in the white noise environment, the realized average emigration probability evolves to be the same as for the density-independent emigration probability (cf. fig. 1). The same pattern results when individuals base their dispersal decision on population size instead of density (figs. 3*C*, 3*D*, 4*C*, 4*D*). From both models, what evolves in this case is a density-independent emigration probability.

Poethke et al. argue that a negative density-dependent emigration probability should, in fact, be expected to evolve. The verbal argument they make is that, on average, under white noise, present competition (N_t/K_t) should be expected to be negatively correlated with the competition experienced by the next generation. We tested for this in both models, finding no evidence for a negative correlation between N_t/K_t and N_{t+1}/K_{t+1}. Rather, the correlation was

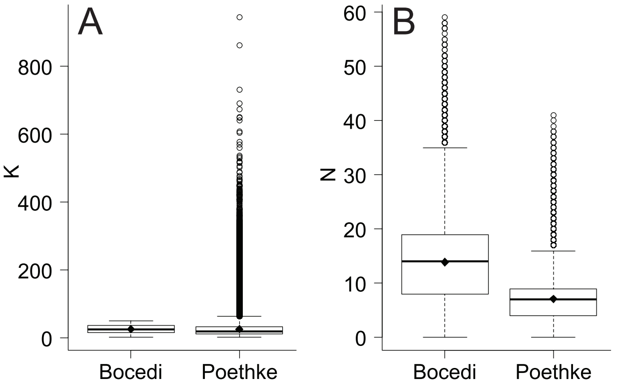

Figure 2: Distribution of carrying capacities (*A*) and population sizes (*B*) emerging from the two models, Bocedi et al. (2012) and Poethke et al. (2016). Data are plotted as medians (solid bands), first and third quartiles (box limits), approximately twice the standard deviation (whiskers), outliers (dots), and means (diamonds) over the last 100 generations over 20 replicate simulations.

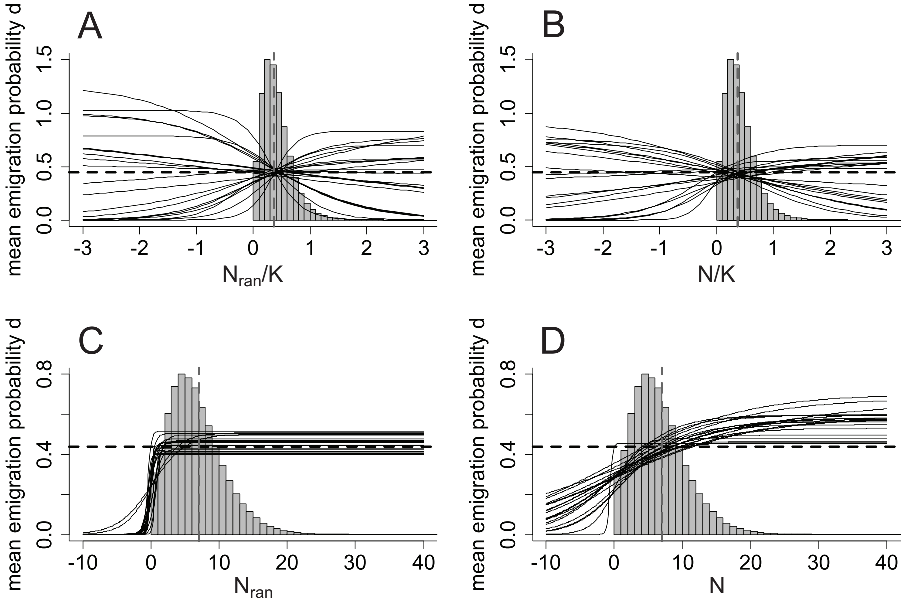

Figure 3: Effect of the type of information used on the evolution of the emigration reaction norm to population density (or size) modeled with the reimplemented Poethke et al. (2016) model. *A*, Individuals randomly guess the population size (N_{ran}) and base their dispersal decision on estimated population density (N_{ran}/K). *B*, Individuals have full knowledge of the population density (N/K). *C*, Individuals base their dispersal decision on a random guess of population size (N_{ran}). *D*, Individuals base their dispersal decision on the true population size (N). Each solid line represents the mean reaction norm evolved in a single replicate (out of 20) at generation 7,000. The black dashed line indicates the evolved mean density-independent emigration probability. Histograms show the distribution of population densities (*A*, *B*) or sizes (*C*, *D*) over the last 100 generations over the 20 replicate simulations, while the gray dashed lines indicate the medians of those distributions.

consistently not significantly different from zero (correlation averaged across patches and replicates -0.003 ± 0.018 SD with Poethke et al.'s model and 0.013 ± 0.099 SD with our model; both mean correlations have been calculated for the scenario with constant noninformed dispersal).

Poethke et al.'s (2016) main critique of our method and, thus, our results was that we restricted the parameters' evolution in a way that allows only positive density-dependence emigration to evolve and that our mutation rule biases parameter values toward the center of the predefined range. Indeed, this is a fair critique, and we realize that the distribution of mutational effects we chose was not ideal as it constrained the range of values parameters could assume. Despite this restrictive assumption, the reimplementation of our model with Poethke and colleagues' mutational effects (fig. 4) shows that our previous results are robust and that what evolves is still a positive density dependence. Note that the differences in emigration probabilities that we originally found between the noninformed strategy and strategy based on low-precision information are smaller when we remove previous evolutionary constraints (cf. fig. 3*D* in Bocedi et al. 2012 and this reply's fig. 1, gray boxes), confirming that, under white noise, what evolves is essentially a noninformed strategy. Poethke et al. further argue that our relatively high mutation rate (0.001), together with relatively low selection pressure on each of the parameters, explains the evolution of a positive density-dependent emigration probability instead of the expected negative density dependence. We show that our results are robust to these assumptions (fig. A1, available online) and that what evolves is consistently a positive density-dependent emigration probability.

Finally, we try to better understand from where the differences in results between the two models stem. We progressively change our model by changing different components into ones implemented by Poethke et al. Hence, we try to break our model (Thiele and Grimm 2015) to the point that it matches Poethke and colleagues' results. On top of having already implemented the authors' initialization rules and distribution of mutational effects, we implement our model with Poethke et al.'s submodels for (*a*) environmental stochasticity (fig. 5*A*); (*b*) population dynamics (fig. 5*B*; although it should be noted that with the current parameterization, the two population dynamics differ only in the value of growth rate); (*c*) both environmental stochasticity and population dynamics (fig. 5*C*); and (*d*) environmental stochasticity, population dynamics, and mutation rate (fig. 5*D*). We restrict the comparison to the case where individuals have full knowledge of the population density, as our N^e/K and Poethke and colleagues' N_{ran}/K are not directly comparable.

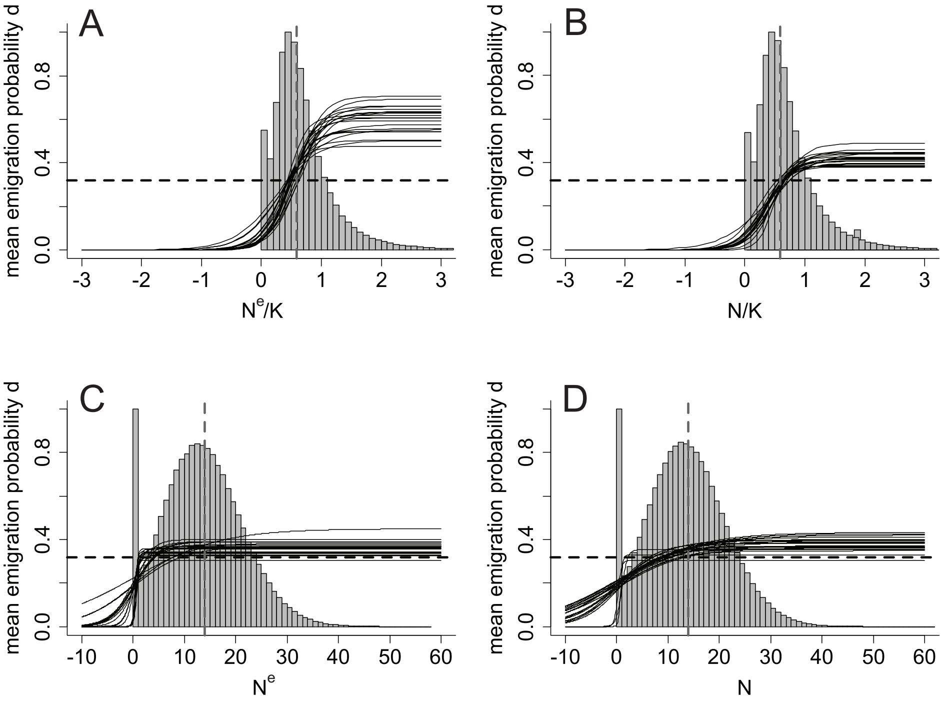

Figure 4: Effect of the type of information used on the evolution of the emigration reaction norm to population density (or size) modeled with the reimplemented Bocedi et al. (2012) model (which uses the same distribution of mutational effects as Poethke et al. 2016). *A*, Individuals estimate the population size (N^e) by sampling from a negative binomial distribution with mean N and $\lambda = 1$, and base their dispersal decision on estimated population density (N^e/K). *B*, Individuals have full knowledge of the population density (N/K). *C*, Individuals base their dispersal decision on the estimate N^e of population size. *D*, Individuals base their dispersal decision on the true population size (N). As in figure 3, each solid line represents the mean reaction norm evolved in a single replicate (out of 20) at generation 7,000. The black dashed line indicates the evolved mean density-independent emigration probability. Histograms show the distribution of population densities (*A*, *B*) or sizes (*C*, *D*) over the last 100 generations over the 20 replicate simulations, while the gray dashed lines indicate the medians of those distributions.

Implementing the different environmental stochasticity submodel in our model led to only 2 out of 40 replicates resulting in negative density-dependent reaction norms (fig. 5*A*), while a consistent positive density dependence was found when changing only the population dynamics submodel (fig. 5*B*). By changing both the environmental stochasticity and the population dynamics submodels at the same time (fig. 5*C*), we obtained a mix of replicates evolving either a negative or positive density-dependent reaction norm. A similar mix of negative and positive density-dependent reaction norms was obtained when we additionally introduced Poethke et al.'s submodel for the mutation rate (fig. 5*D*). We reiterate, however, that calling what evolves here a reaction norm is misleading, as in the range of densities experienced by individuals, emigration is effectively density independent.

Discussion

We have shown that the results presented in Bocedi et al. (2012) withstand the critique recently presented by Poethke et al. (2016), and therefore, there are no reasons to doubt the validity of that study based on these arguments. What was described as a "misleading use" of the term population density, misconceptions concerning the "true informative value of different decision criteria," and "arbitrary constraints" imposed on the evolution of dispersal function do not affect our original results. Under temporally uncorrelated environmental fluctuation (white noise), information about either population density or size has low value as the environment is completely unpredictable. Therefore, noninformed and informed individuals evolve to have the same emigration probability at the more frequently realized population densities (or sizes). Furthermore, when emigration probability is allowed to evolve as a response to population density (or size), individuals evolve a positive density-dependent response.

We agree with Poethke et al. on the point that the evolution of an emigration reaction norm depends on the specific type of information individuals may use. A very interesting question is, on what type(s) of information should individuals base their dispersal decisions, for example,

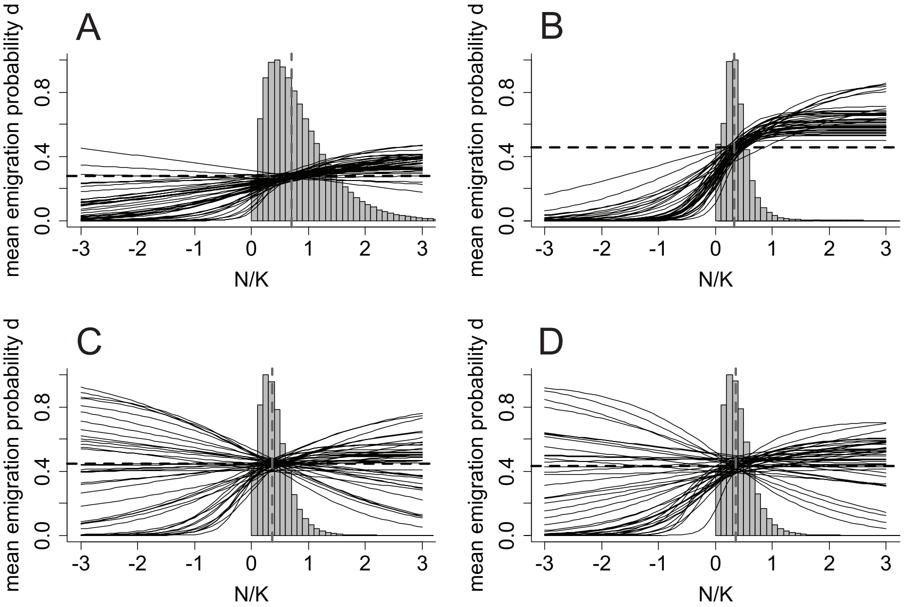

Figure 5: Breaking Bocedi et al.'s (2012) model by implementation of Poethke et al.'s (2016) model features. *A–D*, Mean emigration probability evolved when individuals had full knowledge of the population density (N/K). *A*, Bocedi et al.'s (2012) model with changed submodel for environmental stochasticity. *B*, Bocedi et al.'s (2012) model with changed submodel for population dynamics. *C*, Bocedi et al.'s (2012) model with changed submodels for environmental stochasticity and population dynamics. *D*, As *C*, with the further change of the mutation rate submodel. For all submodel specifications, see table A1. Each solid line represents the mean reaction norm evolved in a single replicate (out of 40) at generation 7,000. For lines and color legend, see figures 3, 4.

population size, density, habitat quality, internal status, or sex ratio? Dispersal decisions are likely to be influenced by a suite of interacting internal and external, abiotic and biotic factors and sources of information, and we are still far from understanding this complexity (Clobert et al. 2009). However, despite the interest and breadth of this question, this was not the objective of our original study, which was, rather, investigating, given one source of information (N/K), the role of information precision and environmental stochasticity on the evolution of emigration probability depending on that particular information. Here, we further demonstrated that not only do our results under white noise hold when using N/K but also when using N as a source of information.

Important Messages for Evolutionary and Ecological Modeling

This debate gives us the opportunity to illustrate and comment on some general issues in evolutionary and ecological modeling. First, it is important to bear in mind that a model is its assumptions, and changing these assumptions means building a new model that may or may not give the same results as the original one. To replicate a model means to reimplement, independently, exactly the same model (Thiele and Grimm 2015). Changing several assumptions at the same time makes it very difficult to nail down what causes eventual differences in results and can lead to misinterpretation, as we show in this case. While the differences between the two models may not seem to be major ones, they create important differences in the selective environment, which lead to the major differences in model outcomes. Replicating and breaking models is indeed a healthy and yet underused practice in ecological and evolutionary modeling (Thiele and Grimm 2015). However, the breaking of a model has to be done systematically to avoid spurious results.

Evolution of dispersal, in common with many other evolutionary questions, has traditionally been investigated with analytical models. It is only recently that evolutionary modeling has started to use a stochastic individual-based approach, and indeed, Poethke and his collaborators have been some of the first to apply this promising approach to the evolution of dispersal (e.g., Poethke and Hovestadt 2002; Poethke et al. 2003, 2007, 2010). In this transition, it is crucial to consider a fundamental difference: individual-based models have often multiple sources of stochasticity, and the results will rarely be deterministic. Thus, to be meaningful, results from an individual-based model must be accompanied by a representation or estimate of the uncertainty around them (Grimm and Railsback 2005). The number of replicates run by Poethke et al. (2016) was not reported;

hence, we could not evaluate the robustness of their results directly from their comment. However, from our reimplementation, we were able to obtain their result of an apparent negative density-dependent emigration probability only in some of the replicates. Furthermore, to obtain those same results with our model, we had to change the submodels for both environmental stochasticity and population dynamics. This example brings us to two more observations.

When modeling the evolution of a trait, and in particular the evolution of a behavioral reaction norm, we need to pay attention to the conditions under which selection is acting on the trait. In the case of Poethke et al.'s (2016) model, because of the particular ecological model implemented, selection on dispersal is acting in a very restricted region of population densities. Hence, the implemented dispersal function will be under strong selection for the values it assumes in that specific region; beyond that, region selection is very weak because individuals very rarely or never experience those densities, making the particular shape of the function irrelevant. In contrast, in our model, which implemented a different ecological submodel, the range of population densities individuals experience is much broader, resulting in a broader portion of the dispersal function being under selection. In this case, evolving the right shape reaction norm is more important for individuals as they are likely to experience a range of conditions, and as we show, what evolves is always positive density dependence. Nevertheless, because of the already mentioned low value of information under white noise, on average, informed individuals emigrate with the same probability as noninformed individuals. A more general question is, therefore, what the appropriate underlying ecological model should be when the objective is investigating the evolution of specific behavioral reaction norms. As reaction norms describe phenotypic responses across a range of environments, in this case, across a range of population densities or sizes, an appropriate underlying ecological model should allow individuals to experience a range of values of the independent variable (i.e., selection should be created across the range of interest) to allow the evolution of a response function rather than a point response. Of course, both methods tell us something, but we should be careful not to extrapolate the results outside the range in which selection operates.

A further observation is about the choice of model for the mutation rate. Poethke et al. use a mutation probability that decays exponentially through time (see also Poethke and Hovestadt 2002; Poethke et al. 2003, 2007, 2010). Particularly, in Poethke et al. (2016), mutation probability decreases from 0.01, in the first generation, to 4.5×10^{-7} at generation 5,000. The rationale behind this approach is "to allow for broad initial genetic variation but selective fine-tuning of decision rules later in the simulations" (Poethke et al. 2016, p. 138). This method is directly derived from the method of optimization by simulated annealing, an approach developed for optimization problems derived from techniques of statistical mechanics (Kirkpatrick et al. 1983). This raises the question of whether evolutionary models are optimization problems and, hence, whether this technique can or should be applied. Looking at the problem from a biological point of view, it seems hard to justify a decaying mutation rate. We are not aware of any examples beyond the above-cited articles of any other evolutionary model that has applied this method (for examples of other evolutionary models that apply a constant mutation rate, cf. Reeve 2000; Jones et al. 2003; Guillaume and Whitlock 2007; Guillaume and Perrin 2009; Hovestadt et al. 2010; Kubisch et al. 2010, 2013; Roff 2010), nor are we aware of any evidence for the existence of a decaying mutation rate in nature. We realize that Poethke et al.'s mutation model is not meant to be genetically realistic and that it is simply a way to get the system to equilibrium. However, we can see a potential problem with it: if the system has not reached equilibrium by the time the mutation rate has decreased to very low values, it can become stuck in a state that is not equilibrium as a consequence of stochastic events that happened in the first part of the simulation. While in this particular case, the choice of mutation model does not result in major differences (cf. figs. 5*C* and 5*D*), we would urge caution in using optimization approaches such as simulated annealing, especially now that computational time is rarely a major limiting factor.

Another question is, what is an appropriate mutation rate? The rate 10^{-3} has been largely used in evolutionary modeling because it is close to what has been empirically estimated for mutational variance (Lynch 1988; Houle et al. 1996; Reeve 2000). Of course, this does not mean that it is the right one to use, and the choice will depend on what we are actually modeling. In this case, we are not modeling explicit alleles but the phenotypic effect of probably many loci, adopting what can be considered a continuum-of-allele model (Kimura 1965; Lande 1976). Hence, a mutation probability of 10^{-3} does not seem particularly high. Generally, mutation rates are applied somewhat arbitrarily in a lot of evolutionary models, partly because information from empirical systems remains very scarce (although see recent progress in Lang and Murray 2008; Zhu et al. 2014; Levy et al. 2015). This calls for a more careful choice of mutation rate and for the need to test the sensitivity of any specific model to it.

In summary, this debate has given us the opportunity to confirm previous results that under temporally uncorrelated environmental variations, information on local density has low value for individual dispersal decisions, and on average, the emigration probabilities that evolve in the presence or absence of information are the same. What type of information individuals are expected to base their dispersal decision on and how different sources of information are integrated remain open questions. Importantly, we have highlighted several issues that require careful consideration when modeling the evolution of reaction norms. Not considering the properties of the underlying ecological model that creates the selective pressure on the evolving trait(s) and the stochasticity inherent to stochastic individual-based models, or comparing models without considering how they differ in their assumptions, can be misleading when interpreting models' results.

Literature Cited

Armsworth, P. R. 2009. Conditional dispersal, clines, and the evolution of dispersiveness. Theoretical Ecology 2:105–117.

Bach, L., J. Ripa, and P. Lundberg. 2007. On the evolution of conditional dispersal under environmental and demographic stochasticity. Evolutionary Ecology Research 9:663–673.

Bocedi, G., J. Heinonen, and J. M. J. Travis. 2012. Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. American Naturalist 179:606–620.

Clobert, J., J.-F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Enfjäll, K., and O. Leimar. 2009. The evolution of dispersal: the importance of information about population density and habitat characteristics. Oikos 118:291–299.

Grimm, V., and S. F. Railsback. 2005. Individual-based modeling and ecology. Princeton University Press, Princeton, NJ.

Guillaume, F., and N. Perrin. 2009. Inbreeding load, bet hedging, and the evolution of sex-biased dispersal. American Naturalist 173:536–541.

Guillaume, F., and M. C. Whitlock. 2007. Effects of migration on the genetic covariance matrix. Evolution 61:2398–2409.

Hassell, M., and H. Comins. 1976. Discrete time models for two-species competition. Theoretical Population Biology 9:202–221.

Houle, D., B. Morikawa, and M. Lynch. 1996. Comparing mutational variabilities. Genetics 143:1467–1483.

Hovestadt, T., A. Kubisch, and H.-J. Poethke. 2010. Information processing in models for density-dependent emigration: a comparison. Ecological Modelling 221:405–410.

Jones, A. G., S. J. Arnold, and R. Bürger. 2003. Stability of the **G**-matrix in a population experiencing pleiotropic mutation, stabilizing selection, and genetic drift. Evolution 57:1747–1760.

Kimura, M. 1965. A stochastic model concerning the maintenance of genetic variability in quantitative characters. Proceedings of the National Academy of Sciences of the USA 54:731–736.

Kirkpatrick, S., C. D. Gelatt, and M. P. Vecchi. 1983. Optimization by simulated annealing. Science 220:671–680.

Kubisch, A., E. A. Fronhofer, H. J. Poethke, and T. Hovestadt. 2013. Kin competition as a major driving force for invasions. American Naturalist 181:700–706.

Kubisch, A., T. Hovestadt, and H.-J. Poethke. 2010. On the elasticity of range limits during periods of expansion. Ecology 91:3094–3099.

Kun, A., and I. Scheuring. 2006. The evolution of density-dependent dispersal in a noisy spatial population model. Oikos 115:308–320.

Lande, R. 1976. The maintenance of genetic variability by mutation in a polygenic character with linked loci. Genetical Research 26:221–235.

Lang, G. I., and A. W. Murray. 2008. Estimating the per-base-pair mutation rate in the yeast *Saccharomyces cerevisiae*. Genetics 178:67–82.

Levy, S. F., J. R. Blundell, S. Venkataram, D. A. Petrov, D. S. Fisher, and G. Sherlock. 2015. Quantitative evolutionary dynamics using high-resolution lineage tracking. Nature 519:181–186.

Lynch, M. 1988. The rate of polygenic mutation. Genetical Research 51:137–148.

Poethke, H. J., A. Gros, and T. Hovestadt. 2011. The ability of individuals to assess population density influences the evolution of emigration propensity and dispersal distance. Journal of Theoretical Biology 282:93–99.

Poethke, H. J., and T. Hovestadt. 2002. Evolution of density- and patch-size-dependent dispersal rates. Proceedings of the Royal Society B: Biological Sciences 269:637–645.

Poethke, H. J., T. Hovestadt, and O. Mitesser. 2003. Local extinction and the evolution of dispersal rates: causes and correlations. American Naturalist 161:631–640.

Poethke, H. J., A. Kubisch, O. Mitesser, and T. Hovestadt. 2016. The adequate use of limited information in dispersal decisions. American Naturalist 187:136–142.

Poethke, H. J., B. Pfenning, and T. Hovestadt. 2007. The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. Evolutionary Ecology Research 9:41–50.

Poethke, H. J., W. W. Weisser, and T. Hovestadt. 2010. Predator-induced dispersal and the evolution of conditional dispersal in correlated environments. American Naturalist 175:577–586.

Reeve, J. P. 2000. Predicting long-term response to selection. Genetical Research 75:83–94.

Roff, D. A. 2010. Modeling evolution. Oxford University Press, Oxford.

Ruokolainen, L., A. Lindén, V. Kaitala, and M. S. Fowler. 2009. Ecological and evolutionary dynamics under coloured environmental variation. Trends in Ecology and Evolution 24:555–563.

Schjørring, S. 2002. The evolution of informed natal dispersal: inherent versus acquired information. Evolutionary Ecology Research 4:227–238.

Thiele, J. C., and V. Grimm. 2015. Replicating and breaking models: good for you and good for ecology. Oikos 124:691–696.

Travis, J. M. J. 2001. The color of noise and the evolution of dispersal. Ecological Research 16:157–163.

Zhu, Y. O., M. L. Siegal, D. W. Hall, and D. A. Petrov. 2014. Precise estimates of mutation rate and spectrum in yeast. Proceedings of the National Academy of Sciences of the USA 111:E2310–E2318.

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