The influence of fluctuating population densities on evolutionary dynamics

Abstract

The causes and consequences of fluctuating population densities are an important topic in ecological literature. Yet, the effects of such fluctuations on maintenance of variation in spatially structured populations have received little analytic treatment. We analyze what happens when two habitats coupled by migration not only differ in their trade-offs in selection but also in their demographic stability – and show that equilibrium allele frequencies can change significantly due to ecological feedback arising from locally fluctuating population sizes. When an ecological niche exhibits such fluctuations, these drive an asymmetry in the relative impact of gene flow, and therefore, the equilibrium frequency of the locally adapted type decreases. Our results extend the classic conditions on maintenance of diversity under selection and migration by including the effect of fluctuating population densities. We find simple analytic conditions in terms of the strength of selection, immigration, and the extent of fluctuations between generations in a continent-island model. Whereas weak fluctuations hardly affect coexistence, strong recurrent fluctuations lead to extinction of the type better adapted to the fluctuating niche – even if the invader is locally maladapted. There is a disadvantage to specialization to an unstable habitat, as it makes the population vulnerable to swamping from more stable habitats.

Introduction

Classic evolutionary theory behind maintenance of variation in natural populations focuses on the balance between selection, migration and mutation (Levene, 1953; Maynard Smith, 1970; Bulmer, 1972). Over decades of research, 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.

Natural populations are often out of equilibrium (Hastings, 2004). The discovery that large and irregular fluctuations can be driven by very simple dynamics (Lorenz, 1963) has led to a surge of interest in ecological theory. Both within- and between-species interactions, such a density dependence and predator-prey interactions can lead to large fluctuations in population sizes (May, 1972, 1974; Levins, 1979). Even chaotic dynamics, arising from overcompensating density dependence *via* intraspecific predation, have been successfully induced in an experimental population of flour beetles (Costantino et al., 1995). While, nonetheless, chaotic dynamics are believed to be rare (Thomas et al., 1980; Ellner and Turchin, 1995), fluctuations in population size are omnipresent. In natural populations, these can be caused by both intra- and inter-specific interactions, as well as purely exogenous abiotic factors such as weather (Framstad et al., 1997; Turchin et al., 2000; Coulson et al., 2001).

Oscillations in population size rarely affect the whole species uniformly. The size of the fluctuations may change through the species' range and at any given time, some subpopulations can even go extinct. These local extinctions may affect the persistence of the whole population (Levins, 1969, 1970; Hanski and Ovaskainen, 2003). 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 whole (meta-)population becomes more stable as immigration from more populated patches pushes local population sizes away from zero (Hanski, 1985, 1991). Notably, even weak migration can dampen chaotic fluctuations arising due to overcompensating density dependence (Ruxton, 1994; Stone and Hart, 1999; Allen et al., 1993).

While dispersal stabilizes the ecological dynamics of a single species in the presence of

disturbances, the effect of the interplay of dispersal and disturbances is more complex once we consider more species or within-species diversity (Holt, 1983b). Strong dispersal can lead to both global and local loss of variation, as some of the locally adapted types get swamped by other, more abundant variants. Interestingly though, diversity can increase with dispersal in the presence of disturbances and specific trade-offs in adaptation at low *vs.* high densities (r/K-selection, MacArthur and Wilson 1967; Pianka 1970). Even in the absence of spatial structure, coexistence on a single resource is possible if the trade-off in resource use leads to a stronger intra-specific competition than inter-specific competition ("relative nonlinearity", Armstrong and McGehee 1980; Chesson 1994). When the balance between the ability to grow fast (high r) *vs.* efficiently (high K) can evolve, selection may favour intermediate values of both r and K (Roughgarden, 1971; Gadgil and Solbrig, 1972; Turelli and Petry, 1980; Lande et al., 2009; Engen et al., 2013; Lande et al., 2017). In contrast to well-mixed populations (Armstrong and McGehee, 1980; Turelli and Petry, 1980; Chesson, 1994), coexistence of multiple types on a single resource becomes considerably more robust when populations are spatially structured. Notably, in an environment with frequent local disturbances, coexistence of a quick ("weedy") coloniser which grows fast from low densities and an efficient user of resources is possible under a broad range of conditions (Hastings, 1980; Comins and Noble, 1985; Tilman et al., 1994; Chesson, 2000; Long et al., 2007; Yodzis, 2013). In the presence of spatial structure, a broad range of r–K trade-offs readily lead to coexistence. Yet, in our study, r and K are properties of the niches: there is no trade-off in r and K which drives coexistence of multiple types when population densities fluctuate. We ask how is coexistence between locally adapted types influenced by out-of-equilibrium population dynamics.

We study coexistence of two discrete types (genotypes, species, bacterial clones) that are locally adapted to two habitats. These are coupled by migration and one (or both) of the habitats exhibit deterministic fluctuations in population size. When the environment varies across space, dispersal between two habitats brings in locally maladapted variants. How is local adaptation affected by the recurrent asymmetric gene flow arising in fluctuating populations? The balance between the trade-offs in selection, and between the flows among the independently-regulated habitats is of known importance: 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). Yet, to our knowledge, it is not known whether the classic predictions are robust when

population dynamics within the niches are taken into account. We start by modeling evolution jointly with discrete-time ecological dynamics, where fluctuations arise from overcompensating density dependence under Ricker's regulation (1954). We then proceed by analyzing a simplification with imposed fluctuations in population size. This leads to explicit analytical conditions which provide 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

Population dynamics are modeled jointly with the dynamics of the change in frequency of two types adapted to two different habitats. Throughout, we interpret these types as two different alleles in a one-locus haploid system, although they could also represent two different species. The trade-off in selection is density-independent. A relatively complex model where local, endogenous density fluctuations arise due to overcompensating density dependence in discrete-time precedes 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 presence of fluctuations. All results presented in the stability analyses are analytic – but lengthy and complicated expressions 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). More details are provided in the supporting information (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 population growth is density-dependent, with Ricker's regulation (Ricker, 1954). In this model, a delayed feedback in density regulation can cause large fluctuations of the population size beyond the carrying capacity.

The life cycle starts with migration, where m_{12} denotes the forward migration rate from deme 1 into deme 2, i.e. m_{12} is the proportion of individuals that emigrate from deme 1. m_{21} is the forward migration rate in the opposite direction. Throughout our analyses, we will mainly focus on the complementary cases of symmetric migration,

$m_{12} = m_{21} = m \leq 1/2$, and unidirectional migration, $m_{12} = 0$ (Fig. 1).

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, primes label the intermediate variables after migration but 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

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

with similar recursions 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 $\overline{w}_i'(t) = p_i'(t)w_{iA} + (1 - p_i'(t))w_{ia}$ denotes the mean fitness after migration in deme i.

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

$$N_i(t + 1) = N_i'(t) \cdot e^{r_i\left(1 - \frac{N_i'(t)}{K_i}\right)\overline{w}_i'(t)} \tag{4}$$

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 (notably, mainland-island model).

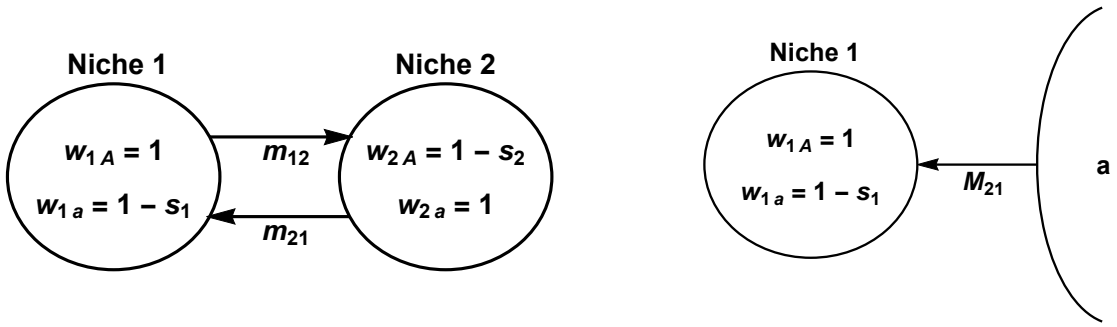

Figure 1: **Evolution and maintenance of variation in the face of gene flow between populations in two divergent habitats.** Left-hand side: Bidirectional migration between two ecological niches with forward migration rates m_{12} and m_{21}. Type A is better adapted to niche 1; type a to niche 2. Right-hand 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.

We are interested in the effects of fluctuations in population size around the carrying capacity on the evolutionary dynamics. In this study, the genetic composition of a population does not influence its carrying capacity (*soft selection*: Wallace 1975; Christiansen 1975), because this would add another layer of interactions between ecology and evolution to the system. We discuss an alternative model choice, where the mean fitness of a population affects its carrying capacity (*hard selection*) in the SI (S7). The core effects remain robust.

Backward migration

For parts of our analysis it will prove helpful to rewrite the allele frequencies after migration to

$$p_1'(t) = \big(1 - \mathcal{M}_1(t)\big) \cdot p_1(t) + \mathcal{M}_1(t) \cdot p_2(t) \tag{5}$$

$$p_2'(t) = \mathcal{M}_2(t) \cdot p_1(t) + \big(1 - \mathcal{M}_2(t)\big) \cdot p_2(t) \tag{6}$$

Here, $\mathcal{M}_i(t)$ is the backward migration rate to deme i, which gives the proportion of new immigrants in the population of deme i at generation t. In our model, the backward migration rates are given by

$$\mathcal{M}_1(t) = \frac{1}{1 + \alpha_1\, n(t)} \qquad \text{and} \qquad \mathcal{M}_2(t) = \frac{\alpha_2\, n(t)}{1 + \alpha_2\, n(t)} \tag{7}$$

where $n(t) = N_1(t)/N_2(t)$ is the proportion of the two population sizes, and $\alpha_1 = (1 - m_{12})/m_{21}$ and $\alpha_2 = m_{12}/(1 - m_{21})$.

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 impose fluctuations D_1 in the population density of niche 1 such that its population size 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). 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. It represents 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 population 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 S10) and two comprehensible inequalities as condition for coexistence.

Results

As explained in detail in the methods, we study the impact of fluctuating population sizes on maintenance of diversity in spatially structured populations *via* a model of two discrete types living in two habitats with migration between them. There is a trade-off in adaptation 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. Numerical demonstrations of the temporal dynamics – showing that allele frequencies can change significantly due to the ecological feedback – precede a stability analysis of the polymorphic equilibrium. 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).

Population dynamics affect evolution

When the density of a subpopulation fluctuates, allele frequencies evolve 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 (see Eq. S4). 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 (Karlin and Campbell (1980) for the proof of global convergence). When the trade-off in selection is symmetric, this equilibrium is always polymorphic in the absence of fluctuations. Hence, even if the focal type is initially rare, it is able to invade and reach high frequencies.

Population densities are not always constant. Fluctuations arise for high intrinsic rates of increase, where recurrent overshooting of the carrying capacity is followed by overcompensating density regulation pushing the population to low densities (Fig. 2C). Such density fluctuations in one of the niches can markedly change the evolutionary outcome. Notably, they are disadvantageous to the type that is better adapted to the "fluctuating" niche. Fig. 2D shows that a high intrinsic rate of increase in one niche, which drives strong fluctuations in the local population size, leads to a decline in the equilibrium frequencies of the locally adapted type – and can ultimately result in its extinction. This

is true even if the focal type is initially abundant and even if its equilibrium frequency in the absence of fluctuations is high (dashed lines).

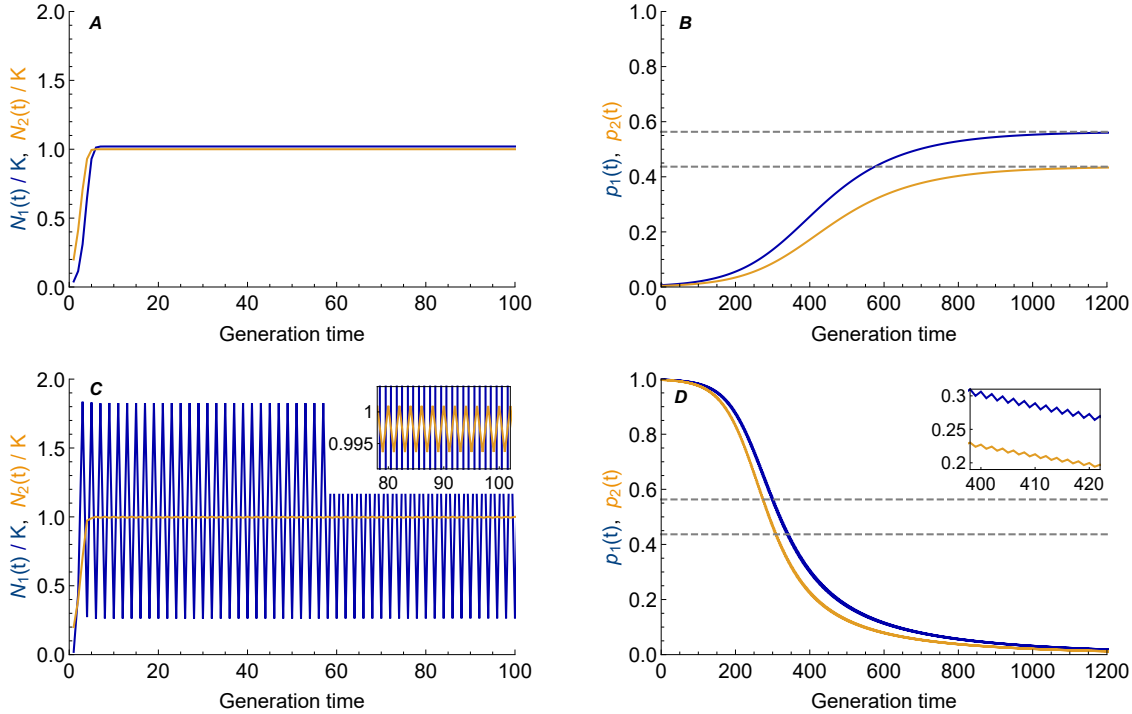

Figure 2: **Ecological dynamics can change the evolutionary predictions.** (A, C): Population dynamics in niche 1 (blue) and niche 2 (dark orange) – under low *vs.* high intrinsic rate of increase in niche 1 (A $r_1 = 1$ *vs.* C $r_1 = 2.5$). (B, D): The allele frequency of the focal type, which is favored in niche 1, is shown in blue for niche 1 and in dark orange for niche 2. The dashed lines represent the expected equilibrium allele frequencies of the focal type in the absence of ecological dynamics. When population sizes evolve 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), the frequency of the locally favored type 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. In (A) the population sizes at equilibrium are equal (N_1/K is offset by 0.02 for visual clarity). (C) In niche 2, intrinsic rate of increase is low enough ($r_2 = 1$) so that the density stays nearly constant at carrying capacity (see inset) despite the strong fluctuations in niche 1. Parameters: $s_1 = s_2 = 0.05$, $m_{12} = m_{21} = 0.1$, $r_1 = 1$ (A, B), $r_1 = 2.5$ (C, D), $r_2 = 1$, $K = K_1 = K_2$.

We analyze the decrease in equilibrium frequency of the type adapted to a niche that

exhibits fluctuations in population size in more detail in the following paragraphs.

The extent of local fluctuations determines the evolutionary equilibrium

How does the equilibrium frequency of the focal type depend on the amplitude of fluctuations in population density? Fig. 3 shows the ecological (A) and evolutionary (B) dynamics at equilibrium for increasing values of the intrinsic rate of increase in niche 1, r_1. For small r_1, the population size reaches a stable equilibrium at carrying capacity ($N_1 = K_1$), and the allele frequencies converge to the stable migration-selection equilibrium predicted by classic population genetic theory. However, as r_1 rises above a threshold, the ecological equilibrium becomes unstable and the population size in niche 1 fluctuates (blue lines in Fig. 3A). Simultaneously, the equilibrium allele frequencies of the type adapted to niche 1 start to decrease in both niches (blue, orange in Fig. 3B).

The larger the intrinsic rate of increase, the stronger are overshooting and overcompensation, which leads to oscillations of higher period and eventually to chaos, whenever migration is absent or really weak. In the absence of migration and selection, the transition to cycling occurs at $r_1 = 2$ for the Ricker model (May and Oster, 1976). Yet, immigration from the second, stable deme stabilizes the ecological dynamics in two ways: First, by pushing the local population density away from zero, even weak migration dampens fluctuations sufficiently so that the long-term dynamics no longer portrait the classic chaotic branching diagram of the single population Ricker model (Ruxton, 1994; Stone and Hart, 1999). Additionally, in our model, the effective intrinsic rate of increase ($r_1 \cdot \overline{w}_1'(t)$) declines with the mean fitness due to immigration of maladapted types, increasing the threshold to cycling as a function of r_1. 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).

Despite wildly fluctuating population dynamics with rising intrinsic rate of increase r_1, the corresponding change in the polymorphic equilibrium is almost linear (Fig. 3A *vs.* B). The higher the variance in the population density of the focal niche, the lower the equilibrium frequency of the locally adapted type – until it dies out: when local fluctuations with increasing r_1 become too strong, the stable polymorphism ceases to exist and the focal type goes extinct; the other type adapted to the stable niche fixes in both niches.

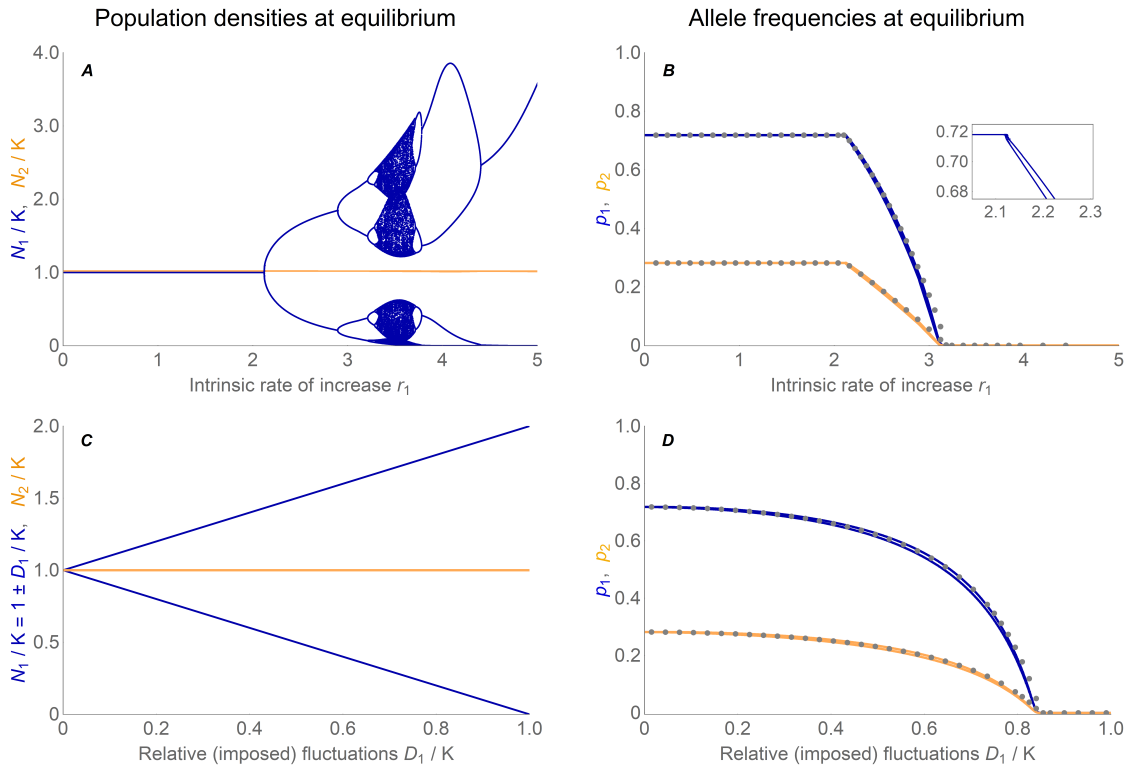

Figure 3: **The evolutionary equilibrium changes continuously as fluctuations in population density increase.** Fluctuations in local population size – whether they arise intrinsically due to overcompensating density dependence (A, blue) or are imposed extrinsically (C, blue) – lead to considerable changes in the evolutionary equilibrium of the focal type (B, D). The stronger the fluctuations in the density of one niche, the lower the equilibrium frequencies of the type that is best adapted to this fluctuating habitat. (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 (see section S2). The population size in the second niche (orange) with a 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 the Ricker-regulated population (blue) differs from the classic one due to the stabilizing effect of dispersal (Fig. S3A). (B) As long as the intrinsic rate of increase leads to stable population sizes, allele frequencies evolve towards the equilibrium predicted in the absence of joint population dynamics. However, with growing intrinsic rate of increase r_1, fluctuations in the population density of niche 1 arise, and thus the equilibrium frequencies of the type favored in this niche decrease in both habitats (blue: p_1 in niche 1, orange: p_2 in niche 2). When fluctuations in the focal niche are strong, the locally adapted type goes extinct. Grey dots are an approximation of the evolutionary equilibrium, obtained by inserting the mean backward migration from the complete model (Fig. 4) into a simplified model with constant backward migration rates. This explains the evolutionary dynamics well unless fluctuations in backward migration rates are really large (see Fig. S6). The decrease in equilibrium frequency is smooth despite the complicated ecological dynamics, with only small fluctuations in the allele frequencies (inset). (C) This analogue to the branching diagram in (A) depicts the population density in niche 1 (blue) for linearly increasing values of imposed fluctuations, expressed relative to the carrying capacity as D_1/K_1. The population size in niche 2 stays constant (orange). (D) The equilibrium frequencies of the focal type decrease as a function of the (imposed) fluctuations in the niche where it is favored. Grey dots give the approximation using mean backward migration. The decrease in equilibrium frequencies is not as abrupt as it is in (B), because the increase in fluctuations is linear. Parameters: $s_1 = s_2 = 0.1$, $m_{12} = m_{21} = 0.05$, $K = K_1 = K_2$.

Also under a simplified model with exogenous fluctuations in the focal niche (Fig. 3C), equilibrium frequencies of the locally adapted type decrease (Fig. 3D). Here, we assume that the external environment imposes periodic fluctuations between two densities (e.g. summer/winter) with constant average density K, but amplitude parametrized by D_1. Fig. 3D shows a decline in the equilibrium frequencies of the locally adapted type with increasing amplitude of the fluctuations, which is entirely analogous to the effect of intrinsic fluctuations under Ricker's regulation. The simplified model with imposed fluctuations demonstrates that the decrease 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.

What is the reason for the decrease in equilibrium frequency of the type that is locally adapted to the niche with oscillating population size? As both types grow reasonably well at low densities, 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 fluctuating niche is low, immigration brings in a significant number of individuals that are adapted to the other niche – resulting in a higher proportion of locally maladapted types in the focal niche. Afterwards, in the transition to a generation with high density, 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. If 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 equilibrium allele frequency of the focal type decreases, i.e. the type that is adapted to the "better" niche, in which a high intrinsic rate of increase leads to fluctuations in density.

We can understand the increased swamping by gene flow due to fluctuations in local population densities in terms of backward migration rates. Backward migration measures the relative strength of immigration to a niche: it gives the proportion of individuals in the local population that immigrated from the other habitat. In contrast to forward migration, it depends on the population size in the focal niche. When densities fluctuate, they drive fluctuations in the backward migration rates (both to the fluctuating niche and to the other niche – light blue and light orange lines in Fig. 4): fluctuations up in local population size correspond to fluctuations down in the backward migration to this niche and *vice versa*. More importantly, fluctuations in the focal niche lead to an

increase in its **average** backward migration rate (dark blue lines in Fig. 4). Indeed, whenever the population size in the focal niche is low, the backward migration to this niche is strongly increased due to the large contribution of immigrants relative to the locals. In contrast, the decrease in the backward migration rate in times of high local density is much smaller.

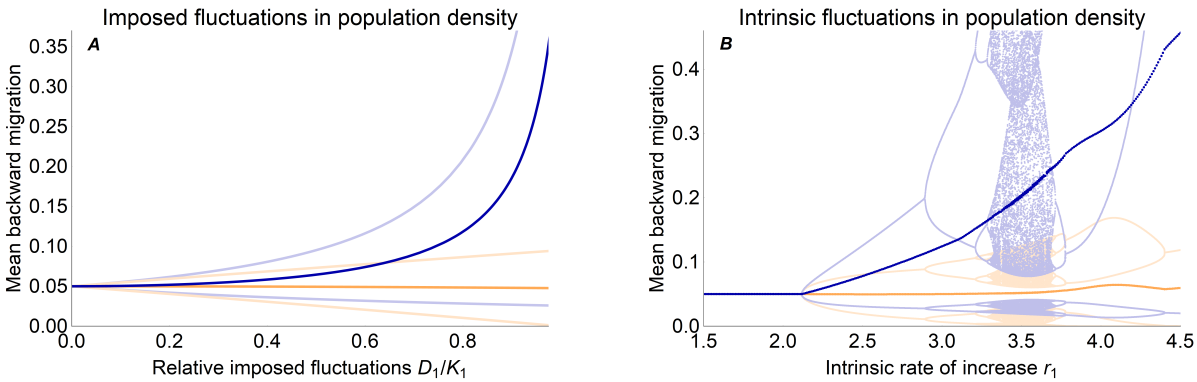

Figure 4: **The mean backward migration to the focal niche increases significantly as fluctuations in the local population size grow.** Because backward migration reflects immigration rates, it rise substantially when local population density is low. Thus, fluctuations in local population densities drive an increase in the average backward migration rate to the fluctuating niche (dark blue lines). (A) Under imposed fluctuations in population density, backward migration rates fluctuate up and down with a period of 2 (migration to niche 1 in light blue, niche 2 in light orange). As fluctuations D_1/K_1 in the density of the focal niche grow, the extent of fluctuations in backward migration rate increases markedly for the focal niche (increasing mean, dark blue), but only about linearly for the stable niche 2 (barely declining mean, dark orange). (B) Under Ricker's regulation, complex fluctuations in backward migration rates arise (light lines) as a high intrinsic rate of increase r_1 drives fluctuations in population density. Again, this leads to a strong increase in mean backward migration to the focal niche, while hardly affecting the one to the stable niche (dark blue *vs.* dark orange). Dark lines were obtained by averaging backward migration over generations $1000 - 1300$. The bump in the mean backward migration rates around $r_1 = 4$ comes from the population size fluctuating to high densities in this regime. Parameters of selection and migration are the same as in Fig. 3.

The rise in "average relative immigration" as density fluctuations grow explains most of the change in the evolutionary equilibrium: using the mean backward migration rates as an approximation for fluctuations leads to a good estimate of the equilibrium allele frequencies under fluctuating population densities (*c.f.* grey dots in Fig. 3). We obtain this close approximation by replacing the migration in a model without joint population dynamics by the mean backward migration from the model with joint ecological

dynamics (and density fluctuations). Hence, the mean backward migration gives a good measure for the strength of fluctuations and their impact on the evolutionary dynamics – especially when fluctuations in backward migration rates are not too strong (SI, section S3.2). When fluctuations in backward migration increase with intensifying density fluctuations, their small effect on equilibrium allele frequencies becomes apparent – and the approximation deviates slightly from the complete model (just before the focal type dies out in Fig. 3).

Strong selection in the focal niche makes the evolutionary dynamics less vulnerable to the recurrent swamping under fluctuating population densities. Higher selection counteracts the rising mean backward migration: the locally adapted type increases in numbers during the growing phase of the fluctuations significantly more than the locally maladapted type does – even if the maladapted type dominates in frequency after migration. Hence, with increasing selection the locally adapted type survives larger fluctuations and the decrease in equilibrium allele frequency driven by density fluctuations flattens (Fig. S7). This holds true even when the trade-off in selection between the niches is symmetric (i.e. also strong in the stable niche): strong symmetric selection, albeit leading to less variation in both niches, stabilizes the polymorphism and maintains diversity for higher intrinsic rate of increase.

The decrease in allele frequency of the type which is best adapted to a fluctuating environment is due to the combination of the ecological instability and immigration of a type adapted to an other, more stable habitat. In the absence of gene flow, the locally adapted type converges to fixation regardless of fluctuations. Yet, given a constant immigration rate, increasing emigration may be essential for survival of the type adapted to the fluctuating niche (see Fig. S8). As fluctuations grow, higher asymmetry between emigration and immigration is necessary for the focal type to persist – the other niche acts as a reservoir of the focal type although it is locally maladapted. Increasing symmetric migration is only advantageous to the focal type under specific conditions, such as when the focal niche is larger (Fig. S9).

Robustness to further scenarios

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. 5). Specifically, when

the population density in the second niche fluctuates, the focal type A benefits from these fluctuations as long as the first niche maintains a more stable density ($r_1 < r_2$). This relative advantage of the focal type declines, and so does its equilibrium frequency, as the amplitude of the fluctuations in the focal niche rises. When the intrinsic rates of increase are the same in both niches and population sizes are fluctuating but not yet chaotic, allele frequencies converge to about the same value as in the absence of fluctuations (intersection of gray dashed lines in Fig. 5B, D, F). This is because mean backward migration rates are identical in both niches when the strength of the fluctuations in their population densities is equal. When more than one subpopulation exhibit density fluctuations, we observe an increase in equilibrium frequency of the type adapted to the niche where fluctuations in population size are the smallest. The less fluctuating niche is subject to the weakest average backward migration, and therefore the type adapted to it swamps niches that undergo stronger fluctuations. This generalizes the phenomenon described in the previous paragraphs: when one niche is significantly less stable than the other niche, the focal type, adapted to the niche where fluctuations are the strongest, goes extinct.

The decline in equilibrium frequency of the type adapted to the less stable niche is independent of the underlying reason for the occurrence of fluctuations. For the evolutionary dynamics, only net fluctuations in population size matter – whether imposed or driven by intrinsic dynamics. Thus, the change in equilibrium frequency is robust also under other forms of population dynamics such as logistic density dependence (Fig. S10, S11). Here, fluctuations are weaker than under Ricker's regulation, and we see that the focal type's equilibrium frequencies decrease continuously even if polymorphism can be maintained under chaotic densities.

The change in equilibrium frequency driven by intrinsic fluctuations in population size is also qualitatively robust to alternative formalizations, where the mean fitness of a population impacts also its carrying capacity. Under hard selection, the decline in equilibrium allele frequency with growing fluctuations is steeper, because mean fitness in the fluctuating niche decreases due to a higher proportion of maladapted immigrants (Fig. S12).

Furthermore, the observed evolutionary phenomenon is qualitatively independent of whether migration precedes selection and population growth (as modeled here) or succeeds them (Fig. S13).

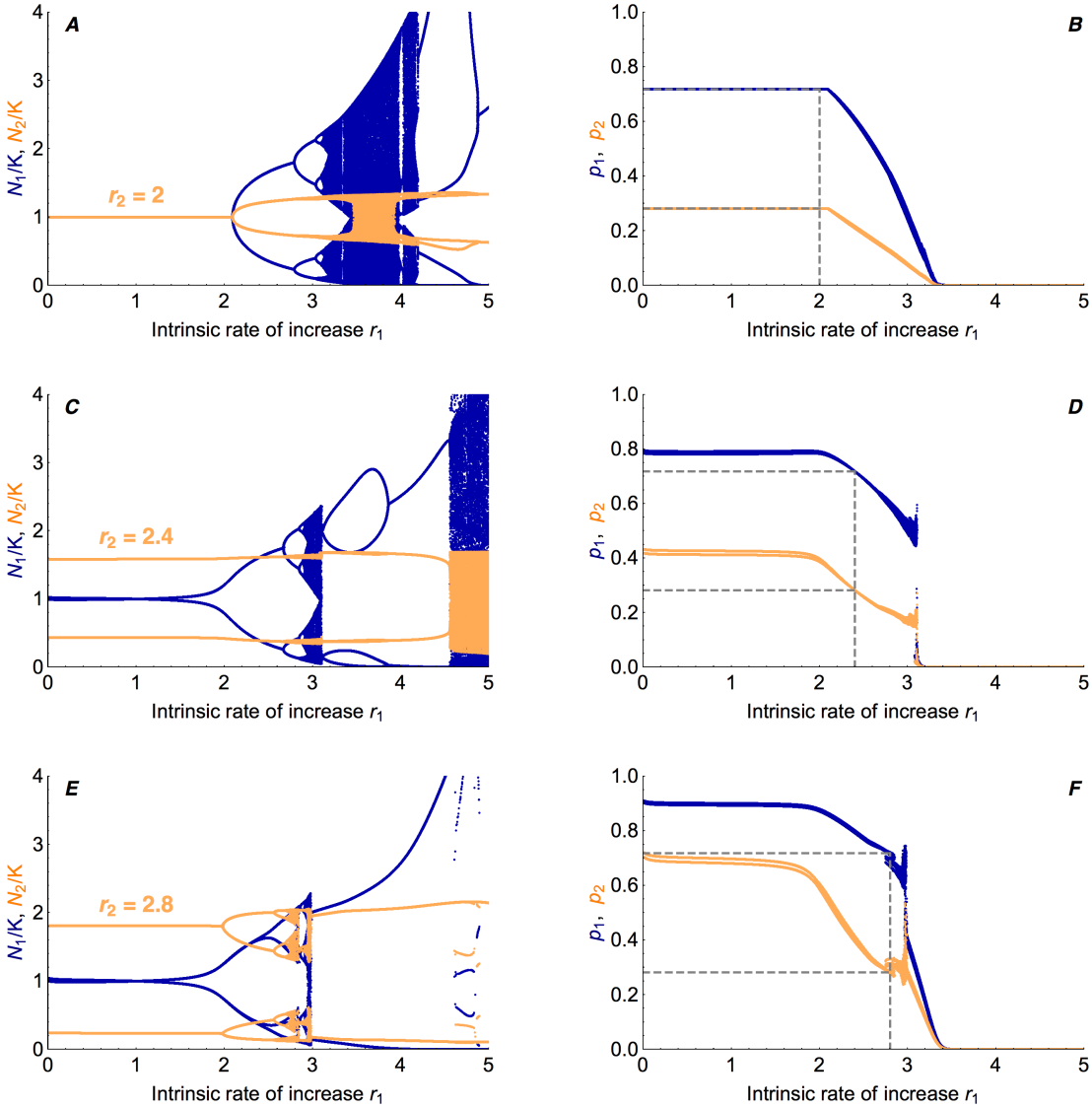

Figure 5: **When both niches exhibit fluctuations, the type better adapted to the more stable niche increases in frequency.** With growing intrinsic rate of increase in niche 2 (from top to bottom: $r_2 = 2$, 2.4, 2.8), fluctuations in population density in niche 2 arise and intensify (A, C, E), leading 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: $s_1 = s_2 = 0.1$, $m = 0.05$

Conditions for stable polymorphism

How do the classic conditions for maintenance of diversity under migration and selection change when local population size fluctuates?

When population dynamics maintain constant densities, simple explicit conditions for a stable polymorphism can be derived (SI, section S1.1). For the general case of arbitrary migration rates and potentially unequal niche sizes these can be found in the SI (Eqs. S5, S6). The condition for coexistence of the two types when population densities are stable (and equal) and migration is symmetric, is given by

$$m \cdot \left| \frac{1}{s_1} - \frac{1}{s_2} \right| < 1 - m \tag{8}$$

We see that both symmetry in selection strength between the niches and low migration stabilize the polymorphism. 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). The formula is similar to the known sufficient conditions for maintenance of polymorphism in diploids and models in continuous time (Maynard Smith, 1970; Bulmer, 1972; Lenormand, 2002; Bürger, 2014). Condition (8) is visualized by the dashed lines in Fig. 6 (also Fig. S1): the stronger the asymmetry in selection, the larger selection needs to be relative to migration for diversity to be maintained. In the absence of fluctuations, if selection is strongly asymmetric, and weak relative to migration, there is no polymorphic equilibrium and allele frequencies converge to fixation.

When population densities fluctuate, the explicit analytic conditions for a globally stable polymorphism are long and complex (SI, section S1.3). They are derived using stability analysis of the model with imposed fluctuations in niche 1 – where this analysis is possible although we do not have an explicit formula for the equilibrium allele frequencies under fluctuating population densities. The conditions for maintenance of diversity under strong imposed fluctuations in the focal niche are shown in Fig. 6 (solid lines, encasing the grey area).

The parameter region where a stable polymorphic equilibrium is maintained changes when a subpopulation's density fluctuates (Fig. 6: solid *vs.* dashed lines). The stabilizing effect of weak migration and strong selection is preserved under both constant and

fluctuating population dynamics: variation is maintained more easily when dispersal is low (Fig. 6A *vs.* B), and the robustness of the polymorphism broadens as symmetric selection gets stronger (polymorphism is maintained for larger fluctuations as selection intensifies). Therefore, 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 stability region is shifted because selection against the focal type (s_2 in niche 2) and density 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.

Under fluctuations in the focal niche, more variation is maintained when the selection trade-off between the niches is asymmetric and benefits the focal type ($s_2 < s_1$). Fluctuations in the first niche lower the equilibrium frequency of the locally favored type (A), while increasing the proportion of the other type (a). Therefore, they reduce the parameter region where the focal type A becomes fixed (Fig. 6: white area, bottom right). Whenever the focal type A has a strong relative selective advantage ($s_2 \ll s_1$), fluctuations in the niche where it is favored, counteract the asymmetry in selection by increasing the proportion of the disadvantaged type a. In that regime, this broadens the region where polymorphism is maintained. On the other hand, when asymmetry in the selection trade-offs imposes a strong disadvantage on the focal type A ($s_2 \gg s_1$), its allele frequencies decrease and fluctuations lead easily to its extinction. Hence, a significantly larger range of parameters leads to fixation of the other type, a, when fluctuations occur in the first niche (Fig. 6: white area, top left). In summary, 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). Fluctuations counteract resp. intensify asymmetry in selection: if asymmetry in selection trade-offs favors the type adapted to the fluctuating habitat, fluctuations in population density can support diversity.

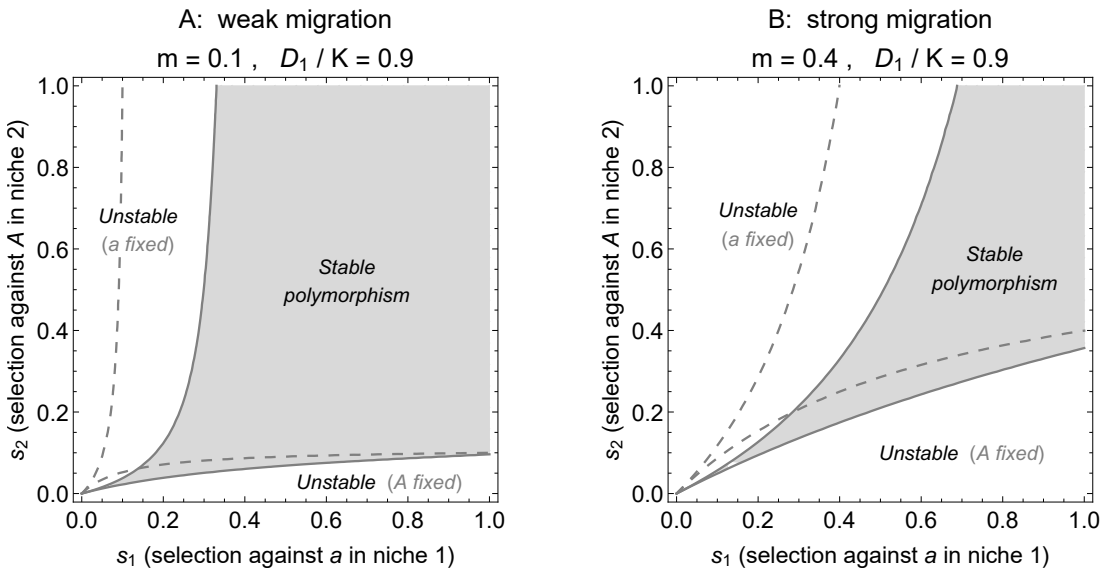

Figure 6: **Fluctuations in the density of niche 1 shift and skew the parameter region where variation is maintained.** Dashed lines give the condition for maintenance of polymorphism in the absence of fluctuations ($m \cdot |1/s_1 - 1/s_2| < 1 - m$, see SI), whilst solid lines delimit the region where 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 analytic conditions for maintenance of polymorphism under imposed fluctuations are extensive and complicated in the model with bidirectional migration (visualization in Fig. 6), it proves useful to analyze a continent-island model with imposed fluctuations on the island. In the SI we demonstrate that the effect of (intrinsic) density fluctuations on the evolutionary dynamics is robust to whether migration is symmetric or unidirectional to the fluctuating niche: the equilibrium frequency of the focal type is simply shifted to lower values under monomorphic immigration (section S9). For the continent-island model, simple explicit conditions for the persistence of the resident type on the island can be derived.

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 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 local selective disadvantage of the immigrants, s_1:

$$\frac{M_{21}}{K_1 + M_{21}} \; < \; s_1 \tag{9}$$

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

In the presence of fluctuations, condition (9) is necessary but not sufficient. The resident type persists on the island if and only if

$$\frac{D_1}{K_1} \; < \; \sqrt{\frac{1}{(2-s_1)s_1} - \left(\frac{1}{(2-s_1)s_1} - 1\right) \cdot \left(1 + \frac{M_{21}}{K_1}\right)^2} \tag{10}$$

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. 7A.

Condition (10) implies and extends the threshold for swamping in the absence of population dynamics (Eq. 9). The critical relative fluctuation size $(D_1/K_1)^*$ is a positive real number, whenever condition (9), which is equivalent to $M_{21}/K_1 < s_1/(1 - s_1)$, is fulfilled. The critical relative fluctuation size 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. In summary, whenever the relative number of immigrants is small enough (Eq. 9), coexistence becomes possible, but depends on the amplitude of fluctuations on the island (Eq. 10).

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 once the balance between selection and immigration allows for coexistence of the two types (see Fig. 7A). Weak fluctuations have a weak effect on the maintenance of diversity on the island.

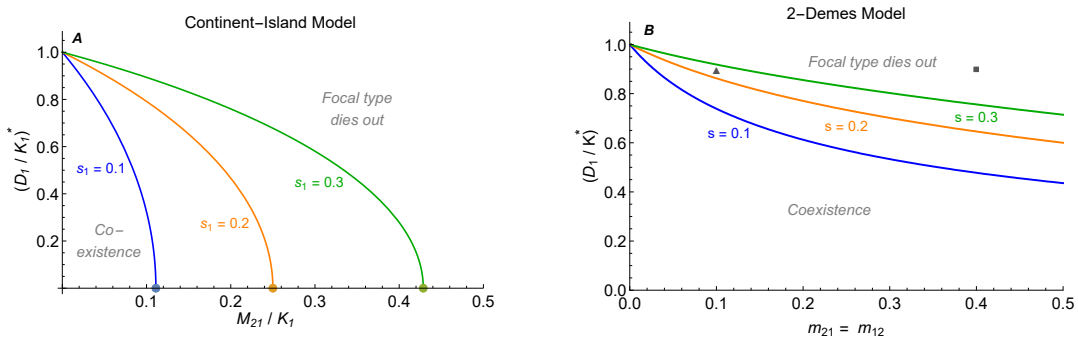

Figure 7: **Strong fluctuations lead to extinction even when migration is weak, but the effect is attenuated under bidirectional migration.** The critical relative fluctuation size is a decreasing function of the migration rate and an increasing function of selection ($s_1 = 0.1$ (blue), 0.2 (orange), 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. (9)), 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. 6 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 immigrants 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. 7A and Fig. S15). 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 discussed in the model with symmetric migration and density dependent population regulation already (Fig. S7).

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 (Fig. 7B)? When there is bidirectional migration between two niches, fluctuations in the focal niche are less detrimental to the locally adapted type than in the continent-island model (Fig. 7A *vs.* B). With bidirectional migration, the other more stable niche 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 locally adapted type: the ability to find refuge in a stable niche is strongly beneficial for its maintenance – even if it is maladapted to that other niche and would go extinct there in the absence of immigration.

Discussion

In nature, the productivity and stability of environments vary through space. Species live across sets of heterogeneous habitats that differ both in their demographic stability and evolutionary optima. For example, many species live both in their natural habitat as well as in strongly human-altered environments such as parks, fields or houses. These habitats favor somewhat different adaptation, and typically differ in their stability as well. Likewise, peripheral populations of species often experience more extreme and unstable environments, inducing fluctuations in population sizes. Our results demonstrate that in such structured populations, recurrent density fluctuations within an ecological niche have a substantial effect on the diversity of the whole population. Whenever local population size is low, the locally adapted type is vulnerable to swamping by migration from a neighboring habitat. The asymmetry in gene flow induced by fluctuating populations is reflected by an increase in average backward migration rate, which measures the mean relative immigration into the focal niche. We obtain simple explicit conditions for persistence of the resident type and show that while small fluctuations hardly affect coexistence, even weak migration may drive the locally adapted type to extinction if fluctuations are strong. 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 fact that migration can balance local disturbances has been recognized early on: "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). Later, Chesson (1985) formalized these ideas of coexistence as a "spatial storage effect" – coexistence is facilitated because differing micro-habitats buffer a species against poor recruitments that occur during periods when the other species has a competitive advantage. In our work, local population sizes fluctuate, but within each habitat, evolutionary optima are stable across time. While dispersal stabilizes the population dynamics, it has a destabilizing effect on the maintenance of polymorphism: weak migration across a heterogeneous habitat increases local variation, but polymorphism cannot be maintained when immigration is too high (reviewed in Lenormand 2002). When population densities fluctuate, swamping by migration becomes very powerful, and the equilibrium frequency of the type which is adapted to the "fluctuating" niche decreases. There is a disadvantage to adaptation to an ecological niche which exhibits fluctuations in population size.

Although it has been known for some time that migration stabilizes population dynamics – and can therefore suppress chaotic fluctuations – our results highlight why it may be difficult to specialize to an unstable environment. A specialist adapted to an environment which induces fluctuations in the population dynamics is sensitive to invasion and replacement by a type common in the surrounding more stable environment – even if that type is locally maladapted to the fluctuating niche. The replacement itself may have a minor stabilizing effect on the ecological dynamics when the effective growth rate decreases with maladaptation (as we assume here, Fig. S3B). Yet, due to ongoing migration, fluctuations of the persisting type are suppressed. Soon after habitats become connected, types adapted to unstable, strongly fluctuating niches will be replaced by their competitors, which benefit from migration from a stable environment.

It is an important assumption of our model that the intrinsic rate of increase is a property of the niche rather than the genotype – as is the case when multiple types use a common abundant resource. Similarly, exogenous fluctuations are imposed on the entire population within a niche. As the fluctuations of a niche apply to its whole subpopulation, they lead to an increase in relative immigration which is independent of evolution and applies to all genotypes at the same rate. Therefore, the recurrent swamping over-

comes the evolutionary trade-off and the type adapted to the most severely fluctuating niche gets swamped by migration from more stable habitats. Its allele frequency declines slowly over many generations of fluctuations in population density. In ecological models where the capacity to grow well from low densities and the trade-off between the types are combined to one parameter (Smith, 1998; Luís et al., 2011), we do not observe the effect that fluctuations in the resource-rich niche ultimately harm the locally more competitive type. This is because fluctuations in population size then only arise due to a dual advantage of this type. The coupling of demography and evolution is an essential feature of our model.

Here, we assume soft selection, so that the carrying capacity does not change with maladaptation. Under hard selection, both intrinsic rate of increase and carrying capacity change with the mean fitness of the population. Then, the decline in frequency of the type adapted to the unstable environment is slightly faster with growing fluctuations (see Fig. S12). This is because the asymmetry in average gene flow increases as the carrying capacity in the focal niche decreases. 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). Here, fluctuations driven by delayed feedback in density regulation arise from discrete time dynamics. Yet, our main results are robust to extrinsically imposed fluctuations and alternative choices of density regulation such as logistic density dependence (see Fig. 3 and Fig. S11). To a good approximation, they can be recovered using mean backward migration rates. Therefore, we believe that our results obtained from discrete-time dynamics extend to continuous time well – as long as the differences in the time scales of fluctuations in the ecological *vs.* evolutionary dynamics are similar as in our model.

Furthermore, 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 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. Conversely though, when one type inhabits multiple fluctuating niches, increasing migration between them stabilizes its population dynamics (Allen et al., 1993; Ruxton, 1994; Stone and Hart, 1999) and hence increases its robustness against gene flow from a neighboring

habitat with a trade-off in adaptation.

We believe that our results are of particular relevance for maintenance of local adaptation to peripheral populations (Sexton et al., 2009; Holt and Barfield, 2011). These often experience more severe fluctuations than more central habitats (Harrison, 1991). Our deterministic model shows that – assuming genetic drift is weak relative to selection – adaptation to local conditions is considerably more difficult when population density fluctuates, and that even weak migration can prevent local adaptation in the presence of strong fluctuations (*c.f.* Holt 1983a,b; Lennon et al. 1997). However, this prediction could change under stochastic dynamics because even weak migration has a strong stabilising effect on density-dependent population dynamics. This beneficial effect of stabilisation by immigration may reduce the strength of genetic drift by keeping the locally adapted type away from very low densities. Therefore, when genetic drift is strong, dispersal could be beneficial even when it brings in also maladapted types. A similar effect is seen in models of evolution to species range margin with a continuously varying resource – once genetic drift becomes important, increasing migration rate improves the adaptation to marginal conditions (Polechová, 2018). The effects of genetic and demographic stochasticity in this simple model, as well as the impact of added instability in peripheral populations on adaptation to marginal conditions would be an interesting subject to dedicated future study.

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). We also believe that our findings, which demonstrate that even under deterministic dynamics the variance in population size is an important factor for maintenance of diversity, are relevant to conservation biology. The equilibrium allele frequencies are strongly affected by density fluctuations, even if the average densities are constant and population size stay large enough so that stochastic extinction is not yet a concern. Our results can be important because large fluctuations in population densities can be induced by extreme weather, which currently appear increasingly often as the stability of the climate is decreasing.

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