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Contents

1 Abstract

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". We assume that the quality of the habitat varies across space, where a differing inherent productivity within each niche determines the attainable intrinsic rate of increase of the local population. Focusing on the question of maintenance of diversity, we illustrate the effects of such spatial variability on coexistence using a simple model: we consider two discrete types inhabiting two demes coupled by migration, and a trade-off in the adaption to the two different demes. In this context, we show that fluctuations, which naturally arise due to endogenous population dynamics with high intrinsic rate of increase, can have a strong influence on the maintenance of diversity in the system. Comparing to the classic conditions for the maintenance of variation in the absence of population dynamics, the richer, less stable environment can get more easily swamped by a species (genotype) which is locally maladapted and that flows in from the more stable environment. Stability in population size can therefore be just as important as the selective advantage within a niche, as locally maladapted types may benefit from fluctuations if they have a stable reservoir available. We explain the conditions for maintenance of diversity (polymorphism) in terms of the relative strength of selection, migration between the habitats, and the extent of fluctuations. Numerical solutions to the full system are complemented by stability analysis and explicit analytic formulas for a simplified model with imposed fluctuations.

Keywords: *Eco-evolutionary dynamics, migration, fluctuating environment, evolution, structured populations, overcompensating density-dependence, migration-selection balance, Ricker model*

2 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 (Slatkin, 1975; Nagylaki and Lou, 2006; Nagylaki, 2009). Yet typically, population dynamics are considered fast enough so that they do not need to be modeled explicitly. In this work, we include population dynamics and analyze how the known predictions and conditions for maintenance of variation in two demes change when local population density fluctuates.

Complex and extensive fluctuations of population density have been in the focus of ecological theory for decades, reaching prominence with the discovery that large and irregular fluctuations can be driven by very simple dynamics (Lorenz, 1963) such as density-dependence or predator-prey interactions (May, 1972, 1974; Turchin et al., 2000; Bjørnstad and Grenfell, 2001). In nature, temporal fluctuations in population density are typically caused by a mixture of endogenous elements and exogenous elements, both biotic and abiotic (Ellner and Turchin, 1995; Higgins et al., 1997; Turchin, 2003). In ecological theory, the importance of out-of-equilibrium population dynamics has been long recognized (Levins, 1979; Hastings, 2004). Whilst disturbances in population size *per se* do not promote diversity (Chesson and Huntly, 1997), coexistence is facilitated by a trade-off in the ability to grow well from low densities *vs.* efficient use of resources at high densities ("r-" *vs.* "K-strategy", Pianka 1970), and facilitated by added spatial structure (Hastings, 1980). In these classes of models, (intermediate) disturbance promotes diversity via density-dependent trade-offs. Yet, whilst the stabilizing effect of spatial structure on diversity is well understood (Levins, 1979; Armstrong and McGehee, 1980; Turelli, 1980; Chesson, 2000), the interaction between spatial structure and disturbances in a simple model with a density-independent trade-off has received little attention.

We phrase the question in the form traditional in evolutionary theory, focusing on coexistence (maintenance of polymorphism) when environments vary across space: when can two discrete types (species, genotypes, bacterial clones) coexist, depending on their trade-off in adaptation to two "niches" represented by two habitats coupled by migration? Is diversity maintained in the presence of population dynamics? In general,

dispersal between the 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). 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 provide a simple model which gives a qualitative insight into the interaction between evolutionary dynamics and potentially complex ecological population dynamics. We focus on the impact of fluctuations in population size, which can arise readily under overcompensating density-dependence (Costantino et al., 1995; Ellner and Turchin, 1995; Turchin et al., 2000; Coulson et al., 2001) or can be imposed by fluctuations in the environment – and in general, are often likely to be driven by the combination of the two (Ellner and Turchin, 1995). While many previous studies focused on complex ecological dynamics arising from within-species interactions, or on evolutionary dynamics in subdivided habitats, we combine the two processes. Here, we investigate the interaction of population dynamics and evolutionary dynamics driven by selection and migration between two habitats which represent two ecological niches.

3 Model and Results

We discuss our analyses first by introducing a relatively complex model and its behavior, and by proceeding to simplified versions of it afterwards in order to enhance our understanding of its characteristics. So, first, we address a two-niche model with joint evolutionary and ecological dynamics, where the latter are modeled by Ricker's regulation (Ricker, 1954). Here, fluctuations may arise due to overcompensating density dependence. Second, we will simplify the ecological dynamics by analyzing the impact of fluctuations when they are imposed in the population size of one niche. In both sections, we explore the marginal cases of symmetric *vs.* unidirectional migration.

3.1 Density dependent regulation of population densities

We start with the description of a model for joint ecological and evolutionary dynamics with migration between two demes, which is then analyzed in the two subsequent parts of this chapter. Focusing on symmetric migration, we first explore the effects of selection and migration on the ecological dynamics. Then, we discuss the impact of population dynamics on the evolutionary equilibrium. Last, we address the differences to these results that arise when migration is unidirectional.

3.1.1 Model for joint eco-evolutionary dynamics

We study the evolution and maintenance of variation in the face of gene flow between populations in two divergent habitats. Crucially, population dynamics are modeled jointly with the dynamics of the change of the frequencies of the two types. These could represent two species or two different alleles in a one locus haploid system – we will use the latter interpretation and denote the alleles by A and a. Importantly, we assume that generations are discrete, where a delayed feedback in density regulation can cause large fluctuations of the population size beyond the carrying capacity. Throughout, 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. At generation t, deme i is described by the population size, $N_i(t)$, and the frequency of allele A, $p_i(t)$. For simplicity, prime ' labels the intermediate variables after migration (before selection and population growth).

Following migration, the number of individuals in deme 1 is

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

and the frequency of allele A in deme 1 is

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

(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 $w_{2a} = 1$. The selection coefficients s_1, s_2 range between 0 and 1. Thus, 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

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

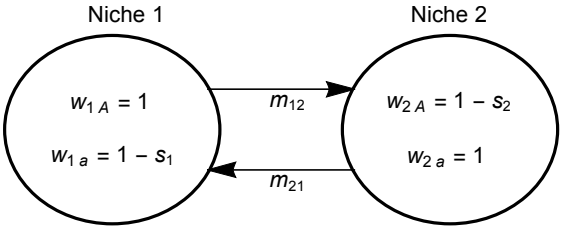

Fig. 1: **Model:** Evolution and maintenance of variation in the face of gene flow between populations in two divergent habitats. Type A is better adapted to niche 1; type a to niche 2.

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

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

Here, r_i denotes the intrinsic rate of increase, which gives the maximum growth rate of the population at low densities. The rate r_i is assumed to be a property of the niche rather than the types. This implies that within a niche the two types compete for the same resource. Importantly, we assume that the effective intrinsic rate of increase declines due to maladaptation (by multiplying the mean fitness $\overline{w}'_i(t)$ to the exponent). This means that a maladapted population is not able to exploit the potential intrinsic rate of increase r_i. The carrying capacity of the entire system, however, remains unaltered by maladaptation and is given by K: with two demes, $c_i K$ describes the carrying capacity of deme i (c_i ranging between 0 and 1, $c_1 + c_2 = 1$). Throughout, we will consider niches with equal carrying capacity, i.e. $c_1 = 1/2$, unless explicitly stated differently.

We now proceed to analyze this model, focusing on symmetric migration between demes. Later, we address unidirectional migration and discuss the impact of immigration to *vs.* emigration from the focal deme.

3.1.2 Symmetric migration

In the following analysis, migration is assumed to be symmetric: m will denote the migration rate, $m = m_{12} = m_{21} \leq 1/2$. Thus, when the population densities in both niches are the same (e.g. both at carrying capacity), migration leads to a balanced exchange of an equal number of individuals.

Effect of evolution and migration on population dynamics

In the absence of evolution and migration, the ecological dynamics with Ricker's regulation are well understood. The population size converges towards a stable equilibrium as long as the intrinsic rate of increase is smaller than 2, which determines the first branching point in the absence of joint evolutionary dynamics (see Fig. 2A and 3A). As the growth rate increases above 2, the population size starts oscillating in a period-2 cycle due to overshooting of the carrying capacity and overcompensating density regulation (May and Oster, 1976). A further rise of the intrinsic rate of increase first leads to other period-doubling bifurcations and finally to chaotic behavior (see orange lines in Fig. 2 A).

With migration and selection, the ecological dynamics change substantially. Fluctuations due to overcompensating density regulation in the focal niche are dampened by

dispersal when the other niche maintains a stable density, as indicated by the blue lines in Fig. 2. Whereas the observation that migration between subpopulations may stabilize all kind of fluctuations has been known for some time (Den Boer, 1968; Reddingius and Den Boer, 1970; Roff, 1974), the extent of the dampening of potentially large and chaotic fluctuations is striking. The stabilizing effect of constant migration into a Ricker regulated population has been explored in detail by Stone and Hart (1999): stabilization occurs because immigration pushes the population size away from zero. Chaotic behavior arises only for larger values of the intrinsic rate of increase, or not at all if migration is strong enough. Interestingly, even if the population size exhibits a phase of chaos, due to immigration it re-stabilizes for even higher intrinsic rate of increase, where fluctuations become periodic again (see Fig. 2, and Dey et al. (2014)). Bidirectional exchange of individuals with a stable niche 2 leads to a slightly stronger stabilization than constant immigration explored by Stone and Hart (1999), because proportional emigration at high densities dampens the fluctuations (see chapter 3.1.3 for more detail).

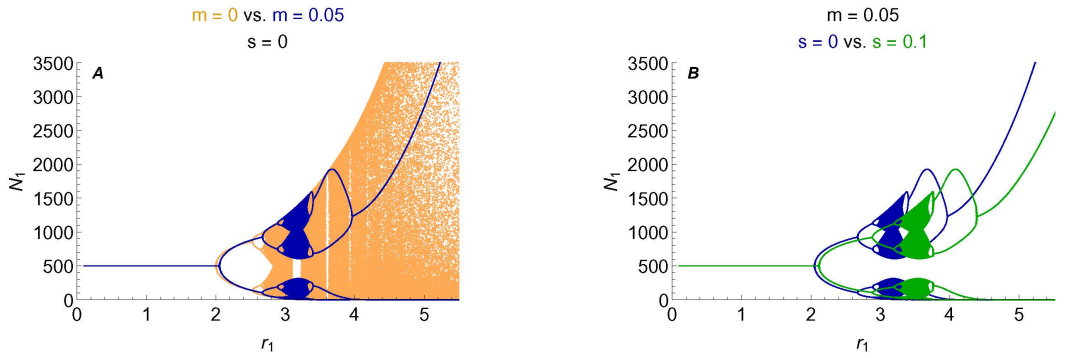

Fig. 2: **Migration and selection stabilize the population dynamics.** Bifurcation diagram showing the long-term behavior of the population size in niche 1 (while the population dynamics in niche 2 are stable with r_2 fixed to 1). (A) Migration from a stable environment dampens fluctuations and chaos which have arisen due to overcompensating density regulation. The standard Ricker model in the absence of migration and evolution is shown in orange. The blue lines depict $N_1(t)$ (after $t = 2^8 - 1$ to $2^8 + 1$ generations) as modeled in equation (5) with symmetric migration $m = 0.05$ (but no selection). (B) Selection shifts the branching points towards higher values: The green lines show the long-term behavior of the population dynamics with symmetric selection ($s_1 = s_2 = 0.1$). This stabilizing effect occurs because, here, the effective intrinsic rate of increase depends on the mean fitness which decreases with maladaptation. Note that the blue lines in (A) and (B) coincide. Parameters: $r_2 = 1$, $K = 1000$, $c_1 = 1/2$.

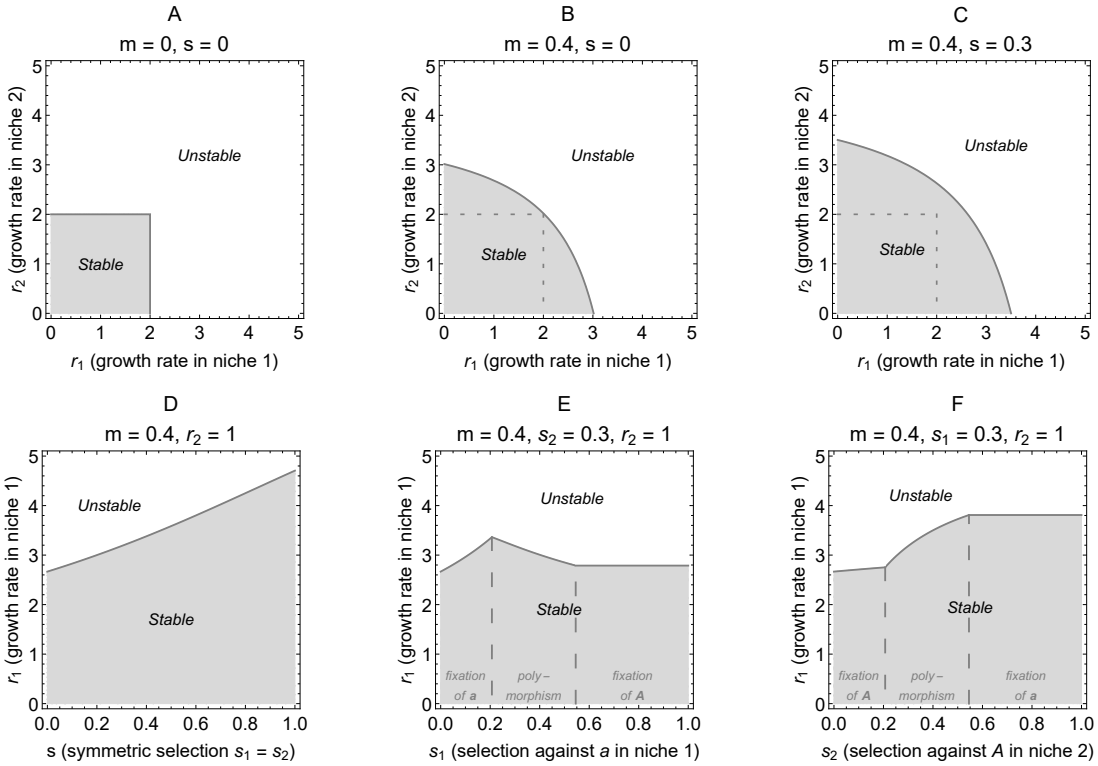

Fig. 3: **Stability of the ecological dynamics (first branching point).** Migration (m) and symmetric selection (s) stabilize the ecological dynamics. (A) In the absence of migration and selection, population size overshoots the carrying capacity for intrinsic rates of increase r_1, $r_2 > 2$ (for the Ricker model of population growth). (B) The stabilizing effect of migration on the population dynamics in niche 1 is stronger, the smaller the growth rate in the other niche, r_2, and vice versa. Strong migration between niches ($m = 0.4$) stabilizes the dynamics for r_1 up to 3 if r_2 is sufficiently small. However, if $r_1 = r_2$, migration has no stabilizing effect (the dashed lines indicate the stable region for $m = 0$, see A). (C, D) Here, strong symmetric selection decreases the mean fitness. This leads to a reduction in the effective intrinsic rate of increase and, thus, to a further stabilization of the population dynamics for large r_1, r_2. Note that in (A)—(D) the evolutionary equilibrium is always polymorphic due to symmetry in selection and migration. However, when selection is asymmetric, more complicated stability properties arise (E, F), as the asymmetry in allele frequencies at equilibrium influences the mean fitness after migration (see Fig. S1 in SI) and, thus, the value of r_1 at the first branching point: (E) Dashed lines indicate the existence of a polymorphic equilibrium. When a is the only type present at equilibrium (left), increasing its local selective disadvantage s_1 corresponds to a decrease of the mean fitness in niche 1. In the middle region, a further increase of s_1 leads to a growing proportion of locally well adapted type A individuals and mean fitness locally increases. When allele frequencies converge to fixation of type A (right), mean fitness in the focal niche equals 1 and the branching point is determined by the stabilizing effect of migration only. (F) An increase in s_2, which determines the selection against A in the other niche, leads to a drop of the equilibrium allele frequency of A in both niches and, thus, to a decrease of the mean fitness in the focal niche (as the frequency of the locally maladapted type a rises).

The leading eigenvalue takes values between -1 and 1 within the gray areas, implying stability. The dark gray lines denote when it equals -1, which indicates instability due to oscillating divergence (see section 5.2.2 in SI for explanation).

In our model, selection also has a stabilizing effect on the population dynamics. This is because we assume throughout that the effective intrinsic rate of increase drops due to maladaptation. Immigration of maladapted individuals leads to a stronger stabilization in the population dynamics of the focal niche, because the more the population is maladapted the less it is able to exploit the potential rate of increase. As $\overline{w}_i'(t)$ decreases, the first branching point occurs for higher values of the intrinsic rate of increase only (see Fig. 2 B).

In Fig. 3 we summarize the stability properties of the population dynamics as a function of the intrinsic rates of increase subject to selection and symmetric migration. In the case of symmetric selection (A, B, C, D) we simply observe the stabilizing effects of migration and selection as described above. However, asymmetry in selection (E, F) alters the behavior: The change in mean fitness $\overline{w}_1'(t)$ (which determines the value of r_1 at the branching point when migration is fixed) as a function of asymmetric selection is non-smooth and its properties depend on whether the equilibrium is polymorphic or not (see also Fig. S1 in SI).

Ecology affects evolution

Under our assumptions, there are two main processes that influence the evolutionary dynamics. First, existence and stability of a polymorphic equilibrium depends on the relative rates of selection and migration. Here, we will show that allele frequencies can also be affected by ecological feedback such as unstable population sizes.

When ecological dynamics are absent or lead to constant population sizes In the absence of population dynamics, the conditions for maintenance of polymorphism, and the predicted amount of variation maintained, are well understood: both symmetry in selection strength between the niches and low migration stabilize the polymorphism (Maynard Smith, 1970; Bulmer, 1972; Lenormand, 2002). In the absence of ecological dynamics, we can predict the allele frequency and asses the stability of the polymorphic equilibrium (see SI, section 5.2.1). These evolutionary predictions continue to be true, when population dynamics are included, as long as the latter leads to a stable, constant ecological equilibrium (see Fig. 4, Fig. 5 A, B).

The stability analysis of the polymorphism is visualized in Fig. 4: the stronger the asymmetry in selection, the larger selection needs to be relative to migration. The

condition for coexistence of the two types is given by

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

(see formulas (S4), (S5) in SI for the general condition with arbitrary m_{12}, m_{21}, c_1). If selection is strongly asymmetric, and weak relative to migration, there is no polymorphic equilibrium and allele frequencies converge to fixation. In Fig. 5 A, B we see that, as long as ecological dynamics lead to stable population sizes, the evolutionary outcome coincides with the predictions in the absence of ecology (dashed lines). So, for growth rates that lead to stable population sizes (see Fig. 3), the expected allele frequencies (and hence the variance) maintained at equilibrium are known (Fig. 5 A, B and 5.2.1 in SI) and polymorphism is kept under the expected and known conditions (Fig. 4).

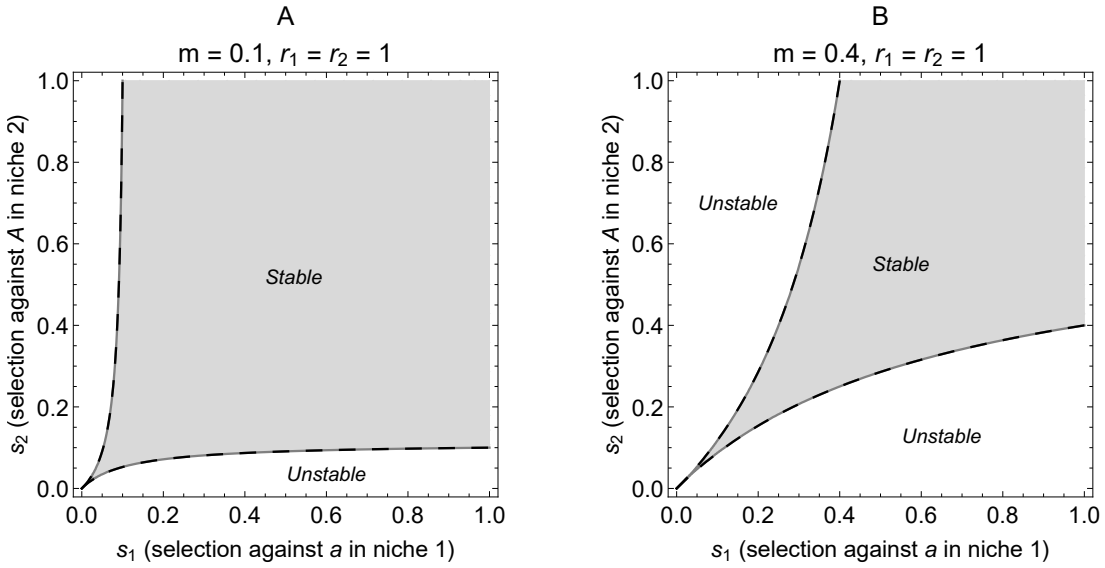

Fig. 4: **Stability of the polymorphic evolutionary equilibrium when ecological dynamics lead to stable population sizes.** For stable polymorphism to be maintained, the stronger the asymmetry in selection, the larger selection needs to be relative to migration (Maynard Smith (1970); Bulmer (1972)). (A) weak migration; (B) strong migration. Migration is symmetric, $m = m_{12} = m_{21}$. Dark gray lines indicate instability due to monotonic divergence, i.e. where the eigenvalue, that describes the direct effect of selection and migration on the evolutionary equilibrium, is equal to 1. This eigenvalue coincides with the leading eigenvalue of the reduced system in the absence of ecological dynamics, which is depicted by the black dashed lines. The condition for stable coexistence is $m \cdot |1/s_1 - 1/s_2| < 1 - m$.

The effect of unstable ecological dynamics on the evolutionary equilibrium However, the fluctuations which arise under a high intrinsic rate of increase due to overcompensating density regulation can markedly change the evolutionary outcome (see Fig. 5 C, D). As the intrinsic rate of increase rises above a value slightly larger than 2 in one niche, the ecological equilibrium becomes unstable and the population size fluctuates. We observe that these fluctuations in one niche are disadvantageous to the

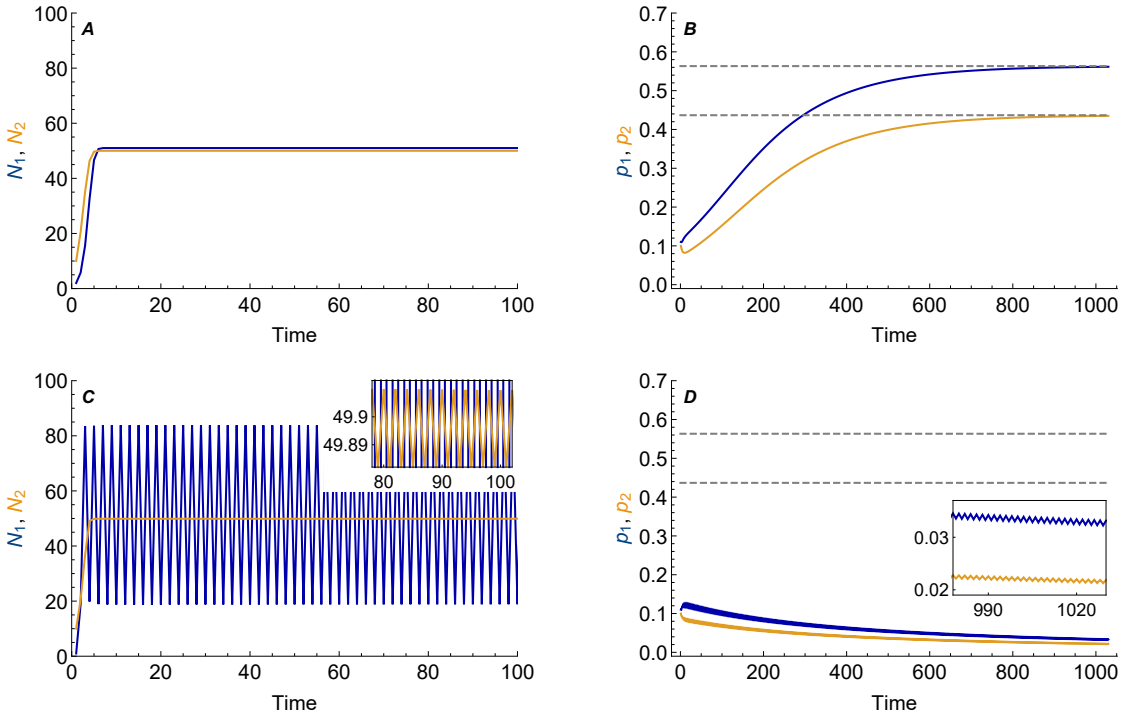

Fig. 5: **Ecological dynamics can change the evolutionary predictions.** (A, C): Population dynamics in deme 1 (blue) and deme 2 (dark orange) – under low vs. high intrinsic rate of increase in deme 1 (A $r_1 = 1$ vs. C $r_1 = 2.5$). In (A) the population sizes at equilibrium are equal (but N_1 is offset by 1 for visual clarity). (C) In deme 2, intrinsic rate of increase is low enough ($r_2 = 1$) so that the density stays (nearly) constant at equilibrium 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 obtained by analyzing 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). However, as the population density fluctuates in niche 1 (C, blue) due to overcompensating density dependence, frequency of the locally favored type A decreases in the whole system (D).
The insets highlight the fluctuations in the population size (C) and in the allele frequencies (D). Parameters: $s_1 = s_2 = 0.05$, $m_{12} = m_{21} = 0.1$, $r_1 = 1$ (A, B), $r_1 = 2.5$ (C, D), $r_2 = 1$, $K = 100$, $c_1 = 1/2$, $N_1(0) = 1$, $N_2(0) = 10$, $p_1(0) = 0.11$, $p_2(0) = 0.1$.

type that is better adapted to this niche. A high intrinsic rate of increase in niche 1 leads to a decline in the allele frequency of A at equilibrium and a gain in type a individuals which are better adapted to the stable niche 2. This phenomenon is not due to a simple drop in the mean population size of niche 1 (compared to the population size in niche 2), as we will show later when we impose exogenous fluctuations in the population density.

When a stable polymorphic equilibrium exists, the corresponding allele frequency of A smoothly decreases as r_1 increases (see Fig. 6). Eventually, fluctuations become so strong that a stable polymorphism present for lower r_1 ceases to exist and type a fixes. Although a growth of the intrinsic rate of increase r_1 leads to complicated fluctuatingpopulation dynamics, the corresponding change in the polymorphic equilibrium is almost linear – until type A dies out. In the case of fluctuating population densities (r_1, r_2 large), we could not determine at what point the frequency of A hits zero, i.e. the stability of the polymorphic equilibrium. Yet, we can obtain such conditions when exogenous fluctuations in population density are imposed – as will be discussed later.

The decrease in frequency of the type better adapted to the niche with overcompensatory density regulation occurs 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 therefore be easily 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, as fluctuations are strong, selection is not capable of compensating the swamping that occurs every second generation. As a result, 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. This evolutionary phenomenon is qualitatively independent of whether migration precedes selection and population growth (as modeled here) or migration succeeds selection and population growth (see Fig. S7 in SI).

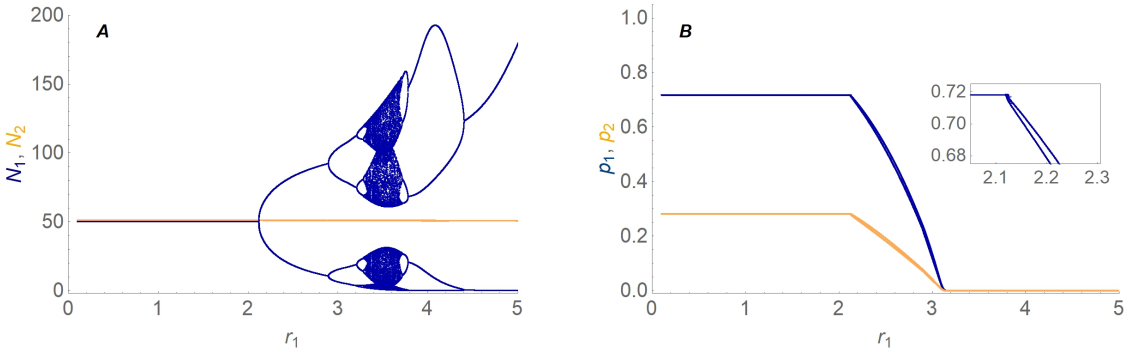

Fig. 6: **Change in the evolutionary dynamics as the density fluctuates due to overcompensatory density-dependence.** The figure depicts the long-term behavior of the ecological (A) and the evolutionary (B) dynamics as a function of the intrinsic rate of increase in niche 1. (A) Fluctuations due to overcompensatory density dependence arise in niche 1 (blue) as the intrinsic rate of increase in niche 1, r_1, increases above a value slightly larger than 2. The population size in the second niche (orange) with a fixed intrinsic rate of increase of $r_2 = 1$ stays close to the carrying capacity. (B) This depicts the equilibrium frequency of A, the type favored in niche 1, as a function of r_1, the intrinsic rate of increase in niche 1. As long as the value of r_1 leads to a stable population size, its increase has no effect on the allele frequency at equilibrium. However, the equilibrium frequency of type A decreases both in niche 1 (p_1, blue) and niche 2 (p_2, orange) as the fluctuations due to overcompensatory density-dependence grow with increasing r_1. With strong fluctuations, the frequency of the focal type approaches zero, and eventually type A dies out. The decrease in its equilibrium frequency is remarkably smooth despite the complicated ecological dynamics in niche 1, with only small fluctuations in the allele frequency induced by the population dynamics (see the inset and Fig. 5).
The branching diagram was obtained by randomizing both the initial conditions and the time of observation. Parameters: $s_1 = s_2 = 0.1$, $m_{12} = m_{21} = 0.05$, $c_1 = 1/2$, $K = 100$. Generation time ranged from 2^{10} to $2^{10} + 10$. The population size in niche 2 (A, orange) is offset by 1 for visual clarity.

The extinction of the locally favorable type A, driven by a high intrinsic rate of increase causing large fluctuations in population size of niche 1, occurs only for a higher r_1 under stronger selection (Fig. 7). There are two reasons for this: Firstly, as selection increases, the timescale of evolution gets closer to the timescale of ecology. When selection is strong, the locally well adapted type increases in number 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 increases, and this in turn stabilizes the polymorphism. Secondly, the robustness of the polymorphism broadens as the symmetric selection gets stronger

(Fig. 4). This matters as fluctuations in deme 1 have a similar effect on the equilibrium allele frequency as selective disadvantage of A has (both decrease the frequency of A at equilibrium). We analyze the effect of the symmetry in strong *vs.* weak selection on the maintenance of polymorphism later, with imposed (exogenous) fluctuations in population density (chapter 3.2.1).

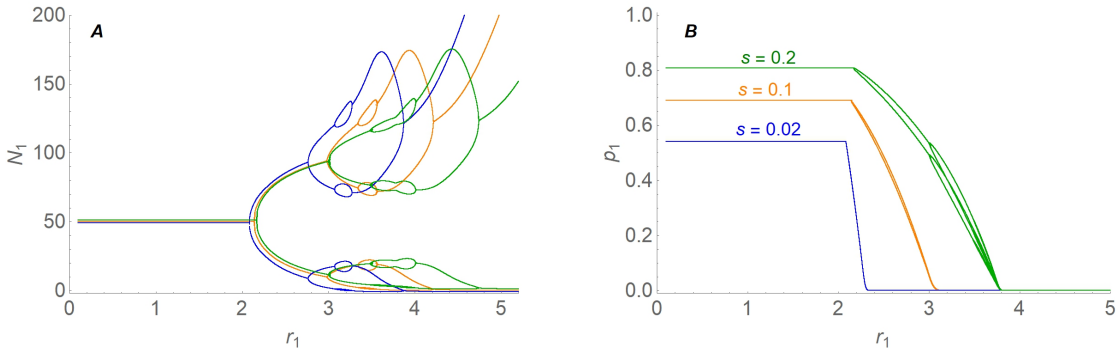

Fig. 7: **Symmetric selection counteracts the deleterious effect of fluctuations (B) and, together with migration, stabilizes the population dynamics (A).** This figure shows the dynamics at equilibrium as a function of the intrinsic rate of increase in niche 1 for three different values of selection ($s_1 = s_2 = 0.02, 0.1, 0.2$). (A) Stronger selection leads to a higher maladaptation on average; lower mean fitness then stabilizes the population dynamics in niche 1 because the effective intrinsic rate of increase decreases – the branching points shift to the right. As migration is slightly larger here comparing to Fig. 6, we observe a stronger stabilization of the fluctuations in the population size. (B) The extinction of the locally favorable type A driven by large fluctuations in population size occurs for a higher r_1 under stronger selection. Mainly, this is because as selection increases, the timescale of evolution becomes comparable to the timescale of ecology, which decreases the impact of ecology on evolution. Note that the multiple branches in the curve for $s = 0.2$ are due to fluctuations in the allele frequency (not to bistability). Parameters: $m = 0.06$, $r_2 = 1$, $c_1 = 1/2$, $K = 100$.

Throughout these analyses, we assumed that one of the niches undergoes fluctuations in population density while the second niche is stable (namely, intrinsic rate of increase in niche 2, r_2, fixed to 1). However, our findings generalize to higher values of r_2 as well: in general, when both niches exhibit fluctuations, the type that is better adapted to the less extreme, more stable habitat, increases in frequency (see SI, Fig. S2). When both growth rates are equal ($r_1 = r_2$) and population dynamics are fluctuating but not yet chaotic, allele frequencies converge to about the same proportion as when population sizes were stable in time.

We now proceed to the analysis of unidirectional migration. We will see that this may be considered a simplification of bidirectional migration that still captures the interesting evolutionary behavior.

3.1.3 Differences between symmetric and unidirectional migration

In the following, we explore how the coupled dynamics change when there is no migration out of niche 1 (i.e., $m_{12} = 0$, $m_{21} > 0$). Note that, as type A individuals are locally maladapted in niche 2, they die out in this niche when it does not receive any immigrants. Therefore – and as the population density in niche 2 will be kept at carrying capacity ($r_2 = 1$) – the model then corresponds to a (potentially fluctuating) focal niche 1 receiving a constant monomorphic influx of locally maladapted individuals. Thus, this approach is akin to a continent-island model that includes population dynamics on the island.

Effect of migration on population dynamics Migration into a Ricker-regulated population has a stabilizing effect on the population dynamics (Stone and Hart, 1999), because it keeps the density away from zero. Yet, migration out ($m_{12} > 0$) can also stabilize population dynamics (see Fig. 8A), as the population size in the fluctuating niche 1 is pushed closer to its carrying capacity by symmetric migration rates ($m_{12} \approx m_{21}$ with niches of comparable size): When population size in the focal niche is high (fluctuating up), more individuals leave it than immigrants arrive from the other niche. Thus, there is a small net decrease in population density in niche 1 whenever the number of individuals is larger than the carrying capacity and the opposite is the case whenever population size is low (fluctuating down).

Effects on evolutionary dynamics The simplification of setting emigration from the focal niche to zero elucidates the role of the second niche as a refuge for the type favored in the niche undergoing strong fluctuations. With immigration only, the equilibrium frequency of the type better adapted to the fluctuating niche (A) is shifted to lower values comparing to bidirectional migration (see Fig. 8B). This is because when migration is unidirectional the allele frequency in niche 2 converges to fixation of type a: there is no immigration to niche 2 and A is locally maladapted. Thus, immigration is monomorphic here, whereas it is polymorphic when migration goes both ways.

The second niche acts as a refuge for type A even if selection is stronger than migration but only when the evolutionary dynamics are slow relative to the population dynamics

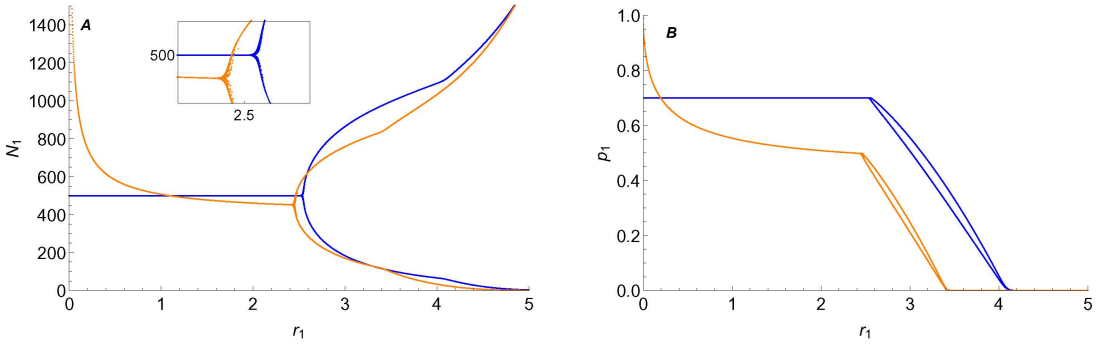

Fig. 8: **Unidirectional immigration has a weaker stabilizing effect on ecology and maintains less variation than a bidirectional exchange of individuals.** (A) The blue lines indicate the population dynamics in niche 1 with migration in both ways (with strong symmetric migration: $m = 0.2$). The outcome of population dynamics in niche 1 only with unidirectional immigration ($m_{21} = 0.2$) from the stable niche 2 ($r_2 = 1$) is shown in orange. The inset highlights the slightly stronger stabilization that occurs when migration is bidirectional. For r_1 small, immigration is stronger than density regulation, which leads to an overpopulation of niche 1. I.e. population density converges to a value above the carrying capacity whenever regulation is weak. In the extreme case of no regulation ($r_1 = 0$) population size in the focal niche goes to infinity over time, where $N_1(t+1) = N_1(t) + m_{21}N_2(t)$. However, for r_1 closer to the branching point, regulation is stronger and overcompensation occurs as a reaction to immigration which results in a slightly underpopulated niche 1. (B) The blue lines indicate the equilibrium allele frequency of A in niche 1 with bidirectional migration, whereas the orange lines show the evolutionary outcome in niche 1 only with immigration from the stable niche 2 ($r_2 = 1$). The equilibrium allele frequency of A is shifted to lower values when migration goes in one way only, as immigration is then monomorphic for type a. The exception is $r_1 \to 0$, where regulation is weak and, thus, outplayed by selection and immigration leading to an increase in equilibrium frequency of A. Parameters: $m_{12} = 0$ and $m_{21} = 0.2$ (orange) *vs.* $m_{12} = m_{21} = 0.2$ (blue), $s_1 = s_2 = 0.3$, $K = 1000$, $c_1 = 1/2$.

(see Fig. 8B). When fluctuations are large (i.e. r_1 is large enough so that selection is weak relative to ecology), migration out of the niche is beneficial for the focal type as some proportion of the migrants survive in the neighboring habitat and may migrate back to the niche to which they are better adapted to, where they help to replenish the population in the growing phase. However, when population dynamics are very slow – for r_1 close to zero – the evolutionary dynamics becomes relatively strong. In this case, monomorphic immigration of the locally maladapted type a leads to higher frequencies of the focal type A than bidirectional migration does (Fig. 8B), because immigration and selection are both stronger than population regulation: As population size in niche

1 increases due to immigration when regulation is weak, the relative immigration decreases (since the absolute number of immigrants stays constant). This drop in relative immigration (which is monomorphic of the locally maladapted type) favors the locally well adapted type, because the timescale of selection remains unchanged.

3.2 Effect of (imposed) fluctuations on evolutionary equilibria

The observed evolutionary phenomena are due to fluctuations in the population density and are therefore not specific to the choice of Ricker's regulation. In the SI (section 5.2.4), we show that the change in equilibrium frequency is robust to different forms of population dynamics that exhibit overcompensating density regulation, such as logistic density dependence (see Fig. S3 and S4). While fluctuations in the population size arising under high intrinsic rate of increase due to overcompensatory 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 model where fluctuations in the population density are imposed. Next, we thus place fluctuations D_1 in the population density of niche 1 to focus on the effect of fluctuations on evolution.

In the following model, 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 N_2 (Fig. S5 in SI). The equations for the evolutionary dynamics remain unchanged. Here, we concentrate on the case $N_2 = K_1$ (analogously to the previous focus on $c_1 = 1/2$).

We analyze the evolutionary dynamics again by addressing the case of symmetric migration rates between the two niches first, and by proceeding to unidirectional immigration to niche 1 afterwards.

3.2.1 Symmetric migration

This simplification captures the interesting evolutionary behavior from the previous model with density dependent regulation: as seen in Fig. 9, the allele frequency of A decreases as a function of the fluctuation size D_1 (a growth in D_1 here compares to increasing the intrinsic rate of increase r_1 in the preceding chapter).

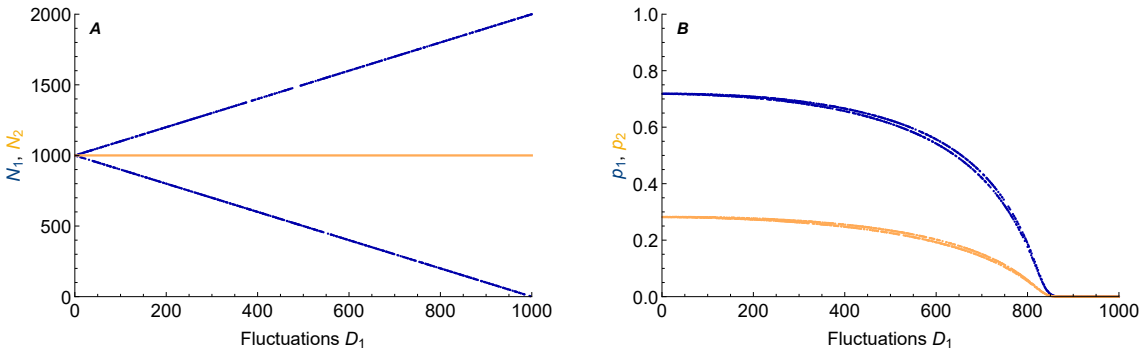

Fig. 9: **Change in the evolutionary dynamics due to imposed fluctuations in the population density.** (A) Fluctuations D_1 are imposed in the population density of niche 1 (blue line). This depicts N_1 for linearly increasing values of D_1 (although over time t fluctuations D_1 remain constant). Population size in niche 2 is constant for all times (orange line). (B) This shows the drop in the equilibrium frequency of type A in both niches as a function of the fluctuations in niche 1. The shape of the decrease of A frequency at equilibrium is not as abrupt as it was before, because here, in contrast to the previous chapter, the increase in fluctuations is linear. Parameters: $s_1 = s_2 = 0.1$, $m = 0.05$, $K_1 = N_2 = 1000$

For the evolutionary dynamics, only the net fluctuations in population size matter and the precise reason for occurrence of fluctuations is not important. Here, the population density in niche 1 fluctuates symmetrically around a "carrying capacity" K_1, i.e. we keep the mean population size in niche 1 constant and equal to the one in niche 2 ($K_1 = N_2$). This is not the case with Ricker's regulation. Therefore, this simplification proves that the decrease in the frequency of the locally adapted allele A is not simply caused by a decline in the mean population size of niche 1 when fluctuations arise.

We are now able to asses the stability analysis of the polymorphism (see SI, first part of section 5.2.5): although we still do not have an explicit solution for the allele frequencies at equilibrium, we know the expression for the population density as it is imposed. The conditions for maintenance of polymorphism are visualized in Fig. 10. Fluctuations lead to a shift in the parameter region for which variation is maintained (*c.f.* dashed lines; Fig. 4).

Even as fluctuations occur, variation is maintained more easily when migration is weak and polymorphism allows for more asymmetry in selection when selection is stronger (the shape of the stable region remains unchanged). However, fluctuations in one niche, while the other niche is stable, introduce an asymmetry in the range of selec-

tion coefficients for which variation is maintained (stable region is askew). This is because selective disadvantage of A (s_2 in niche 2) and fluctuations in niche 1 have a similar deleterious impact on the allele frequency of A at equilibrium: both lead to a decrease in the proportion of the focal type. Namely, the parameter space where the evolutionary dynamics converge to fixation of the other type a increases when fluctuations arise in niche 1, as the locally maladapted individuals benefit from the fluctuations: when asymmetry in selection is strongly discriminating against type A individuals (namely, if $s_2 \gg s_1$), then fluctuations in niche 1 intensify their struggle for survival, and lead to a further increase in proportion of the other type a. Thus,

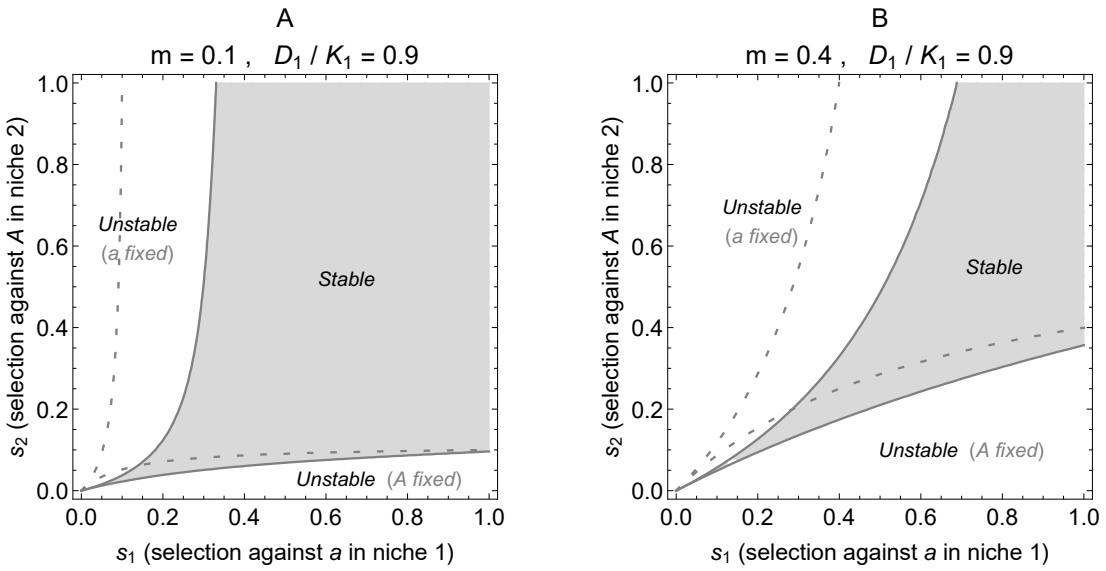

Fig. 10: **Fluctuations imposed in the population size of niche 1 shift and skew the parameter region for which variation is maintained.** This picture visualizes the conditions for maintenance of polymorphism under weak (A) and strong migration (B), when population density in niche 1 fluctuates between 10 and 190 (while population size in niche 2 is fixed to 100). The dashed lines indicate stability when fluctuations D_1 equal 0 (these lines are the same as in Fig. 4). If selection against type A is relatively strong ($s_1 \ll s_2$), then fluctuations make it even harder for A to survive. This causes the enlargement of the parameter space that leads to fixation of the other type a. However, if $s_1 \gg s_2$, then fluctuations counteract the selective asymmetry favoring A and polymorphism is maintained more easily: the region where type A gets fixed decreases. When fluctuations are absent (dashed lines), the magnitude of migration determines how tight symmetry in selection must be for polymorphism to be maintained (A *vs.* B). In the presence of fluctuations, the selective advantage of the type best adapted to the fluctuating niche must be comparatively higher: the stability region shifts to the right, at a rate which is nearly independent of the strength of migration.

the upper boundary line in Fig. 10 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 which prove deleterious for this type (by decreasing its equilibrium frequency). So, whenever type A has a relative overall 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 other type a.

Furthermore, Fig. 10 confirms the phenomenon observed in Fig. 7: the stronger symmetric selection, the stronger fluctuations need to be in order to have a lethal impact on allele A (which happens whenever the line $s_1 = s_2$ lies within the region of fixation of a in Fig. 10).

3.2.2 Unidirectional migration (continent-island model)

Finally we analyze the most simplified setting, with unidirectional migration and imposed fluctuations. Now we can find an explicit solution for the allele frequency of A at equilibrium (see SI, section 5.2.5 on unidirectional migration) and two comprehensible inequalities as condition for coexistence.

Every generation, a constant absolute number M_{21} (corresponding to $m_{21}N_2 = m_{21}K_1$) 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.) We obtain conditions for persistence of the locally well adapted type A in terms of selective disadvantage of the immigrating type, s_1, the relative fluctuation size on the island, D_1/K_1, and the mean ratio of immigrants to locals (at the beginning of the life cycle), $M_{21}/K_1 = m_{21}$, which we call the rate of immigration.

First, extinction of type A 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, selection needs to satisfy

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

I.e. 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. 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).

Now, whenever (7) is satisfied, it depends on the size of the fluctuations in the population density on the island whether the resident allele A actually survives or not. This leads us to a condition on the relative size of the fluctuations: Type A survives on the island if and only if

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

For simplicity, we denote by $(D_1/K_1)^*$ the critical relative fluctuation size at which A dies out (right-hand side of (8)). This threshold is a function of the selection coefficient s_1 and the rate of immigration M_{21}/K_1, and is illustrated in Fig. 11A.

The actual relative fluctuation size D_1/K_1 can satisfy inequality (8) only when the threshold $(D_1/K_1)^*$ is a positive real number. This is the case whenever condition (7), equivalent to $M_{21}/K_1 < s_1/(1-s_1)$, is true. The critical relative fluctuation size $(D_1/K_1)^*$ equals zero if and only if $M_{21}/K_1 = s_1/(1-s_1)$. Then, as the rate of immigration M_{21}/K_1 decreases below the critical value $s_1/(1-s_1)$, the critical relative fluctuation size $(D_1/K_1)^*$ increases. I.e. whenever the relative number of immigrants is small enough, coexistence becomes possible, and the weaker immigration is, the larger fluctuations may be without leading to extinction of the resident type.

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 A in the absence of fluctuations and, thus, the stronger the fluctuations in population density have to be to prove lethal to the locally advantaged type A. However, once the balance between selection and immigration allows for coexistence of the two types, small fluctuations do not yet lead to extinction of A (see Fig. 11A). Weak fluctuations have a weak effect on the maintenance of diversity on the island.

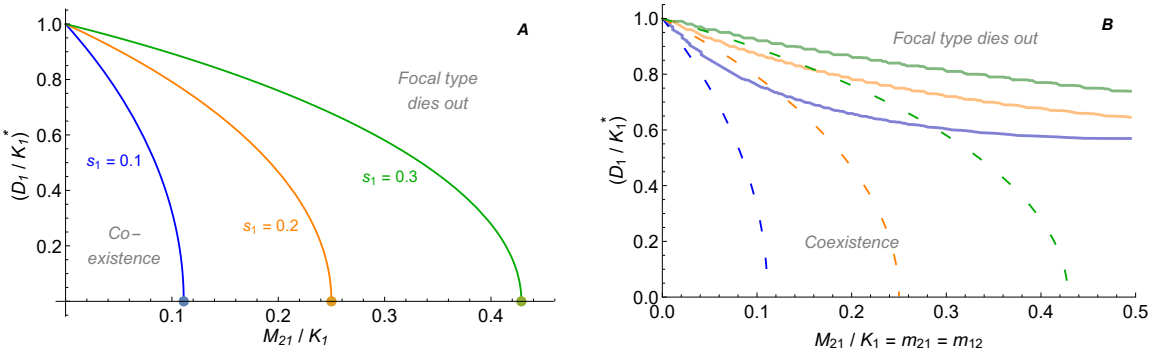

Fig. 11: **The critical relative fluctuation size is a decreasing function of the immigration rate and an increasing function of selection.** (A) The critical relative fluctuations, $(D_1/K_1)^*$, as a function of the immigration rate, M_{21}/K_1, for different values of the immigrants' selective disadvantage on the island: $s_1 = 0.1, 0.2, 0.3$. When immigration is too strong ($M_{21}/K_1 \geq s_1/(1-s_1)$, see (7)), the locally maladapted immigrants swamp the island and extinction of the resident type A is certain. At $M_{21}/K_1 = s_1/(1-s_1)$ the critical relative fluctuation size equals zero as indicated by the dots. Once the relative immigration falls below the critical value $s_1/(1-s_1)$, coexistence becomes possible and the critical relative fluctuation size $(D_1/K_1)^*$ increases abruptly. Thus, weak fluctuations have a weak effect on the maintenance of diversity on the island. When the resident type A has a strong relative advantage ($M_{21}/K_1 \ll s_1/(1-s_1)$), fluctuations must be severe in order to lead to its extinction. The critical fluctuation size approaches its maximum (D_1 is bounded by K_1) when immigration is close to zero. There, the dependency between critical relative fluctuation size and the rate of immigration is almost linear – the stronger the selection against the immigrating type (blue, orange, green), the more is the resident type robust to the fluctuations.
(B) When migration rates are symmetric, fluctuations have a weaker effect on the maintenance of diversity in the two habitats: Solid lines depict an approximation for the critical relative fluctuation size when there is bidirectional symmetric migration between niches. The lines are obtained by simulations and hence their algebraic expression is unknown. Unlike the continent-island model, even strong migration does not lead to extinction of a type, when migration rates are symmetric and fluctuations are absent or weak, because immigration into the focal niche is polymorphic. Note that selection is symmetric ($s_1 = s_2 = 0.1, 0.2, 0.3$), so that in the absence of fluctuations, polymorphism is always maintained.

The fluctuation size D_1 is obviously bounded by K_1 (the mean population size on the island). There are two cases when fluctuations can be close to their maximum K_1 without leading to extinction of the resident type (i.e. when $(D_1/K_1)^* \to 1$): if immigration goes to zero ($M_{21} \to 0$), or if selection of a goes to one ($s_1 \to 1$). These are the scenarios where the island is monomorphic for type A, because the immigrants of type a cannot survive there. The dependency between critical relative fluctuation size and immigration rate is almost linear when the resident type A has a strong rel-

ative advantage (i.e. when fluctuations have to be large in order to lead to extinction of A). Initially, the critical relative fluctuation size $(D_1/K_1)^*$ as a function of the immigration rate M_{21}/K_1 decreases with the negative slope $-1/[(2-s_1)s_1]+1$ (see SI, Fig. S6). When the selection against the immigrating type, s_1, is very small, then $1/[(2-s_1)s_1] \approx 1/(2s_1)$ becomes very large, and the critical relative fluctuation size declines quickly with increasing immigration (the resident type dies out for smaller fluctuations already). Conversely, the stronger the selection, the larger fluctuations need to be to prove lethal to the locally well adapted type – a phenomenon that we observed in the model with density dependent population regulation already (Fig. 7).

When there is a 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. 11B). 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. Thus, migration out of the fluctuating niche can be essential for persistence of the focal type.

3.3 Summary

Fluctuations in population densities may influence the evolutionary dynamics. In a habitat consisting of two niches with a trade-off in fitness and migration between them, fluctuations in the population size of one niche are deleterious for the type that is better adapted to this niche. Whenever the local population density is low, this type then gets easily swamped by the migration from the neighboring, stable habitat. For maintenance of variation, stability in population size can therefore be just as important as the selective advantage within a niche, as locally maladapted types may benefit from fluctuations if they have a stable refuge/source available.

We started by observing that fluctuations in population dynamics, arising due to overcompensating density dependence, have an impact on the evolutionary equilibrium. While evolutionary predictions in the absence of ecological dynamics still hold when population densities are stable in time, this is no longer true when instabilities arise. In the **model with density dependent regulation and symmetric migration**, a high growth rate in the focal niche proves deleterious for the type that is better adapted to this niche, which is then fluctuating. This effect is stronger, the weaker

the selection in the focal niche – even if the trade-off in selection is symmetric. Thus, the impact of ecological dynamics on evolution is stronger when evolution is weak/slow.

Most of the results hold with **unidirectional migration** to the niche that exhibits the fluctuations. Compared to bidirectional migration, the frequency of the focal type A at equilibrium is simply shifted to lower values due to monomorphic immigration. The decline in frequency of this type caused by fluctuations is still observable and has a similar shape, as long as the rate of increase in the focal niche is not close to zero (then immigration and selection are stronger than regulation which has a particular effect on the evolutionary equilibrium).

Further on, simplified ecological dynamics with **imposed fluctuations** capture qualitatively the evolutionary behavior and give more insight. First, with bidirectional migration, we explore the balance between evolutionary effects (selection) and ecological effects (fluctuations) on the evolutionary equilibrium. The fluctuations in the focal niche and the selective disadvantage of the locally adapted type have a similar impact on the evolutionary dynamics: both lead to a decrease in equilibrium allele frequency of the type A that is better adapted to the deme where fluctuations in population size occur. Therefore, fluctuations counteract asymmetry in selection whenever it favors type A, whereas they intensify asymmetry in selection whenever it favors the other type.

Last, for a continent-island model with imposed fluctuations on the island, we obtain simple explicit conditions for maintenance of polymorphism on the island. The local selective disadvantage of the immigrating type needs to be strong enough to prevent swamping. If this is the case, coexistence becomes possible but depends on the size of the fluctuations on the island. The critical relative fluctuation size at which polymorphism ceases to exist is an increasing function of the selection of the locally maladapted immigrants and a decreasing function of the immigration rate.

4 Discussion

We demonstrate that ecological dynamics with population densities naturally fluctuating around the carrying capacity – no matter if they are due to endogenous or exogenous factors – can significantly alter both the conditions for maintenance of polymorphism and the amount of variation maintained.

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). While we do retrieve this ecological phenomenon in our work, the effect of migration is more complex when evolution is taken into account. As a result of migration within a heterogeneous habitat, we observe a destabilizing effect on the maintenance of polymorphism.

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. The locally maladapted immigrants can then grow to high frequencies, exploiting the phase of low population density in the focal fluctuating niche.

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. Even if fluctuations were randomized (stochastic ecological dynamics), we'd still expect to observe a decrease in the (quasi-)equilibrium frequency of the type that is best adapted to the niche exhibiting these fluctuations in population

density. Yet, when stochasticity arises in evolutionary dynamics, the complete impact of migratory movement on the maintenance of variation becomes more complex. Because migration stabilizes the ecological dynamics and keeps the subpopulations away from very low densities (Roff, 1974), it will lessen the effect of genetic drift, thereby preserving more variation. In this paper, we concentrate on the effects of dispersal in fluctuating structured populations when the effect of drift is weak relative to selection, and leave the effect of genetic drift to a dedicated future study (*c.f.* Whitlock 2003 for constant population sizes).

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 decrease in equilibrium frequency of the focal allele, as different timescales in evolutionary and ecological dynamics apply. 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. 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. In this case, competition between the types and population growth are intrinsically tied to each other – where fluctuations in the population size are driven by a dual advantage of one type: increasing a species' growth rate ultimately increases its competitiveness and vice versa.

The decline in equilibrium frequency conditioned by endogenous fluctuations arising due to overcompensating density dependence occurs because the intrinsic rate of increase is assumed to be a property of the niche (such as due to a common abundant resource) and applies to all types inhabiting that niche. Likewise, when exogenous fluctuations are imposed on the population size of the focal niche, they apply to individuals of all types. Conversely, if the growth rate is a property of the types and fluctuations in a niche are due to a high fitness of the locally best adapted type only (via the coupling between evolution and ecology), while the intrinsic rate of increase in the niche stays fixed, we do not recover the decrease in frequency of the focal type.

The focal type then profits from the increased fitness more than it suffers from the fluctuations arising due to its high fitness, and hence, its equilibrium frequency does not decline in the way it does when fluctuations are due to a niche-wide increase in the growth rate.

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 can 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).

5 Appendix

5.1 Deutsche Zusammenfassung (German summary)

Schwankungen in Populationsdichten können einen großen Einfluss auf evolutionäre Dynamiken haben. Wir modellieren ein Habitat, das aus zwei Nischen besteht, die durch einen Trade-Off in Fitness gekennzeichnet und durch Migration miteinander verbunden sind. In diesem Kontext führen fluktuierende Populationsdichten einer Nische auf lange Sicht zu einer Abnahme jener Individuen, die besser an diese Nische angepasst sind. In Generationen, wo die Größe der lokalen Population gering ist, werden Individuen diesen Typs von der Migration aus der zweiten, stabileren Nische überschwemmt. Um die genetische Vielfalt zu erhalten, kann Stabilität in Populationsgrößen also genauso wichtig sein wie der Selektionsvorteil in einer Nische: Lokal schlecht angepasste Individuen können von ökologischen Schwankungen profitieren, wenn ihnen ein stabiler Rückzugsort zur Verfügung steht.

Zu Beginn analysieren wir, wie sich Populationsdynamiken, die aufgrund von überkompensierendem, dichteabhängigen Wachstum Fluktuationen aufweisen, auf das evolutionäre Gleichgewicht des Systems auswirken. Evolutionäre Vorhersagen, die in Abwesenheit von ökologischen Prozessen gemacht werden, bleiben unter Inkludierung von Populationsdynamiken korrekt, wenn diese zu konstanten Populationsdichten führen – nicht aber wenn Schwankungen auftreten. In einem **Modell mit dichteabhängiger Populationsregulation und symmetrischer Migration** führt eine hohe Wachstumsrate in der ersten Nische, die damit Fluktuationen aufweist, auf lange Sicht zu einer insgesamt niedrigeren Häufigkeit des Typs, der besser an diese Nische angepasst ist. Dieses Phänomen ist stärker, je schwächer die Selektion in dieser Nische ist – sogar wenn die Selektionsnachteile (trade-off) in den Nischen symmetrisch sind. Der Einfluss ökologischer Dynamiken auf die Evolution ist also stärker, je schwächer (langsamer) Evolution ist.

Die meisten dieser Ergebnisse behalten ihre Gültigkeit, wenn **Migration nur einseitig** in die Nische, die Fluktuationen aufweist, stattfindet. Im Vergleich zu symmetrischen Migrationsraten konvergiert die Proportion des lokal angepassten Typs hier schlicht zu niedrigeren Werten, da die Immigration monomorph ist. Die durch Fluktuationen bedingte Abnahme seiner Häufigkeit ist weiterhin beobachtbar und hat eine ähnliche Form wie zuvor (solange die Wachstumsrate der betrachteten Nische nicht gegen Null geht).

Darüber hinaus geben vereinfachte Populationsdynamiken mit **festgesetzten Schwankungen** weitere Einblicke in die evolutionären Entwicklungen, ohne diese qualitativ zu verändern. Zunächst analysieren wir im Fall von symmetrischer Migration das Gleichgewicht zwischen evolutionären Einflüssen (Selektion) und ökologischen Einflüssen (Stärke der Schwankungen) auf das evolutionäre Gleichgewicht. Die Fluktuationen in der ersten Nische haben auf den lokal gut angepassten Typ ähnliche Auswirkungen wie dessen habitatweiter Selektionsnachteil: beide führen auf lange Sicht zu einer Abnahme seiner Häufigkeit. Das bedeutet, dass Schwankungen in der Populationsdichte einer Nische habitatweiten, selektiven Asymmetrien entgegenwirken, wann immer diese den lokal am besten angepassten Typ bevorzugen, wohingegen sie Asymmetrien verstärken, wann immer diese insgesamt den lokal schlechter angepassten Typ begünstigen.

Schließlich betrachten wir ein Kontinent-Insel-Modell mit festgesetzten Fluktuationen auf der Insel, und erhalten einfache, explizite Bedingungen für den Erhalt von Polymorphismus auf der Insel. Der lokale Selektionsnachteil des immigrierenden Typs muss stark genug sein, um eine Überschwemmung der Insel durch die Immigration zu verhindern. Wenn das gegeben ist, so wird Koexistenz möglich, hängt aber von der Größe der Populationsschwankungen auf der Insel ab. Die kritische relative Fluktuationsgröße, die zu einem Aussterben des ortsansässigen Typs führt, ist eine zunehmende Funktion der Selektion (gegen die lokal schlechter angepassten immigrierenden Individuen), und eine abnehmende Funktion der Immigrationsrate.

5.2 Supporting information (SI)

5.2.1 Analyzing evolution in the absence of ecology

To reach a better understanding of the model's behavior we start by analyzing a simplification that takes into account evolution only. For this, we assume that population dynamics are in equilibrium and fix the population sizes to a constant value. We set

$$N_i(t) = c_i K. \tag{S1}$$

Thus, the formulas for the allele frequency after migration, $p_i'(t)$, equal

$$p_1'(t) = \frac{(1-m_{12})p_1(t)c_1 + m_{21}p_2(t)(1-c_1)}{(1-m_{12})c_1 + m_{21}(1-c_1)} \tag{S2}$$

because K cancels out (and conversely for niche 2). I.e. we analyze a system of two recurrences for p_1 and p_2:

$$p_i(t+1) = p_i'(t) \cdot \frac{w_{iA}}{p_i'(t)w_{iA} + (1-p_i'(t))w_{ia}} \tag{S3}$$

We obtain the formula for a polymorphic equilibrium by solving a system of two equations for p_1 and p_2. Namely,

$$\begin{aligned} &\frac{(1-m_{12})p_1c_1 + m_{21}p_2(1-c_1)}{(1-m_{12})c_1 + m_{21}(1-c_1)} \cdot \\ &\quad \cdot \frac{w_{1A}}{\frac{(1-m_{12})p_1c_1+m_{21}p_2(1-c_1)}{(1-m_{12})c_1+m_{21}(1-c_1)} w_{1A} + \left(1 - \frac{(1-m_{12})p_1c_1+m_{21}p_2(1-c_1)}{(1-m_{12})c_1+m_{21}(1-c_1)}\right) w_{1a}} \; + \\ &- \; p_1 \quad = \quad 0 \end{aligned}$$

and a second equation with 1 and 2 interchanged. Note, that we assume $m_{12}, m_{21} < \frac{1}{2}$. We obtain the following equation for the allele frequency of A at equilibrium, p_i^*:

$$\begin{aligned} p_1^* = 1 - \frac{1}{2c_1^2(1-m_{12})(1-m_{12}-m_{21})s_1^2s_2} \cdot \Big(& m_{12}m_{21}s_1s_2 - m_{12}^2m_{21}s_1s_2 + m_{12}m_{21}s_1^2 - m_{12}^2m_{21}s_1^2 + \\ & s_1^2s_2 - m_{21}s_1^2s_2 - 2m_{12}s_1^2s_2 + m_{12}^2s_1^2s_2 + m_{12}^2m_{21}s_1^2s_2 + (1-c_1)^2(1-m_{12}-m_{21})s_1((1- \\ & m_{12})s_1s_2 - m_{21}(s_2(2-m_{12}(1-s_1)-s_1) - m_{12}s_1)) + (1-c_1)s_1(-2(1-m_{12})^2s_1s_2 + \\ & m_{21}(1-m_{12})(-2m_{12}s_1 + s_2(2-2m_{12}(1-s_1)+s_1)) + m_{21}^2(m_{12}s_1 - s_2(2-m_{12}-s_1 + \\ & m_{12}s_1))) - c_1\sqrt{(1-m_{12}-(1-c_1)(1-m_{12}-m_{21}))^2s_1^2((1-m_{12})^2s_1^2s_2^2 + \\ & 2m_{21}(1-m_{12})s_1s_2(m_{12}(2-s_2(1-s_1)-s_1) - s_1s_2) + \\ & m_{21}^2(s_1^2s_2^2 - 2m_{12}s_1s_2(2-s_1-s_2+s_1s_2) + m_{12}^2(s_1+s_2-s_1s_2)^2))} \Big). \end{aligned}$$

Note that the allele frequency of a in niche 1 equals $1-p_1^*$ at equilibrium. Due to symmetry reasons, the equilibrium allele frequency of a in niche 2 equals the above formula with all 1 and 2 interchanged. Thus, p_2^* equals 1 minus the equation for p_1^* with 1s and 2s switched.

In order to find conditions for stability we investigate the conditions for a protected polymorphism (i.e. the circumstances under which allele frequencies converge to fixation), as this approach simplifies the calculations and yields reasonably short equations: Instability of both monomorphic equilibria $p_1 = p_2 = 0$ and $p_1 = p_2 = 1$ implies stability of the polymorphic fixed point (because we consider a two-dimensional system of haploids: there is a unique, stable and globally attracting equilibrium (Karlin and Campbell, 1980)). So, we compute the Jacobi matrices J_0 and J_1 of the system at 0

and 1 respectively. Now, 0 is stable if and only if both eigenvalues of J_0 are in absolute value < 1. One can either compute the eigenvalues or use the following condition: Both eigenvalues of J_0 are in absolute value < 1 if and only if $|\mathrm{Tr}(J_0)| < 1 + \mathrm{Det}(J_0) < 2$. We did the latter for both J_0 and J_1 and obtained the equation that is stated in the article: for arbitrary migration rates m_{12}, m_{21} and niche sizes c_1, c_2 the polymorphic equilibrium (p_1^*, p_2^*) is stable if and only if

$$s_1 > \frac{c_2 m_{21} s_2 [1 - m_{21} - c_1(1 - m_{12} - m_{21})]}{[m_{21} + c_1(1 - m_{12} - m_{21})] \cdot [c_1 m_{12} + c_2 s_2 (1 - m_{21})]} \tag{S4}$$

and

$$s_2 > \frac{c_1 m_{12} s_1 [1 - m_{12} - c_2(1 - m_{12} - m_{21})]}{[m_{12} + c_2(1 - m_{12} - m_{21})] \cdot [c_1 s_1 (1 - m_{12}) + c_2 m_{21}]} \tag{S5}$$

For $m_{12} = m_{21} = m$ and $c_1 = c_2 = 1/2$ this simplifies to

$$s_1 > \frac{m s_2}{m + (1 - m) s_2} \quad \text{and} \quad s_2 > \frac{m s_1}{m + (1 - m) s_1}. \tag{S6}$$

Rearranging these inequalities yields $m/s_1 - m/s_2 < 1 - m$ and $-m/s_1 + m/s_2 < 1 - m$, which in turn leads to the condition stated in the main text.

Finally, we want to check whether the stability properties of the polymorphic equilibrium are the same in the absence of ecological dynamics and when they lead to stable population size – i.e. whether the above conditions represent an approximation or the exact solution. (By visual comparison such as in Fig. 4 in the main text, we know that they are at least very similar.)
In order to do this, we compute the two eigenvalues of the system in the absence of ecology. (We choose not to include them in this text as they would take a few pages.) It turns out (computer algebra system) that the leading eigenvalue (which we determined visually by plotting both eigenvalues) of the simplified system is the same as the one eigenvalue of the complete system that captures the direct effects of selection and migration on evolution (we determined this eigenvalue visually, too – see Fig. 4 in the main text). Therefore, the equations above are a precise condition for the stability of the polymorphic equilibrium in case of stable population dynamics, too.

5.2.2 Coupled system

From the previous analysis, we know the behavior of the system up to the first branching point. We therefore want to reach a better understanding of that branching point. For this, we compute the Jacobian of the system. All results in this section are analytic. However, as this analysis yields extremely long and complex expressions, we choose to evaluate them and illustrate the results visually (see Fig. 3 in the main text). The Jacobian matrix has four eigenvalues, whereof two are of no interest as they are always smaller in absolute value than the other two. However, two of the eigenvalues are important and determine the stability of the equilibrium (p_1^*, p_2^*, c_1K, c_2K). One of them, let's call it λ_1, captures the direct effects of selection and migration on the evolutionary equilibrium. It describes the stability of the polymorphic equilibrium as a function of s_1, s_2 and m_{12}, m_{21} and is depicted in Fig. 4 in the main text. The second eigenvalue of importance, λ_2, is shown in the main text in Fig. 3. It describes the ecological stability, that is to say, the influence of selection and migration on the first branching point of the population dynamics.
If selection and migration are symmetric, allele frequencies always converge to a polymorphic equilibrium. Thus, we can simply compute the Jacobian matrix of the system at the polymorphic equilibrium for p_1, p_2 and the population densities in equilibrium $N_1 = c_1K$, $N_2 = (1 - c_1)K$. As polymorphism always exists, $|\lambda_1| < 1$ and we only need to consider λ_2 in order to understand the stability properties of the population dynamics. This is shown in Fig. 3 A, B, C, D in the main text.

However, as the evolutionary dynamics influence the value of r_i at the first branching point, we have to be a bit more careful as soon as we investigate asymmetric selection. Here, we need to distinct the cases of convergence to fixation or convergence to polymorphism: In the regime where a stable polymorphism exists, we can use the eigenvalue λ_2 that we obtained in the previous step (by calculating the Jacobian at the polymorphic equilibrium). This regime is depicted by λ_1. I.e. λ_1 tells us whether λ_2 is valid or not. In the regime, where polymorphism doesn't exist, we need to compute λ_2 differently. We have to compute two other Jacobian matrices of the system: Once for the equilibrium $p_1 = p_2 = 0$ and once for the equilibrium $p_1 = p_2 = 1$. So, for parameter ranges that lead to fixation of A we plot the λ_2 that we obtained from the Jacobian computed at $p_1 = p_2 = 1$ and vice versa for fixation of a. This is shown in Fig. 3 E and F of the main text. The resulting picture in Fig. 3 E and F is due to the change in $\overline{w}_i'(t)$ as a function of asymmetric selection. This can be seen easily in Fig. S1.

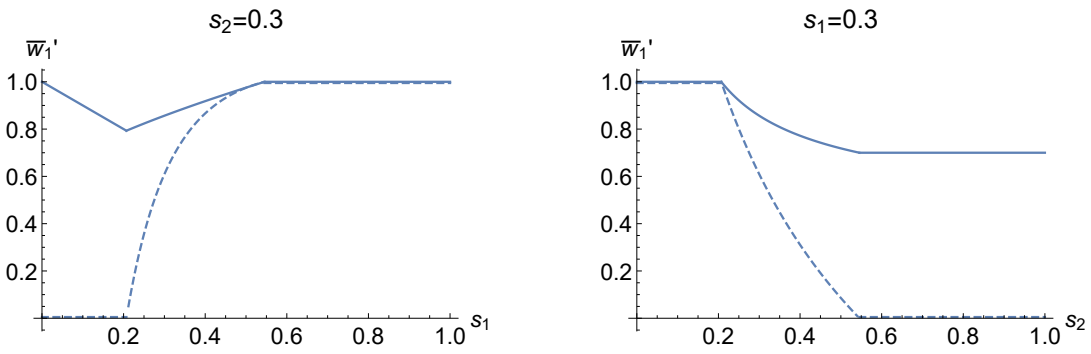

Fig. S1: **The mean fitness at evolutionary equilibrium changes as the asymmetry in selection is varied.** Solid lines indicate the values of the mean fitness after migration in the focal niche 1 (once evolutionary dynamics are in equilibrium), $\overline{w}_1'(t)$, as a function of one selection coefficient when the other is fixed. Dashed lines indicate the corresponding equilibrium allele frequency of A in niche 1. The parameters here are the same as in Fig. 3 E, F (main text).
Left-hand side: Here, the selection against A in the other niche, s_2, is fixed to 0.3, while the selective disadvantage of a in the focal niche 1, s_1, is varied. For small values of s_1, $\overline{w}_1'(t)$ decreases, because no individuals of type A are present at equilibrium: an increase of s_1 leads to a higher maladaption of a, which is the only type present. Then, a polymorphic equilibrium emerges and a further growth of s_1 leads to an increasing proportion of A, which are perfectly adapted to niche 1, and mean fitness increases. Finally, for large s_1, allele frequencies converge to fixation of A and mean fitness equals 1, as $w_{1A} = 1$.
Right-hand side: Now, $s_1 = 0.3$ and we consider $\overline{w}_1'(t)$ as a function of the maladaptation of A in niche 2, s_2. As long as A is the only type present at equilibrium (for small s_2), mean fitness equals the fitness of A, which is 1 in the focal niche. As s_2 increases, the allele frequency of A at equilibrium eventually decreases (in niche 2 and, thus, in niche 1, too). Mean fitness decreases as the locally maladapted type a increases. For large values of s_2, allele frequencies converge to fixation of a and, thus, mean fitness in niche 1 equals $1 - s_1 = 0.7$.

5.2.3 High intrinsic rate of increase in both niches

Throughout our analyses, we assumed that one of the niches undergoes fluctuations in population density while the second niche is stable. Namely, in niche 2 we considered only a fixed intrinsic rate of increase: $r_2 = 1$.
However, our findings generalize to higher values of r_2 as well: in general, it can be said that, when both niches exhibit fluctuations, the type which is better adapted to the less extreme, more stable habitat, increases in frequency (see Fig. S2). I.e. when population density in niche 2 fluctuates due to a high intrinsic rate of increase (r_2 fixed to some value above 2), then the focal type A benefits from these fluctuations as

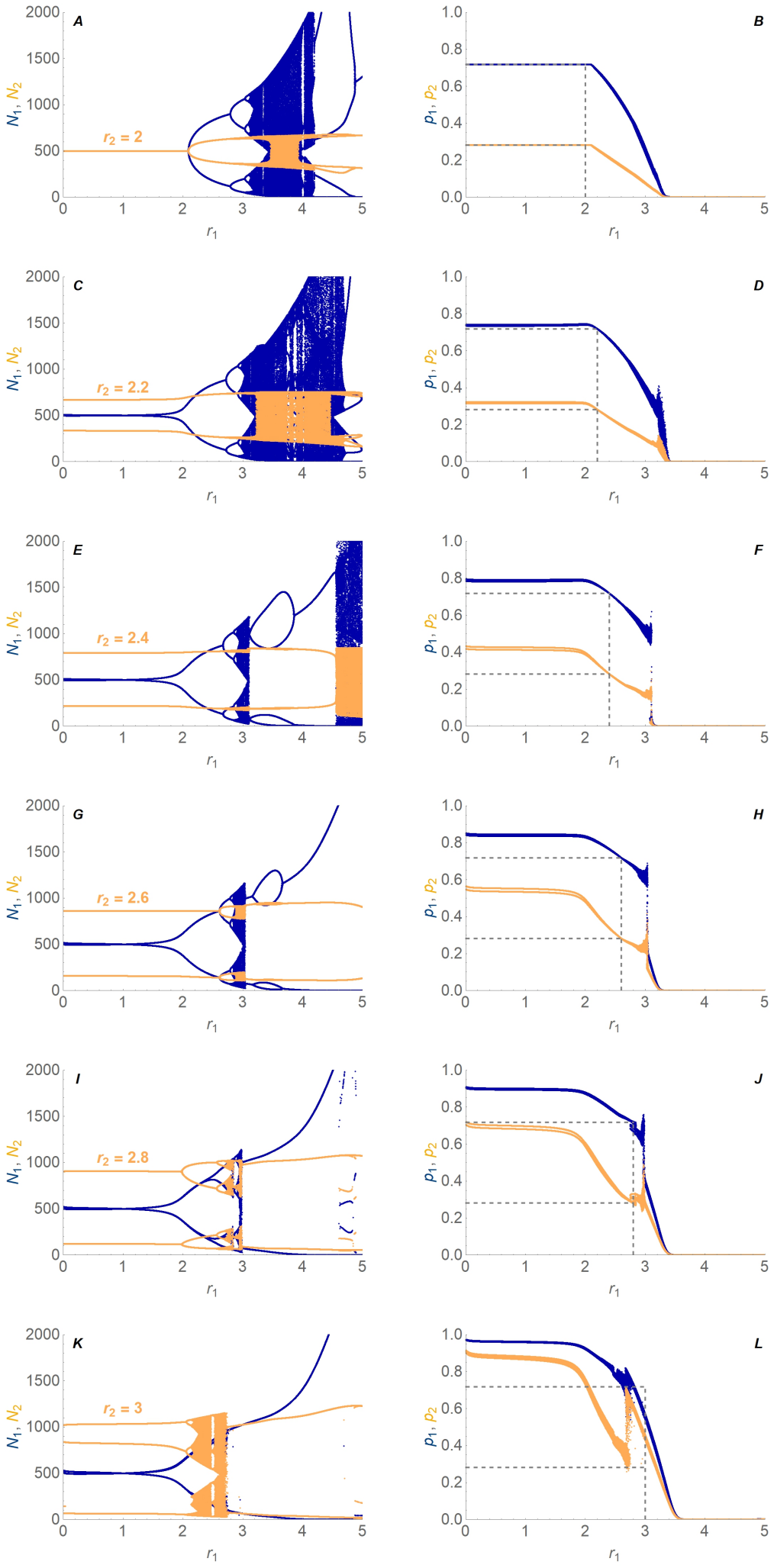
A
B
C
D
E
F
G
H
I
J
K
L
$r_2 = 2$
$r_2 = 2.2$
$r_2 = 2.4$
$r_2 = 2.6$
$r_2 = 2.8$
$r_2 = 3$
N_1, N_2
p_1, p_2
r_1

Fig. S2: **When both niches exhibit fluctuations, the type, which is better adapted to the more stable niche, increases in frequency.** The impact of population dynamics (left, long-term behavior as a function of r_1) on the corresponding evolutionary dynamics (right) in both niches (niche 1 in blue, niche 2 in orange) depends on the value of r_2. From top to bottom: $r_2 = 2$, 2.2, 2.4, 2.6, 2.8, 3. Gray dashed lines indicate the amount of variation 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 (r_1 small enough), while niche 2 exhibits fluctuations ($r_2 > 2$), the focal type reaches higher equilibrium frequencies than predicted in the absence of fluctuations (compare the equilibrium frequency on the left of the vertical dashed lines ($r_1 < r_2$) to the horizontal dashed lines). Here, equilibrium frequencies of the focal type increases with r_2 (the intrinsic rate of increase in the second niche, to which the other type is better adapted). The relative advantage vanishes once $r_1 \approx r_2$ (vertical dashed lines), 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, H and J). When $r_1 > r_2$ (to the right of the vertical dashed lines), niche 1 is less stable than niche 2. This leads to a decrease in the equilibrium frequency of the focal type, and eventually (for sufficiently large r_1) to its extinction. (L) When $r_2 = 3$, population dynamics are chaotic for relatively small r_1, and post-chaotic for $r_1 = 3$ (re-stabilization as a result of migration, see section 3.1.2 and Dey et al. (2014)). Due to the partly chaotic ecological dynamics, allele frequencies exhibit a phase of chaos for $2 < r_1 < r_2 = 3$, too. Hence, for $r_1 = r_2$ they do not converge to the proportion predicted in the absence of ecology. Parameters: $s_1 = s_2 = 0.1$, $m = 0.05$

long as niche 1 is more stable (in terms of $r_1 < r_2$). When the intrinsic rate of increase in niche 1, r_1, approaches the intrinsic rate of increase in niche 2, r_2, the relative advantage of A declines and, thus, so does its equilibrium frequency. When both growth rates are equal ($r_1 = r_2$) and population dynamics are not yet chaotic, allele frequencies converge to about the same proportion as when population sizes were stable in time (see gray dashed lines in Fig. S2 B, D, F, H, J). Once $r_1 > r_2$, the population density in niche 1 exhibits stronger fluctuations than in niche 2 and, therefore, the phenomenon inverses: the equilibrium frequency of type A decreases even further, eventually leading to extinction of A.

5.2.4 Logistic growth

We want to explore the system when population dynamics are modeled by logistic growth rather than Ricker's regulation. The equations for p_1 and p_2 remain unchanged, but the dynamics of the population density become

$$N_i(t+1) = N_i'(t) + N_i'(t) \cdot r_i \left(1 - \frac{N_i'(t)}{c_i K}\right) \cdot \overline{w}_i'(t). \tag{S7}$$

For the actual computations (Fig. S3 and S4) we furthermore force $N_i(t)$ to be non-negative. I.e. whenever the equations would lead to negative population sizes, we set them to zero instead and use that value to calculate the density in the next generation.

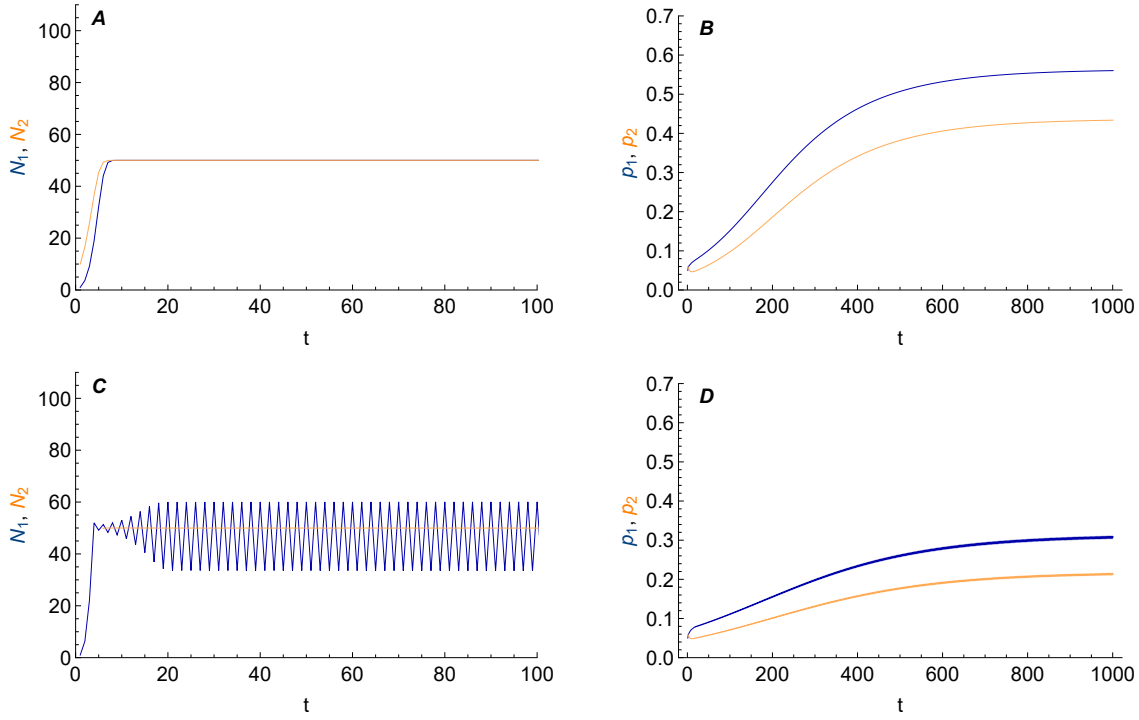

Fig. S3: **The qualitative behavior is preserved when Ricker's regulation is replaced by logistic growth.** The parameters here are the same as in Fig. 5 in the main text. Ecological dynamics modeled by logistic growth may affect the allele frequency at equilibrium. Compared to ecological dynamics that lead to stable population sizes (A, B), fluctuating population densities in niche 1 (C) lead to lower allele frequencies of A at equilibrium (D).

In Fig. S3 we see that the allele frequency of A at equilibrium is lower for fluctuating population dynamics (D) than it is for stable population dynamics (B). Hence, the decline in the equilibrium value of p_1 as a function of r_1 still exists when Ricker's regulation is replaced by logistic growth. Fig. S4 depicts the change in the allele frequency at equilibrium when r_1 is varied. The qualitative effect of population dynamics on evolution, i.e. the drop in allele frequencies of A, corresponds to what we observe in the main text, although there are quantitative differences. Comparing Fig. 6 (main text) and Fig. S4 (same parameters), we notice that with logistic growth the decrease is slighter in the beginning. This is because the fluctuations in N_1 between first and

second branching point are much weaker with logistic growth. Then, as chaotic population sizes arise for far smaller r_1 already than they do with Ricker's regulation, equilibrium allele frequencies may still be polymorphic when chaos arises in the ecological dynamics. Thus, chaos is transmitted to the evolutionary dynamics and the decrease in p_1 eventually shows a certain amount of noise rather than being a distinct line.

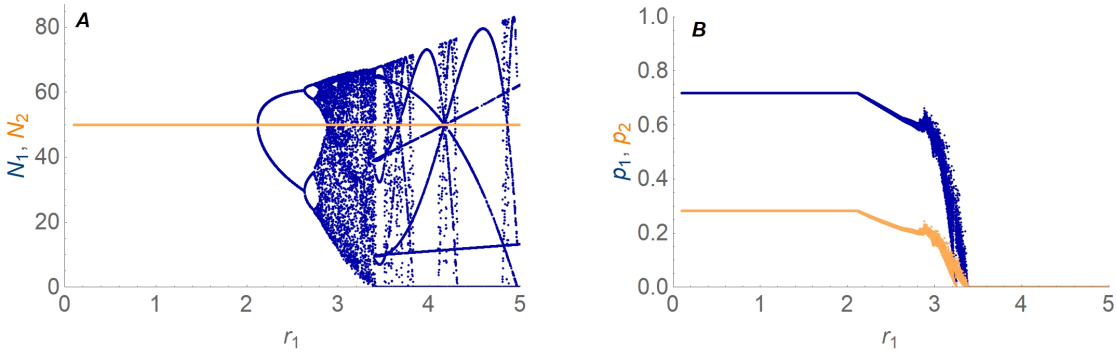

Fig. S4: **The qualitative long term behavior is preserved when Ricker's regulation is replaced by logistic growth.** The parameters here are the same as in the main text, Fig. 6 (only difference: here, generation time ranges from $2^{13} - 1$ to $2^{13} + 1$ as convergence is slower). In the allele frequency of A at equilibrium (B), a slight decrease (due to small fluctuations in the population size) is followed by are more drastic and rather chaotic one (as chaos arising in the population dynamics is transmitted to the evolutionary dynamics).

5.2.5 Imposed fluctuations

We consider a simplification of the model, where population densities are imposed: in niche 1, population size fluctuates between $K_1 + D_1$ and $K_1 - D_1$ (K_1, D_1 constant), while the density in niche 2 is fixed to $N_2 = K_1$ (see Fig. S5).

Symmetric migration When migration is bidirectional we are not able to predict the amount of variation maintained under fluctuating population densities, even when the fluctuations are imposed. Therefore, we assessed the stability analysis of the polymorphic equilibrium (Fig. 10 main text) again by investigating the protected polymorphism conditions instead (polymorphism is stable when both monomorphisms are unstable). As we trivially know the population densities $N_1 = K_1 \pm D_1$ and $N_2 = K_1$, we are able to analyze the stability of the monomorphic equilibria $p_1 = p_2 = 0$ and $p_1 = p_2 = 1$ (even in the presence of fluctuations).
Here, in order to capture the fluctuations in population density, we analyze the

stability of the monomorphisms under two consecutive generations. I.e. we compute the Jacobi matrices J_0 and J_1 of the iterated system, that describes the change in allele frequency after two generations, at 0 and 1.

As before, this analysis yields complex expressions that are illustrated in Fig. 10 in the main text, where we visualize the leading eigenvalues of the two Jacobi matrices: in the parameter space, where the leading eigenvalue of J_1 is in absolute value < 1, allele frequencies converge to fixation of the focal type A. Conversely, in the region where the absolute value of the leading eigenvalue of J_0 is smaller than 1 allele frequencies converge to fixation of the other type a. The region in between leads to polymorphism.

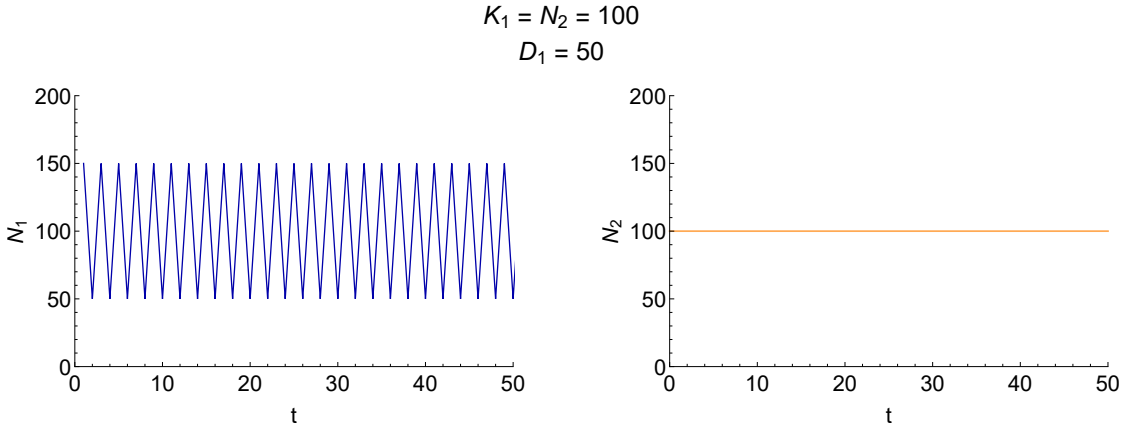

Fig. S5: **Imposing fluctuations D_1 in the population size of niche 1, while fixing the density in niche 2 to a constant value.** Population density in niche 1 periodically fluctuates between $K_1 + D_1$ and $K_1 - D_1$. Population size in niche 2 remains at N_2. (Parameters: $K_1 \pm D_1 = 100 \pm 50$, $N_2 = 100$.)

Unidirectional migration In the continent-island model with imposed fluctuations on the island, the formula for the allele frequency of the resident type equals

$$p_1(t+1) = p_1'(t) \cdot \frac{1}{p_1'(t) + [1 - p_1'(t)][1 - s_1]} \tag{S8}$$

where

$$p_1'(t) = \frac{p_1(t) N_1(t)}{N_1(t) + M_{21}} \tag{S9}$$

as immigration (M_{21} is the total number of immigrants per generation) is monomorphic and, thus, $p_2 = 0$. The population size at the beginning of every life cycle equals $N_1(t) = K_1 + D_1$ or $N_1(t) = K_1 - D_1$, in subsequent generations. Here, we are able

to solve for the equilibrium frequency of the resident type on the island. I.e. there are two relatively simple algebraic solutions to the equation

$$p_1(t+2) - p_1(t) = 0. \tag{S10}$$

Strictly speaking, as (equilibrium) allele frequencies fluctuate a bit due to the fluctuations in the population size, the frequency of type A is converging to a two-cycle rather than a fixed point. Therefore, one of the two solutions to (S10) corresponds to the quasi-equilibrium frequency of A in generations where population size on the island is high. The other, slightly smaller solution corresponds to the lower branch of the two-cycle. E.g. for the amount of variation maintained in generations where the population size on the island fluctuates up, we obtain the expression

$$\begin{aligned} p_1^* \; = & \frac{1}{2(K_1 - D_1)\Big((K_1 + D_1)(2 - s_1) + M_{21}(1 - s_1)\Big)s_1} \cdot \\ & \cdot \Bigg((K_1^2 - D_1^2)(2 - s_1)s_1 - M_{21}(2K_1 + M_{21})(1 - s_1)^2 + \\ & + \sqrt{((K_1^2 - D_1^2)(2 - s_1)s_1 - M_{21}(2K_1 + M_{21})(1 - s_1)^2)^2} \Bigg) . \end{aligned}$$

The conditions for persistence of the resident type A (inequalities (7) and (8) in the main text) were obtained by setting both solutions for p_1^* to zero. I.e. we calculated under which conditions type A dies out (and then reversed the unequal signs).

The critical relative fluctuation size $(D_1/K_1)^*$ is the smallest fluctuation size that leads to extinction of the resident type.

$$\left(\frac{D_1}{K_1}\right)^* \; = \; \sqrt{\frac{1}{(2 - s_1)s_1} - \left(\frac{1}{(2 - s_1)s_1} - 1\right) \cdot \left(1 + \frac{M_{21}}{K_1}\right)^2} . \tag{S11}$$

If $(D_1/K_1)^*$ equals zero, or is a complex value, extinction of A is certain – no matter if the population size on the island fluctuates or not.

The first order series of $(D_1/K_1)^*$ around $M_{21}/K_1 = 0$ is given by expression (S12). This is the rate at which the critical relative fluctuation size initially decreases as a function of the immigration rate M_{21}/K_1 (see Fig. S6): the approximation holds whenever M_{21}/K_1 is small. Approximation (S13) is true, if also s_1 is small.

$$\left(\frac{D_1}{K_1}\right)^* \approx 1 - \frac{M_{21}}{K_1}\left(\frac{1}{(2-s_1)s_1} - 1\right) \tag{S12}$$

$$\approx 1 - \frac{M_{21}}{K_1}\left(\frac{1}{2s_1} - 1\right) \tag{S13}$$

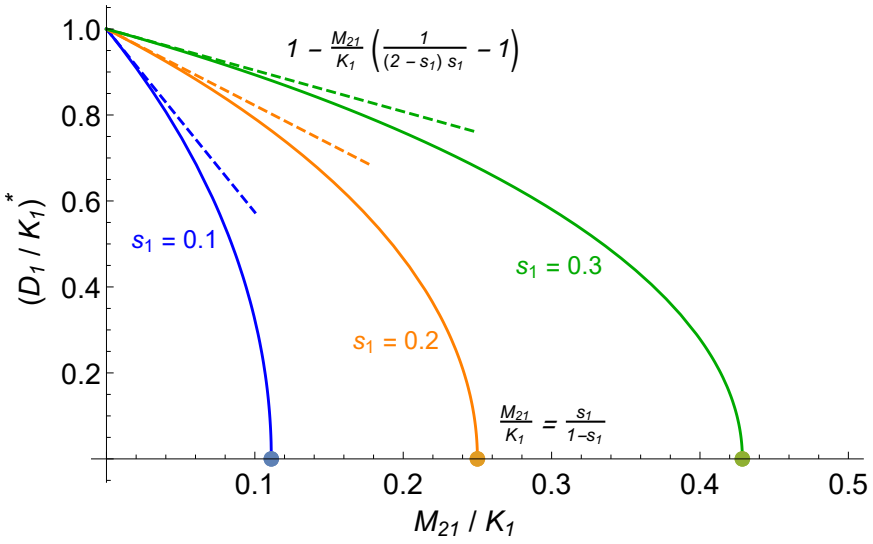

Fig. S6: **The decrease in critical relative fluctuation size as a function of the immigration rate is determined by the strength of selection against the immigrating type.** When immigration is weak (close to zero), the critical relative fluctuation size decreases with slope $-1/((2-s_1)s_1)+1$. Hence, the weaker the selection s_1 against the immigrating type, the more detrimental proves its immigration M_{21}/K_1 to the resident type. At $M_{21}/K_1 = s_1/(1-s_1)$ the resident type dies out, no matter how strong are the fluctuations on the island.

5.2.6 Order of the life cycle

When the order of the life cycle is switched, i.e. when migration happens last – after selection and population growth, the equations turn into

$$N_1(t+1) = (1-m_{12}) \cdot \hat{N}_1(t) + m_{21} \cdot \hat{N}_2(t) \tag{S14}$$

and

$$p_1(t+1) = \frac{1}{N_1(t+1)} \cdot \left[(1-m_{12}) \cdot p_1(t)\frac{w_{1A}}{\overline{w}_1(t)} \cdot \hat{N}_1(t) + m_{21} \cdot p_2(t)\frac{w_{2A}}{\overline{w}_2(t)} \cdot \hat{N}_2(t)\right] \tag{S15}$$

where

$$\overline{w}_i(t) = p_i(t) \cdot w_{iA} + (1 - p_i(t)) \cdot w_{ia} \tag{S16}$$

equals the mean fitness in niche i before migration, and

$$\hat{N}_i(t) = N_i(t) e^{r_i \left(1 - \frac{N_i(t)}{c_i K}\right) \overline{w}_i(t)} \tag{S17}$$

is the number of individuals in niche i after selection (before migration).

Whether migration precedes selection and density regulation (as modeled in the main text) or migration succeeds selection and density regulation has no qualitative influence on the evolutionary dynamics. If selection (and population growth) occurred first, all individuals would reproduce according to the parameters of their current niche and offspring would migrate afterwards. This would lead to an increased coupling of the population dynamics between the niches: fluctuations in one niche would be transferred more strongly to the second niche (see Fig. S7).

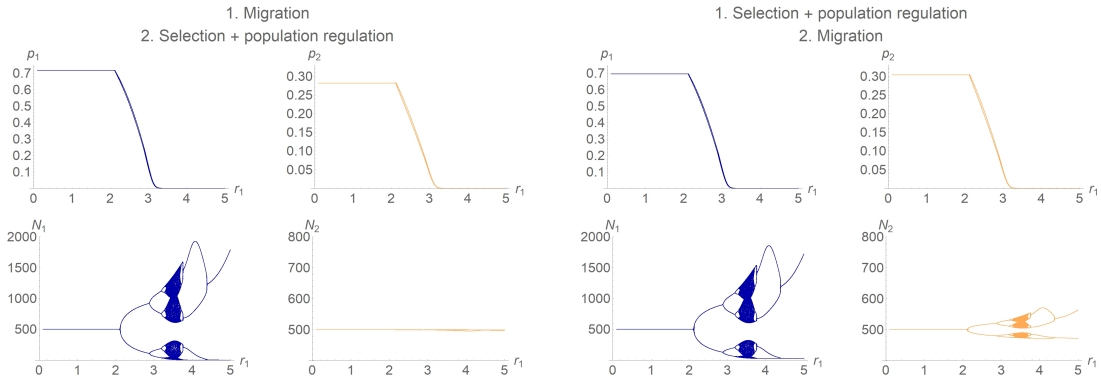

Fig. S7: **The influence of the order of the life cycle on the qualitative behavior of the system.** Left-hand side: The system as it is modeled in the main text. Migration precedes selection and population regulation. Alternatively (right-hand side), if migration comes last, we observe that the population size in niche 2 is coupled to the fluctuations in niche 1. How strongly the fluctuations are transmitted to the population density in niche 2 depends on the migration rate. Parameters: $r_2 = 1$, $s_1 = s_2 = 0.1$, $m_{12} = m_{21} = 0.05$.

5.3 Mathematica code

Evolution only

Find the formula for a polymorphic equilibrium:

```
p1p2EquilibriumAll =
  Solve[{(1 - m12) p1 c1 + m21 p2 (1 - c1)) / ((1 - m12) c1 + m21 (1 - c1)) *
      (1 / (((1 - m12) p1 c1 + m21 p2 (1 - c1)) / ((1 - m12) c1 + m21 (1 - c1)) +
        (1 - ((1 - m12) p1 c1 + m21 p2 (1 - c1)) / ((1 - m12) c1 + m21 (1 - c1))) (1 - s1))) -
    p1 == 0, ((1 - m21) p2 (1 - c1) + m12 p1 c1) / ((1 - m21) (1 - c1) + m12 c1) *
     ((1 - s2) / ((((1 - m21) p2 (1 - c1) + m12 p1 c1) / ((1 - m21) (1 - c1) + m12 c1))
       (1 - s2) + 1 - ((1 - m21) p2 (1 - c1) + m12 p1 c1) /
       ((1 - m21) (1 - c1) + m12 c1))) - p2 == 0}, {p1, p2}] // Simplify;
p1p2Equilibrium := {p1p2EquilibriumAll[[3, 1, 2]], p1p2EquilibriumAll[[3, 2, 2]]};
(* Extract the relevant solution only and make it a function *)
```

Find the conditions for a protected polymorphism:

1. Compute the Jacobian matrices at 0 and 1 resp.

In[170]:=
```
jacobi = D[{(1 - m12) p1 c1 + m21 p2 (1 - c1)) / ((1 - m12) c1 + m21 (1 - c1)) *
     (1 / (((1 - m12) p1 c1 + m21 p2 (1 - c1)) / ((1 - m12) c1 + m21 (1 - c1)) +
       (1 - ((1 - m12) p1 c1 + m21 p2 (1 - c1)) / ((1 - m12) c1 + m21 (1 - c1)))
       (1 - s1))), ((1 - m21) p2 (1 - c1) + m12 p1 c1) / ((1 - m21) (1 - c1) + m12 c1) *
     ((1 - s2) / ((((1 - m21) p2 (1 - c1) + m12 p1 c1) / ((1 - m21) (1 - c1) + m12 c1))
       (1 - s2) + 1 - ((1 - m21) p2 (1 - c1) + m12 p1 c1) /
       ((1 - m21) (1 - c1) + m12 c1)))}, #] & /@ {p1, p2} // Simplify;

jacobiZero = jacobi /. {p1 → 0, p2 → 0} // Simplify ;
jacobiOne = jacobi /. {p1 → 1, p2 → 1} // Simplify ;
```

2. Compute trace (s) and determinant (d) of both matrices

```
dZero = Det[jacobiZero] // Simplify;
sZero = Tr[jacobiZero] // Simplify;

dOne = Det[jacobiOne] // Simplify;
sOne = Tr[jacobiOne] // Simplify;
```

3. Now, 0 is stable iff |sZero| < 1 + dZero < 2
and 1 is stable iff |sOne| < 1 + dOne < 2

```
Reduce[Abs[sZero] < 1 + dZero < 2 && 0 < m12 < 1 / 2 &&
    0 < m21 < 1 / 2 && 0 < s1 < 1 && 0 < s2 < 1 && 0 < c1 < 1] // Simplify
Reduce[Abs[sOne] < 1 + dOne < 2 && 0 < m12 < 1 / 2 && 0 < m21 < 1 / 2 &&
    0 < s1 < 1 && 0 < s2 < 1 && 0 < c1 < 1] // Simplify
```

4. Reverse the unequal signs to obtain conditions for stability of the polymorphic equilibrium

To obtain the condition stated in the main text ($m* \mid 1/s_1 - 1/s_2 \mid < 1 - m$) set $c_1 = 1/2$ and $m_{12} = m_{21} = m$:

```
c1 = 1 / 2;   m =.; m12 = m; m21 = m;
((-1 + c1) m21 (1 - m21 + c1 (-1 + m12 + m21)) s2) /
   ((-m21 + c1 (-1 + m12 + m21)) (s2 - m21 s2 + c1 (m12 + (-1 + m21) s2))) // Simplify
(c1 m12 (-m21 + c1 (-1 + m12 + m21)) s1) /
   ((1 - m21 + c1 (-1 + m12 + m21)) ((-1 + c1) m21 + c1 (-1 + m12) s1)) // Simplify
```

Density dependent regulation

Simulations

CompleteModel [s1, s2, m12, m21, p1, p2, N1, N2, c1, r1, r2, kk, tm] iterates the system (for initial conditions p1, p2, N1, N2) tm times and creates a list {... { $p_1(t)$, $p_2(t)$, $N_1(t)$, $N_2(t)$ } ...} of the results:

In[151]:=
```
CompleteModel[s1_, s2_, m12_, m21_,
  p1_, p2_, N1_, N2_, c1_, r1_, r2_, kk_, tm_] :=
 Module[{w1A = 1, w1a = 1 - s1, w2A = 1 - s2, w2a = 1, c2 = 1 - c1}, NestList[{
    ((1 - m12) #[[1]] #[[3]] + m21 #[[2]] #[[4]]) /
      ((1 - m12) #[[3]] + m21 #[[4]]) *
     (w1A / ((((1 - m12) #[[1]] #[[3]] + m21 #[[2]] #[[4]]) / ((1 - m12) #[[3]] + m21 #[[4]])) *
         w1A + (1 - (((1 - m12) #[[1]] #[[3]] + m21 #[[2]] #[[4]]) /
             ((1 - m12) #[[3]] + m21 #[[4]])) * w1a)),
    ((1 - m21) #[[2]] #[[4]] + m12 #[[1]] #[[3]]) /
      ((1 - m21) #[[4]] + m12 #[[3]]) * (w2A /
       ((((1 - m21) #[[2]] #[[4]] + m12 #[[1]] #[[3]]) / ((1 - m21) #[[4]] + m12 #[[3]])) * w2A +
         (1 - (((1 - m21) #[[2]] #[[4]] + m12 #[[1]] #[[3]]) / ((1 - m21) #[[4]] + m12 #[[3]])) *
         w2a)),
    ((1 - m12) #[[3]] + m21 #[[4]]) Exp[r1 (1 - ((1 - m12) #[[3]] + m21 #[[4]]) / (c1 kk))]
      ((((1 - m12) #[[1]] #[[3]] + m21 #[[2]] #[[4]]) / ((1 - m12) #[[3]] + m21 #[[4]])) * w1A +
        (1 - (((1 - m12) #[[1]] #[[3]] + m21 #[[2]] #[[4]]) / ((1 - m12) #[[3]] + m21 #[[4]])) *
        w1a)],
    ((1 - m21) #[[4]] + m12 #[[3]]) Exp[r2 (1 - ((1 - m21) #[[4]] + m12 #[[3]]) / (c2 kk))]
      ((((1 - m21) #[[2]] #[[4]] + m12 #[[1]] #[[3]]) / ((1 - m21) #[[4]] + m12 #[[3]])) * w2A +
        (1 - (((1 - m21) #[[2]] #[[4]] + m12 #[[1]] #[[3]]) / ((1 - m21) #[[4]] + m12 #[[3]])) *
        w2a)]} &, {p1, p2, N1, N2}, tm]]
```

With this, we can create **Fig. 5** for example:

In[152]:=
```
m = 0.1; m12 = m; m21 = m;
s = 0.05; s1 = s; s2 = s;
r2 = 1;
kk = 100; c1 = 1 / 2;
N1 = 1; N2 = 10;
p1 = 0.11; p2 = 0.1;
tm = 2^10 + 5;
```

In[155]:=
```
r1 = 1;  modelR1 =
 Transpose[CompleteModel[s1, s2, m12, m21, p1, p2, N1, N2, c1, r1, r2, kk, tm]];
```

In[156]:=
```
r1 = 2.5;  modelR25 =
 Transpose[CompleteModel[s1, s2, m12, m21, p1, p2, N1, N2, c1, r1, r2, kk, tm]];
```

In[157]:=
```
p1 = modelR1[[1]]; p2 = modelR1[[2]]; N1 = modelR1[[3]]; N2 = modelR1[[4]];
p1Fluct = modelR25[[1]]; p2Fluct = modelR25[[2]];
N1Fluct = modelR25[[3]]; N2Fluct = modelR25[[4]];
```

In[159]:=
```
GraphicsGrid[
 {{ListPlot[{N1 + 1, N2}, PlotRange → {{-0.01, 100}, {0, 100}}, Joined → True],
   Show[ListPlot[{p1, p2}, PlotRange → {-0.01, 0.7}, Joined → True],
    Plot[p1p2Equilibrium, {t, 0, tm}, PlotStyle → {Dashed, Gray}]]},
  {ListPlot[{N1Fluct, N2Fluct}, PlotRange → {{-0.01, 100}, {0, 100}},
    Joined → True], Show[ListPlot[{p1Fluct, p2Fluct},
     PlotRange → {-0.01, 0.7}, Joined → True], Plot[p1p2Equilibrium,
     {t, 0, tm}, PlotStyle → {Dashed, Gray}]]}}, ImageSize → 900]
```

CompleteModelLast [s1, s2, m12, m21, p1, p2, N1, N2, c1, r1, r2, kk, tm] does the same iteration as “CompleteModel”, but saves only the last element $\{p_1(\text{tm}),\ p_2(\text{tm}),\ N_1(\text{tm}),\ N_2(\text{tm})\}$, i.e. we use it to analyze the long-term behavior (by choosing tm large enough):

In[2]:=
```
CompleteModelLast = Compile[{{s1, _Real}, {s2, _Real}, {m12, _Real},
    {m21, _Real}, {p1, _Real}, {p2, _Real}, {N1, _Integer}, {N2, _Integer},
    {c1, _Real}, {r1, _Real}, {r2, _Real}, {kk, _Real}, {tm, _Integer}},
   Module[{w1A = 1, w1a = 1 - s1, w2A = 1 - s2, w2a = 1, c2 = 1 - c1}, Nest[{
     (((1 - m12) #[[1]] #[[3]] + m21 #[[2]] #[[4]]) / ((1 - m12) #[[3]] + m21 #[[4]])) *
      (w1A / ((((1 - m12) #[[1]] #[[3]] + m21 #[[2]] #[[4]]) / ((1 - m12) #[[3]] + m21 #[[4]])) *
          w1A + (1 - (((1 - m12) #[[1]] #[[3]] + m21 #[[2]] #[[4]]) /
              ((1 - m12) #[[3]] + m21 #[[4]])) * w1a)),
     (((1 - m21) #[[2]] #[[4]] + m12 #[[1]] #[[3]]) / ((1 - m21) #[[4]] + m12 #[[3]])) *
      (w2A / ((((1 - m21) #[[2]] #[[4]] + m12 #[[1]] #[[3]]) / ((1 - m21) #[[4]] + m12 #[[3]])) *
          w2A + (1 - (((1 - m21) #[[2]] #[[4]] + m12 #[[1]] #[[3]]) /
              ((1 - m21) #[[4]] + m12 #[[3]])) * w2a)),
     ((1 - m12) #[[3]] + m21 #[[4]]) Exp[r1 (1 - ((1 - m12) #[[3]] + m21 #[[4]]) / (c1 kk))]
       ((((1 - m12) #[[1]] #[[3]] + m21 #[[2]] #[[4]]) / ((1 - m12) #[[3]] + m21 #[[4]])) * w1A +
        (1 - (((1 - m12) #[[1]] #[[3]] + m21 #[[2]] #[[4]]) /
            ((1 - m12) #[[3]] + m21 #[[4]])) * w1a)],
     ((1 - m21) #[[4]] + m12 #[[3]]) Exp[r2 (1 - ((1 - m21) #[[4]] + m12 #[[3]]) / (c2 kk))]
       ((((1 - m21) #[[2]] #[[4]] + m12 #[[1]] #[[3]]) / ((1 - m21) #[[4]] + m12 #[[3]])) * w2A +
        (1 - (((1 - m21) #[[2]] #[[4]] + m12 #[[1]] #[[3]]) / ((1 - m21) #[[4]] + m12 #[[3]])) *
         w2a)]} &, {p1, p2, N1, N2}, tm]]];
```

Using the function CompleteModelLast, we can run simulations for a large set of parameters, and create the bifurcation diagrams for the **figures 2, 6, 7 and 8**. Namely, we choose tm large and compute CompleteModelLast (i.e. the equilibrium) repetitively for different values of the growth rate in niche 1, r_1 (to obtain a bifurcation diagram as a function of r_1). The initial population size in niche 1, $N_1(0)$, is being varied, too (because of sensitivity to initial conditions of the population size), while selection, migration, carrying capacity and r_2 are fixed throughout one simulation. Every equilibrium is saved in a list (which can then be plotted).

E.g. for **Fig. 6**: (**Fig. 2**, **Fig. 7** and **Fig. 8** are generated similarly)

```
(* Fixed parameters: *)
m12 = 0.05; m21 = 0.05;
s1 = 0.1; s2 = 0.1;
c1 = 1 / 2; kk = 100; N2 = (1 - c1) kk;
r2 = 1;
p1 = 0.1; p2 = 0.1;
tm = 2^10;
(* Simulations for r1 ranging from 0.1 to 5.2, and N1(0) between 5 and 50: *)
s01m005Longterm = Transpose[Flatten[ParallelTable[
     MapThread[{#1, #2} &, {{r1, r1, r1, r1}, CompleteModelLast[s1, s2, m12,
        m21, p1, p2, N1, N2, c1, r1, r2, kk, tm + RandomInteger[{0, 10}]]}],
     {r1, 0.1, 5.2, 0.0003}, {N1, Round[c1 kk / 10], Round[c1 kk], 5}], 1]];
```

```
(* Plot (Fig. 6): *)
GraphicsGrid[
 {{Show[ListPlot[s01m005Longterm[[3]], PlotRange → {{0, 5}, {-2, 4 c1 kk}},
     PlotStyle → {PointSize[0.003], Darker[Blue]}],
    ListPlot[{#[[1]], #[[2]] + 1} & /@ s01m005Longterm[[4]],
     PlotStyle → {PointSize[0.003], Lighter[Orange]}]],
   Show[ListPlot[s01m005Longterm[[1]], PlotRange → {{0, 5}, {-0.01, 1.05}},
     PlotStyle → {PointSize[0.003], Darker[Blue]}],
    ListPlot[s01m005Longterm[[2]], PlotStyle →
      {PointSize[0.003], Lighter[Orange]}]]}, ImageSize → 900]
```

Stability analysis

To simplify the long and extensive computations, we restrict this analysis to the case $c_1 = c_2 = 1/2$ and $m_{12} = m_{21} = m$.

As long as the growth rates are small enough, such that the ecological dynamics lead to constant population sizes, the population densities converge to $c_1 K$ and $c_2 K$, in niche 1 and 2 respectively. In this regime (without fluctuations, and for symmetric migration), the values of selection determine whether the evolutionary dynamics lead to a polymorphic equilibrium or to fixation of one of the two types. Hence, we conduct the stability analysis for the following equilibria and combine the results as needed.

- (p1p2Equilibrium[s1, s2, m12, m21, c_1], c_1K, c_2K)
- (1, 1, c_1K, c_2K)
- (0, 0, c_1K, c_2K)

```
c1 = 1 / 2; c2 = 1 - c1;
CompleteModel1Generation[s1_, s2_, m_, p1_, p2_, N1_, N2_ , r1_, r2_, kk_] :=
  {((1 - m) p1 N1 + m p2 N2) / ((1 - m) N1 + m N2) *
     (w1A / (((1 - m) p1 N1 + m p2 N2) / ((1 - m) N1 + m N2) * w1A +
        (1 - ((1 - m) p1 N1 + m p2 N2) / ((1 - m) N1 + m N2)) * w1a)),
    ((1 - m) p2 N2 + m p1 N1) / ((1 - m) N2 + m N1) *
     (w2A / (((1 - m) p2 N2 + m p1 N1) / ((1 - m) N2 + m N1) * w2A +
        (1 - ((1 - m) p2 N2 + m p1 N1) / ((1 - m) N2 + m N1)) * w2a)),
    ((1 - m) N1 + m N2) Exp[r1 (1 - ((1 - m) N1 + m N2) / (c1 kk))
       (((1 - m) p1 N1 + m p2 N2) / ((1 - m) N1 + m N2) * w1A +
        (1 - ((1 - m) p1 N1 + m p2 N2) / ((1 - m) N1 + m N2)) * w1a)],
    ((1 - m) N2 + m N1) Exp[r2 (1 - ((1 - m) N2 + m N1) / (c2 kk))
       (((1 - m) p2 N2 + m p1 N1) / ((1 - m) N2 + m N1) * w2A +
        (1 - ((1 - m) p2 N2 + m p1 N1) / ((1 - m) N2 + m N1)) * w2a)]} /.
   {w1A → 1, w1a → 1 - s1, w2A → 1 - s2, w2a → 1};
```

Start by computing the Jacobian matrix:

```
s1 =.; s2 =.; m =.; p1 =.; p2 =.; N1 =.; N2 =.; r1 =.; r2 =.; kk =.;
jac = D[CompleteModel1Generation[s1, s2, m, p1, p2, N1, N2, r1, r2, kk], #] & /@
    {p1, p2, N1, N2} // Simplify;
```

1. Stability of 1/2K with polymorphic equilibrium:

```
jacPoly = jac /. {p1 → p1p2Equilibrium[[1]],
     p2 → p1p2Equilibrium[[2]], N1 → 1 / 2 kk, N2 → 1 / 2 kk} // Simplify;
EVcompletePoly = Eigenvalues[jacPoly] // Simplify;
```

2. Stability of 1/2K with monomorphic equilibria:

```
jacOne = jac /. {p1 → 1, p2 → 1, N1 → 1 / 2 kk, N2 → 1 / 2 kk} // Simplify;
EVcompleteOne = Eigenvalues[jacOne] // Simplify;
```

```
jacZero = jac /. {p1 → 0, p2 → 0, N1 → 1 / 2 kk, N2 → 1 / 2 kk} // Simplify;
EVcompleteZero = Eigenvalues[jacZero] // Simplify;
```

Any of these computations yields extremely long and complex expression for four eigenvalues. Thus, we choose to analyze them visually using the ContourPlot function. When doing so, we see that there are two leading eigenvalues per equilibrium:
- in EVcompletePoly only second and third eigenvalue are of interest
- in EVcompleteOne it's the first and third eigenvalue
- and in EVcompleteZero only first and third eigenvalue are important.

Now, these eigenvalues describe different effects:
EVcompletePoly[[2]], EVcompleteOne[[3]] and EVcompleteZero[[3]] determine the stability of the evolutionary equilibrium as a function of s_1, s_2 and m given that the ecological dynamics lead to stable population sizes 1/2K: these eigenvalues capture the direct effects of selection and migration on polymorphism/monomorphism. I.e.
- as long as | EVcompletePoly[[2]] | < 1, polymorphism is stable
- when | EVcompleteOne[[3]] | < 1, then 1 (fixation of *A*) is stable
- | EVcompleteZero[[3]] | < 1 implies stability of 0 (fixation of *a*)

EVcompleteOne[[3]] and EVcompleteZero[[3]] combined, yield the same picture as EVcompletePoly[[2]]: here, instability of the monomorphisms is equivalent to stability of the polymorphism (system of haploids in two demes: protected polymorphism <=> stable polymorphism). So, for the further analysis it suffices to consider EVcompletePoly[[2]].

Remark: EVcompletePoly[[2]] coincides with the leading eigenvalue of the "evolution only" Jacobi matrix (see above):

```
s1 =.; s2 =.; m =.; m12 = m; m21 = m; c1 = 1 / 2;
EVEvoOnly =
  Eigenvalues[jacobi /. {p1 → p1p2Equilibrium[[1]], p2 → p1p2Equilibrium[[2]]}][[2]] //
   Simplify;
```

```
Reduce[EVcompletePoly[[2]] == EVEvoOnly && 0 < s1 < 1 && 0 < s2 < 1 && 0 < m < 1 / 2]
```

Out[279]= $0 < m < \frac{1}{2}$ && $0 < s2 < 1$ && $0 < s1 < 1$

Fig. 4 is a visualization of EVcompletePoly[[2]] (and the simple condition obtained with evolution only):

```
s1 =.;
s2 =.;
m =.;
r1 = 1;
r2 = 1;
kk = 50; c1 = 1 / 2; m01 = 0.1; m04 = 0.4;
GraphicsGrid[
 {{Show[ContourPlot[Evaluate[EVcompletePoly[[2]] /. {m → 0.1}], {s1, 0, 1},
     {s2, 0, 1}, ContourStyle → None, Contours → {1},
     ContourShading → {LightGray, White}],
    ContourPlot[Evaluate[(EVcompletePoly[[2]] /. {m → 0.1}) == 1],
     {s1, 0, 1}, {s2, 0, 1}, ContourStyle → Gray],
    ContourPlot[Abs[m01 (1 / s1 - 1 / s2)] == 1 - m01, {s1, 0, 1},
     {s2, 0, 1}, ContourStyle → {Black, Dashing[Large]}]],
   Show[ContourPlot[Evaluate[EVcompletePoly[[2]] /. {m → 0.4}],
     {s1, 0, 1}, {s2, 0, 1}, ContourStyle → None,
     Contours → {1}, ContourShading → {LightGray, White}],
    ContourPlot[Evaluate[(EVcompletePoly[[2]] /. {m → 0.4}) == 1],
     {s1, 0, 1}, {s2, 0, 1}, ContourStyle → Gray],
    ContourPlot[Abs[m04 (1 / s1 - 1 / s2)] == 1 - m04, {s1, 0, 1},
     {s2, 0, 1}, ContourStyle → {Black, Dashing[Large]}]]},
 ImageSize →
  800]
```

EVcompletePoly[[3]], EVcompleteOne[[1]] and EVcompleteZero[[1]] determine the stability of 1/2K, i.e. the stability of the population dynamics given that the corresponding evolutionary equilibrium (polymorphism, one, zero) is stable:
- when the evolutionary dynamics lead to a polymorphic equilibrium, EVcompletePoly[[3]] tells us about the first branching point of the population dynamics,
- when the evolutionary dynamics lead to fixation of either allele *A* or allele *a*, then the stability of the population dynamics is given by EVcompleteOne[[1]] or EVcompleteZero[[1]], respectively.

This leads us to **Fig. 3**:
In (A)---(D), the trade-off in selection is symmetric and, thus, evolutionary dynamics always converge to a polymorphic equilibrium as long as fluctuations are absent. Therefore, it suffices to plot EVcompletePoly[[3]] to obtain information about the first branching point of the system.

E.g. Fig. 3B:

```
s1 = 0.01; s2 = 0.01; m = 0.4; r1 =.; r2 =.; kk = 50; c1 = 1 / 2;
Show[
 ContourPlot[Evaluate[EVcompletePoly[[3]]],
  {r1, 0, 5}, {r2, 0, 5}, ContourLabels → None, Contours → {-1},
  ContourShading → {White, LightGray}, ContourStyle → None],
 ContourPlot[Evaluate[EVcompletePoly[[3]] == -1],
  {r1, 0, 5}, {r2, 0, 5}, ContourStyle → Gray],
 ContourPlot[r1 == 2, {r1, 0, 5}, {r2, 0, 2},
  ContourStyle → {Gray, Thickness[0.0065], Dashing[{0.01, 0.055}]}],
 ContourPlot[r2 == 2, {r1, 0, 2}, {r2, 0, 5},
  ContourStyle → {Gray, Thickness[0.0065], Dashing[{0.01, 0.055}]}]]
```

E.g. Fig. 3D:

```
s1 =.; s2 =.; m =.; r1 =.; r2 =.; kk =.; c1 =.; s =.;
EVcompletePolySymmSel = EVcompletePoly[[3]] /. {s1 → s, s2 → s};

m = 0.4; r2 = 1; kk = 50; c1 = 1 / 2;
Show[
 ContourPlot[Evaluate[EVcompletePolySymmSel],
  {s, 0, 1}, {r1, 0, 5}, ContourLabels → None, Contours → {-1},
  ContourShading → {White, LightGray}, ContourStyle → None],
 ContourPlot[Evaluate[EVcompletePolySymmSel == -1],
  {s, 0, 1}, {r1, 0, 5}, ContourStyle → Gray]]
```

In (E) and (F), we keep one of the selection coefficients fixed, while varying the other. Therefore, the evolutionary equilibrium does not always converge to polymorphism anymore. If the asymmetry in selection is too strong, allele frequencies converge to fixation of one type. Hence, we have to plot a combination of EVcompletePoly[[3]], EVcompleteOne[[1]] and EVcompleteZero[[1]]. Which eigenvalue applies where, is determined by EVcompletePoly[[2]] (the stability of the evolutionary dynamics).

E.g. Fig. 3E:

```
s1 =.; s2 = 0.3; m = 0.4; kk = 50; c1 = 1 / 2;
Solve[EVcompletePoly[[2]] == 1, s1]
```

Out[340]= $\{\{s1 \to -0.0532742\}, \{s1 \to 0.206897\}, \{s1 \to 0.545455\}\}$

In[343]:=
```
lower = 0.20689655172413;
upper = 0.54545454545454;

Solve[(EVcompletePoly[[3]] /. {s1 → lower, s2 → 0.3, m → 0.4, r2 → 1}) == -1, r1]
Solve[(EVcompletePoly[[3]] /. {s1 → upper, s2 → 0.3, m → 0.4, r2 → 1}) == -1, r1]
```

$\{\{r1 \to -1.38772 \times 10^{11}\}, \{r1 \to 3.36232\}\}$

$\{\{r1 \to 2.78788\}\}$

In[345]:=
```
Rlower = 3.3623188406304783;
Rupper = 2.7878787877539657;

s2 = 0.3; m = 0.4; r2 = 1; kk = 50; c1 = 1 / 2;
Show[
 ContourPlot[Evaluate[EVcompletePoly[[3]]], {s1, 0, 1}, {r1, 0, 5},
  ContourStyle → None, Contours → {-1}, ContourShading → {White, LightGray},
  RegionFunction → Function[{s1, r1}, lower < s1 < upper]],
 ContourPlot[Evaluate[EVcompletePoly[[3]] == -1],
  {s1, lower, upper}, {r1, 0, 5}, ContourStyle → Gray],
 ContourPlot[Evaluate[EVcompleteZero[[1]]], {s1, 0, lower}, {r1, 0, 5},
  ContourStyle → None, Contours → {-1}, ContourShading → {White, LightGray}],
 ContourPlot[Evaluate[EVcompleteZero[[1]] == -1],
  {s1, 0, lower}, {r1, 0, 5}, ContourStyle → Gray],
 ContourPlot[Evaluate[EVcompleteOne[[1]]], {s1, upper, 1}, {r1, 0, 5},
  ContourStyle → None, Contours → {-1}, ContourShading → {White, LightGray}],
 ContourPlot[Evaluate[EVcompleteOne[[1]] == -1],
  {s1, upper, 1}, {r1, 0, 5}, ContourStyle → Gray],
 ContourPlot[Evaluate[EVcompletePoly[[2]] == 1], {s1, 0, lower + 0.05},
  {r1, 0, Rlower}, ContourStyle → {Gray, Dashing[{0.05, 0.09}]}],
 ContourPlot[Evaluate[EVcompletePoly[[2]] == 1], {s1, upper - 0.05, 1},
  {r1, 0, Rupper}, ContourStyle → {Gray, Dashing[{0.05, 0.09}]}]]
```

Imposed population densities (fluctuations)

Simulations

Here, we compute the population sizes differently:
Population density in niche 1 fluctuates between N1 + D1 and N1 - D1, population size in niche 2 is fixed to N2.

```
s1 =.; s2 =.; m12 =.; m21 =.; p1 =.; p2 =.; N1 =.; D1 =.; N2 =.; tm =.;

ImposedModel[s1_, s2_, m12_, m21_, p1_, p2_, N1_ , D1_, N2_, tm_] :=
 Module[{w1A = 1, w1a = 1 - s1, w2A = 1 - s2, w2a = 1}, NestList[{
      (1 - m12) #[[1]] #[[3]] + m21 #[[2]] N2 / (1 - m12) #[[3]] + m21 N2 * (w1A /
        ((((1 - m12) #[[1]] #[[3]] + m21 #[[2]] N2) / ((1 - m12) #[[3]] + m21 N2)) * w1A + (1 -
            ((1 - m12) #[[1]] #[[3]] + m21 #[[2]] N2) / ((1 - m12) #[[3]] + m21 N2)) * w1a)),
      (1 - m21) #[[2]] N2 + m12 #[[1]] #[[3]] / (1 - m21) N2 + m12 #[[3]] * (w2A /
        ((((1 - m21) #[[2]] N2 + m12 #[[1]] #[[3]]) / ((1 - m21) N2 + m12 #[[3]])) * w2A + (1 -
            ((1 - m21) #[[2]] N2 + m12 #[[1]] #[[3]]) / ((1 - m21) N2 + m12 #[[3]])) * w2a)),
    #[[3]] + (-1)^#[[4]] 2 D1,
    #[[4]] + 1} &, {p1, p2, N1 + D1, 1}, tm]]
```

```
ImposedModelLast[s1_, s2_, m12_, m21_, p1_, p2_, N1_ , D1_, N2_, tm_] :=
 Module[{w1A = 1, w1a = 1 - s1, w2A = 1 - s2, w2a = 1}, Nest[{
    ((1 - m12) #[[1]] #[[3]] + m21 #[[2]] N2) / ((1 - m12) #[[3]] + m21 N2) * (w1A /
       ((((1 - m12) #[[1]] #[[3]] + m21 #[[2]] N2) / ((1 - m12) #[[3]] + m21 N2)) * w1A + (1 -
          ((1 - m12) #[[1]] #[[3]] + m21 #[[2]] N2) / ((1 - m12) #[[3]] + m21 N2)) * w1a)),
    ((1 - m21) #[[2]] N2 + m12 #[[1]] #[[3]]) / ((1 - m21) N2 + m12 #[[3]]) * (w2A /
       ((((1 - m21) #[[2]] N2 + m12 #[[1]] #[[3]]) / ((1 - m21) N2 + m12 #[[3]])) * w2A + (1 -
          ((1 - m21) #[[2]] N2 + m12 #[[1]] #[[3]]) / ((1 - m21) N2 + m12 #[[3]])) * w2a)),
    #[[3]] + (-1)^#[[4]] 2 D1,
    #[[4]] + 1} &, {p1, p2, N1 + D1, 1}, tm]]
```

The simulations are now easier than they were before. It suffices to run the computations for increasing values of the fluctuation size D1.

Fig. 9:

In[397]:=
```
s1 = 0.1; s2 = 0.1; m = 0.05;
p1 = 0.5; p2 = 0.5; N1 = 1000; N2 = 1000;
D1 = .; tm = 500;

s01m005LongtermImposed = Transpose[ParallelTable[
    MapThread[{#1, #2} &,
     {{D1, D1, D1}, {ImposedModelLast[s1, s2, m, m, p1, p2, N1 , D1, N2,
         tm + RandomInteger[{0, 1}]][[1]], ImposedModelLast[s1, s2, m, m, p1, p2,
         N1 , D1, N2, tm + RandomInteger[{0, 1}]][[2]],
       ImposedModelLast[s1, s2, m, m, p1, p2, N1 , D1, N2,
         tm + RandomInteger[{0, 1}]][[3]]}}], {D1, 1, 1000, 1}]];
```

In[401]:=
```
GraphicsGrid[
 {{Show[ListPlot[s01m005LongtermImposed[[3]], PlotStyle → {PointSize[0.005],
       Darker[Blue]}, PlotRange → {{0, N1}, {0, 2 N1}}],
    Plot[N2, {t, 0, N2}, PlotStyle → {Thickness[0.005], Lighter[Orange]}]],
   Show[ListPlot[s01m005LongtermImposed[[1]], PlotRange → {{0, N1}, {0, 1}},
     PlotStyle → {PointSize[0.005], Darker[Blue]}],
    ListPlot[s01m005LongtermImposed[[2]], PlotStyle →
      {PointSize[0.005], Lighter[Orange]}]]}}, ImageSize → 1000]
```

Stability analysis

As we are not able to solve for the equilibrium frequency, we analyze the stability of the polymorphic equilibrium again by evaluating the conditions for a protected polymorphism. To capture the fluctuations in population size, we consider two consecutive generations:

```
s1 = .; s2 = .; m12 = .; m21 = .; p1 = .; p2 = .; KK = .; D1 = .; N2 = .;
```

```
NextGenerationUp[s1_, s2_, m12_, m21_, p1_, p2_, KK_ , D1_, N2_] :=
 Module[{w1A = 1, w1a = 1 - s1, w2A = 1 - s2, w2a = 1, N1 = KK + D1},
  {((1 - m12) p1 N1 + m21 p2 N2)/((1 - m12) N1 + m21 N2) *
    (w1A/((((1 - m12) p1 N1 + m21 p2 N2)/((1 - m12) N1 + m21 N2)) * w1A +
       (1 - (((1 - m12) p1 N1 + m21 p2 N2)/((1 - m12) N1 + m21 N2))) * w1a)),
   ((1 - m21) p2 N2 + m12 p1 N1)/((1 - m21) N2 + m12 N1) * (w2A/
      ((((1 - m21) p2 N2 + m12 p1 N1)/((1 - m21) N2 + m12 N1)) * w2A +
        (1 - (((1 - m21) p2 N2 + m12 p1 N1)/((1 - m21) N2 + m12 N1))) * w2a))}]

NextGenerationDown[s1_, s2_, m12_, m21_, p1_, p2_, KK_ , D1_, N2_] :=
 Module[{w1A = 1, w1a = 1 - s1, w2A = 1 - s2, w2a = 1, N1 = KK - D1},
  {((1 - m12) p1 N1 + m21 p2 N2)/((1 - m12) N1 + m21 N2) *
    (w1A/((((1 - m12) p1 N1 + m21 p2 N2)/((1 - m12) N1 + m21 N2)) * w1A +
       (1 - (((1 - m12) p1 N1 + m21 p2 N2)/((1 - m12) N1 + m21 N2))) * w1a)),
   ((1 - m21) p2 N2 + m12 p1 N1)/((1 - m21) N2 + m12 N1) *
    (w2A/((((1 - m21) p2 N2 + m12 p1 N1)/((1 - m21) N2 + m12 N1)) * w2A +
       (1 - (((1 - m21) p2 N2 + m12 p1 N1)/((1 - m21) N2 + m12 N1))) * w2a))}]

TwoGenerationsUpDown[s1_, s2_, m12_, m21_, p1_, p2_, KK_ , D1_, N2_] :=
 NextGenerationDown[s1, s2, m12, m21,
  NextGenerationUp[s1, s2, m12, m21, p1, p2, KK, D1, N2][[1]],
  NextGenerationUp[s1, s2, m12, m21, p1, p2, KK, D1, N2][[2]], KK, D1, N2]

TwoGenerationsDownUp[s1_, s2_, m12_, m21_, p1_, p2_, KK_ , D1_, N2_] :=
 NextGenerationUp[s1, s2, m12, m21,
  NextGenerationDown[s1, s2, m12, m21, p1, p2, KK, D1, N2][[1]],
  NextGenerationDown[s1, s2, m12, m21, p1, p2, KK, D1, N2][[2]], KK, D1, N2]
```

Remark: The results are the same no matter if we consider N1 + D1 or N1 - D1 in the first generation. We choose to run the computations for TwoGenerationsUpDown[s1, s2, m12, m21, p1, p2, KK, D1, N2] (i.e. for N1 + D1 in the first and N1 - D1 in the subsequent generation):

```
jacImposedUpDown =
  D[TwoGenerationsUpDown[s1, s2, m12, m21, p1, p2, KK, D1, N2], #] & /@ {p1, p2} //
   Simplify;

jacImposedUpDownZero = jacImposedUpDown /. {p1 → 0, p2 → 0} // Simplify;
EVImposedUpDownZero = Eigenvalues[jacImposedUpDownZero] // Simplify;

jacImposedUpDownOne = jacImposedUpDown /. {p1 → 1, p2 → 1} // Simplify;
EVImposedUpDownOne = Eigenvalues[jacImposedUpDownOne] // Simplify;
```

In both cases, the second eigenvalue of the Jacobi matrix is the leading eigenvalue (again, we assessed that by visual analysis). These two leading eigenvalues -- EVImposedUp-DownZero[[2]] and EVImposedUpDownOne[[2]] -- determine the stable region of the monomorphisms 0 and 1, respectively.

The polymorphism is stable when both monomorphisms are unstable. I.e. the region where

both, EVImposedUpDownZero[[2]] and EVImposedUpDownOne[[2]], are in absolute value larger than 1, leads to a stable polymorphic equilibrium.

Fig. 10:

```
s1 =.; s2 =.;
m =.; m12 = m;  m21 = m;
KK = 100; D1 =.;
N2 = 100;
GraphicsGrid[{{
    Show[
     RegionPlot[(EVImposedUpDownOne[[2]] /. {m → 0.1, D1 → 90}) > 1 &&
       (EVUpDownZero[[2]] /. {m → 0.1, D1 → 90}) > 1, {s1, 0, 1},
      {s2, 0, 1}, PlotStyle → LightGray, BoundaryStyle → None],
     ContourPlot[Evaluate[(EVImposedUpDownOne[[2]] /. {m → 0.1, D1 → 0}) == 1],
      {s1, 0, 1}, {s2, 0, 1}, ContourStyle → {Gray, Dashing[{0.01, 0.045}]}],
     ContourPlot[Evaluate[(EVImposedUpDownZero[[2]] /. {m → 0.1, D1 → 0}) == 1],
      {s1, 0, 1}, {s2, 0, 1}, ContourStyle → {Gray, Dashing[{0.01, 0.045}]}],
     ContourPlot[Evaluate[(EVImposedUpDownOne[[2]] /. {m → 0.1, D1 → 90}) == 1],
      {s1, 0, 1}, {s2, 0, 1}, ContourStyle → Gray],
     ContourPlot[Evaluate[(EVImposedUpDownZero[[2]] /. {m → 0.1, D1 → 90}) == 1],
      {s1, 0, 1}, {s2, 0, 1}, ContourStyle → Gray]],

    Show[
     RegionPlot[(EVImposedUpDownOne[[2]] /. {m → 0.4, D1 → 90}) > 1 &&
       (EVUpDownZero[[2]] /. {m → 0.4, D1 → 90}) > 1, {s1, 0, 1},
      {s2, 0, 1}, PlotStyle → LightGray, BoundaryStyle → None],
     ContourPlot[Evaluate[(EVImposedUpDownOne[[2]] /. {m → 0.4, D1 → 0}) == 1],
      {s1, 0, 1}, {s2, 0, 1}, ContourStyle → {Gray, Dashing[{0.01, 0.045}]}],
     ContourPlot[Evaluate[(EVImposedUpDownZero[[2]] /. {m → 0.4, D1 → 0}) == 1],
      {s1, 0, 1}, {s2, 0, 1}, ContourStyle → {Gray, Dashing[{0.01, 0.045}]}],
     ContourPlot[Evaluate[(EVImposedUpDownOne[[2]] /. {m → 0.4, D1 → 90}) == 1],
      {s1, 0, 1}, {s2, 0, 1}, ContourStyle → Gray],
     ContourPlot[Evaluate[(EVImposedUpDownZero[[2]] /. {m → 0.4, D1 → 90}) == 1],
      {s1, 0, 1}, {s2, 0, 1}, ContourStyle → Gray]]}}, ImageSize → 800]
```

Continent-island model

Finally, we analyze the continent-island model with imposed fluctuations on the island. M21 denotes the number of immigrants (per generation) arriving on the island.

First, we compute the equilibrium frequency (more precisely: the two-cycle) of the resident type, again by considering two consecutive generations:

In[512]:=
```
K1 =.; D1 =.; s1 =.; M21 =.;
p1t0 =.;
N1t0 =.;
N1t1 =.;
N2 =.;
p2 =.; (* "fixed allele frequency of the focal type on the continent" ->
 will be set to zero *)

p1t1 =
 (p1t0 N1t0 + p2 M21)/(N1t0 + M21) * (1/((p1t0 N1t0 + p2 M21)/(N1t0 + M21) + (1 - (p1t0 N1t0 + p2 M21)/(N1t0 + M21)) * (1 - s1)));

p1t2 =
 (p1t1 N1t1 + p2 M21)/(N1t1 + M21) * (1/((p1t1 N1t1 + p2 M21)/(N1t1 + M21) + (1 - (p1t1 N1t1 + p2 M21)/(N1t1 + M21)) * (1 - s1)));
```

We obtain two solutions: one for generations where the local population density is low, the other for generations where the local population density is high. The allele frequency of the resident type *A* at equilibrium exhibits small fluctuations:

In[519]:=
```
N1t0 = K1 - D1;
N1t1 = K1 + D1;
Reduce[
 p1t2 - p1t0 == 0 && 0 < s1 < 1 && 0 < M21 && 0 < D1 < K1 && 0 < p2 < 1, p1t0, Reals]

N1t0 = K1 + D1;
N1t1 = K1 - D1;
Reduce[
 p1t2 - p1t0 == 0 && 0 < s1 < 1 && 0 < M21 && 0 < D1 < K1 && 0 < p2 < 1, p1t0, Reals]
```

Take the relevant solution from both computations (second one in both cases):

In[522]:=
```
p1EquilibriumIslandPoly[s1_, D1_, K1_, M21_, p2_] :=
 {(-2 K1 M21 - M21^2 - 2 D1^2 s1 + 2 K1^2 s1 + 4 K1 M21 s1 + 2 M21^2 s1 -
      2 D1 M21 p2 s1 - 2 K1 M21 p2 s1 - 2 M21^2 p2 s1 + D1^2 s1^2 - K1^2 s1^2 -
      2 K1 M21 s1^2 - M21^2 s1^2 + 2 K1 M21 p2 s1^2 + 2 M21^2 p2 s1^2 - M21^2 p2^2 s1^2) /
    (2 (D1 - K1) s1 (-2 D1 - 2 K1 - M21 + D1 s1 + K1 s1 + M21 s1 - M21 p2 s1)) +
   1/2 Sqrt((4 K1^2 M21^2 + 4 K1 M21^3 + M21^4 + 8 D1^2 K1 M21 s1 - 8 K1^3 M21 s1 + 4 D1^2 M21^2 s1 -
        20 K1^2 M21^2 s1 - 16 K1 M21^3 s1 - 4 M21^4 s1 - 16 D1^2 K1 M21 p2 s1 + 16 K1^3 M21 p2 s1 -
        8 D1^2 M21^2 p2 s1 + 24 K1^2 M21^2 p2 s1 + 16 K1 M21^3 p2 s1 + 4 M21^4 p2 s1 + 4 D1^4 s1^2 -
        8 D1^2 K1^2 s1^2 + 4 K1^4 s1^2 - 20 D1^2 K1 M21 s1^2 + 20 K1^3 M21 s1^2 - 10 D1^2 M21^2 s1^2 +
        34 K1^2 M21^2 s1^2 + 24 K1 M21^3 s1^2 + 6 M21^4 s1^2 + 24 D1^2 K1 M21 p2 s1^2 -
        24 K1^3 M21 p2 s1^2 + 16 D1^2 M21^2 p2 s1^2 - 56 K1^2 M21^2 p2 s1^2 - 44 K1 M21^3 p2 s1^2 -
        12 M21^4 p2 s1^2 - 4 D1^2 M21^2 p2^2 s1^2 + 20 K1^2 M21^2 p2^2 s1^2 + 20 K1 M21^3 p2^2 s1^2 +
        6 M21^4 p2^2 s1^2 - 4 D1^4 s1^3 + 8 D1^2 K1^2 s1^3 - 4 K1^4 s1^3 + 16 D1^2 K1 M21 s1^3 -
        16 K1^3 M21 s1^3 + 8 D1^2 M21^2 s1^3 - 24 K1^2 M21^2 s1^3 - 16 K1 M21^3 s1^3 - 4 M21^4 s1^3 -
        16 D1^2 K1 M21 p2 s1^3 + 16 K1^3 M21 p2 s1^3 - 12 D1^2 M21^2 p2 s1^3 + 44 K1^2 M21^2 p2 s1^3 +
        40 K1 M21^3 p2 s1^3 + 12 M21^4 p2 s1^3 + 4 D1^2 M21^2 p2^2 s1^3 - 20 K1^2 M21^2 p2^2 s1^3 -
        32 K1 M21^3 p2^2 s1^3 - 12 M21^4 p2^2 s1^3 + 8 K1 M21^3 p2^3 s1^3 + 4 M21^4 p2^3 s1^3 +
        D1^4 s1^4 - 2 D1^2 K1^2 s1^4 + K1^4 s1^4 - 4 D1^2 K1 M21 s1^4 + 4 K1^3 M21 s1^4 -
        2 D1^2 M21^2 s1^4 + 6 K1^2 M21^2 s1^4 + 4 K1 M21^3 s1^4 + M21^4 s1^4 + 4 D1^2 K1 M21 p2 s1^4 -
        4 K1^3 M21 p2 s1^4 + 4 D1^2 M21^2 p2 s1^4 - 12 K1^2 M21^2 p2 s1^4 - 12 K1 M21^3 p2 s1^4 -
        4 M21^4 p2 s1^4 - 2 D1^2 M21^2 p2^2 s1^4 + 6 K1^2 M21^2 p2^2 s1^4 + 12 K1 M21^3 p2^2 s1^4 +
        6 M21^4 p2^2 s1^4 - 4 K1 M21^3 p2^3 s1^4 - 4 M21^4 p2^3 s1^4 + M21^4 p2^4 s1^4) /
      ((D1 - K1)^2 s1^2 (-2 D1 - 2 K1 - M21 + D1 s1 + K1 s1 + M21 s1 - M21 p2 s1)^2)),
  (-2 K1 M21 - M21^2 - 2 D1^2 s1 + 2 K1^2 s1 + 4 K1 M21 s1 + 2 M21^2 s1 + 2 D1 M21 p2 s1 -
      2 K1 M21 p2 s1 - 2 M21^2 p2 s1 + D1^2 s1^2 - K1^2 s1^2 - 2 K1 M21 s1^2 -
      M21^2 s1^2 + 2 K1 M21 p2 s1^2 + 2 M21^2 p2 s1^2 - M21^2 p2^2 s1^2) /
    (2 (D1 + K1) s1 (-2 D1 + 2 K1 + M21 + D1 s1 - K1 s1 - M21 s1 + M21 p2 s1)) +
   1/2 Sqrt((4 K1^2 M21^2 + 4 K1 M21^3 + M21^4 + 8 D1^2 K1 M21 s1 - 8 K1^3 M21 s1 + 4 D1^2 M21^2 s1 -
        20 K1^2 M21^2 s1 - 16 K1 M21^3 s1 - 4 M21^4 s1 - 16 D1^2 K1 M21 p2 s1 + 16 K1^3 M21 p2 s1 -
        8 D1^2 M21^2 p2 s1 + 24 K1^2 M21^2 p2 s1 + 16 K1 M21^3 p2 s1 + 4 M21^4 p2 s1 + 4 D1^4 s1^2 -
        8 D1^2 K1^2 s1^2 + 4 K1^4 s1^2 - 20 D1^2 K1 M21 s1^2 + 20 K1^3 M21 s1^2 - 10 D1^2 M21^2 s1^2 +
        34 K1^2 M21^2 s1^2 + 24 K1 M21^3 s1^2 + 6 M21^4 s1^2 + 24 D1^2 K1 M21 p2 s1^2 -
        24 K1^3 M21 p2 s1^2 + 16 D1^2 M21^2 p2 s1^2 - 56 K1^2 M21^2 p2 s1^2 - 44 K1 M21^3 p2 s1^2 -
        12 M21^4 p2 s1^2 - 4 D1^2 M21^2 p2^2 s1^2 + 20 K1^2 M21^2 p2^2 s1^2 + 20 K1 M21^3 p2^2 s1^2 +
        6 M21^4 p2^2 s1^2 - 4 D1^4 s1^3 + 8 D1^2 K1^2 s1^3 - 4 K1^4 s1^3 + 16 D1^2 K1 M21 s1^3 -
        16 K1^3 M21 s1^3 + 8 D1^2 M21^2 s1^3 - 24 K1^2 M21^2 s1^3 - 16 K1 M21^3 s1^3 - 4 M21^4 s1^3 -
        16 D1^2 K1 M21 p2 s1^3 + 16 K1^3 M21 p2 s1^3 - 12 D1^2 M21^2 p2 s1^3 + 44 K1^2 M21^2 p2 s1^3 +
        40 K1 M21^3 p2 s1^3 + 12 M21^4 p2 s1^3 + 4 D1^2 M21^2 p2^2 s1^3 - 20 K1^2 M21^2 p2^2 s1^3 -
        32 K1 M21^3 p2^2 s1^3 - 12 M21^4 p2^2 s1^3 + 8 K1 M21^3 p2^3 s1^3 + 4 M21^4 p2^3 s1^3 +
        D1^4 s1^4 - 2 D1^2 K1^2 s1^4 + K1^4 s1^4 - 4 D1^2 K1 M21 s1^4 + 4 K1^3 M21 s1^4 -
        2 D1^2 M21^2 s1^4 + 6 K1^2 M21^2 s1^4 + 4 K1 M21^3 s1^4 + M21^4 s1^4 + 4 D1^2 K1 M21 p2 s1^4 -
        4 K1^3 M21 p2 s1^4 + 4 D1^2 M21^2 p2 s1^4 - 12 K1^2 M21^2 p2 s1^4 - 12 K1 M21^3 p2 s1^4 -
        4 M21^4 p2 s1^4 - 2 D1^2 M21^2 p2^2 s1^4 + 6 K1^2 M21^2 p2^2 s1^4 + 12 K1 M21^3 p2^2 s1^4 +
        6 M21^4 p2^2 s1^4 - 4 K1 M21^3 p2^3 s1^4 - 4 M21^4 p2^3 s1^4 + M21^4 p2^4 s1^4) /
      ((D1 + K1)^2 s1^2 (-2 D1 + 2 K1 + M21 + D1 s1 - K1 s1 - M21 s1 + M21 p2 s1)^2))}
```

Set p2 = 0 (monomorphic immigration from the continent):

In[523]:=
```
p1EquilibriumIsland[s1_, D1_, K1_, M21_] :=
 p1EquilibriumIslandPoly[s1, D1, K1, M21, 0] // Simplify
```

Finally, we obtain conditions for persistence of the resident type by setting its equilibrium frequency to zero and then reversing the unequal signs:

In[525]:=
```
Reduce[p1EquilibriumIsland[s1, D1, K1, M21] == 0 &&
   0 < s1 < 1 && 0 < M21 && 0 < D1 < K1, D1, Reals] // Simplify
```

Out[525]=
$$M21 > 0 \&\& K1 > 0 \&\& D1 < K1 \&\& \left(\left(0 < D1 \&\& 0 < s1 \&\& s1 \le \frac{M21}{K1 + M21}\right) \,||\, \left(\frac{M21}{K1 + M21} < s1 \&\& s1 < 1 \&\& \sqrt{\left(\left(2\,K1\,M21\,\left(-1+s1\right)^2 + M21^2\,\left(-1+s1\right)^2 + K1^2\,\left(-2+s1\right)\,s1\right) \Big/ \left(\left(-2+s1\right)\,s1\right)\right)} \le D1\right)\right)$$

Simplify $D1 < \sqrt{\frac{2\,K1\,M21\,(-1+s1)^2+M21^2\,(-1+s1)^2+K1^2\,(-2+s1)\,s1}{(-2+s1)\,s1}}$ to obtain condition (8) in the main text.

Fig. 11A:

In[509]:=
```
s1 =.; MM =.;
DD = Sqrt[(1/((2 - s1) s1) - (1/((2 - s1) s1) - 1)) * (1 + MM)^2];

Show[Plot[DD /. s1 → 0.1, {MM, 0, 0.45}, PlotStyle → Blue],
 Plot[DD /. s1 → 0.2, {MM, 0, 0.5}, PlotStyle → Orange],
 Plot[DD /. s1 → 0.3, {MM, 0, 0.5}, PlotStyle → Darker[Green]],
 ListPlot[{{#/(1 - #), 0}} & /@ {0.1, 0.2, 0.3},
  PlotStyle → {PointSize[0.02] & /@ {Blue, Orange, Darker[Green]}}]]
```

Fig. 11B:

In order to compare the above result to the equilibrium frequency of *A* with bidirectional migration, we rescale the formulas for bidirectional migration by dividing through K1:

$$\frac{(1-m)\,N_1\,p_1 + m\,N_2\,p_2}{(1-m)\,N_1 + m\,N_2} = \frac{(1-m)\,(K_1 +- D_1)\,p_1 + m\,K_1\,p_2}{(1-m)\,(K_1 +- D_1) + m\,K_1} = \frac{(1-m)\left(1 +- \frac{D_1}{K_1}\right)p_1 + m\,p_2}{(1-m)\left(1 +- \frac{D_1}{K_1}\right) + m}$$

```
D1K1ImposedModelLast[s1_, s2_, m_, p1_, p2_, D1K1_, tm_] :=
 Module[{w1A = 1, w1a = 1 - s1, w2A = 1 - s2, w2a = 1}, Nest[{
    ((1 - m) #[[1]] (1 + #[[3]]) + m #[[2]])/((1 - m) (1 + #[[3]]) + m) *
     (w1A/((((1 - m) #[[1]] (1 + #[[3]]) + m #[[2]])/((1 - m) (1 + #[[3]]) + m)) * w1A +
       (1 - (((1 - m) #[[1]] (1 + #[[3]]) + m #[[2]])/((1 - m) (1 + #[[3]]) + m)) * w1a)),
    ((1 - m) #[[2]] + m #[[1]] (1 + #[[3]]))/((1 - m) + m (1 + #[[3]])) * (w2A/
      ((((1 - m) #[[2]] + m #[[1]] (1 + #[[3]]))/((1 - m) + m (1 + #[[3]]))) * w2A +
        (1 - (((1 - m) #[[2]] + m #[[1]] (1 + #[[3]]))/((1 - m) + m (1 + #[[3]]))) * w2a)),
    (-1)^#[[4]] Abs[#[[3]]],
    #[[4]] + 1} &, {p1, p2, D1K1, 1}, tm]]
```

I.e. in the list generated through D1K1ImposedModelLast we have the following entries:

#[[1]] = p_1 (as before)

#[[2]] = p_2 (as before)

#[[3]] = +- $\frac{D_1}{K_1}$ = +- D1K1 (D1K1 = D_1/K_1 and, thus, ranges between zero and one)

E.g. simulations for $s_1 = 0.1$ (blue line in Fig. 11B):

```
s = 0.1;  (* change the value of s to obtain the other lines in Fig. 11B *)
s1 = s; s2 = s;  p1 = 0.5; p2 = 0.5;
m =.;  (* m = m*K1/K1 = M21/K1 *)
D1K1 =.;  (* D1K1 = D1/K1 -> between 0 and 1 *)
tm = 2^12;

SimBiUniMS01 =
  Transpose[Flatten[ParallelTable[MapThread[{#1, #2, #3} &, {{m, m, m, m},
       {D1K1, D1K1, D1K1, D1K1}, D1K1ImposedModelLast[s1, s2, m, p1, p2,
        D1K1, tm + RandomInteger[{-1, 1}]]]],
     {m, 0.001, 0.5, 0.005}, {D1K1, 0, 0.99, 0.01}], 1]];
```

We choose a threshold of 10^{-10} for "extinction of A":

```
Show[Plot[DD /. s1 → 0.1, {MM, 0, 0.5},
  PlotStyle → {Dashing[{0.02, 0.06}], Blue}, PlotRange → {{0, 0.5}, {0, 1.05}}],
 ListContourPlot[SimBiUniMS01[[1]], Contours → {10^-10},
  ContourStyle → {{Darker[Blue], Thickness[0.006]}}, ContourShading → None]]
```

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