The influence of fluctuating population densities on evolutionary dynamics

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Abstract

The causes and consequences of disturbances and fluctuating population densities have been an important topic in ecological literature for decades. Whilst it is understood that certain types of disturbances can promote diversity, the effects of fluctuations on maintenance of variation in spatially structured population have received little analytical treatment. Here, we study a simple model where two discrete types inhabit two habitats with migration between them and a trade-off in selection. Starting with a model where fluctuations arise due to overcompensating density dependence, we then reduce it to a mainland-island system with imposed fluctuations to obtain simple conditions for maintenance of diversity under fluctuating densities. We explain these conditions in terms of the strength of selection, migration between the habitats, and the extent of fluctuations. Whereas weak fluctuations hardly affect coexistence, strong recurrent fluctuations lead to extinction of the type better adapted to the fluctuating habitat even when dispersal is low. There is a disadvantage to specialization to a habitat with a high intrinsic rate of increase, as it makes the population vulnerable to swamping from more stable habitats – even if the invader is maladapted. This result is consistent with the difficulties of finding chaos in nature.

Keywords: *eco-evolutionary dynamics, fluctuating environment, migration-selection balance, Ricker model, discrete time, haploid*

Introduction

The evolutionary theory behind maintenance of variation in natural populations often focuses on the balance between selection, migration and mutation (Levene, 1953; Maynard Smith, 1970; Bulmer, 1972) and over time, the conditions for maintenance of polymorphism have been analyzed for increasingly complex systems with many loci, alleles and demes (reviewed in Bürger 2014). Yet typically, population dynamics are considered fast enough so that they do not need to be modeled explicitly – an assumption that we relax in this work.

The importance of out-of-equilibrium population dynamics has been long recognized in ecological theory (Levins, 1979; Hastings, 2004). Large temporal fluctuations in population density can arise under overcompensating density dependence in both natural and experimental populations (Costantino et al., 1995; Turchin et al., 2000; Coulson et al., 2001) or can be imposed by fluctuations in the environment. In general, they are likely to be driven by a combination of the two (Ellner and Turchin, 1995; Grenfell et al., 1998). With the discovery that large and irregular (chaotic) fluctuations can be driven by very simple dynamics (Lorenz, 1963) such as density dependence or predator-prey interactions (May, 1972, 1974), they have gained prominence in ecological modeling.

Local disturbances creating large fluctuations in the size of the affected subpopulations can lead to local extinctions and may affect the persistence of the whole population. Yet, dispersal among subpopulations can strongly mitigate the extent of fluctuations, diminishing the risk of extinction in spatially structured populations (Den Boer, 1968; Reddingius and Den Boer, 1970; Roff, 1974). The balancing impact of migration on demographic stability has received more theoretical attention since. Specifically, fluctuations due to overcompensating density dependence are strongly dampened by dispersal between subpopulations (Ruxton, 1994; Stone and Hart, 1999), as immigration from more populated patches pushes the local population size away from zero. Thus, overshooting of the carrying capacity due to delayed feedback is diminished and the population densities remain closer to the carrying capacity. Even weak migration can have a strong stabilizing effect such that no chaotic dynamics in the system ever build up.

Whilst dispersal stabilizes ecological dynamics of a single species in the presence of disturbances, the effect of the interplay of dispersal and disturbances on diversity is a lot less clear. A large body of ecological theory focuses on finding conditions which promote

coexistence. In spatially structured habitats, local disturbances, leading to fluctuations in population size, can promote diversity when there are specific trade-offs related to colonization ability and/or adaptation at low *vs.* high densities (Hastings, 1980; Comins and Noble, 1985; Tilman et al., 1994; Chesson, 2000; Yodzis, 2013). The inferior competitors persist by virtue of greater dispersal ability or lower mortality rates (Tilman et al., 1997).

In contrast, evolutionary theory typically assumes that there is a trade-off in adaptation to a heterogeneous environment which is independent of population dynamics. Ecological parameters like dispersal ability and intrinsic rate of increase are often held constant – or demographic dynamics are fully neglected. When the environment varies across space, dispersal between two habitats brings in locally maladapted variants – whilst this increases local variation, it may ultimately lead to swamping of all habitats by the type with a higher geometric mean fitness (reviewed in Lenormand 2002). For stable polymorphism to be maintained, the stronger the migration between the niches, the tighter must be the symmetry between the selection underlying the negative trade-offs in fitness in the different niches (Maynard Smith, 1970; Bulmer, 1972; Bürger, 2014). The balance between the trade-offs in selection, and between the flows among the independently-regulated habitats is of known importance. Yet, to our knowledge, it is not known whether the classic predictions are robust when population dynamics within the niches are taken into account.

Here, we extend the classic evolutionary theory by asking how the conditions for maintenance of diversity change when population density fluctuates. Specifically, we study coexistence of two discrete types (genotypes, species, bacterial clones) with a trade-off in adaptation to two habitats which are coupled by migration. Many previous studies focused either on evolutionary dynamics in subdivided habitats or on complex ecological dynamics arising from overcompensating density dependence (Ruxton, 1994; Costantino et al., 1997; Stone and Hart, 1999). We start by modeling these two processes jointly and then analyze a simplification with imposed fluctuations in population size. We thus obtain a qualitative insight into the effect of fluctuations in population densities on evolutionary dynamics – whether these are due to extrinsic disturbances or arise from complex ecological population dynamics.

Models and methods

To study the influence of fluctuations in population density on deterministic evolutionary dynamics, population dynamics are modeled jointly with the dynamics of the change in frequency of two types. These could represent two species or two different alleles in a one locus haploid system – we will use the latter interpretation and focus on maintenance of polymorphism. A relatively complex model where local endogenous fluctuations may arise due to overcompensating density dependence in two divergent habitats, is followed by a simplified version with exogenous fluctuations imposed on a subpopulation's density.

We start with numerical demonstrations of temporal dynamics, and progress to stability analyses in the absence as well as in the presence of fluctuations. All results presented in the stability analyses are analytic. However, as most expressions are rather extensive and complicated, they are evaluated numerically and visualized in graphics. The stability analysis was assessed via the leading eigenvalues of the corresponding systems, and by the conditions for a protected polymorphism (which – in the case of two haploids in two demes – implies global convergence; Karlin and Campbell 1980). For more details see the supporting information (SI, section S1).

Density dependent regulation of population densities (endogenous fluctuations)

First, we address a two-niche model with migration and joint evolutionary and ecological dynamics, where the latter are modeled by Ricker's regulation (Ricker, 1954). Importantly, as we assume discrete generations, a delayed feedback in density regulation can cause large fluctuations of the population size beyond the carrying capacity. We consider niche optima which are stable in time.

The life cycle starts with migration, where m_{12} denotes the migration rate from deme 1 into deme 2, and m_{21} the migration rate in the opposite direction. Throughout our analyses, we will mainly focus on the special case of symmetric migration $m_{12} = m_{21} = m \leq 1/2$.

At generation t, deme i is described by the population size, $N_i(t)$, and the frequency of the focal allele A, $p_i(t)$. (We denote the second allele by a.) For simplicity, prime ' labels the intermediate variables after migration (before selection and population growth).

Following migration, the number of individuals in deme 1 is

$$N_1'(t) = (1 - m_{12})N_1(t) + m_{21}N_2(t) \tag{1}$$

and the frequency of allele A in deme 1 is given by

$$p_1'(t) = \frac{(1 - m_{12})p_1(t)N_1(t) + m_{21}p_2(t)N_2(t)}{N_1'(t)} \tag{2}$$

(and conversely for deme 2).

We assume there is a negative trade-off in the fitness of the alleles A and a in the two niches. The fitnesses of allele A are $w_{1A} = 1$ and $w_{2A} = 1 - s_2$ in niches 1 and 2 respectively, and the corresponding fitnesses of allele a are $w_{1a} = 1 - s_1$ and $w_{2a} = 1$ (see left-hand side of Fig. 1 for visualization). The selection coefficients s_1, s_2 range between 0 and 1. Thus, the focal allele A has a fitness advantage in niche 1 whereas a is better adapted to niche 2. In the next generation (after migration and selection), allele frequency of A in each deme i is

$$p_i(t+1) = p_i'(t) \cdot \frac{w_{iA}}{\overline{w}_i'(t)} \tag{3}$$

where $\overline{w}_i'(t)$ denotes the mean fitness after migration in deme i. It is given by

$$\overline{w}_i'(t) = p_i'(t)w_{iA} + (1 - p_i'(t))w_{ia} \tag{4}$$

Population growth is density-dependent, following Ricker's regulation (Ricker, 1954). The population size in each deme i after migration and selection is

$$N_i(t+1) = N_i'(t) \cdot e^{r_i\left(1 - \frac{N_i'(t)}{K_i}\right)\overline{w}_i'(t)} \tag{5}$$

Here, r_i denotes the intrinsic rate of increase, which gives the maximum growth rate of the population at low densities. Importantly, the rate r_i is assumed to be a property of the niche rather than the types. This is a valid assumption when both types compete for the same resource within a niche. However, we suppose that the effective intrinsic rate of increase declines due to maladaptation (by multiplying the mean fitness $\overline{w}_i'(t)$ to the exponent): a maladapted population is not able to exploit the potential intrinsic rate of increase r_i. The carrying capacity of a niche, though, remains unaltered by maladaptation and is given by K_i. Throughout, we will consider niches with equal

carrying capacity, i.e. $K = K_1 = K_2$, unless explicitly stated differently.

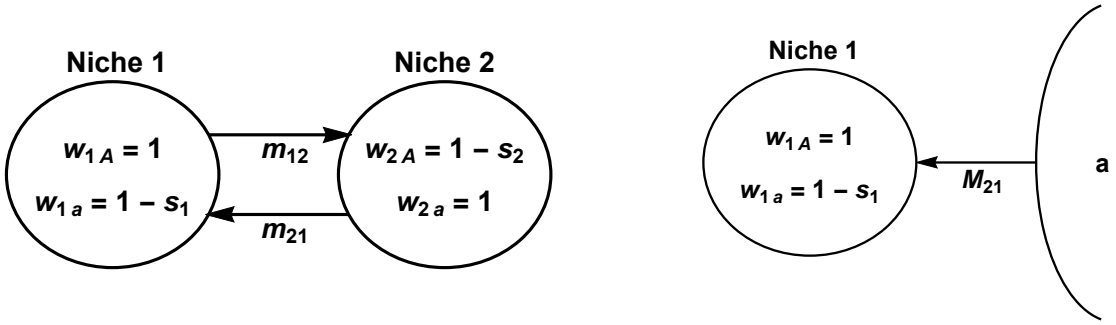

Figure 1: **Evolution and maintenance of variation in the face of gene flow between populations in two divergent habitats.** Left-hand side: Bidirectional migration between two ecological niches with forward migration rates m_{12} and m_{21}. Type A is better adapted to niche 1; type a to niche 2. Right-hand side: Continent-island model with monomorphic immigration of the locally maladapted type a to the island. M_{21} denotes the absolute number of immigrants per generation.

Imposed population densities (exogenous fluctuations)

While fluctuations in the population size arising under high intrinsic rate of increase due to overcompensating density regulation such as over-exploitation of the resource or cannibalism are well documented (Symonides et al. 1986; Costantino et al. 1995; Turchin et al. 2000), it is useful to examine a simpler system where fluctuations in the population density are imposed.

In this second model, we place fluctuations D_1 in the population density of niche 1: we assume that the population size in niche 1 periodically fluctuates between two densities $K_1 - D_1$ and $K_1 + D_1$ whereas the population in niche 2 maintains a constant density K_2 (Fig. S2 in SI). Again, we concentrate on the case $K = K_1 = K_2$. The equations for the evolutionary dynamics remain unchanged.

Finally, we analyze the most simplified setting, with unidirectional migration and imposed fluctuations, i.e. a continent-island model with a monomorphic continent and imposed fluctuations on the island (see right-hand side of Fig. 1): every generation, a constant absolute number M_{21} (corresponding to $m_{21}K_2 = m_{21}K_1$) of type a individuals migrate to the island, where they are locally maladapted ($w_{1a} = 1 - s_1$). The population size on the island fluctuates between $K_1 + D_1$ and $K_1 - D_1$ in subsequent generations. (We assume that "regulation" is strong enough to counteract the ecological effects of

immigration.) In this context, we can find an explicit solution for the equilibrium frequency of the focal type A on the island (see SI, section S7) and two comprehensible inequalities as condition for coexistence.

Results

The impact of fluctuating population sizes on maintenance of diversity in spatially structured populations is studied using a simple model of two discrete types living in two habitats with migration between them. There is a trade-off in the adaption to the two habitats which also differ in their inherent productivity. The productivity of a habitat determines the attainable intrinsic rate of increase of the local population – where a high intrinsic rate of increase can lead to overcompensation and naturally fluctuating population densities. Numerical demonstrations of the temporal dynamics – showing that allele frequencies can change significantly due to ecological feedback arising from fluctuating population sizes – are followed by a stability analysis of the polymorphic equilibrium. This extends the classic conditions on maintenance of diversity under selection and migration by including the effect of fluctuating population densities.

We prove that the outcome of evolution strongly depends on whether the ecological dynamics maintain constant densities or exhibit fluctuations (which can arise from intrinsic dynamics or can be imposed extrinsically). When the density of a subpopulation fluctuates, allele frequencies converge to a different equilibrium than predicted for population densities that are stable in time – see Fig. 2.

In the absence of ecological dynamics, we can predict the allele frequencies maintained at equilibrium. These evolutionary predictions continue to be true when population dynamics are included as long as they lead to a stable, constant density (Fig. 2B, dashed lines). Whenever population densities tend to (and remain at) carrying capacity, allele frequencies converge to the unique, stable and globally attracting equilibrium predicted in the absence of ecology (see Karlin and Campbell (1980) for the proof of global convergence, and S1.1 for the analytic expression of the polymorphism). When the trade-off in selection is symmetric, this equilibrium is always polymorphic in the absence of fluctuations. Hence, even if the focal, locally adapted, type is initially rare, it is able to invade and reach high frequencies.

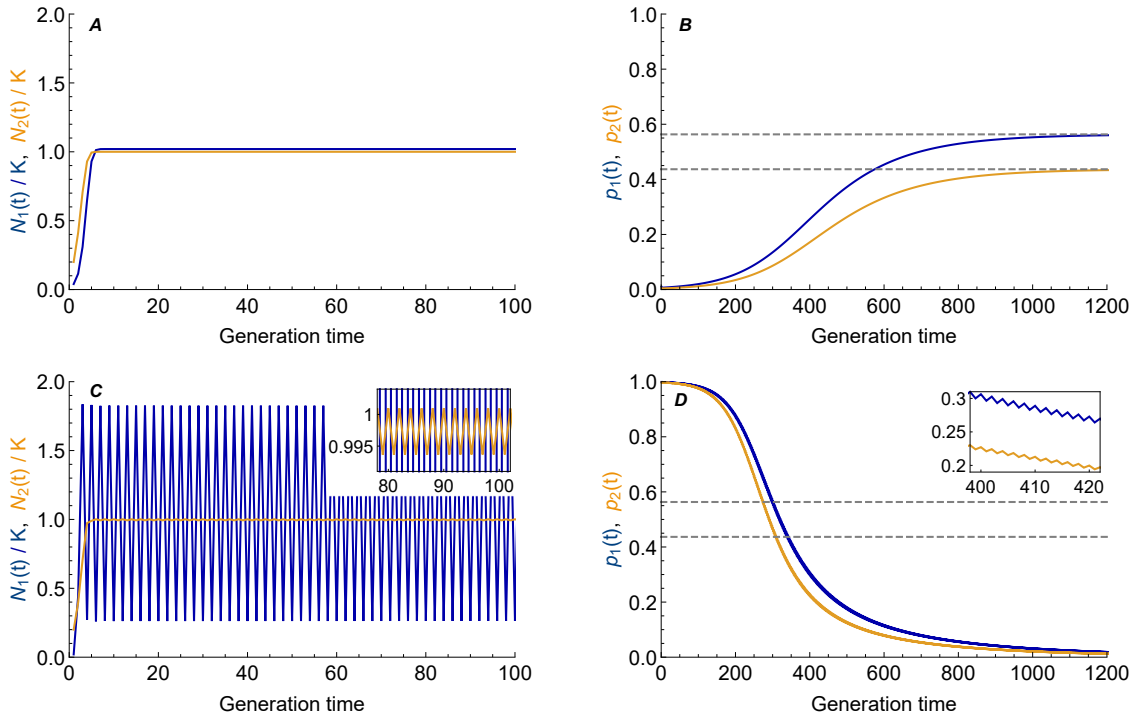

Figure 2: **Ecological dynamics can change the evolutionary predictions.** (A, C): Population dynamics in deme 1 (blue) and deme 2 (dark orange) – under low vs. high intrinsic rate of increase in deme 1 (A $r_1 = 1$ *vs.* C $r_1 = 2.5$). In (A) the population sizes at equilibrium are equal (but N_1/K is offset by 0.02 for visual clarity). (C) In deme 2, intrinsic rate of increase is low enough ($r_2 = 1$) so that the density stays nearly constant (see inset) at carrying capacity despite the strong fluctuations in deme 1. (B, D): The allele frequency p of type A, which is favored in niche 1, is shown in blue for deme 1 and in dark orange for deme 2. The dashed lines represent the expected allele frequencies of the system in the absence of ecology. When population dynamics lead to a stable constant equilibrium (A), evolutionary dynamics behave as predicted (B, dashed lines): even when initially rare ($p_1(0) = 0.01$, $p_2(0) = 0.005$), the focal type is able to invade and its frequency converges to the globally asymptotically stable evolutionary equilibrium predicted in the absence of population dynamics. However, as the population density in niche 1 fluctuates due to overcompensating density dependence (C, blue), frequency of the locally favored type A decreases in the whole system (D). Although initially very frequent ($p_1(0) = 0.999$, $p_2(0) = 0.997$), the focal type eventually dies out due to the fluctuations in the niche where it is better adapted to. The inset highlights the fluctuations in the allele frequencies, which are due to the fluctuating population density. Parameters: $s_1 = s_2 = 0.05$, $m_{12} = m_{21} = 0.1$, $r_1 = 1$ (A, B), $r_1 = 2.5$ (C, D), $r_2 = 1$, $K = K_1 = K_2$.

In nature, population densities are not always constant. Fluctuations may arise under a high intrinsic rate of increase, where population size starts overshooting the carrying capacity and delayed feedback in density regulation leads to overcompensation (Fig. 2C).

Such fluctuations occurring in the density within one of the niches can markedly change the evolutionary outcome. Notably, fluctuations are disadvantageous to the type that is better adapted to this "fluctuating" niche. Fig. 2D shows that a high intrinsic rate of increase in niche 1 leads to a decline in the equilibrium frequency of the type adapted to this niche (which then exhibits fluctuations in population size). Strong fluctuations in the density of a subpopulation can ultimately lead to extinction of the type that is best adapted to the focal environment. This is true even if the focal type is initially abound and even if it would converge to high frequencies in the absence of fluctuations.

The focus of this paper lies in explaining the phenomenon that fluctuations in the density of a subpopulation may ultimately lead to extinction of the type which is best adapted to the niche where these fluctuations occur.

The effect of population dynamics on the evolutionary equilibrium depends on the strength of the fluctuations

How does the equilibrium frequency of the focal type depend on the amplitude of fluctuations in population density? First, for fluctuations arising due to overcompensating density dependence, we need to understand the phases that the population dynamics undergo as the intrinsic rate of increase rises (Fig. 3A). The population size converges towards a stable equilibrium at carrying capacity as long as the intrinsic rate of increase is smaller than a threshold. In the absence of selection and migration from a neighboring niche, this threshold equals 2 for the Ricker model (May and Oster, 1976). As the intrinsic rate of increase within a niche rises above this threshold, the ecological equilibrium becomes unstable and the population size within that niche oscillates due to overshooting of the carrying capacity and overcompensating density regulation. The larger the intrinsic rate of increase, the stronger are overshooting and overcompensation, which leads to oscillations of higher period and eventually to chaotic behavior, whenever migration is absent or really weak. With migration, however, the ecological dynamics is substantially stabilized: fluctuations due to overcompensating density regulation in the focal niche are dampened by dispersal when the other niche maintains a more stable density. By pushing the population density away from zero, even weak migration dampens fluctuations sufficiently so that the long-term behavior of the population dynamics in the focal niche (Fig. 3A) does no longer portrait the classic chaotic branching diagram of a single population under Ricker's regulation (Stone and Hart, 1999). Additionally, in our model selection lowers the mean fitness and hence the effective intrinsic rate of increase (see Eq. 5) – therefore, the stronger the selection, the higher the threshold for

branching. A detailed analysis of Ricker's regulation, the population dynamics, their stability analysis, branching points and how they are influenced by migration and selection can be found in the SI, section S2 (Fig. S3, S4).

The amplitude of endogenous fluctuations rises with the intrinsic rate of increase, which thus changes the evolutionary equilibrium. As long as the intrinsic rate of increase r_1 is smaller than the threshold discussed above and therefore supporting stable population sizes, the allele frequencies maintained at equilibrium are independent of the population dynamics (Fig. 2A, B). In contrast, above the threshold, the population size in niche 1 keeps fluctuating around the carrying capacity, thus driving a decline in the equilibrium frequency of the locally adapted type A (see Fig. 3B). Eventually, when fluctuations become too strong, the stable polymorphism present for lower r_1 ceases to exist and the focal type goes extinct; the type adapted to the stable niche fixes in both niches. Despite wildly fluctuating population dynamics underlying the complicated branching diagram due to a rising intrinsic rate of increase r_1, the corresponding change in the polymorphic equilibrium is almost linear – until the focal type dies out. Although we could not determine the point at which this happens in the case of fluctuating population densities due to a large intrinsic rate of increase r_1, we can obtain conditions for stability of a polymorphic equilibrium when exogenous fluctuations in population density are imposed (Fig. 3C, D). We discuss the stability of the polymorphic equilibrium under imposed fluctuations in the next section.

When exogenous fluctuations are imposed, equilibrium frequencies of the locally adapted type decrease just as they do with endogenous fluctuations (see Fig. 3C, D). The decline in equilibrium frequency is independent of the underlying reason for the occurrence of fluctuations, because for the evolutionary dynamics, only net fluctuations in population size matter – whether imposed or driven by intrinsic dynamics. The change in equilibrium frequency is remarkably robust to other forms of population dynamics that exhibit overcompensating density regulation, such as logistic density dependence (S3). Likewise, the simplified model with imposed fluctuations – symmetric around the carrying capacity – further corroborates the robustness of the phenomenon. It also demonstrates that the drop in equilibrium frequency of the focal type is not simply caused by a drop in the mean population size within the focal niche when fluctuations arise.

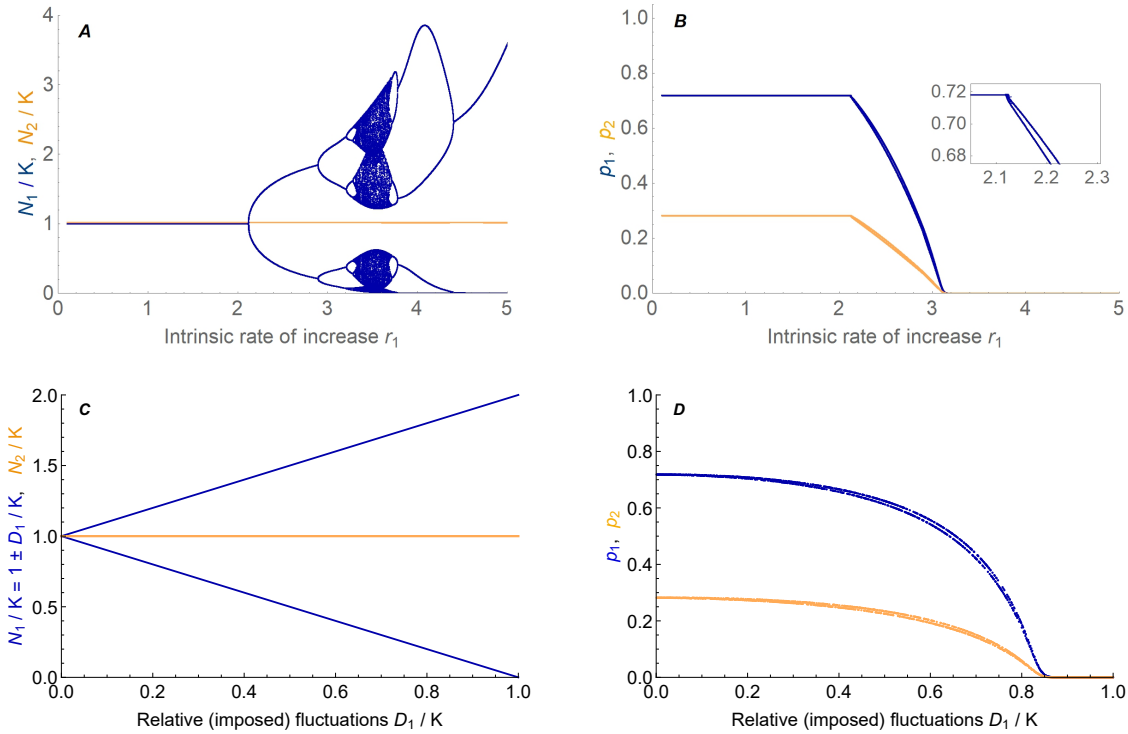

Figure 3: **The evolutionary equilibrium changes continuously as the fluctuations in population density increase.** The long-term behavior of the system is similar under overcompensatory density-dependence (A, B), and when fluctuations in the population density are imposed (C, D). (A) Fluctuations due to overcompensating density dependence arise in niche 1 (blue) as the local intrinsic rate of increase, r_1, increases above a threshold slightly larger than 2. The population size in the second niche (orange) with fixed intrinsic rate of increase, $r_2 = 1$, stays close to the carrying capacity. (N_2/K is offset by 0.02 for visual clarity.) The bifurcation diagram of a Ricker-regulated population (niche 1, blue) under migration with a second stable environment (niche 2) differs from the classic bifurcation diagram (see Fig. S3A) due to the stabilizing effect of migration. (B) The equilibrium frequency of the type favored in niche 1 changes as a function of the intrinsic rate of increase in niche 1. As long as the intrinsic rate of increase leads to a stable population size, its increase has no effect on the allele frequency at equilibrium. However, the equilibrium frequency of the focal type decreases both in niche 1 (p_1, blue) and niche 2 (p_2, orange) as fluctuations due to overcompensating density-dependence arise with growing intrinsic rate of increase r_1. With increasing fluctuations, the frequency of the focal type approaches zero, and eventually it dies out. This decrease in equilibrium frequency is smooth despite the complicated ecological dynamics, with only small fluctuations in the allele frequency induced by the unstable densities (inset). (C) The population density in niche 1 (blue) "branches" as imposed fluctuations D_1/K increase, whilst population size in niche 2 stays constant (orange). This analogue to the branching diagram in (A), depicts N_1/K for linearly increasing values of relative fluctuations D_1/K. (D) The equilibrium frequency of the focal type decreases as a function of the (exogenous) fluctuations in niche 1. The shape of the decrease of its equilibrium frequency is not as abrupt as it is in (B), because the increase in fluctuations is linear. Parameters: $s_1 = s_2 = 0.1$, $m_{12} = m_{21} = 0.05$, $K = K_1 = K_2$.

What is the reason for the decrease in equilibrium frequency of the type better adapted to the niche with oscillating population size? As both types grow reasonably well at low densities (assuming selective disadvantage for the maladapted type is not close to lethal), the fluctuations in the focal niche can easily be exploited by types immigrating from the more stable environment, even if they are locally maladapted. In generations where the population density in the niche undergoing fluctuations is low, immigration brings in a significant number of individuals that are better adapted to the other niche – resulting in a higher proportion of the locally maladapted type a in the focal niche (where type A is better adapted). Afterwards, in the growing phase, both types increase in number as the ecological dynamics are much faster than the evolutionary dynamics. That is, in generations where the local density is low, the focal niche gets swamped by the other, more stable habitat. As fluctuations are strong, selection is not capable of compensating the recurrent swamping that occurs over a long time of repeated oscillations around the carrying capacity. Hence, the allele frequency at equilibrium decreases for the type that is adapted to the "better" niche, in which, a high intrinsic rate of increase leads to fluctuations in density.

Strong selection in the focal niche makes the evolutionary dynamics less vulnerable to fluctuations in population density. As selection increases, evolution becomes faster, its timescale getting closer to the timescale of ecology. Thus, the locally adapted type increases in numbers during the growing phase of the fluctuations significantly more than the maladapted type does. This is the case even if the locally maladapted type dominates in frequency after migration. The potential for the maladapted immigrants to exploit the fluctuations decreases as selection against it increases. This holds true even when the trade-off in selection between the niches is symmetric. Strong symmetric selection, albeit leading to less variation in both niches, stabilizes the polymorphism and maintains diversity for higher intrinsic rate of increase r_1. With increasing selection, the decrease in equilibrium allele frequency p_1 as a function of r_1 flattens (Fig. S8). Hence, the locally adapted type survives larger fluctuations.

The decrease in allele frequency of the type which is best adapted to the most extreme environment is due to the combination of the ecological instability (namely, fluctuations in population size) and migration from the other, more stable habitat. If an ecologically unstable habitat is favoring one type and there is no exchange of individuals with any other habitat, then in a deterministic model the allele frequencies converge to fixation of the favored type even if population density fluctuates. Yet, the focal type suffers from

such fluctuations if migration connects it with another habitat, which is stable in time and favoring a different type (which then grows to high frequencies, exploiting the phase of low population density in the focal fluctuating niche).

So far, we have assumed that one of the niches undergoes fluctuations in population density while the second niche is stable, but our findings generalize to oscillations in both niches. When both niches exhibit fluctuations, the type which is better adapted to the less extreme, more stable habitat, increases in frequency (see Fig. 4). Specifically, when population density in the second niche fluctuates due to a high intrinsic rate of increase (r_2 above the first branching point), then the focal type A benefits from these fluctuations as long as the focal niche maintains a more stable density ($r_1 < r_2$). This relative advantage declines, and so does the equilibrium frequency of the focal type, as the amplitude of the fluctuations in the focal niche rises, approaching the one in the second niche. When the strength of the fluctuations is equal in both niches ($r_1 = r_2$) and population dynamics are fluctuating but not yet chaotic, allele frequencies converge to about the same value as in the absence of population dynamics (intersection of gray dashed lines in Fig. 4B, D, F). However, the equilibrium frequency of the focal type decreases even further, once the population density in the focal niche exhibits stronger fluctuations than in the second niche ($r_1 > r_2$). This generalizes the phenomenon described throughout most of this work: when the focal niche is significantly less stable than the other niche, the focal type, adapted to the niche where fluctuations are the strongest, goes extinct. In summary, when all subpopulations exhibit fluctuations in density, we observe an increase in equilibrium frequency of the type adapted to the niche where fluctuations in population size are the weakest.

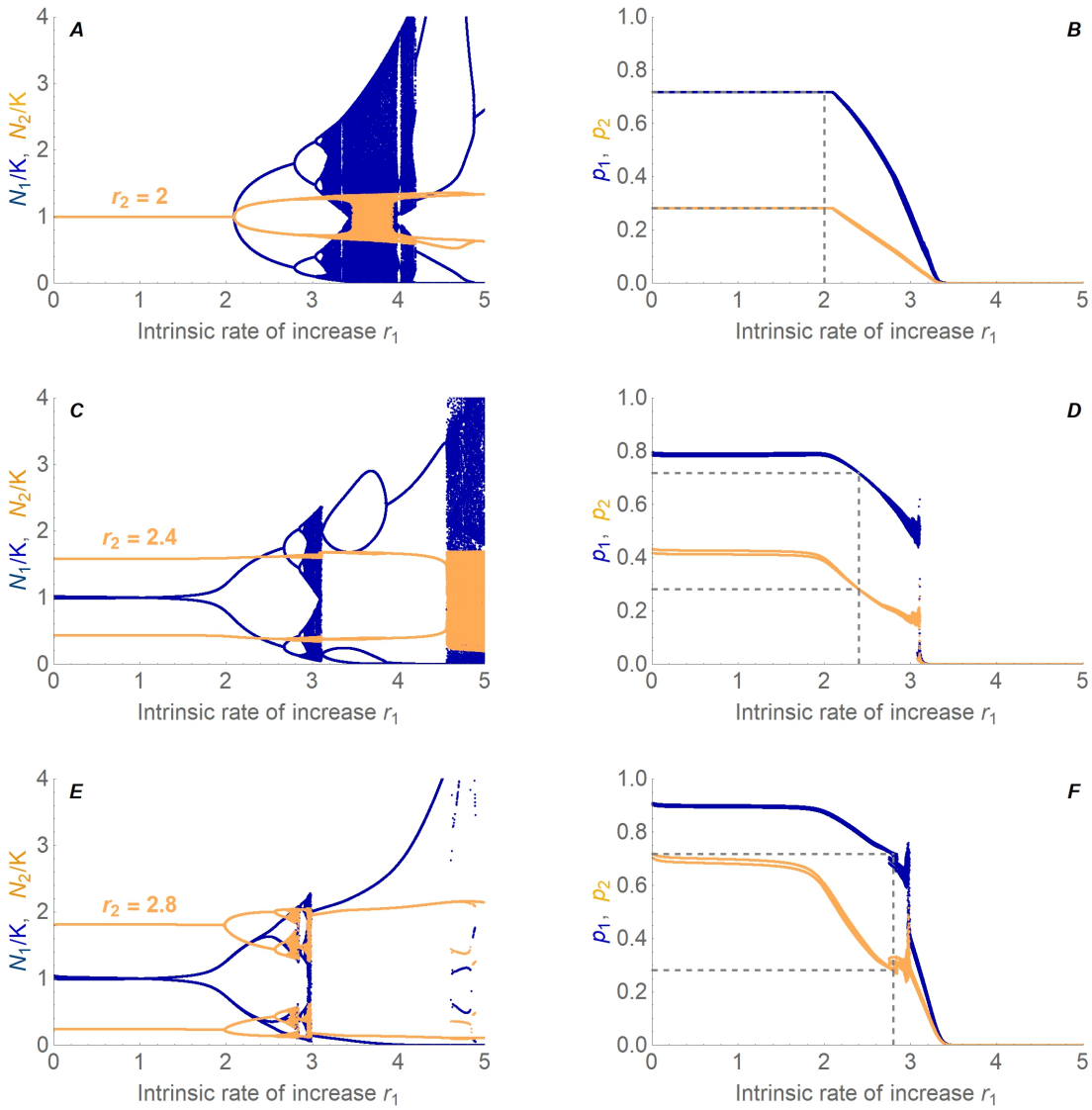

Figure 4: **When both niches exhibit fluctuations, the type better adapted to the more stable niche increases in frequency.** With growing intrinsic rate of increase in niche 2 (from top to bottom: $r_2 = 2$, 2.4, 2.8), fluctuations in population density in niche 2 arise and intensify (A, C, E), leading to higher equilibrium frequencies of the focal type (B, D, F) because it is able to swamp the second niche whenever the population density in niche 2 is low. Blue lines show the long-term behaviour in niche 1, orange lines describe niche 2. Gray dashed lines indicate the diversity maintained if population densities were constant (horizontal), and the value of r_2 (vertical). When the population density in niche 1 stays close to the carrying capacity whilst niche 2 exhibits fluctuations ($r_2 > 2$, $r_1 < r_2$ – note that the branching point in niche 1 depends on the amplitude of fluctuations in niche 2), the focal type reaches higher equilibrium frequencies than predicted in the absence of fluctuations (horizontal dashed lines in D, F). The relative advantage of the focal type vanishes once $r_1 \approx r_2$ (vertical dashed lines in D, F), where equilibrium frequencies are about the same as for constant population densities as long as r_1 and r_2 are not too large (intersection of vertical with horizontal dashed lines in B, D, F). When $r_1 > r_2$ (right of vertical dashed lines), niche 1 is less stable than niche 2, which leads to a decrease in the equilibrium frequency of the focal type – and eventually, as r_1 increases, to its extinction. Parameters: $s_1 = s_2 = 0.1$, $m = 0.05$

The observed evolutionary phenomenon is qualitatively independent of whether migration precedes selection and population growth (as modeled here) or succeeds them (see Fig. S9 in SI).

Stability of evolutionary polymorphism

We have established that fluctuations in the focal niche make the locally adapted type more susceptible to extinction. We proceed to quantify how the conditions for maintenance of polymorphism under migration and selection change when population density fluctuates. This is possible although we do not have an explicit solution for the equilibrium allele frequencies once the population density starts to fluctuate. The conditions for globally stable polymorphism are derived using stability analysis under imposed fluctuations in niche 1 (see S1.3), which yield (long) explicit analytical expressions.

When population dynamics maintain a constant density, explicit conditions for a stable polymorphism can be readily derived. Both symmetry in selection strength between the niches and low migration stabilize the polymorphism. The condition for coexistence of the two types when population densities are stable and migration is symmetric, is given by

$$m \cdot \left| \frac{1}{s_1} - \frac{1}{s_2} \right| < 1 - m \tag{6}$$

This balance between migration and selection expresses a necessary and sufficient condition for maintenance of polymorphism in the case of two haploids inhabiting two demes in the absence of population dynamics (or, when they are included but lead to a stable, constant ecological equilibrium). This formula is similar to the known sufficient conditions for maintenance of polymorphism in diploids (Maynard Smith, 1970; Bulmer, 1972; Lenormand, 2002). We also derive the general condition for maintenance of diversity with arbitrary migration rates and potentially unequal niche sizes (see (S4), (S5)). The stability analysis of the polymorphism in the absence of fluctuations is visualized by the dashed lines in Fig. 5: the stronger the asymmetry in selection, the larger selection needs to be relative to migration for diversity to be maintained. If selection is strongly asymmetric, and weak relative to migration, there is no polymorphic equilibrium and allele frequencies converge to fixation.

The parameter region where a stable polymorphic equilibrium is maintained changes when population density fluctuates (Fig. 5: solid lines encasing the gray area indicate the parameter region where a stable polymorphism exists in the presence of fluctua-

tions *vs.* dashed lines which depict the conditions in the absence of ecological dynamics). Variation is maintained more easily when migration is weak, even when fluctuations are present (Fig. 5A *vs.* B). The robustness of the polymorphism broadens as symmetric selection gets stronger: the polymorphism is maintained for larger fluctuations as selection intensifies. As the stabilizing effect of weak migration and strong selection is preserved under both constant and fluctuating population dynamics, the shape of the stability region is fairly robust to fluctuations in density. However, fluctuations in one niche, while the other niche is stable, introduce an asymmetry in the range of selection coefficients for which variation is maintained. The stable region is shifted by fluctuations in population density, because selection against the focal type (s_2 in niche 2) and fluctuations in the focal niche 1 have a similar impact on the evolutionary dynamics: both lead to a decrease in equilibrium allele frequency of the focal type.

Because fluctuations in the first niche lower the equilibrium frequency of the focal type, more variation is maintained when the selection trade-off between the niches is asymmetric and benefits the focal type ($s_2 < s_1$). Namely, the parameter space where the evolutionary dynamics converge to fixation of the other type, a, increases when fluctuations arise in niche 1, because the locally maladapted type benefits from the fluctuations. When asymmetry in selection is strongly deleterious for the focal type A individuals ($s_2 \gg s_1$), then fluctuations in niche 1 intensify their struggle for survival. Fluctuations decrease the equilibrium frequency of the focal type, and lead to a further increase in proportion of the other type, a. Thus, the upper boundary line in Fig. 5 is shifted to the right and a larger range of parameters lead to fixation of the other type, a, when fluctuations occur. On the other hand, the parameter region where the focal type A becomes fixed in both demes decreases due to fluctuations in niche 1, as these prove deleterious for the focal type (by decreasing its equilibrium frequency). Hence, whenever the focal type A has a strong relative selective advantage ($s_2 \ll s_1$), fluctuations in the niche where it is better adapted to, counteract this asymmetry by increasing the proportion of the disadvantaged other type, a – broadening the region where polymorphism is maintained. In the presence of fluctuations, polymorphism is maintained for stronger selection against maladapted immigrants (s_1), and weaker selection against the focal type in the stable niche (s_2).

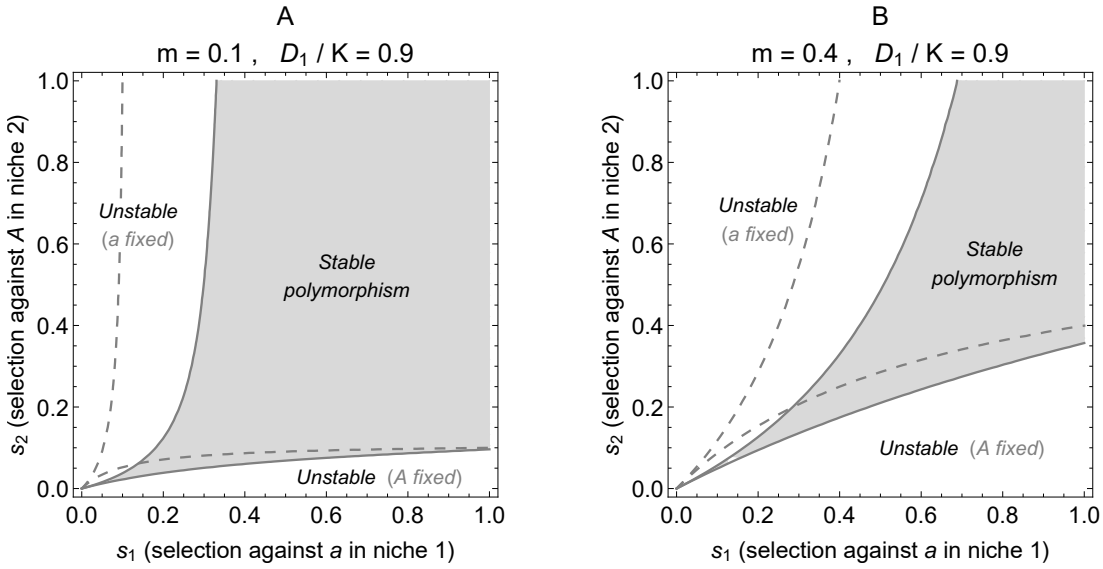

Figure 5: **Fluctuations in the density of niche 1 shift and skew the parameter region where variation is maintained.** Dashed lines give the condition for maintenance of polymorphism in the absence of fluctuations ($m \cdot |1/s_1 - 1/s_2| < 1 - m$, see SI), whilst solid lines delimit the region where polymorphism is stable (grey area) under strong imposed fluctuations in the population density in niche 1 ($D_1/K = 0.9$). To prevent extinction of the type adapted to the fluctuating niche, its selective advantage must be comparatively higher than when the densities are stable: the stability region shifts to the right, at a rate which is nearly independent of the strength of migration (A *vs.* B). Fluctuations broaden the parameter space that leads to fixation of the type a adapted to the stable niche by increasing the pressure on the focal type A. However, if asymmetry in selection favors the focal type ($s_1 \gg s_2$), then fluctuations counteract that asymmetry and polymorphism is maintained more easily: the region where type A gets fixed shrinks.

Imposed fluctuations in a continent-island model

Since the analytical conditions for maintenance of polymorphism under imposed fluctuations are extensive and complicated when migration is symmetric (visualization in Fig. 5), it proves useful to analyze a continent-island model with imposed fluctuations on the island. Then, simple explicit conditions for persistence of the resident type on the island can be derived. A simple extension of our earlier analysis under density dependent population dynamics demonstrates that the evolutionary dynamics are qualitatively independent of whether migration is symmetric or unidirectional to the niche that exhibits the fluctuations: compared to bidirectional migration, the frequency of the focal type at equilibrium is simply shifted to lower values due to monomorphic immigration (SI,

section S6). The observation that the decrease in equilibrium frequency of the focal type as a function of the intrinsic rate of increase is robust to asymmetry in migration, indicates that an analysis of a continent-island model is appropriate.

We obtain conditions for persistence of the locally adapted type in terms of selective disadvantage of the immigrating type, s_1, the relative fluctuation size on the island, D_1/K_1, and the "rate of immigration" – the mean ratio of immigrants to locals (at the beginning of the life cycle), $M_{21}/K_1 = m_{21}$.

Extinction of the locally adapted resident type on the island is certain whenever the local selective disadvantage of the immigrating type is not strong enough to prevent swamping by the continent. Namely, for survival of the resident type to be possible, the relative strength of immigration at the time of selection, $M_{21}/(K_1 + M_{21}) = m_{21}/(1 + m_{21})$, needs to be weaker than the selective disadvantage of the immigrants, s_1:

$$\frac{M_{21}}{K_1 + M_{21}} \; < \; s_1 \tag{7}$$

This condition recovers the known threshold for survival of a locally well adapted type in a continent-island model in the absence of population dynamics (Haldane, 1930; Wright, 1931).

In the presence of fluctuations, condition (7) is necessary but not sufficient. The resident type persists on the island if and only if

$$\frac{D_1}{K_1} \; < \; \sqrt{\frac{1}{(2-s_1)s_1} - \left(\frac{1}{(2-s_1)s_1} - 1\right) \cdot \left(1 + \frac{M_{21}}{K_1}\right)^2} \tag{8}$$

This threshold, which we denote by $(D_1/K_1)^*$, gives the critical relative fluctuation size at which the resident type dies out. It increases with the selection coefficient s_1 and decreases with the rate of immigration M_{21}/K_1, as illustrated in Fig. 6A.

Condition (8) implies and extends the threshold for swamping in the absence of population dynamics (Eq. 7). The critical relative fluctuation size $(D_1/K_1)^*$ is a positive real number, only when condition (7), equivalent to $M_{21}/K_1 < s_1/(1 - s_1)$, is fulfilled. It equals zero when $M_{21}/K_1 = s_1/(1 - s_1)$, and increases to positive values as the rate of immigration decreases below this threshold for swamping: $(D_1/K_1)^* > 0 \;\; \Leftrightarrow \;\; (7)$. In

summary, whenever the relative number of immigrants is small enough (Eq. 7), coexistence becomes possible, but depends on the amplitude of fluctuations on the island.

This result corresponds to our previous findings: the fewer locally maladapted immigrants arrive on the island and the stronger their maladaptation, the higher the frequency of the resident type in the absence of fluctuations. Therefore, the locally adapted type becomes more robust to fluctuations. In general, small fluctuations do not yet lead to extinction of the resident type (see Fig. 6A) once the balance between selection and immigration allows for coexistence of the two types. Weak fluctuations have a weak effect on the maintenance of diversity on the island.

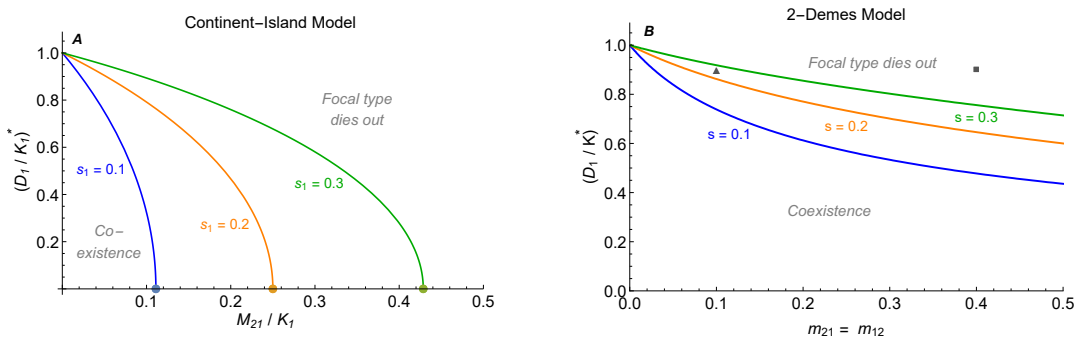

Figure 6: **Strong fluctuations lead to extinction even when migration is weak, but the effect is attenuated under bidirectional migration.** The critical relative fluctuation size is a decreasing function of the migration rate and an increasing function of selection ($s_1 = 0.1$ (blue), 0.2 (orange), 0.3 (green)). (A) In the continent-island model, locally maladapted immigrants swamp the island when immigration is too strong. Just once the relative immigration falls below the critical value (solid dots: $M_{21}/K_1 = s_1/(1 - s_1)$, see Eq. (7)), coexistence becomes possible. Then the critical relative fluctuation size $(D_1/K_1)^*$ increases abruptly: weak fluctuations have a weak effect on the maintenance of diversity on the island. When migration is weak relative to selection ($M_{21}/K_1 \ll s_1/(1-s_1)$), the dependency between critical relative fluctuation size and the rate of immigration becomes almost linear – the stronger the selection against the immigrating type, the more is the resident type robust to fluctuations. (B) In the 2-demes model, migration can be polymorphic, and hence even strong dispersal does not necessarily lead to extinction of the focal type. The lines depict the critical relative fluctuation size when migration and selection are symmetric ($m_{12} = m_{21}$, $s_1 = s_2$). The triangle ($m = 0.1$) and square ($m = 0.4$) provide a reference to Fig. 5 which depicts the stability of the system for variable selection ($s_1 \neq s_2$) but a fixed value of fluctuations ($D_1/K = 0.9$).

There are two cases when fluctuations can be extensive without leading to extinction of the resident type: when immigration tends to zero, or when selection against the immi-

grants is lethal, $s_1 \to 1$. These are the scenarios where the island is monomorphic for the resident type because the immigrants cannot survive there. As immigration increases from zero, the critical relative fluctuation size decreases almost linearly, with a negative rate of $-1/\big((2-s_1)s_1\big)+1$ (Fig. 6 and Fig. S11). This rate flattens as selection against the immigrating type increases. Thus, the critical relative fluctuation size declines faster with increasing immigration when selection is weak. Conversely, the stronger the selection, the larger are the fluctuations under which the resident type is still able to survive – a phenomenon that we observed in the model with symmetric migration and density dependent population regulation already (Fig. S8).

How does the critical relative fluctuation size in the continent-island model compare to the critical relative fluctuation size in the model with two niches and symmetric migration between them? When there is bidirectional migration between two demes – as opposed to the continent-island model – fluctuations in the focal niche are less detrimental to the locally adapted type (see Fig. 6B). With bidirectional migration, the other more stable niche (the "continent" in the case of unidirectional migration) is inhabited by both types, leading to a polymorphic (rather than monomorphic) immigration into the focal niche. Hence, migration out of the fluctuating niche can be essential for persistence of the focal type.

Discussion

In nature, environments vary in their productivity and stability, and there may be a strong negative correlation between the two due to delayed population regulation, called "overcompensating density dependence". Fluctuations can arise due to endogenous factors such as overcompensating density dependence, or exogenous factors such as a fluctuating resource. We demonstrate that while classic evolutionary predictions, obtained in the absence of ecological dynamics, still hold when population densities are stable in time, this is no longer true when instabilities arise. Both the conditions for maintenance of polymorphism and the amount of variation maintained can significantly change when population densities fluctuate around their carrying capacity.

Under overcompensating density dependence, a high intrinsic rate of increase leads to fluctuations which prove deleterious for the type better adapted to the focal niche. Whenever the local population density is low, the locally adapted type gets easily swamped by migration from a neighboring, stable habitat. This effect becomes stronger the weaker the selection is, even if the trade-off in selection between the habitats is symmetric. However, if the asymmetry in selection trade-off favors the type adapted to the fluctuating habitat, fluctuations in population density can support diversity. This is because fluctuations in population density and selection against the locally adapted type have a similar impact on the evolutionary dynamics: both lead to a decrease in equilibrium frequency of the focal type. To understand the interplay of migration, selection and fluctuations, we model an island population which experiences both imposed fluctuations in its density and migration of maladapted individuals from the mainland. This leads to simple explicit conditions for persistence of the resident type: strong recurrent fluctuations lead to its extinction even under weak migration. Conversely, weak fluctuations hardly affect coexistence. We thus show that stability in population size can be just as important for maintenance of diversity as the selective advantage within a niche.

In the 60s and 70s, ecological instability and chaotic dynamics were in the focus of attention (May, 1972, 1974; Levins, 1979), and the balancing impact of migration in diversified environments has been known: "The effect of extreme conditions in one place will be leveled out to some degree by less extreme conditions in others. Migration can contribute to the leveling influence of spatial heterogeneity." (Den Boer, 1968). We retrieve this well-known phenomenon, but show that the effect of dispersal is more complex when evolution and ecology are analyzed jointly. Migration stabilizes the population dy-

namics, but it has a destabilizing effect on the maintenance of polymorphism: whilst weak migration across a heterogeneous habitat increases local variation, polymorphism cannot be maintained when swamping by migration is too high (reviewed in Lenormand 2002). When population densities fluctuate, swamping becomes very powerful, and the equilibrium frequency of the type which is best adapted to the "fluctuating" niche decreases.

It remains to be explored what happens if both genetic and demographic stochasticity were included. Immigration by locally maladapted variants still keeps the subpopulations away from very low densities (Roff, 1974), which stabilizes the population dynamics. This reduces the strength of genetic drift and thus stochastic extinction of the type adapted to the fluctuating niche can become less likely in the presence of migration. Furthermore, it is possible that in the presence of stochasticity, the stable niche serves as a "refuge" for types which are best adapted to the productive but unstable environment. We leave the exploration of a stochastic model to a dedicated future study. In this paper, we concentrate on the effects of dispersal in fluctuating structured populations when the effect of drift is weak relative to selection.

Although fluctuations in population density are very common in nature, evidence for chaotic dynamics is sparse. Overcompensatory density dependence can drive chaos in some experimental systems (Costantino et al. 1995; *c.f.* Thomas et al. 1980), whereas in nature, fluctuations rarely exceed limit-cycle dynamics (Ellner and Turchin, 1995; Framstad et al., 1997; Turchin et al., 2000; Coulson et al., 2001). Often populations fluctuate due to a combination of intrinsic dynamics, between-species interactions, and environmental fluctuations (Grenfell et al., 1998; Turchin, 2003). We believe that our work can contribute to the debate why we see chaos so rarely: the type which is better adapted to the more productive but fluctuating niche is sensitive to invasion by the type which is common in the surrounding stable environment. Hence, intrinsic fluctuations in population density are selected against in the presence of spatial structure: as they increase, they lead to a decrease in the frequency of the type fluctuating with the highest amplitude. Evolution has thus the tendency to replace unstable types by more stable competitors – which is consistent with the relative rarity of chaos in natural and experimental systems.

The coupling of ecology and evolution is an essential feature of our model. Importantly, treating intrinsic rates of increase and selection coefficients as two independent

parameters leads to the observed decrease in equilibrium frequency of the focal allele as evolutionary and ecological dynamics have different timescales. The selection coefficients (and the trade-off between them) are typically much weaker than the intrinsic rate of increase determined by the niche's productivity. As the intrinsic rate of increase is assumed to be a property of the niche (such as due to a common abundant resource), it limits the ability to grow well from low densities for all types inhabiting that niche. (Similarly, exogenous fluctuations are imposed on the entire population within a niche.) A type's capacity to exploit the potential intrinsic rate of increase depends on its local adaptation. However, as evolution is much slower than the ecological dynamics, the recurrent swamping (that occurs whenever the fluctuating population density is low) overcomes the evolutionary trade-off. It is the small changes in allele frequency that take place over many generations of fluctuations in population density which lead to the observed effect. A solely ecological model cannot account for this phenomenon. When the trade-off between the types is merged with their growth rate – such as when a type's capacity to grow well (from low densities) increases with its competitiveness (Smith, 1998; Luís et al., 2011) – we do not observe the direct deleterious effect of fluctuations in the resource-rich niche on the locally more competitive type. When competition between the types and population growth are intrinsically tied to each other, fluctuations in the population size are driven by a dual advantage of one type. Increasing a species' growth rate then ultimately increases its competitiveness and vice versa.

We have started with the Ricker model of a population's density dependent growth, as it is established in theoretical literature and there are examples where it gives good fit to experimental data (Thomas et al., 1980). However, we demonstrate that our results are independent of this choice of density regulation: the decrease in variation maintained arises due to fluctuations in population size – no matter where these fluctuations come from. In general, we expect to observe a decrease in equilibrium frequency of the type that is adapted to the niche exhibiting the most severe fluctuations in population density. Although we restrict ourselves to the study of two types inhabiting two heterogeneous niches, we believe that our results generalize to n types in m niches with various trade-offs in fitness between the niches. The deleterious effect of fluctuations would then be observable as a decrease in equilibrium frequency of the type(s) that is/are best adapted to the environment(s) that exhibit(s) fluctuations in population density.

We hope that our study will bring attention to important effects of considering population dynamics and evolution jointly, and helps elucidating the role of

disturbances/fluctuations on the maintenance of diversity – an important phenomenon of natural populations, which has recently become again a focus of experimental studies (Buckling et al., 2000; Rainey et al., 2000; Buckling et al., 2007).

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