

Spatially heterogeneous stochasticity and the adaptive diversification of dormancy

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Abstract

Diversified bet-hedging, a strategy that leads several individuals with the same genotype to express distinct phenotypes in a given generation, is now well established as a common evolutionary response to environmental stochasticity. Life-history traits defined as diversified bet-hedging (e.g. germination or diapause strategies) display marked differences between populations in spatial proximity. In order to find out whether such differences can be explained by local adaptations to spatially heterogeneous environmental stochasticity, we explored the evolution of bet-hedging dormancy strategies in a metapopulation using a two-patch model with patch differences in stochastic juvenile survival. We found that spatial differences in the level of environmental stochasticity, restricted dispersal, increased fragmentation and intermediate survival during dormancy all favour the adaptive diversification of bet-hedging dormancy strategies. Density dependency also plays a major role in the diversification of dormancy strategies because: (i) it may interact locally with environmental stochasticity and amplify its effects; however, (ii) it can also generate chaotic population dynamics that may impede diversification. Our work proposes new hypotheses to explain the spatial patterns of bet-hedging strategies that we hope will encourage new empirical studies of this topic.

Introduction

The role of environmental stochasticity in the evolution of life-history traits has been studied both theoretically and empirically (Cohen, 1966; Tuljapurkar & Orzack, 1980; Cooper & Kaplan, 1982; Bulmer, 1984; Ellner, 1985a,b; Seger & Brockmann, 1987; Menu & Debouzie, 1993; Philippi, 1993a,b; Menu *et al.*, 2000). The main finding has been that bet-hedging strategies, which favour low variance rather than a high arithmetic mean in generational fitness, are more likely to evolve in a stochastically variable environment because they increase the geometric mean of reproductive rates (Seger & Brockmann, 1987; Philippi & Seger, 1989; Yoshimura & Clark, 1991). The strategy that drives several individuals (with the same genotype) to express distinct phenotypes in a given generation, known as diversified

bet-hedging (Seger & Brockmann, 1987; Philippi & Seger, 1989), is predicted to emerge as a response to environmental stochasticity (note that the distribution of phenotypes can be considered to be either discrete or continuous, see Sasaki & Ellner, 1995, for an example of the latter). Such a strategy, which can be described by the common saying 'don't put all your eggs in one basket', may confer an adaptive advantage if the conditions that favour each of the phenotypes expressed occur randomly. Some theoretical studies have determined which diversified bet-hedging strategies, defined as the set of probabilities that each phenotype will be expressed, are expected to evolve in a given, spatially homogeneous, ecological context (Cohen, 1966; Bulmer, 1984; Ellner, 1985a,b; Seger & Brockmann, 1987; Menu *et al.*, 2000).

Since the pioneering investigations that were conducted in desert plants, dormancy strategies have been considered to be adaptive responses to environmental stochasticity (Cohen, 1966; Philippi, 1993a,b; Clauss & Venable, 2000; Evans *et al.*, 2007). Many plants are capable of producing seeds with various different

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dormancy phenotypes, some of them being capable of germinating readily the following season, and the remainder keeping dormant for one or more years. Although such strategies are obviously costly (lost reproductive opportunities and mortality during dormancy), they prevent all the individuals carrying the same genotype from simultaneously encountering an environment that makes it unlikely that they will survive to reproductive maturity or that is unsuitable for their reproduction. Dormancy of variable length has also been considered as a diversified bet-hedging strategy in animals, as, for example, in insects (Menu & Debouzie, 1993; Menu, 1993; Danforth, 1999; Menu & Desouhant, 2002) and crustaceans (Hairston & Munns, 1984). An analogy with dormancy strategies has also recently been put forward to explain prolonged latency in viruses (Stumpf *et al.*, 2002; Jansen & Stumpf, 2005). The concept of bet-hedging has also been applied to life-history traits other than dormancy. For example, it helps to explain why different sexual morphs are expressed by aphids (Halkett *et al.*, 2004), and the switching between two forms in the [PSI⁺] prion (Masel, 2005; King & Masel, 2007) and in the bacterium *Escherichia coli* (Balaban *et al.*, 2004; Kussell *et al.*, 2005; Kussell & Leibler, 2005).

Between-population variability of bet-hedging strategies has seldom been investigated, except in a few field studies reporting marked differences between dormancy duration distributions among neighbouring populations of given species (*Lepidium lasiocarpum*, Philippi, 1993a; *Plantago insulari*, Clauss & Venable, 2000; *Curculio elephas*, Oberli, 2001; *Daphnia pulicaria*, Cáceres & Tessier, 2003; *Oenothera californica* and *Oenothera arizonica*, Evans *et al.*, 2007). One would expect bet-hedging dormancy strategies to vary between localities, as other traits do, as a result of local adaptations to particular ecological conditions (see the review from Kawecki & Ebert, 2004 on local adaptation). Theoretical studies on bet-hedging dormancy strategies have already considered a metapopulation structure in a stochastically variable environment (Bulmer, 1984; Klinkhamer *et al.*, 1987; Venable & Brown, 1988; McPeck & Holt, 1992; Mathias *et al.*, 2001; Mathias & Kisdi, 2002). However, only Mathias & Kisdi (2002) have studied the adaptive diversification of bet-hedging dormancy strategies in a permanently heterogeneous landscape. They explored the evolution of germination rate in plants depending on survival during dormancy that was constant within each patch but differed between the patches. In our study, we highlight the role of spatial differences of environmental stochasticity in the diversification of bet-hedging dormancy strategies.

Local differences in the level of environmental stochasticity may occur in many taxa in which bet-hedging strategies have evolved. Studying desert plants, Clauss & Venable (2000) found a relationship between the locally variable germination rates in *P. insulari* and the precipitation gradient in their natural habitat, which the

authors suppose to be correlated with the local level of environmental stochasticity. Furthermore, the impact of a climatic stochastic event (e.g. rainfall) on the fitness of a germinating plant may depend on local parameters (e.g. the slope of the ground). In *D. pulicaria*, Cáceres & Tessier (2003) suggested that differences in the proportion of dormant eggs among populations could be explained in part by differences in the ability of the active form to persist seasonally between the lakes in which they live. Moreover, Lytle & Poff (2004) reported that hatching asynchrony in stoneflies has evolved in some aquatic species in response to natural flow regimes, which may vary strongly both within a given river (upstream and downstream of a dam, for instance) and between different rivers. In many systems, distinct stochastic environments could therefore select for distinct bet-hedging strategies, and possibly favour their local adaptation. This may, however, depend considerably on the spatial dispersal rate between localities, which can impede local adaptation of bet-hedging due to gene flow.

In this study, we aim to explore the conditions that promote the diversification of bet-hedging dormancy strategies in response to spatially heterogeneous levels of unpredictable environmental variation. We set up a two-patch model, in which good and bad years succeed each other stochastically, and are associated with high and low juvenile survival rates respectively. The level of environmental stochasticity in a given patch is measured by the local variance in juvenile survival (given that there is no temporal autocorrelation), which increases with: (i) the local probability that a bad year will occur and/or (ii) the local ratio of good-to-bad juvenile survival rates. We analyse the effect of a spatial difference in these two variables, as we expect the diversification of dormancy strategies to be favoured by marked differences in the level of environmental stochasticity between the patches. According to the theory of local adaptation (Kawecki & Ebert, 2004), one would also expect different dormancy strategies to coexist within the metapopulation when the dispersal rate is low and the habitat fragmentation is high. The model includes a locally density-dependent fecundity, which can cause chaotic population dynamics that may lead to the evolution of dormancy in the absence of environmental stochasticity (Bulmer, 1984; van Dooren & Metz, 1998; Lalonde & Roitberg, 2006). This might play a role in the adaptive diversification of dormancy. We therefore use adaptive dynamics (Metz *et al.*, 1992, 1996; Kisdi & MeszÉna, 1993; Geritz *et al.*, 1998; Waxman & Gavrilets, 2005) to explore the conditions for diversification of bet-hedging dormancy strategies. We consider the effects of dispersal, of differences in the levels of environmental stochasticity, of habitat fragmentation, of survival throughout dormancy and of the shape of the density dependency function on the diversification of dormancy strategies.

The model

General description

The life cycle is shown in Fig. 1. The model includes two types of individuals: the Active type (*A*), which can disperse and reproduce, and the Inactive type (*I*) which is dormant (for example, dormant eggs or larvae). The individuals are distributed over two patches with equal carrying capacity (i.e. they have the same density-dependent function for fecundity, defined below). Those who become Active at the beginning of year *t* disperse from one patch to the other with a probability *m* (independent of which patch they were born in). The probability that individuals will survive during dispersal is *S_m*; this parameter can be regarded as an indicator of habitat fragmentation, assuming that a greater distance between the patches increases the risk that individuals will not survive the journey from one patch to the other (e.g. dying as a result of predation or energy depletion). Once dispersal has occurred, Active individuals reproduce with fecundity *F*(*n_{A(t)}*) (eqn 1), where *n_{A(t)}* is the total number of Active individuals in the patch (i.e. nondispersed individuals that have remained in the patch where they were born plus dispersers from the other patch). Reproduction is assumed to be clonal.

$$F(n_{A(t)}) = \frac{F_{\max}}{1 + \exp[\beta(n_{A(t)} - N_{0.5})]}, \quad (1)$$

where *N_{0.5}* is the population size for which the fecundity equals *F_{max}*/2. All else being equal, this correlated with the maximum size of the population. *β* is responsible for the shape of the density-dependent function. After

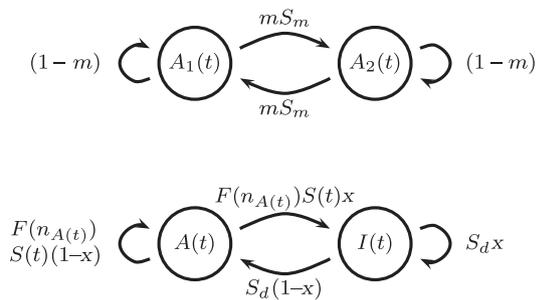


Fig. 1 Life cycle. (Top) Dispersal of Active (*A*) individuals (the subscript number on the life cycle indicates the patch in which they live). An individual may either disperse from one patch to the other, with probability *m*, or stay in its native patch. *S_m* is the probability of surviving dispersal. Active individuals disperse before reproduction, whereas Inactive individuals (not shown) do not. (Bottom) Demography within a patch. *F*(*n_{A(t)}*) is the density-dependent fecundity; *S*(*t*) is the survival of newborn individuals, which varies stochastically; *x* is the probability that an individual will become or remain Inactive (*I*) at *t* + 1 (in the case of individuals which were either newborn or Inactive at *t*); *S_d* is the probability of survival in the Inactive stage. See text for more details.

reproducing, Active individuals die. The probability that a newborn individual will survive throughout (the rest of) the year *t* is *S*(*t*), and this randomly takes a high (*S_G*) or a low (*S_B*) value, with probabilities $(1 - p_B)$ and p_B respectively. The geometric mean of *S*(*t*), *G_S*, has a constant value of 0.3 in each patch. This enables us to focus on the influence of the variation of *S*(*t*) (eqn 2):

$$G_S = S_B^{p_B} S_G^{1-p_B} \quad (2)$$

We define the ratio of good-to-bad survival as $r_{G/B} = S_G/S_B$. We consider the level of environmental stochasticity to be a variable linked to the variance in *S*(*t*). Hence, in our view, any increase in *r_{G/B}* or *p_B* increases the level of environmental stochasticity (note that this is only true if $p_B \leq 0.5$). Values of *S_G* and *S_B* are calculated as in eqn 3, as functions of *r_{G/B}* and *p_B*:

$$\begin{aligned} S_G &= \exp[\log(G_S) + p_B \log(r_{G/B})] \\ S_B &= \exp[\log(G_S) + (p_B - 1) \log(r_{G/B})] \end{aligned} \quad (3)$$

The two patches are independent, which means that there is no correlation between their values of *S*(*t*) for year *t*. However, an analysis of the impact of spatial autocorrelation is reported in Appendix S1 (supplementary online material). We also assume that there is no temporal autocorrelation, so that the value of *S*(*t*) in a given patch at time *t* does not depend on the value at another time step.

At *t* + 1, individuals born during year *t* become either Inactive, with probability *x*, or Active, with probability $(1 - x)$. Similarly, individuals that are Inactive in year *t* either remain Inactive or become Active at *t* + 1, with the same probabilities [*x* and $(1 - x)$ respectively]. The value of *x* designates the dormancy strategy (a higher *x* value means a higher proportion of Inactive individuals). The probability that an Inactive individual will survive throughout a year in dormancy is *S_d*.

Adaptive dynamics

We use adaptive dynamics (Metz *et al.*, 1992, 1996; Geritz *et al.*, 1998; Waxman & Gavrilets, 2005) to study conditions for diversification of the dormancy frequency *x*. Here, we report just a brief outline of our approach, and a detailed modelling procedure is available in Appendix S2 (supplementary online material). Our results were tested for robustness (see Appendix S3 in the supplementary online material).

The first step in our analysis consists of identifying the conditions required for diversification of the dormancy frequency to occur. To do this, we carry out an analysis based on the invasion capacity of a mutant in a large monomorphic resident population (Metz *et al.*, 1992, 1996), assuming that mutations are rare and have only a small effect. There are two possible results: (i) a strategy that can be reached by a series of mutational steps, and that then remains stable against invasion, and (ii) a

strategy that can also be attained but which can subsequently be invaded by all nearby mutants. A type (i) dormancy strategy is the expected outcome of the evolutionary process, and should not lead to a diversification. A type (ii) dormancy strategy is known as a 'branching point', and can be expected to be the starting point of an evolutionary diversification.

Whenever diversification is expected to occur, we want to find out precisely which frequencies of dormancy will evolve and coexist in the metapopulation. We therefore perform an analysis, which is also based on the invasion capacity of a mutant but assumes a population that is dimorphic with regard to the dormancy frequency. From this analysis, we determine the expected polymorphism of dormancy frequencies (x_1, x_2), and we take the absolute difference between them as a measure of diversification (see Figs 2–6). As the polymorphisms that we found in the dimorphic cases were stable against invasion by nearby mutants, we did not consider the case of a population with three or more residents. It is worth noting that we have checked that our results are consistent with those predicted by a simulation approach, which allows a theoretically infinite number of coexisting strategies within a polymorphism, and in which the effects of mutations are normally distributed (see Appendix S2, supplementary online material).

Parameter values

We focus on the influence of spatial differences in the levels of environmental stochasticity (i.e. differences in the variance of juvenile survival, $S(t)$, between the patches), on the adaptive diversification of dormancy strategies. Each patch has a particular stochastic regime, characterized by the probability that a bad year will occur in patch 1 [$(p_B)_1$] and in patch 2 [$(p_B)_2$] and by the ratio of good-to-bad juvenile survival in patch 1 [$(r_{G/B})_1$] and in patch 2 [$(r_{G/B})_2$].

The between-patch difference in $r_{G/B}$, $(r_{G/B})_1 - (r_{G/B})_2$, is denoted Δ_R . We study the influence of this difference for a between-patch mean value $E(r_{G/B})$ of 6 [$E(r_{G/B}) = [(r_{G/B})_1 + (r_{G/B})_2]/2$]. The value of $r_{G/B}$ is then $(r_{G/B})_1 = E(r_{G/B}) + (\Delta_R/2)$ in patch 1, and $(r_{G/B})_2 = E(r_{G/B}) - (\Delta_R/2)$ in patch 2. The range of Δ_R is [0 : 10].

The conditions for dormancy strategies to diversify in response to a spatial difference in the probability that a bad year will occur, p_B , are studied for a between-patch mean value of p_B , $E(p_B)$, of 0.25 [$E(p_B) = [(p_B)_1 + (p_B)_2]/2$]. The difference in p_B between the patches is noted as Δ_P , and p_B can be calculated in patch 1 as $(p_B)_1 = E(p_B) + (\Delta_P/2)$ and in patch 2 as $(p_B)_2 = E(p_B) - (\Delta_P/2)$. The range of Δ_P is [0 : 0.5]. For example, $\Delta_P = 0.3$ means that the probability that a bad year will occur is 0.4 in patch 1 and 0.1 in patch 2. Increasing Δ_P and Δ_R values are associated with a greater environmental stochasticity in patch 1 and weaker stochasticity in patch 2. It is worth noting that a null value of either Δ_R or Δ_P means that there is no difference in the

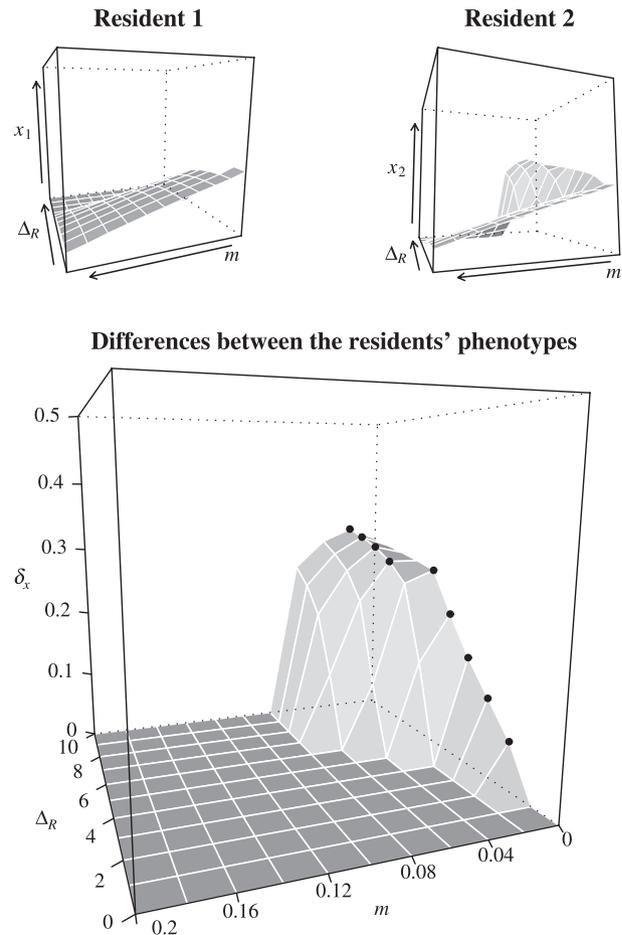
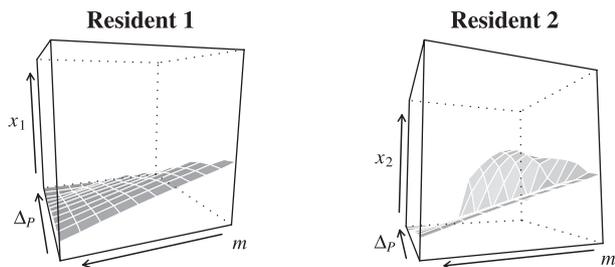


Fig. 2 Evolution of the prolonged dormancy frequency, x , as a response to both the spatial dispersal rate, m , and the difference in the ratio of good-to-bad year survival rates, $r_{G/B}$, between the two patches (Δ_R). The expected strategy for each resident is shown in the top two panels (Resident 1 and Resident 2), and the resulting difference expected in the population, δ_x , is represented in the bottom panel (Differences between the residents' phenotypes). The greatest difference between the strategies of resident 1 and resident 2 is indicated by a solid circle for each value of Δ_R . The probability that a bad year will occur, p_B , is 0.25 in both patches ($\Delta_P = 0$). The values of the other parameters are given in the description of the model. Note that the dotted lines of the delimiting cube are in the back, and that the plotted surface is transparent.

level of stochasticity between the patches, and that the highest values that we used account for a high variance of $S(t)$ in patch 1 and no variance of $S(t)$ in patch 2.

We also studied the influence of the survival rates during dormancy and dispersal (S_d and S_m respectively) on the diversification of dormancy strategies in a landscape with spatial disparities in the level of environmental stochasticity ($\Delta_R = 8$, $\Delta_P = 0$). In all other simulations, the values of S_d and S_m were set to 0.7.

The values for the parameters of the density dependency function, F_{max} and $N_{0.5}$, were fixed on the basis of



Differences between the residents' phenotypes

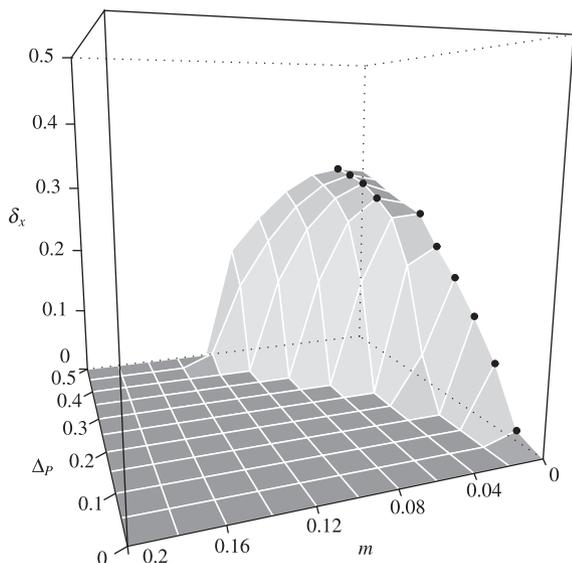
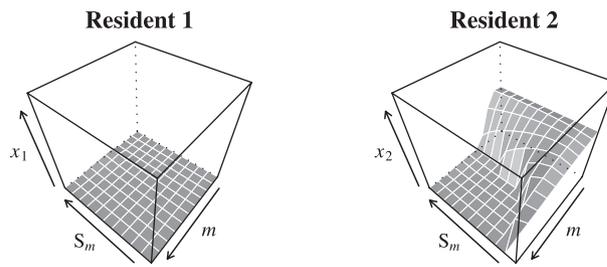


Fig. 3 Evolution of the prolonged dormancy frequency, x , in response to both the spatial dispersal rate, m , and the difference between the patches (Δp) in the probability that a bad year will occur, p_B . The ratio of good-to-bad year survival, r_{GIB} , is 6 in both patches ($\Delta_R = 0$). The values of the other parameters are given in the description of the model. See Fig. 2 for further details.

estimations made in natural populations of the chestnut weevil, *C. elephas* ($F_{max} = 7$ and $N_{0.5} = 500$ respectively; Menu *et al.*, 2000; Debouzie *et al.*, 2002), even though the present model is much simpler. Density dependency can lead to nonlinear population dynamics, which can in turn lead to the evolution of delayed maturation strategies (Bulmer, 1984; van Dooren & Metz, 1998; Lalonde & Roitberg, 2006). We therefore analysed the effect of density dependency on diversification, by means of a sensitivity analysis to β . We used a default value of β (0.007) for which: (i) the population dynamics is stable and (ii) a null dormancy frequency is expected to evolve in the absence of environmental stochasticity (see Appendix S4, supplementary online material).

The influence of a given parameter on the diversification of x was studied as a response to the dispersal rate, m . In this context, a parameter is considered to influence the diversification of x if: (i) it increases the



Differences between the residents' phenotypes

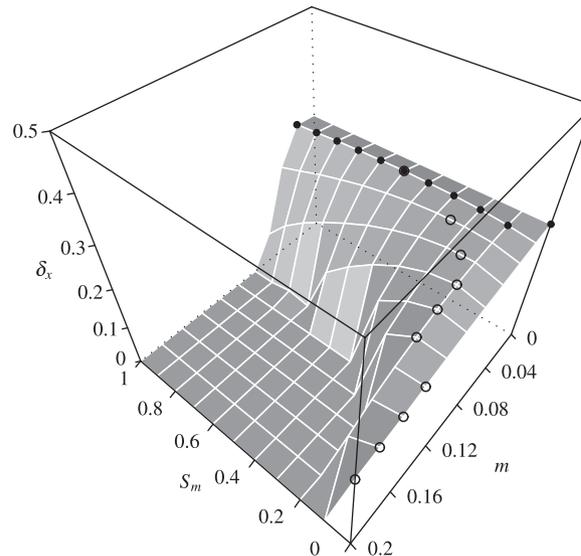


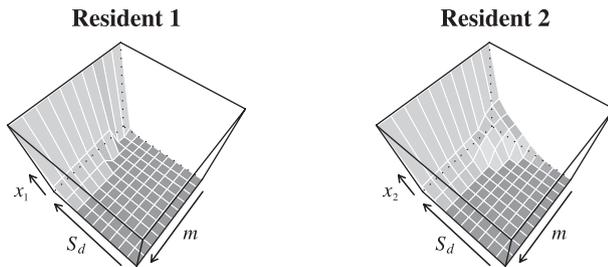
Fig. 4 Evolution of the prolonged dormancy frequency, x , in response to the spatial dispersal rate, m , and to the survival rate during dispersal, S_m . The greatest difference between the strategies of resident 1 and resident 2 is denoted by a solid circle for each value of S_m , and by an open circle for each value of m . The probability that a bad year will occur, p_B , is 0.25 in both patches ($\Delta p = 0$), and the ratio of the good-to-bad year survival rates, r_{GIB} , is 10 in patch 1 and 2 in patch 2 ($\Delta_R = 8$). The values of the other parameters are given in the description of the model. See Fig. 2 for further details.

difference of x between the patches, for a given value of the dispersal rate m and/or (ii) it increases the range of values of m for which diversification occurs. We used three-dimensional representations to study the joint influences on diversification of dispersal and of the parameter of interest.

Results

Diversification of dormancy strategies driven by heterogeneous stochasticity

Figs 2 and 3 show the change in the diversification of dormancy frequencies in response to both the dispersal rate and the difference in the levels of stochasticity



Differences between the residents' phenotypes

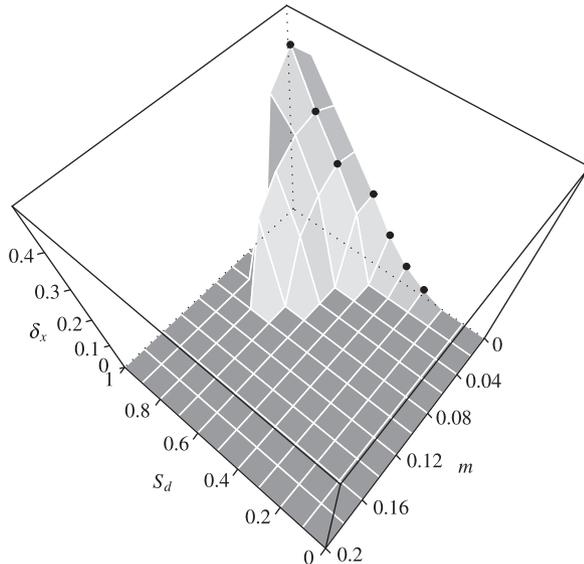
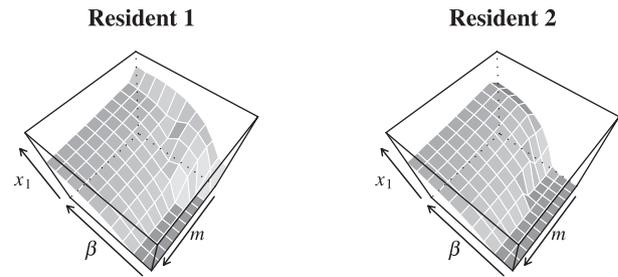


Fig. 5 Evolution of the prolonged dormancy frequency, x , in response to the spatial dispersal rate, m , and to the survival rate during dormancy, S_d . The maximum difference between the strategies of resident 1 and resident 2 is indicated by a solid circle for each value of S_d . The probability that a bad year will occur, p_B , is 0.25 in both patches ($\Delta_p = 0$), and the ratio of the good-to-bad year survival rates, $r_{G/B}$, is 10 in patch 1 and 2 in patch 2 ($\Delta_R = 8$). The values of other parameters are given in the description of the model. See Fig. 2 for further details.

between the two patches. The latter is expressed as the difference in the ratio of good-to-bad year survival rates $r_{G/B}$, Δ_R (Fig. 2), and as the difference in the probability that a bad year will occur p_B , Δ_p (Fig. 3), between the two patches. The diversification of dormancy strategies is quantified by the absolute difference between the evolutionarily expected dormancy frequencies within the metapopulation, δ_x . This variable is shown in the bottom panels of Figs 2–6, and the expected dormancy frequencies in each patch (x_1 and x_2) are shown in the two upper plots of these figures. The relationship that describes the diversification of dormancy frequencies as a response to the level of environmental stochasticity is very similar, whether the latter is due to a difference in $r_{G/B}$ ($\Delta_R > 0$, Fig. 2) or in p_B ($\Delta_p > 0$, Fig. 3). As expected, when the



Differences between the residents' phenotypes

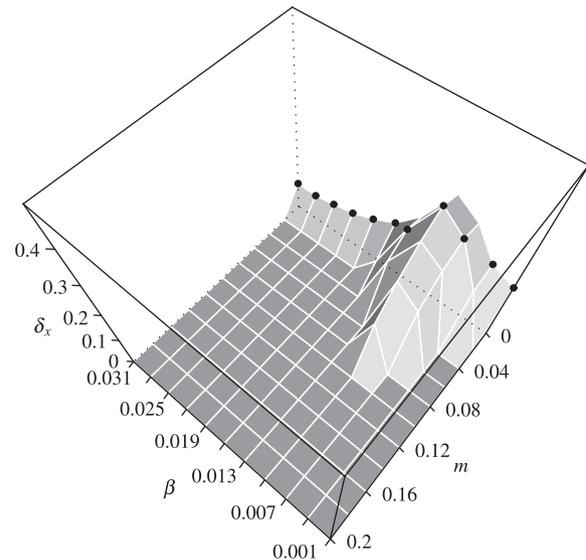


Fig. 6 Evolution of the prolonged dormancy frequency x as a response to the spatial dispersal rate m and to the density dependency parameter β . The maximal difference between resident 1 and resident 2 strategies is indicated by a solid circle for each value of β . The probability for a bad year to occur, p_B , equals 0.25 in each patch ($\Delta_p = 0$), and the ratio of good-to-bad year survival, $r_{G/B}$, equals 10 in patch 1 and 2 in patch 2 ($\Delta_R = 8$). Values of other parameters are given in the model description. See Fig. 2 for further details.

two patches have the same level of stochasticity ($\Delta_p = 0$ and $\Delta_R = 0$), no diversification occurs. At low values of Δ_R and Δ_p , a difference between the dormancy strategies emerges, but only when the dispersal rate is low. As the difference in the stochasticity levels between the two patches increases, diversification occurs at higher dispersal rates. However, when the spatial heterogeneity of the environmental stochasticity is high, diversification of dormancy frequencies occurs at higher dispersal rates if this heterogeneity involves p_B (Fig. 3) rather than $r_{G/B}$ (Fig. 2). Overall, the general trend is for the expected difference between the evolutionarily expected dormancy strategies to increase as the dispersal rate, m , decreases and as the spatial heterogeneity of stochasticity (Δ_R or Δ_p) increases.

Effect on diversification of habitat fragmentation and survival during dormancy

As shown in Fig. 4, a low survival rate during dispersal favours diversification, as does a low dispersal rate. Fragmentation may reduce successful dispersal by reducing survival during dispersal, and thus favour the diversification of dormancy strategies.

We also studied the influence of survival during dormancy, S_d (Fig. 5). The mean selected dormancy rate increases with S_d (see upper panels in Fig. 5). The diversification of dormancy strategies is favoured by an increase in survival during dormancy (for S_d values up to 0.8): both the range of dispersal rates at which diversification occurs and the difference in dormancy strategies for a given value of m increase with S_d . For higher values of S_d , diversification of dormancy strategies becomes less likely, as the range of dispersal rates at which diversification occurs and the difference δ_x both decrease with S_d .

Impact of density dependency

The effect of the density-dependent function is investigated by means of a sensitivity analysis to parameter β (Fig. 6). Increasing values of this parameter lead to an accelerating decrease in the fecundity as the population size increases towards $N_{0.5}$ (see eqn 1 and Appendix 4, supplementary online material). In the context of no environmental stochasticity ($S(t) = 0.3$ each year), the population dynamics become cyclic as $\beta > 0.007$ (assuming that $x = 0$ and $m = 0$, Appendix S4, Fig. S5). Accordingly, a null frequency of dormancy ($x = 0$) can be expected to evolve with the value of β used elsewhere in our study ($\beta = 0.007$) if no environmental stochasticity is considered (Appendix S4).

Environmental stochasticity can drive the evolution of dormancy frequencies, even when β is very low (e.g. 0.001; Fig. 6). In this case, diversification is only expected when the dispersal rate is low, and it is expected to be slight. We found a similar pattern for high values of β . The diversification of dormancy strategies is therefore expected to be the greatest for intermediate values of β ($\beta = 0.01$).

Over-diversification at low dispersal rates

We found a counterintuitive relationship between diversification and dispersal, for high values of Δ_R and Δ_P (see Figs 2–6): the highest diversity of dormancy frequencies in the metapopulation is not expected when no dispersal occurs, but rather when a small number of individuals disperse. We designate this phenomenon as ‘over-diversification’, as the expected spatial difference in the trait is higher than that expected in the absence of dispersal. The dispersal rate, m , at which diversification is maximized increases with Δ_R , Δ_P and S_m (Figs 2–4). One can see

in Fig. 6 that such an over-diversification occurs for intermediate values of the density dependency parameter β , at which diversification is favoured.

Discussion

Theoretically, low dispersal and selection against genotypes adapted to other localities are two necessary conditions for the evolution of local adaptations (Kawecki & Ebert, 2004). We confirmed that major differences in the level of environmental stochasticity between the patches, combined with a low dispersal rate, should favour the adaptive diversification of dormancy frequencies. When environmental stochasticity displays marked spatial disparities and the dispersal rate is low, natural selection should favour genotypes that have specialized to cope with the levels of stochasticity encountered within each patch. As the dispersal rate increases, individuals with a dormancy frequency specialized to suit one patch have less evolutionary advantage because they are increasingly likely to encounter stochastic environments (frequency of bad years, amplitude of the difference between bad and good years) to which they are not adapted (after migrating to the other patch). Hence, when the dispersal rate is high, an intermediate dormancy strategy (i.e. a generalist strategy) can be expected to be selected because it confers higher mean fitness at the metapopulation level than either local specialist.

An increase in the survival rate during dispersal, S_m , is expected to impede the adaptive diversification of dormancy frequencies. Accordingly, diversification may depend on the rate of successful dispersal, which is determined by both the dispersal rate and survival during dispersal. Hence, diversification of dormancy frequencies is expected to be favoured in a fragmented landscape (i.e. a landscape with a low S_m) with spatial differences of environmental stochasticity.

As one would expect from previous studies (Cohen, 1966; Bulmer, 1984; Ellner, 1985a,b; Menu *et al.*, 2000), we found that the frequency of dormancy expected in each patch increases with the probability of surviving throughout dormancy (S_d). However, the greatest diversification is expected for high values of this survival rate, but not 1 (for example, in Fig. 5, maximum diversification is expected for $S_d = 0.9$ when $m = 0.02$). As Ellner, 1985a) pointed out, in the unlikely case of S_d reaching a value of 1, a dormancy frequency of 1 can be considered an ESS because the number of dormant individuals becomes constant and cannot decrease. As the same strategy is selected in each patch, no diversification is predicted when $S_d = 1$, and maximum diversification is instead expected to occur at intermediate values of survival during dormancy.

The evolution of dormancy frequencies is expected to be driven by: (i) environmental stochasticity, (ii) density dependency (the regulation of the population growth

rate as a function of density) and (iii) the interaction between these two factors, known as ‘chaotic stochasticity’ (Rand & Wilson, 1991). The pattern of diversification according to the density dependency parameter β , i.e. maximum diversification at intermediate values of β (Fig. 6), is then explained by at least one of these factors.

First, according to Lalonde & Roitberg (2006), we show that density dependency alone may play a considerable role in the evolution of the mean dormancy frequency in the metapopulation (Appendix S4, supplementary online material). However, in our model, the same density dependency function is used in both patches, and accordingly density dependency alone cannot account for the diversification observed. Second, spatial differences in the level of environmental stochasticity can lead to the evolution of different dormancy strategies within the metapopulation. Nevertheless, environmental stochasticity, which is independent of the value of parameter β , cannot explain the pattern of diversification according to β . The interaction between environmental stochasticity and density dependency is therefore crucial for explaining the pattern of spatial differences in the frequency of dormancy. Such an interaction may find two nonexclusive explanations: (i) the difference in the level of environmental stochasticity should lead to different population dynamics between the patches and/or (ii) the impact of environmental stochasticity on fecundity should depend on the value of β .

Explanation (i) implies that cyclic or chaotic dynamics occur at lower values of β in the most variable patch, so that there is a range of values for this parameter at which population dynamics are cyclic or chaotic in the most variable patch but not in the less variable one (this is due to a difference in juvenile survival during good years; see Appendix S5, supplementary online material, for detailed results and discussion). In that range of β values, variability in population densities due to chaotic dynamics is thus increased in the most variable patch, which should favour the evolution of a high dormancy frequency, whereas it is not the case in the less variable patch. This difference in population dynamics between the patches is due to a difference in juvenile survival during good years, which is higher in the most variable patch (see eqn 3 and Appendix S5). This hypothesis, however, does not seem to explain completely the pattern of diversification observed: at the value of β maximizing the difference in dormancy frequencies between the patches ($\beta = 0.01$), population dynamics in good year conditions are also unstable in the less variable patch, which should reduce the differences in variability of population densities between the patches and thus hinder the diversification of dormancy (Appendix S5).

Explanation (ii) considers that the impact of environmental stochasticity on fecundity depends on the value of β (see Appendix S6, supplementary online material, for detailed results and discussion). When β increases towards 0.01, a given change in population density due

to environmental stochasticity leads to a greater change in fecundity. Hence, one can expect the local effects of environmental stochasticity to be amplified in that context, and to a greater extent when β approaches 0.01. Such amplification should increase the difference in the variance of population densities between the patches, and thus increase the diversification of dormancy frequencies. However, as β increases over 0.01, chaotic dynamics frequently lead population densities to be either high or low (Fig. S9, Appendix S6). The density dependency function is flat for such densities, and thus a given change in population density due to environmental stochasticity leads to a small change in fecundity. In that context, fluctuations in population densities due to environmental stochasticity are poorly amplified and the dormancy frequencies tend to be similar in both patches.

We found that the greatest diversity within the metapopulation is sometimes obtained with a dispersal rate that is low, but not null, and we have designated this phenomenon as ‘over-diversification’. This outcome could be explained by the qualitative change in competition in the more variable patch due to dispersal. The strength of competition should depend on the kind of year because individuals dispersing from the patch with low variability, and so which are less likely to enter dormancy, may increase in frequency as they encounter favourable conditions. In order to avoid periods of strong competition with the specialist of the patch with low variability, dispersal may thus favour an increase in the dormancy frequency of the resident adapted to the highly variable patch. As far as we are aware, such a pattern has never previously been reported in a context of local adaptation. However, the increase in the diversity of dormancy frequencies due to over-diversification is low in our results, and further theoretical work is needed before we can infer whether it is specific to stochastic environments and bet-hedging, or can be extrapolated to other contexts.

We showed that local adaptation of bet-hedging dormancy strategies is a possible outcome in a landscape characterized by spatially heterogeneous stochasticity. We propose that the between-population variability of dormancy strategies, which has been reported from empirical studies (Philippi, 1993a; Oberli, 2001; Cáceres & Tessier, 2003), can be attributed, at least in part, to differences in the level of environmental stochasticity between localities. Clauss & Venable (2000) found a relationship between dormancy strategies in populations of *P. insulari* and fluctuation rates in the annual precipitation that they encounter. These findings are consistent, at least to some extent, with local adaptation of these populations. However, there is an urgent need for further empirical investigations of the bet-hedging strategies adopted in different localities, together with the levels of environmental stochasticity encountered by these populations, and with the connections between them as a result of dispersal. It is also crucial to determine the shape of the density dependency function, as our

model shows that this parameter can greatly influence the diversification of dormancy strategies.

The paucity of such integrative studies may be linked to the difficulty of conducting long-term field surveys. They could be facilitated by using very dissimilar populations, either with very different levels of environmental stochasticity or among which very different bet-hedging strategies are observed. A few species in which bet-hedging dormancy strategies have been studied for several years (e.g. *P. insulari*, Clauss & Venable, 2000; *D. pulicaria*, Cáceres & Tessier, 2003; *C. elephas*, Menu & Debouzie, 1993; Menu & Desouhant, 2002) are good candidates for studying local adaptation in the field. Studies of micro-organisms could also be helpful because of their short generation time, which would make it possible to choose the stochastic regime they encounter in the laboratory, or/and to carry out accurate and quick determinations of the stochastic regime they encounter in the field.

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References

- Balaban, N.Q., Merrin, J., Chait, R., Kowalik, L. & Leibler, S. 2004. Bacterial persistence as a phenotypic switch. *Science* **305**: 1622–1625.
- Bulmer, M.G. 1984. Delayed germination of seeds: Cohen's model revisited. *Theor. Popul. Biol.* **26**: 367–377.
- Cáceres, C.E. & Tessier, A.J. 2003. How long to rest: the ecology of optimal dormancy and environmental constraint. *Ecology* **84**: 1189–1198.
- Clauss, M.J. & Venable, D.L. 2000. Seed germination in desert annuals: an empirical test of adaptive bet hedging. *Am. Nat.* **155**: 168–186.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.* **12**: 119–129.
- Cooper, W.S. & Kaplan, R.H. 1982. Adaptive "coin-flipping": a decision-theoretic examination of natural selection for random individual variation. *J. Theor. Biol.* **94**: 135–151.
- Danforth, B.N. 1999. Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. *Proc. R. Soc. Lond. B Biol. Sci.* **266**: 1985–1994.
- Debouzie, D., Desouhant, E., Oberli, F. & Menu, F. 2002. Resource limitation in natural populations of phytophagous insects. A long-term study case with the chestnut weevil. *Acta Oecol.* **23**: 31–39.
- van Dooren, T.J.M. & Metz, J.A.J. 1998. Delayed maturation in temporally structured populations with non-equilibrium dynamics. *J. Evol. Biol.* **11**: 41–62.
- Ellner, S. 1985a. Ess germination strategies in randomly varying environments. I. Logistic-type models. *Theor. Popul. Biol.* **28**: 50–79.
- Ellner, S. 1985b. Ess germination strategies in randomly varying environments. II. Reciprocal yield-law models. *Theor. Popul. Biol.* **28**: 80–116.
- Evans, M.E.K., Ferriere, R., Kane, M.J. & Venable, D.L. 2007. Bet hedging via seed banking in desert evening primroses (oenothera, onagraceae): demographic evidence from natural populations. *Am. Nat.* **169**: 184.
- Geritz, S., Kisdi, E., Meszéna, G. & Metz, J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**: 35–57.
- Hairston, N.G.J. & Munns, W.R.J. 1984. The timing of copepod diapause as an evolutionarily stable strategy. *Am. Nat.* **123**: 733–751.
- Halkett, F., Harrington, R., Hullé, M., Kindlmann, P., Menu, F., Rispé, C. & Plantegenest, M. 2004. Dynamic of production of sexual forms in aphids: Theoretical and experimental evidence for adaptive "coin-flipping" plasticity. *Am. Nat.* **163**: E112–E125.
- Jansen, V.A.A. & Stumpf, M.P.H. 2005. Making sense of evolution in an uncertain world. *Science* **309**: 2005–2007.
- Kawecki, T.J. & Ebert, D. 2004. Conceptual issues in local adaptation. *Ecol. Lett.* **7**: 1225–1241.
- King, O.D. & Masel, J. 2007. The evolution of bet-hedging adaptations to rare scenarios. *Theor. Popul. Biol.* **72**: 560–575.
- Kisdi, É. & Meszéna, G. 1993. Density dependent life history evolution in fluctuating environments. *Lect. Notes Biomath.* **98**: 26–62.
- Klinkhamer, P.G.L., Jong, T.J.D., Metz, J.A.J. & Vai, J. 1987. Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theor. Popul. Biol.* **32**: 127–156.
- Kussell, E. & Leibler, S. 2005. Phenotypic diversity, population growth, and information in fluctuating environments. *Science* **309**: 2075–2078.
- Kussell, E., Kishony, R., Balaban, N.Q. & Leibler, S. 2005. Bacterial persistence a model of survival in changing environments. *Genetics* **169**: 1807–1814.
- Lalonde, R.G. & Roitberg, B.D. 2006. Chaotic dynamics can select for long-term dormancy. *Am. Nat.* **168**: 127–131.
- Lytte, D.A. & Poff, N.L.R. 2004. Adaptation to natural flow regimes. *Trends Ecol. Evol.* **19**: 94–100.
- Masel, J. 2005. Evolutionary capacitance may be favored by natural selection. *Genetics* **170**: 1359–1371.
- Mathias, A. & Kisdi, E. 2002. Adaptive diversification of germination strategies. *Proc. R. Soc. Lond. B Biol. Sci.* **269**: 151–155.
- Mathias, A., Kisdi, E. & Olivieri, I. 2001. Divergent evolution of dispersal in a heterogeneous landscape. *Evolution* **55**: 246–259.
- McPeck, M.A. & Holt, R.D. 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* **140**: 1010–1027.
- Menu, F. 1993. Strategies of emergence in the chestnut weevil *Curculio elephas* (coleoptera: Curculionidae). *Oecologia* **96**: 383–390.
- Menu, F. & Debouzie, D. 1993. Coin-flipping plasticity and prolonged diapause in insects: example of the chestnut weevil *Curculio elephas* (coleoptera: Curculionidae). *Oecologia* **93**: 367–373.
- Menu, F. & Desouhant, E. 2002. Bet-hedging for variability in life cycle duration: bigger and later-emerging chestnut weevils have increased probability of a prolonged diapause. *Oecologia* **132**: 167–174.
- Menu, F., Roebuck, J. & Viala, M. 2000. Bet-hedging diapause strategies in stochastic environments. *Am. Nat.* **155**: 724–734.

- Metz, J., Nisbet, R. & Geritz, S. 1992. How should we define 'fitness' for general ecological scenarios? *Trends Ecol. Evol.* **7**: 198–202.
- Metz, J.A.J., Geritz, S.A.H., Mesz ena, G., Jacobs, F.J.A. & van Heerwaarden, J.S. 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: *Stochastic and Spatial Structures of Dynamical Systems* (S.J. Van Strien & S.M. Verduyn Lunel, eds), pp. 183–231. Amsterdam, North Holland.
- Oberli, F. 2001. *Influence de l'hote vegetal et de l'heterogeneite spatiale et temporelle de l'environnement sur l'evolution des traits d'histoire de vie chez les insectes phytophages. Exemple du balanin de la chataigne, Curculio elephas Gyll.* (Coleoptere, Curculionidae). PhD thesis, Universit  Lyon 1.
- Philippi, T. 1993a. Bet-hedging germination of desert annuals: beyond the first year. *Am. Nat.* **142**: 474–487.
- Philippi, T. 1993b. Bet-hedging germination of desert annuals: variation among populations and maternal effects in *Lepidium lasiocarpum*. *Am. Nat.* **142**: 488–507.
- Philippi, T. & Seger, J. 1989. Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* **4**: 41–44.
- Rand, D.A. & Wilson, H.B. 1991. Chaotic stochasticity: a ubiquitous source of unpredictability in epidemics. *Proc. Biol. Sci.* **246**: 179–184.
- Sasaki, A. & Ellner, S. 1995. The evolutionarily stable phenotype distribution in a random environment. *Evolution* **49**: 337–350.
- Seger, J. & Brockmann, H.J. 1987. What is bet-hedging? *Oxford Surveys Evol. Biol.* **4**: 182–211.
- Stumpf, M.P.H., Laidlaw, Z. & Jansen, V.A.A. 2002. Herpes viruses hedge their bets. *Proc. Natl Acad. Sci. USA* **99**: 15234–15237.
- Tuljapurkar, S.D. & Orzack, S.H. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theor. Popul. Biol.* **18**: 314–342.
- Venable, D.L. & Brown, J.S. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* **131**: 360–384.
- Waxman, D. & Gavrillets, S. 2005. Target review: 20 questions on adaptive dynamics. *J. Evol. Biol.* **18**: 1139–1154.
- Yoshimura, J. & Clark, C.W. 1991. Individual adaptations in stochastic environments. *Evol. Ecol.* **5**: 173–192.

Supporting information

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

Appendix S1 Sensitivity to spatial autocorrelation.

Appendix S2 Simulation procedures.

Appendix S3 Robustness of the results.

Appendix S4 Role of density dependency.

Appendix S5 Interaction between environmental stochasticity and density dependency. I. Differences in population dynamics between the patches.

Appendix S6 Interaction between environmental stochasticity and density dependency. II. Impact of stochasticity as a function of β .

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