

SHORT COMMUNICATION

Evolution of reproductive effort in viscous populations: the importance of population dynamics

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Abstract

I present two ecological models for the evolution of reproductive effort in viscous populations with empty sites. In contrast with previous studies, I show that limited dispersal needs not have a positive effect on the evolutionarily stable allocation of resources to fecundity versus survival. Rather, depending on the feedback between the trait and the population dynamics, population viscosity may have no effect or even lead to a decrease in the evolutionarily stable reproductive effort when individuals can degrade their environment during their lifetime. I show that the different evolutionary outcomes can be explained by the asymmetry in the level of kin competition resulting from investing into juveniles or into adults.

A central point in life history theory is to understand how ecological conditions affect reproductive effort, that is, the division of resources between reproduction and survival (Stearns, 1992; Charnov, 1993; Roff, 2002). In the theoretical and empirical literature, however, this question is usually investigated under restrictive ecological assumptions, which often neglect the feedback between reproductive effort and the environment (Metz *et al.*, 1992; Mylius & Diekmann, 1995; Metz *et al.*, 2008a,b). Yet, this feedback can be expected to be a determining factor, because an increased reproductive effort will affect population density, which may in turn affect competition between individuals and alter the selective pressures on reproductive effort.

The effects of competition on reproductive effort are likely to be particularly determining in populations in which juvenile dispersal is local. In such viscous populations, the selective pressures on reproductive effort may be different from those in a well-mixed population, because limited dispersal leads to higher levels of relatedness between locally interacting individuals, thereby increasing the possibility for individuals to reap inclusive fitness benefits, but also the extent to which they compete with relatives (Queller, 1992; Taylor, 1992; West *et al.*, 2002). Understanding how these opposite

factors shape the selective pressures on reproductive effort is the topic of the present note.

This study is not the first to address the evolution of reproductive effort in viscous populations. Pen (2000) analysed a patch-structured population following the island model of dispersal (Wright, 1931; Taylor, 1992; Rousset, 2004) and showed that, when dispersal increases, individuals should shift their allocation of resources from reproduction to survival, and thus the optimal reproductive effort should decrease. Pen (2000) showed that this occurred because, in a viscous population, adults experience relatively more competition with relatives than juveniles, making juveniles more valuable. As juvenile dispersal increases, however, this asymmetry in kin competition disappears. Similar results were obtained by Ronce & Olivieri (1997) in a metapopulation model with extinction and recolonization dynamics.

There are reasons to expect, however, that different assumptions on life cycle or population dynamics could have a significant impact on the evolution of reproductive effort in a spatially structured population. The aim of this article is to show that it is indeed the case. To that effect, I explore two different ecological scenarios. First, I study a spatial demographic model in which reproduction is conditional to the availability of empty sites either in the neighbourhood of the mother (local reproduction) or at a random location in the population (global reproduction). As an increased reproductive effort can be expected to decrease the availability of empty sites for

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reproduction, this analysis explicitly takes into account the feedback between reproductive effort and habitat saturation. A crucial feature of the model is that, at a given time, each site can either be empty or occupied. The model therefore retains the discreteness of individuals and accounts for kin selection effects (Durrett & Levin, 1994a; Lion & van Baalen, 2008).

Second, I consider the evolution of reproductive effort in a model of negative ecosystem engineering (Odling-Smee *et al.*, 1996, 2003; Jones *et al.*, 1997). I extend the previous model by assuming that individuals degrade their local habitat during their lifetime and adding a habitat recovery process. The resulting habitat degradation or autotoxicity (van der Putten *et al.*, 1993; Boeken & Shachak, 1994; Mazzoleni *et al.*, 2007; Bonanomi *et al.*, 2008). I show that different predictions for the evolutionarily stable reproductive effort are obtained under those two ecological scenarios.

Because the theory used to obtain these results may be unfamiliar to some readers, this note can be read at two different levels. The shortest path is to read section 1 and then to hitchhike from figure to figure to the discussion, which provides a summary of the main results, as well as a more general discussion about the need to take into account population dynamics in life history evolution. The longest route meanders through a more mathematical landscape, but also provides a more formal underpinning of the interplay between kin competition and population dynamics in the two models.

Ecological model

Individuals live on a network of sites. Each site has n neighbours and can be either empty (o) or occupied by one individual (\times). Each individual can either die at rate d or reproduce at rate b . Reproduction depends on the availability of empty sites and can be either global (with probability P) or local (with probability $1 - P$). It is further assumed that long-distance dispersal may be costly, so juveniles have a probability σ of surviving. After competition for empty sites, successful juveniles become adults immediately. Figure 1 provides a schematic description of the demographic processes in the model. When $P = 0$, the model collapses to the contact process (Harris, 1974; Durrett & Levin, 1994b; van Baalen & Rand, 1998; Lion, 2009; Lion & Gandon, 2009). When $P = 1$, the population is effectively well mixed. The biological assumptions are similar to Pen's (2000) model, except for the fact that Pen (2000) used a patch model with discrete generations.

If we denote by $q_{o/\times}$ the average local density of empty sites experienced by an individual, and by p_o the global density of empty sites, the dynamics of the density of individuals, p_\times , follows the differential equation

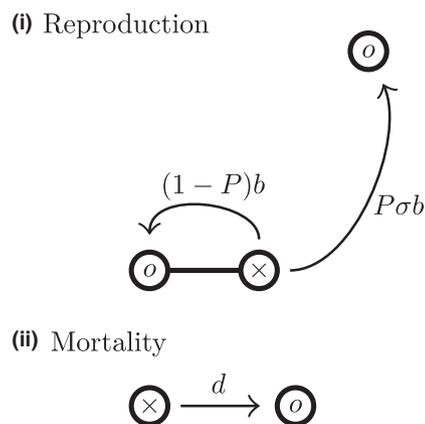


Fig. 1 Schematic description of the demographic events in the model. (i) Local vs. global reproduction into empty sites. (ii) Death of an individual.

$$\frac{dp_\times}{dt} = [(1 - P)bq_{o/\times} + P\sigma bp_o - d]p_\times \quad (1)$$

The first two terms between brackets represent the contribution of local and global reproduction to the dynamics of the density of individuals. Note that local reproduction depends on the *local* availability of empty sites in the neighbourhood of an individual ($q_{o/\times}$), whereas global reproduction depends on the *global* availability of empty sites (p_o).

At equilibrium, the global and local densities of empty sites are linked although the equilibrium condition

$$(1 - P)q_{o/\times} + P\sigma p_o = \frac{d}{b} \quad (2)$$

The left-hand side of that equation is the overall probability of landing on an empty site, which is equal at equilibrium to the death-to-birth ratio d/b . This indicates that a change in reproductive effort may affect the availability of empty sites. For instance, if an increase in reproduction is accompanied by a smaller increase in mortality, the availability of empty sites will decrease, and thus habitat saturation will increase.

Evolution of reproductive effort

Now suppose that individuals can allocate resources to reproduction or to survival and that they vary with respect to their reproductive effort e . If individuals have a constant amount of resources to allocate, they can only increase their fecundity rate if they also increase their mortality rate, and this defines a trade-off between fecundity $b(e)$ and mortality $d(e)$. In the remainder of this note, I will assume a concave-down trade-off (i.e. fecundity is a saturating function of mortality). In this case, classical non-spatial theory predicts evolution of intermediate levels of reproductive efforts (Gadgil & Bossert, 1970; Charnov & Schaffer, 1973; Schaffer, 1974).

We are interested in the evolutionarily stable reproductive effort (ESRE), and in how it varies with the probability of long-distance dispersal.

Selection gradient

Consider a mutant M with reproductive effort e' in a resident population of individuals R with trait e . The per capita growth rate of mutant individuals is

$$\lambda_M = (1 - P)b(e')q_{o/M} + P\sigma b(e')p_o - d(e') \tag{3}$$

where $q_{o/M}$ is the average local density of empty sites experienced by a mutant individual. As long as the mutants are globally rare, it is reasonable to assume that the resident population stays on its ecological attractor, so the global density of empty sites p_o can be approximated as the equilibrium value of the monomorphic population. However, mutants will not necessarily experience the same local environment, so one expects a change in reproductive effort to affect the local density of empty sites $q_{o/M}$.

Using the shorthand notation $\Delta \equiv \partial/\partial e'|_{e=e'}$, we can compute the selection gradient $\Delta\lambda_M$ as (Appendix S2)

$$\Delta\lambda_M = [(1 - P)q_{o/\times} + P\sigma p_o]\Delta b - \Delta d + (1 - P)b\Delta q_{o/M} \tag{4}$$

The first term represents the selective pressure on reproduction, weighted by the probability of colonizing an empty site, and the second term is the selective pressure on survival. The third term $(1 - P)b\Delta q_{o/M}$ measures the effect of an increase in reproductive effort on the local availability of empty sites. Thus, it encapsulates the effect of reproductive effort on local competition for empty sites. This selective pressure vanishes in a well-mixed population ($P = 1$), but in a viscous population it is likely to play an important role. Using eqn 2, we can finally rewrite the selection gradient as

$$\Delta\lambda_M = d\Delta S + (1 - P)b\Delta q_{o/M} \tag{5}$$

where $\Delta S \equiv \Delta b/b - \Delta d/d$. The ESRE is the solution of $\Delta\lambda_M = 0$.

Well-mixed population

In a well-mixed population ($P = 1$), eqn 5 reduces to $\Delta S = 0$, and the ESRE is the solution of

$$\frac{\Delta b}{\Delta d} = \frac{b}{d}$$

which is a version of the marginal value principle (Charnov, 1976). This implies that, under those life cycle assumptions, the ESRE is the value of e which maximizes the reproductive ratio b/d (Fig. 2). Following Pen (2000), the ratio $\Delta b/b$ can be interpreted as the marginal benefit of reproduction measured in units of adult reproductive value, whereas the ratio $-\Delta d/d$ measures the marginal cost of reproduction measured in units of offspring

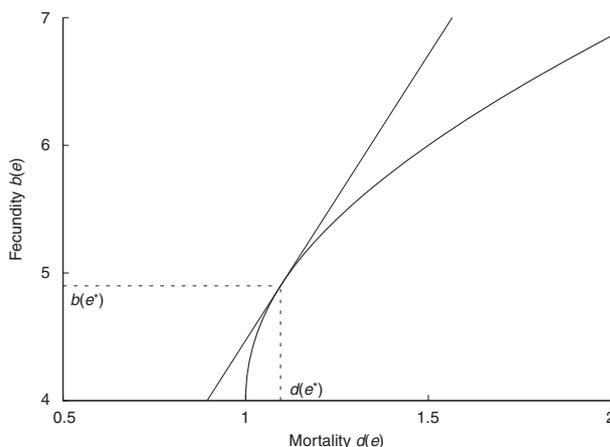


Fig. 2 Evolutionarily stable reproductive effort (ESRE) in a well-mixed population. The straight line gives the tangent to the trade-off curve that goes through the origin. Throughout the article, I use the functions $d(e) = d_0\sqrt{1 + 0.8e^2}$ and $b(e) = b_0\sqrt{1 + e}$, which yields the ESRE $e^* = 0.5$ in the well-mixed population. Note however that the qualitative predictions are independent of the trade-off function and only depend on the trade-off being concave-down. Parameters: $b_0 = 4$, $d_0 = 1$.

reproductive value. At equilibrium in a well-mixed population, juveniles and adults are equally valuable.

Viscous population

The ESRE in a viscous population will depend on how local competition is affected by the reproductive effort and by dispersal. Extending previous analyses (van Baalen & Rand, 1998; Lion & Gandon, 2009), I show in Appendix S2 that $\Delta q_{o/M}$ can be computed from the dynamics of pairs of sites, using an argument of separation of time scales. This yields

$$b\Delta q_{o/M} = \frac{d}{q_{o/\times}(1 + q_{o/\times}) + P\sigma(p_o - q_{o/\times})} \left[-q_{o/\times}r \left(\frac{\Delta b}{b} - \frac{\Delta d}{d} \right) + 2\bar{\phi}\Delta q_{o/M} \right] \tag{6}$$

where $\bar{\phi} = (n - 1)/n$ and $q_{o/oM}$ is the average local density of empty sites in the neighbourhood of an empty site connected to a mutant individual. Equation 6 is enlightening, because it allows the selective pressure because of competition for neighbouring empty sites to be split into two components. The first term in the brackets, $-q_{o/\times}r(\Delta b/b - \Delta d/d) = -q_{o/\times}r\Delta S$, depends on the marginal effects of reproductive effort on fecundity and survival and is weighted by the local density of empty sites $q_{o/\times}$ and by the relatedness between nearest neighbours r , which is simply $q_{M/M}$, the local density of mutants in the neighbourhood of a mutant (van Baalen & Rand, 1998; Lion & van Baalen, 2007; Lion, 2009; Lion & Gandon, 2009). This first term tells us that, if the marginal effect on fecundity is larger than the marginal effect on survival ($\Delta S > 0$), an

increase in reproductive effort will increase local competition for empty sites. The competitive effects of reproduction effort are twofold. First, increasing adult mortality opens new empty sites. Second, producing more juveniles increases the rate at which empty sites are filled. The magnitude of this competitive effect depends on both habitat saturation (through the local density $q_{o/\times}$) and relatedness r . Note that this effect will be greater when competition for empty sites tends to occur with related individuals (r high) and is therefore a measure of kin competition. In other words, what matters is really competition with relatives, as found by Pen (2000).

The second term $2\phi\Delta q_{o/oM}$ depends on how much a small increase in the trait will affect the local density of empty sites two steps away. Note that eqn 6 represents a spatial moment expansion of the effect of reproductive effort on the local density of empty sites. A rigorous treatment would allow us to pursue this expansion by computing $\Delta q_{o/oM}$, and so on, but, if obtainable at all, the resulting expression would be too intricate to yield much analytical insight. However, we expect the effect of reproductive effort on the local density of empty sites to decrease in magnitude as the distance with the focal individual decreases. In the following, I will therefore assume that the evolutionary dynamics are mostly determined by the effect of reproductive effort on the immediate neighbourhood of mutants and neglect the term $\Delta q_{o/oM}$ in eqn 6. The analytical expression for the selection gradient obtained with this approximation is more interpretable and can be understood as giving the first-order effect of spatial structure on the selection gradient.¹

Combining eqns 5 and 6 and setting $\Delta q_{o/oM}$ to zero, we find that the selection gradient takes the form

$$\Delta\lambda_M = d \left(1 - \frac{(1-P)q_{o/\times}r}{q_{o/\times}(1+q_{o/\times}) + P\sigma(p_o - q_{o/\times})} \right) \Delta S \quad (7)$$

Equation 7 depends on d , on the local density of empty sites $q_{o/\times}$, on the probability P and cost σ of long-distance dispersal and on the relatedness r between nearest neighbours. Note that both $q_{o/\times}$ and r depend on the ecological parameters d , b , P and σ .

From eqn 2, it can be shown that $p_o > q_{o/\times}$, and this implies that the parenthesis in eqn 7 is positive. Hence, the sign of $\Delta\lambda_M$ is given by the sign of

$$\Delta S = \frac{\Delta b}{b} - \frac{\Delta d}{d} \quad (8)$$

Thus, as in the well-mixed population, the candidate ESRE when dispersal is limited is the value of e that maximizes the reproductive ratio b/d . In contrast with Pen's (2000) result, dispersal (and population viscosity in general) has therefore no effect on the ESRE in our ecological model. Although this relies on the fact that

¹It is therefore exact on some networks, such as random regular networks.

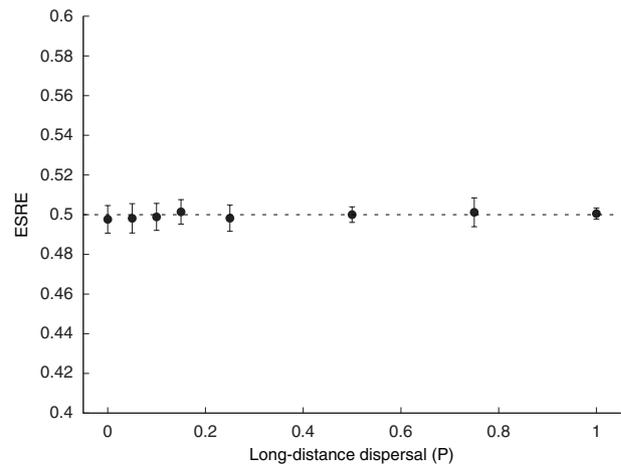


Fig. 3 Evolutionarily stable reproductive effort (ESRE) as a function of long-distance dispersal (P). The mean and standard deviation of eight runs of the stochastic process on a 100×100 square lattice are presented. Mutations occurred at rate 0.005. Mutation effects were drawn from a normal distribution with zero mean and standard deviation 0.005. The mean equilibrium for each run was estimated as the average value of the trait between $t = 60\,000$ and the simulation end time $t = 100\,000$. The dashed line gives the theoretical ESRE in a well-mixed population. Parameters: $\sigma = 1$. Other parameters as in Fig. 2.

$\Delta q_{o/oM}$ can be neglected, evolutionary simulations of the ecological model suggest that this term has a negligible effect (Fig. 3). It is worth noting that a similar result has been implicitly obtained in a deme-structured population with empty sites following the island model of dispersal (see Wild *et al.* (2009) and discussion).

Equation 6 offers a simple analytical explanation for this result. Indeed, it shows that the weighting factors in front of the marginal effects $\Delta b/b$ and $\Delta d/d$ are equal, which implies that investing into juveniles and investing into adults leads to the same amount of kin competition. Thus, although limited dispersal does increase kin competition, the increased competition is equally distributed among juveniles and adults, so the ESRE is independent of dispersal. The asymmetry in kin competition between juveniles and adults observed in Pen's (2000) model therefore disappears under the life cycle I assume.

Long-distance dispersal, relatedness and habitat saturation do however affect the magnitude of selection through their effect on kin competition. Examining the factor between brackets, which measures the speed of selection, it is possible to use eqn 2 to show that this factor increases with P . Thus, population viscosity decreases the speed of evolution.

The role of life cycle assumptions

How can we understand the difference between the predictions of Pen (2000) and those generated by the model presented in this article? Here, the importance of

life cycle assumptions, or more generally of population dynamics, becomes most significant. Indeed, the two models make different assumptions on the timing of events. In my model, reproduction and mortality events are asynchronous, whereas Pen's (2000) model uses a sequence of synchronous demographic events (all individuals produce juveniles, some adults die according to their survival probability, and juveniles compete for empty sites). This has important consequences for the evolution of reproductive effort (I. Pen, personal communication).

To understand why, let us simulate the life cycle of Pen (2000) on a lattice and assume that, as in my model, local dispersal means that juveniles can disperse to nearest neighbours, but that, as in Pen's (2000) model, a juvenile can also compete for its own mother's site. This is impossible in my model by construction, but because in Pen's (2000) model mortality occurs after juveniles are produced, each juvenile has a positive probability of replacing its mother when she dies, if the dispersal neighbourhood includes the mother's site as well as its nearest neighbours. Simulations of this process then show that reproductive effort increased with population viscosity, as predicted by Pen's (2000) model (Fig. 4). However, this result is very sensitive to the dispersal neighbourhood, and if we exclude the mother's site and allow juveniles to compete only for nearest neighbouring empty sites, then reproductive

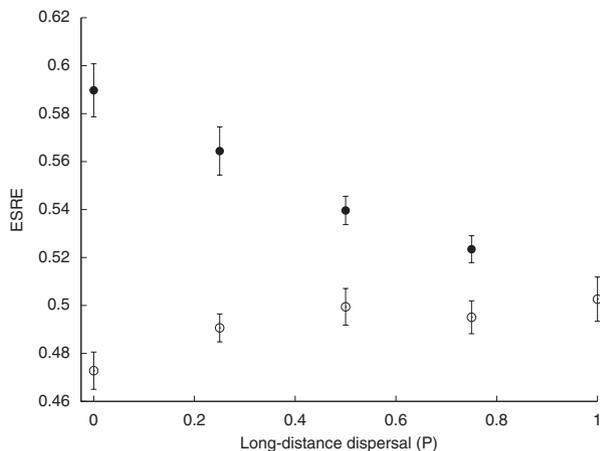


Fig. 4 Evolution of reproductive effort in stochastic simulations implementing the life cycle of Pen (2000) on a square lattice. At each time step, juveniles produced at site i compete for empty sites either locally or globally. The local dispersal neighbourhood is either restricted to the four nearest neighbours of site i (4-site neighbourhood, open circles) or is extended to include site i itself (5-site neighbourhood, filled circles), in which case offspring can settle only if the mother dies during the same time step. The mean and standard deviation of eight runs of the stochastic process are shown. The mean equilibrium for each run was estimated as the average value of the trait between $t = 60\,000$ and the simulation end time $t = 100\,000$. Parameters as in Fig. 3.

effort is predicted to slightly decrease when dispersal decrease (Fig. 4).

This shows that the ability of juveniles to replace their own mother is a crucial component of Pen's (2000) result. This is intuitive, because if juveniles can 'profit' from their own mother dying, it may pay to invest more in reproductive effort, even if this leads to increased mortality of the mother. However, this clearly illustrates the need to be specific about the details of population dynamics, especially in a spatial context. For instance, the order of life history events in discrete-time models is known to strongly affect the dynamics of spatial models (McCauley *et al.*, 1993). This example shows that this can have important evolutionary consequences. The model developed in the next section will show that, in continuous time as well, the interplay between ecological dynamics and selection can lead to evolutionary outcomes that significantly differ from the predictions of non-spatial theory.

Evolution of reproductive effort in a degraded habitat

The previous result demonstrates that increasing population viscosity needs not lead to the asymmetry in kin competition between adults and juveniles that was observed by Pen (2000). However, different ecological conditions may be expected to have different effects on competition between individuals.

Let us now consider a slightly different ecological scenario, in which individuals degrade their local environment during their lifetime, so that the death of one individual leaves a degraded site (u) that may become colonisable again (o) at rate v (Fig. 5a). This can be interpreted as a simple model of negative ecosystem engineering (Odling-Smee *et al.*, 1996, 2003; Jones *et al.*, 1997), such as the overexploitation of a resource through overgrazing (Boeken & Shachak, 1994), or negative plant-soil feedback through nutrition depletion, autotoxicity as a result of the release of phytotoxic compounds during organic matter decomposition and the build-up of soil pathogen populations (van der Putten *et al.*, 1993; van der Putten & Peters, 1997; Mazzoleni *et al.*, 2007; Bonanomi *et al.*, 2008). A related model was considered for the evolutionary ecology of local facilitation in arid ecosystems by Kéfi *et al.* (2007, 2008).

It turns out that, in the habitat degradation model, the selection gradient also takes the form (Appendix S3)

$$\Delta\lambda_M = d\Delta S + (1 - P)b\Delta q_{o/M} \quad (9)$$

with $\Delta S = \Delta b/b - \Delta d/d$. Thus, if habitat degradation has an effect on reproductive effort, it will be through the competition term $(1 - P)b\Delta q_{o/M}$. It follows that, in a well-mixed population ($P = 1$), the ESRE in this model is

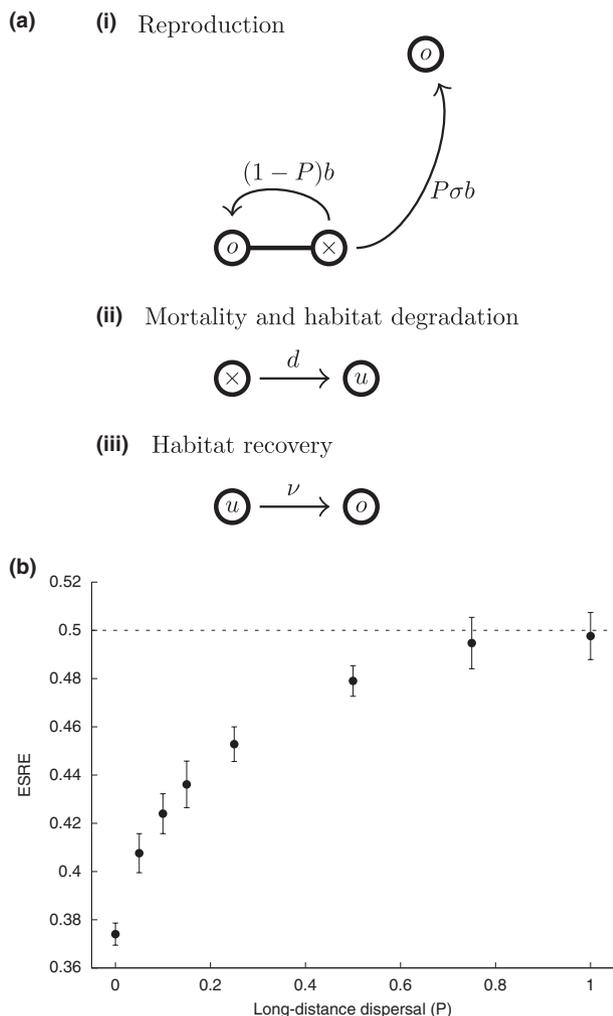


Fig. 5 Habitat degradation model. (a) Schematic description of the demographic events in the habitat degradation model. (i) Local vs. global reproduction into empty sites. (ii) Death of an individual, leaving a degraded site u . (iii) Habitat recovery: the site becomes colonisable again. (b) Evolutionarily stable reproductive effort (ESRE) as a function of long-distance dispersal (P) in the habitat degradation model. The mean and standard deviation of eight runs of the stochastic process on a 100×100 square lattice are presented. Mutations occurred at rate 0.005. Mutation effects were drawn from a normal distribution with zero mean and standard deviation 0.005. The mean equilibrium for each run was estimated as the average value of the trait between $t = 100\,000$ and the simulation end time $t = 200\,000$. The dashed line gives the theoretical ESRE in a well-mixed population. Parameters: $v = 1$, $\sigma = 1$. Other parameters as in Fig. 2.

also the value of e that maximizes the reproductive ratio b/d . When dispersal is high, habitat degradation has therefore no effect on the evolution of reproductive effort.

What happens in a viscous population? Let us focus on a purely viscous population ($P = 0$). In Appendix S3, it is shown that

$$b\Delta q_{o/M} = -\frac{d}{1 + q_{u/x} + (k+1)q_{o/x}} \left[(r + k(r - q_{x/x} + q_{x/u})) \frac{\Delta b}{b} - r \frac{\Delta d}{d} \right]$$

where $k = 2d/v$ and $q_{o/x} = d/b$. We see that the marginal effects of reproductive effort on juveniles and adults are weighted by different factors, which means that an increase in fecundity and an increase in survival have asymmetric effects on kin competition. This asymmetry disappears when the rate at which degraded sites become colonisable is high ($v \rightarrow \infty$), in which case $k \rightarrow 0$. In this limit, the model reduces to the one studied in the previous section.

For smaller values of v ($k > 0$), it follows from eqn 10 that juveniles cause relatively more kin competition than adults, because $r > q_{x/x} - q_{x/u}$ (Appendix S3). Therefore, under a saturating trade-off between fecundity and mortality, the ESRE in a purely viscous population is predicted to be actually *lower* than the ESRE in a well-mixed population (Appendix S3). This result is borne out by the results of stochastic evolutionary simulations (Fig. 5b).

In summary, population viscosity can also select for a decrease in reproductive effort. The impact of dispersal on the evolution of reproductive effort therefore depends crucially on the details of the ecology, in particular on how population dynamics affect kin competition.

Discussion

The main result of this study is that population viscosity can have contrasting effects on the selective pressures on reproductive effort. Earlier theoretical results (Pen, 2000) predicted that one should expect the optimal reproductive effort to decrease with the probability of long-distance dispersal. The rationale was that, in a viscous population, adults would experience more local competition with relatives than juveniles, and therefore juveniles would be more valuable. As long-distance dispersal increases, this asymmetry decreases and the optimal allocation shifts towards higher adult survival.

In this note, I show that, although kin competition constitutes the main selective force driving the evolution of reproductive effort, the asymmetry between juveniles and adults actually depends crucially on population dynamics – an aspect that is sometimes overlooked. For the simple birth-death model, I find that juveniles and adults experience the same amount of competition with relatives, irrespective of the scale of offspring dispersal. The ESRE is therefore the same as the ESRE in a well-mixed population. Moreover, I provide an ecological model of habitat degradation in which the ESRE increases with dispersal rate, in contrast with Pen's (2000) predictions, because investing into adult survival leads to a higher amount of competition with relatives compared to investing into juveniles. Thus, reproductive

effort can evolve in different ways depending on the life cycle and ecological assumptions.

The results of the article do not appear to depend strongly on the spatial model used (i.e. network model vs. patch model). Indeed, similar results as those of section 2 were implicitly obtained in a recent study of Wild *et al.* (2009). Their model is an extension of an island model with demography introduced by Alizon & Taylor (2008). Although the model considers the evolution of parasite virulence under a transmission-virulence trade-off, the problem the authors consider is analogous to the one I consider here in the limit of high host fecundity (in which case susceptible hosts play the role of empty sites, and infected hosts the role of individuals in my model). Their Fig. S2 shows that, in this limit, the impact of dispersal on the optimal allocation between transmission and virulence becomes negligible, which is consistent with the results obtained here.

This study shows that a kin selection perspective allows us to better understand the balance between increased reproductive effort and increased kin competition. It also suggests that kin selection models need to address the impact of life history traits on population dynamics, especially in a spatial context. In particular, I show that the precise effects of kin competition on juveniles and adults depend on the details of population dynamics. Although it is well appreciated that ecological factors influence the role of kin competition in the evolution of traits such as helping or dispersal (Taylor, 1992; West *et al.*, 2002; Lion & van Baalen, 2008; Platt & Bever, 2009), this study stresses that the interplay between kin competition and population dynamics also determines the evolution of simpler life history traits such as reproductive effort. It would be interesting to extend this study to analyse in more detail the interplay between reproductive effort and other life history traits, such as senescence or maturation rate. The role of maturation, in particular, could be explored using an extension of the model developed by Lion & van Baalen (2007).

The habitat degradation model I present can be interpreted as a general model of negative ecosystem engineering and can be expected to be particularly suited for modelling plant populations that have a negative impact on their local habitat, through nutrient depletion, autotoxicity or the accumulation of plant pathogens in the soil (van der Putten *et al.*, 1993; Jones *et al.*, 1997; Mazzoleni *et al.*, 2007; Bonanomi *et al.*, 2008). In this context, the model offers the testable prediction that plant-induced habitat degradation should lead to lower reproductive effort in plant populations with local dispersal compared to plant populations with global dispersal. This prediction can be tested empirically in experimental plant populations in which seed dispersal and habitat degradation are controlled for. At a more applied level, the fact that allocation of resources to seeds can evolve to lower levels through selection has potential implications for applied ecological fields, as, for instance,

plant-induced habitat degradation is a common phenomenon in agriculture (van der Putten *et al.*, 1993). Other potential applications extend to the field of conservation biology. This calls for further theoretical studies that explicitly take into account the interplay between plant ecology, seed dispersal and selection. For instance, a limitation of the model used here is that the survival and reproduction of a plant do not depend on the deterioration of the habitat during its lifetime. This may affect the prediction, and could be investigated using an age-structured model. More generally, this study shows that, from an economic or conservation management perspective, predictions need to rely on ecologically explicit models, as variations in life cycle or environmental dynamics may strongly affect the evolutionary predictions.

It is possible to draw an enlightening analogy with the evolution of virulence in host-parasite interactions. Indeed, the birth-death model is equivalent to a susceptible-infected model. Identifying empty sites σ with susceptible individuals S , and R and M individuals with individuals infected by a resident parasite (I) or a mutant parasite (J), we can use the predictions generated by the model to investigate the evolution of virulence under a transmission-virulence trade-off. The conclusion then is that population viscosity should have no effect on virulence evolution, as found in the simulation results of Claessen & de Roos (1995). Most spatial models of host-parasite interactions have shown however that population viscosity should select for lower virulence if host demography (Boots & Sasaki, 1999; Haraguchi & Sasaki, 2000) or recovery dynamics [SIR model; van Baalen (2002)] are taken into account. (Note that the degradation model presented in section 4 is actually equivalent to the SIR model with constant host population size.)

This note has wider implications for the field of life history evolution. Despite the growing awareness that the evolution of life history traits crucially depends on the feedback loop between ecology and evolution (Metz *et al.*, 1992; Mylius & Diekmann, 1995; Metz *et al.*, 2008a,b), most of the empirical and theoretical literature is pervaded by the often unwitting misconception that evolutionary correlations between life history traits should be fairly independent of the details of population dynamics. This assumption forms the implicit underpinning of across-species meta-analyses. This study suggests that averaging across a wide range of ecological conditions and population dynamics could lead to artefacts when trying to determine evolutionary correlations between life history traits.

To conclude, even when a proper ESS argument is used rather than an *ad hoc* optimization principle, care must be taken when inferring conclusions based on models with constant population size. This article shows that taking into account the details of the interaction between the evolving trait and its environment yields different predictions on the impact of population

viscosity on the evolution of reproductive effort. This calls for further theoretical and empirical studies of the impact of population viscosity and population dynamics on the evolution of reproductive effort. In particular, even qualitative predictions should be based on a careful examination of the population dynamics and life history of the population under study.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Monomorphic population.

Appendix S2 Deriving the selection gradient.

Appendix S3 Habitat degradation.

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