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Dispersal and good habitat quality promote neutral genetic diversity in metapopulations *

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Abstract

Dispersal is a fundamental and crucial ecological process for a metapopulation to survive in heterogeneous or changing habitats. In this paper, we investigate the effect of the habitat quality and the dispersal on the neutral genetics diversity of a metapopulation. We model the metapopulation dynamics on heterogeneous habitats using a deterministic system of ordinary differential equations. We decompose the metapopulation into several neutral genetic fractions seeing as they could be located in different habitats. By using a mathematical model which describes their temporal dynamics inside the metapopulation, we provide the analytical results of their transient dynamics, as well as their asymptotic proportion in the different habitats. The diversity indices show how the genetic diversity at a global metapopulation scale is preserved by the correlation of two factors: the dispersal of the population, as well as the existence of adequate and sufficiently large habitats. The diversity indices show how the genetic diversity at a global metapopulation scale is preserved by the correlation of two factors: the dispersal of the population as well as the existence of adequate and sufficiently large habitats. Moreover, they ensure genetic diversity at the local habitat scale. In a source-sink metapopulation, we demonstrate that the diversity of the sink can be rescued if the condition of the sink is not too deteriorated and the migration from the source is larger than the migration from the sink. Furthermore, our study provides an analytical insight on the dynamics of the solutions of the systems of ordinary differential equations.

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1 Introduction.

Environmental changes such as climate change or habitat alterations, often due to human activity, occur at varying rates and intensities among the regions. The result are heterogeneous landscapes composed of local habitats with potentially altered suitability. In particular, if the environmental changes in some local habitats exceed species tolerance; or if the acclimation and the adaptation of the species are insufficient to allow them to persist (Visser, 2008), their dispersal capabilities could be the key for their survival (Travis et al., 2012; Ponchon et al., 2015; Malanson and Cairns, 1997; Iverson et al., 1999; Schwartz et al., 2001). However, dispersal is also a main force that influences population gene flow (Slatkin, 1987; Bohonak, 1999) as well as genetic diversity (Hewitt, 2000; Roques et al., 2012; Bonnefon et al., 2014).

Within heterogeneous environments, many species persist as a metapopulation consisting in a collection of local populations, living in different habitats, which are connected through dispersal. It is well known that the suitability of the different habitats as well as the dispersal ability of the species crucially determines its survival within this environment (e.g. Husband and Barrett, 1996; Freckleton and Watkinson, 1990; Levin et al., 2003). Whats more, these different endogenous and exogenous factors may also influence the neutral genetic structure and the diversity of the metapopulations (Pannell and Charlesworth, 2000; Slatkin, 1985; Lynch, 1988; Lande, 1992).

Using the classical neutral theory of molecular evolution, Wright (1949) and Lynch (1988) have shown that for a selectively neutral quantitative character, dispersal between two identical habitat patches enhances genetic variance within the populations, while it reduces the variance among the populations. Therefore, in a metapopulation, the effect of dispersal on genetic diversity might depend on the spatial scale being used (Slatkin, 1985). Various other factors may also affect the genetic diversity of the metapopulations; they include mutations, local genetic drift, local selection, hitchhiking, population size and long distance dispersal (Smith and Haigh, 1974; Barton, 2000; Lande, 1992; Charlesworth et al., 1993; Pannell and Charlesworth, 2000; Bohrer et al., 2005). However, little is known about the influence of these factors on the local dynamics and geographical structure of a population of neutral genes. In order to tackle this issue, a deterministic model is used to describe the interactions among conspecific populations linked by migration (Levin and Paine, 1974; Holt, 1985; Gyllenberg et al., 1993). This model allows us to understand the effect that migration and local habitat quality have on the dynamics of neutral gene populations. Our work differs from the studies based on stochastic metapopulation models because they only deal with the interactions among local

populations.

This paper investigates how the divergent dynamics of local populations and their exchange through dispersal determine the neutral genetic diversity of metapopulations at a local and global scale. More precisely, we aim to describe the dynamics of the neutral genetic fractions inside a metapopulation. Clearly, the neutral fractions originating in favorable habitats should have a higher persistence probability when compared with those in less favorable habitats. Thus, they might eventually invade the whole metapopulation; and this invasion would result in a reduction of the diversity of the population in the unsuitable habitats relative to the suitable habitats. However, this shift from the unsuitable or less suitable habitats to the more suitable habitats should promote genetic mixing in the more suitable habitats and thus restore balance to the genetic diversity of the metapopulation. In the following paper, we focus on two specific metapopulations: a source–sink metapopulation and a spatially–structured metapopulation, both existing in favorable habitats. A source–sink metapopulation is composed, on the one hand, of finite local populations with negative growth rates, the *sink* populations. These sink populations go extinct without migration from the *source* populations which are, on the other hand, finite populations with a sufficiently high growth rate to persist without migration. Finally, a metapopulation in a favorable environment is exclusively composed of finite local source populations with conceivably different intrinsic growth rates and carrying capacities.

In this paper, we consider a metapopulation of genes or haploid individuals composed of local populations living in different habitat patches linked by dispersal. Our metapopulation model describes the population density $\mathbf{N}(t) = (N_1(t), \ldots, N_\omega(t))$, including the population density $N_k(t)$ in each habitat patch k at time t, over ω habitat patches. Our metapopulation model takes the form

$$\mathbf{N}'(t) = \mathbf{F}[\mathbf{N}(t)]\mathbf{N}(t) + \mathbf{D}\mathbf{N}(t), \ t > 0 \tag{1}$$

indicating that the density $\mathbf{N}(t)$ evolves in time under the combined effect of the dispersal ($\mathbf{D}$) and the growth ($\mathbf{F}$). The dispersal matrix $\mathbf{D}$ describes the migration rate between the ω habitat patches ($\sum_l d_{kl} = 0$ for all k). We either consider a symmetric dispersal, $d_{kl} = d_{lk}$ or a directional dispersal where the dispersal rates might be different, $d_{kl} \neq d_{lk}$. The growth (birth and death) is embodied in the growth matrix $\mathbf{F}[\mathbf{N}(t)] = \mathrm{diag}(f_k(N_k(t)))$ where the function f_k describes the per capita growth rate in each habitat patch $k \in \{1, \ldots, \omega\}$ where ω is the number of habitat patches.

These models have commonly been used to describe the metapopulation dynamics in finite habitat patches. Moreover, they have also been utilized to describe the change of allele frequencies in

a population located in two niches connected by dispersal (Edwards, 1963; Parsons, 1963; Moody, 1981). Recently, Garnier et al. (2012) and Roques et al. (2012) introduced a new mathematical tool to study the spatio–temporal dynamics of the neutral genetic diversity in a range–expanding population modeled through reaction–diffusion equations. Their framework, inspired from a simulation study of Hallatschek and Nelson (2008), had already been applied to a wide class of reaction–dispersion model (Bonnefon et al., 2014). However, little has been done in a fully heterogeneous environment and with a system of equations. Thus, our analysis extends the early work of Roques et al. (2012) to a new class of equations. Our paper demonstrates innovative mathematical modeling that combines a population dynamics model with a population genetics model, effective for describing the evolution of neutral fractions inside a metapopulation.

Our idea is to assume that the metapopulation is initially composed of several distinct neutral fractions located in different habitats. We provide a mathematical analysis of the temporal dynamics of these neutral fractions in each habitat composing the metapopulation. This analysis contrasts with more classic approaches that use dynamical systems which focus on the stability of equilibrium. Here we describe the inner functioning of inside dynamics system solutions which may converge to equilibrium. In this paper, we provide mathematical insights on the following theoretical issues:

- How do the densities of the various neutral fractions evolve inside an equilibrium generated by a dynamical system? Do any fractions survive? Which fractions generate the equilibrium?
- In a sourcesink metapopulation, is the diversity in the sink less than that of the source? Do the dispersal rates from the sources and from the sinks play a symmetric role in the maintenance of neutral genetic diversity?
- In metapopulations within favorable habitats, which characteristic of the habitat influences the fraction dynamics most? Does dispersal enhance or reduce genetic diversity within the habitats and between the habitats?

2 Materials and methods

2.1 Inside dynamics and neutral fractions.

To study the dynamics of the neutral genetic fractions inside a metapopulation, we use the mathematical framework of *inside dynamics* developed in (Roques et al., 2012; Bonnefon et al., 2014). The main idea is to assume that the metapopulation of genes (or individuals) $\mathbf{N} = (N_1, \ldots, N_\omega)$ is made

of several neutral fractions $\mathbf{n}_i = (n_{i1}, \dots, n_{i\omega})$ (see Fig. 1 for a schematic representation). This means that in each habitat k, the population N_k of the metapopulation $\mathbf{N}$ satisfying (1), is equal to the sum of the fractions which are present in habitat k:

$$N_k(t) = \sum_{i=1}^{I} n_{ik}(t) \quad \text{with} \quad n_{ik}(t) \geq 0, \quad \text{for any } k \in \{1, \dots, \omega\},$$

where I is the total number of neutral fractions inside the metapopulation.

Since the fractions are neutral, the genes (or the individuals) belonging to each fraction only differ by their initial location and their alleles (or their labels). In particular, they share the same dispersal ability as any genes in the metapopulation. Moreover, in each habitat the genes (or individuals) have the same growth rate as the population in this habitat. More precisely, in each habitat k the fraction $n_{ik}(t)$ grows according to the fitness of the population $f_k(N_k(t))$ in this habitat. In addition, the migration ability of each fraction $\mathbf{n}_i$ is described by the dispersal matrix $\mathbf{D}$ of the metapopulation. Each fraction density $\mathbf{n}_i(t) = (n_{i1}(t), \dots, n_{i\omega}(t))$ therefore satisfies the following linear coupled dynamical system:

$$\begin{cases} \mathbf{n}_i'(t) = \mathbf{F}[\mathbf{N}(t)]\mathbf{n}_i(t) + \mathbf{D}\mathbf{n}_i(t), \ t > 0 \\ \\ 0 \leq n_{ik}(0) \leq N_k(0) \quad \text{for all} \quad k \in \{1, \dots, \omega\} \end{cases} \tag{2}$$

where the fractions $\mathbf{n}_i$ initially satisfy

$$N_k(0) = \sum_{i=1}^{I} n_{ik}(0) \quad \text{with} \quad n_{ik}(0) \geq 0, \quad \text{for any } k \in \{1, \dots, \omega\}.$$

The equation (2) is linear with respect to $\mathbf{n}_i$. Therefore the sum $\sum_i \mathbf{n}_i$ of all the fractions $\mathbf{n}_i$ also solves the equation (2).

2.2 Measure of local and global genetic diversities.

Our decomposition method gives a mathematical framework to describe and to analyze the neutral genetic diversity dynamics of the metapopulation. More precisely, for each fraction $i \in \{1, \dots I\}$, we can both define its frequency p_{ik} in each habitat for any $k \in \{1, \dots, \omega\}$ and its mean frequency in the metapopulation $\bar{p}_i$:

$$p_{ik}(t) = \frac{n_{ik}(t)}{N_k(t)} \quad \text{for all } k \in \{1, \dots, \omega\} \quad \text{and} \quad \bar{p}_i(t) = \sum_{k=1}^{\omega} P_k(t) p_{ik}(t) \quad \text{with} \quad P_k(t) = \frac{N_k(t)}{\sum_{l=1}^{\omega} N_l(t)},$$

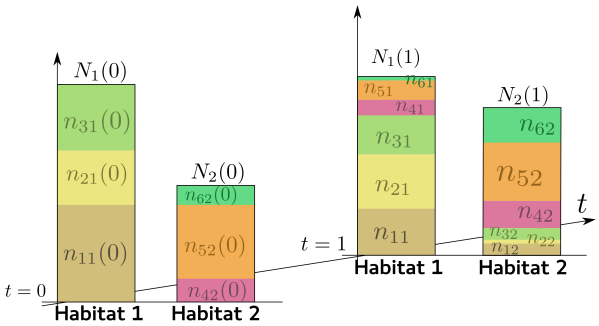


Figure 1: A schematic representation of a metapopulation $\mathbf{N}(t) = (N_1(t), N_2(t))$ described by (1) and composed of six fractions, evolving in two habitats (Habitat 1 and Habitat 2). Each neutral fraction is depicted with a different colour and with a thickness corresponding, in each habitat, to the density $\mathbf{n}_i = (n_{i1}, n_{i2})$ of the fraction.

where P_k corresponds to the proportion of the metapopulation living in habitat k.

At the metapopulation scale, we describe the neutral γ–diversity, corresponding to the total neutral genetic diversity in the metapopulation through the following index γ-$Div(t)$ defined by:

$$\gamma\text{-}Div(t) = \left(\sum_{i=1}^{I} (\bar{p}_i(t))^2 \right)^{-1} \quad \text{for any time} \quad t > 0. \tag{3}$$

This diversity index corresponds to the inverse of the Simpson index (Simpson, 1949) which describes the probability that two individuals sampled randomly in habitat k at time t belong to the same fraction i. It is also the inverse of the total homozygosity in the metapopulation. A high index of diversity indicates high diversity or a true evenness in the population: γ-Div is maximal when all the fractions frequencies are equal, i.e., when $\bar{p}_1 = \cdots = \bar{p}_I = 1/I$.

At the scale of habitat, we describe the neutral α–diversity corresponding to the mean neutral genetic diversity within habitats by the mean of local diversity indices γ-$Div_k(t)$ in habitat k weighted by the proportion P_k of the metapopulation living in habitat k.

$$\alpha\text{-}Div(t) = \left(\sum_{k=1}^{\omega} P_k(t) \big(\gamma\text{-}Div_k(t)\big)^{-1} \right)^{-1} \quad \text{with} \quad \gamma\text{-}Div_k(t) = \left(\sum_{i=1}^{I} (p_{ik}(t))^2 \right)^{-1} \quad \text{for } k \in \{1, \ldots, \omega\}. \tag{4}$$

This index is also the inverse of the mean homozygosity across habitats.

With these two diversity indices, we also quantify the β–diversity corresponding to the mean neutral genetic diversity among habitats by the following ratio of γ–diversity and α–diversity

$$\beta\text{-}Div(t) = \frac{\gamma\text{-}Div(t)}{\alpha\text{-}Div(t)}$$

2.3 Dispersal and demographic models.

In order to understand the interplay effect of local dynamics and dispersal, we assume that our environment is composed of only two habitat patches. The dispersal matrix $\mathbf{D}$ thus takes the following form:

$$\mathbf{D} = \begin{pmatrix} -\varepsilon_{12} & \varepsilon_{21} \\ \varepsilon_{12} & -\varepsilon_{21} \end{pmatrix},$$

where $\varepsilon_{kl} \geq 0$ corresponds to the migration rate from the habitat k to the habitat l when $k \neq l$. The diagonal coefficients are non positive because they describe the proportion of individuals that leave the habitats. In addition, we focus on two different scenarios: (1) favorable environment and (2) source–sink environment.

Scenario 1: Metapopulation in favorable heterogeneous environments. Under this scenario, the two habitats are favorable but may have different characteristics and qualities. In each habitat k, the per capita growth rate function f_k satisfies the following assumption:

$$\begin{aligned} &f_k(K_k) = 0, \;\; f_k > 0 \;\; \text{on } [0, K_k) \;\; \text{and } f_k < 0 \text{ on } (K_k, \infty) \\ &\text{and} \;\; f_k(u) \leq f_k(0) := r_k \text{ on } (0, \infty), \end{aligned} \tag{H1}$$

where $K_k > 0$ and r_k are respectively the carrying capacity and the intrinsic growth rate of habitat k. We only assume density–dependence but no Allee effects. A classical example is the logistic growth function:

$$f_k(u) = r_k\Big(1 - \frac{u}{K_k}\Big). \tag{5}$$

Using these assumptions, we know that any solution $\mathbf{N}(t) = (N_1(t), N_2(t))$ of the model (1) converges to the positive equilibrium $\mathbf{N}^* = (N_1^*, N_2^*)$ satisfying $\mathbf{0} = \mathbf{F}[\mathbf{N}^*]\mathbf{N}^* + \mathbf{D}\mathbf{N}^*$. We know that habitat quality and dispersal are crucial to this positive equilibrium (Holt, 1985).

Scenario 2: Metapopulation in source–sink environments. In this scenario, only the source habitat is favorable, whereas the sink habitat is detrimental in the sense that its per capita growth rate is always negative. To explain it more precisely, the source labelled 1 in the sequel, has a favorable growth function satisfying hypothesis (H1). On contrary, the sink labelled 2, has a negative growth function of the form $f_2(u) = -r_2$ with $r_2 > 0$. Therefore in absence of migration from the source, the population in the sink will become extinct at an exponential rate r_2. However, the migration from the

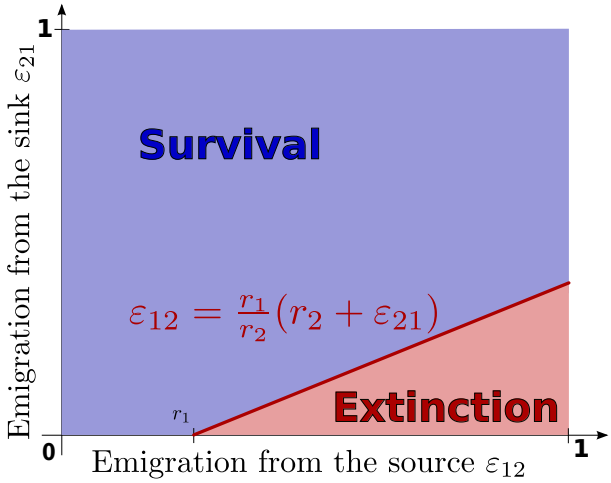


Figure 2: Schematic representation of the behavior of the population density $\mathbf{N}$ as a function of dispersal parameters ε_{12} and ε_{21}. Only a population with a large migration rate from the source and a sufficient migration rate from the sink can survive.

source ε_{12} might prevent local as well as global extinction if the additional hypothesis is reached.

$$\varepsilon_{12} \leq \frac{r_1}{r_2}(r_2 + \varepsilon_{21}). \tag{H2}$$

Under this hypothesis, any solution $\mathbf{N}(t)$ of the model (1) converges to the stable positive equilibrium $\mathbf{N}^* = (N_1^*, N_2^*)$, satisfying $\mathbf{0} = \mathbf{F}[\mathbf{N}^*]\mathbf{N}^* + \mathbf{D}\mathbf{N}^*$. We could not explicitly compute the equilibrium. Yet, the relative number of individuals in the sink compared to the number of individuals in the source attains equilibrium at:

$$P^* = \frac{N_2^*}{N_1^*} = \frac{\varepsilon_{12}}{r_2 + \varepsilon_{21}}.$$

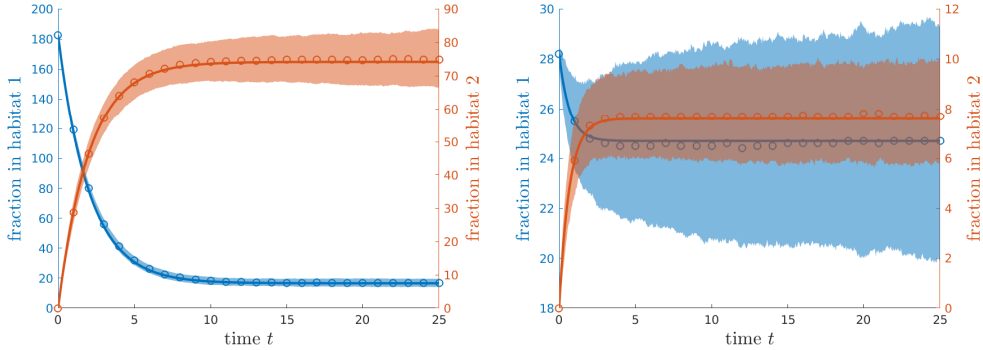
3 Results

Henceforth, we assume that the metapopulation is at equilibrium $\mathbf{N}(t) = \mathbf{N}^*$ and that is composed of I neutral fractions, whose densities $\mathbf{n}_i(t)$ satisfy (2). We study the dynamics of each neutral fraction $\mathbf{n}_i(t)$ and the associated diversity measures γ-*Div*, α-*Div* and β-*Div*.

3.1 Global richness of neutral genetic fractions enhances local richness.

For both scenarios, we consider an arbitrary fraction $\mathbf{n}_i$ satisfying (2), denoted as $\mathbf{n}$ in the sequel. The fraction density $\mathbf{n}$ therefore satisfies:

$$\mathbf{n}'(t) = \mathbf{F}[\mathbf{N}^*]\mathbf{n}(t) + \mathbf{D}\mathbf{n}(t), t > 0 \ . \tag{6}$$



(a) Favourable environment (b) Source–sink environment

Figure 3: Dynamics of a fraction inside a metapopulation composed of two habitats: (a) two favorable habitats with respectively $r_1 = 0.3$ and $K_1 = 100$ in habitat 1 and $r_2 = 0.3$ and $K_2 = 1000$ in habitat 2; (b) source–sink environment with $r_1 = 0.3$ and $K_1 = 100$ for the source and $r_2 = 0.3$ in the sink. The plain lines corresponds to solution of (2). The circles correspond to the empirical density of individuals of the fraction in the habitats, averaged over 10^3 replicates of the individual-based simulations ($N = 10$ individuals). Shading envelope is interval between the 0.05 and 0.95 quantiles of the distribution of the empirical density of fraction in the habitats obtained from the individual-based model.

At time $t = 0$, the fraction $\mathbf{n}(0) = (n_1(0), n_2(0))$ occupies a part $n_k(0)$ of the population N_k^* in each habitat k.

Using the properties of the dispersal matrix $\mathbf{D}$ and the characteristics of the equilibrium $\mathbf{N}^*$, we are able to describe the dynamics of the neutral fraction $\mathbf{n}$ in the metapopulation.

Theorem 1. *For any initial condition $\mathbf{n}(0)$, the density $\mathbf{n}$ of the fraction converges to a proportion p^* of the metapopulation $\mathbf{N}^*$, at an exponential rate $(\varepsilon_{21}N_2^*/N_1^* + \varepsilon_{12}N_1^*/N_2^*)$, that is, $\mathbf{n}(t) \to p^*\mathbf{N}^*$ as $t \to \infty$. The proportion p^* can be computed explicitly as follows:*

$$p^* = \frac{n_1(0)\varepsilon_{12}N_1^* + n_2(0)\varepsilon_{21}N_2^*}{\varepsilon_{12}(N_1^*)^2 + \varepsilon_{21}(N_2^*)^2}. \tag{7}$$

Theorem 1, proved in section 6, describes the evolution of the fractions inside the metapopulation composed of two habitats which are either favorable or source–sink (see Fig. 3). It shows that, as long as migration occurs away from an habitat patch k ($\varepsilon_{kl} > 0$, for some l), then any fraction initially represented in this habitat k with positive density $n_k(0) > 0$, persists in this habitat k and spreads to the other habitats (in Fig. 3 the red curve starts from 0 and eventually goes to positive values).

From an ecological perspective, our result shows that migration preserves global genetic richness, or, in other words, the number of genetic fractions with positive density in at least one habitat. Moreover, migration may enhance local genetic richness, with a direct correlation to the number of

positive density genetic fractions in a particular habitat. Indeed, the spread of persistent fractions over the metapopulation will enhance the richness of the habitat insofar as the initial richness is sustained.

The formula (7) also demonstrates that the absence of migration between habitats might lead to the extinction of some neutral fractions, which as a consequence could decrease the global richness of the metapopulation. In particular, if a neutral fraction is initially present in only one habitat with no migration from this habitat ($\varepsilon_{kl} = 0$ for any l) then, the fraction will become extinct ($\mathbf{n}(t) \to 0$ as $t \to \infty$). For instance, in the classic sourcesink model, if migration from the sink does not occur, the fractions initially present in the sink will vanish; the remaining metapopulation will be composed of the fractions initially located in the source. In other words, the sink does not contribute to the diversity of the metapopulation.

The formula (7) also provides precise information about the effect of local demographic dynamics as well as the dispersal on the neutral genetic diversity. First, the formula shows that the asymptotic proportion p^* of a neutral fraction does not coincide with its initial proportion in the metapopulation $p_0 = (n_1(0)+n_2(0))/(N_1^*+N_2^*)$. Indeed, the initial global proportion of a neutral fraction is preserved only if the fluxes between the habitats are identical; that is $\varepsilon_{12}N_1^* = \varepsilon_{21}N_2^*$. In any other case, the asymptotic proportion of the neutral fraction differs from its initial proportion and thus the local dynamics as well as dispersal play a crucial role in the dynamics of neutral genetic diversity. In particular, if we assume that the sizes of the populations in each habitat are identical, that is $N_1^* = N_2^* = N > 0$, the asymptotic proportion is given by:

$$p^* = \frac{p_1(0)\varepsilon_{12} + p_2(0)\varepsilon_{21}}{\varepsilon_{12} + \varepsilon_{21}}, \quad \text{with} \quad p_1(0) = \frac{n_1(0)}{N} \quad \text{and} \quad p_2(0) = \frac{n_2(0)}{N}$$

where $p_k(0)$ corresponds to the initial proportion of the fraction in habitat k. So in this case, the asymptotic proportion p^* only depends on the dispersal between the habitats. The local dynamics of the population does not play any role if the population sizes are identical. However, if the population sizes are different, due to the migration rate and the habitat characteristics, this will have a crucial impact on the asymptotic proportion.

In the source–sink metapopulation scenario, we can provide an analytical expression of the asymptotic proportion of a neutral fraction with initial density $\mathbf{n}(0) = (n_1(0), n_2(0))$:

$$p^* = \frac{p_1(0) + p_2(0)\dfrac{\varepsilon_{12}\varepsilon_{21}}{(r_2+\varepsilon_{21})^2}}{1 + \dfrac{\varepsilon_{12}\varepsilon_{21}}{(r_2+\varepsilon_{21})^2}}$$

where $p_i(0) = n_i(0)/N_i^*$ is the initial proportion of the neutral fraction $\mathbf{n}$ in the habitat i. We see from this expression that the asymptotic proportion of the neutral fraction does not depend on the habitat quality of the source r_1 neither on its carrying capacity K_1. It only depends on the migration rates ε_{kl} and the quality of the sink r_2.

The formula (7) also provides precise information regarding the effect of both dispersal and local dynamics on diversity. In the following sections, we derive precise quantitative effect of the migration rates ε_{kl} and the intrinsic growth rates r_k on the asymptotic local and global diversity indices, γ-Div, α-Div and β-Div. Our result shows that since the asymptotic proportions of the fraction are the same over all the habitats, the asymptotic α and γ–diversity are identical, resulting in the β–diversity index being equal to 1 asymptotically in any situation. In addition, the convergence rate provided by our result gives the temporal dynamics of these diversity indices. Moreover, we show that the differentiation among habitats decreases at an exponential rate $(\varepsilon_{21}N_2^*/N_1^* + \varepsilon_{12}N_1^*/N_2^*)$ which itself depends on the migration rates as well as the ratio of effective population sizes N_2^*/N_1^*. When the migration rates are identical, $\varepsilon_{12} = \varepsilon_{21} = \varepsilon$, and the effective population sizes are identical $N_1^* = N_2^*$, we show that the differentiation among habitats decreases toward 0 at a rate 2ε. Lynch (1988) has already observed in this situation a decrease of variance among habitats.

Finally, our result provides a verified approximation of an individual–based model in which individuals live in two separate density dependent habitats where they reproduce, die and move between habitats at an exponential rate. (see appendix B for more details on the individual–based model). If we label individuals with neutral markers in this stochastic model, and track their dynamics, we obtain on average the curves with circle markers in Fig. 3. Our deterministic model provides a good approximation of the dynamics of those fractions. Moreover, when the metapopulation is at equilibrium, we are able to analytically describe the entire dynamics of the neutral fractions $\mathbf{n}(t)$ (see proof of Theorem 1).

3.2 Genetic diversity and habitat quality of the environment.

Our first result gives some insight into the richness of the neutral genetic diversity of both source–sink metapopulations and spatially–structured metapopulations within favorable habitats. Now, we aim to understand the effect of habitat quality on the equilibrium of diversity through α–diversity at local habitat scale, and through γ–diversity at global scale. Our first result already shows that the diversity indices at both local and global scales are identical when taken asymptotically in time. Thus, if the initial metapopulation is composed of I fractions with density $\mathbf{n}_i$, the diversity indices γ-$Div(t)$ and

α-$Div(t)$ defined respectively by (3) and (4), will converge to the following asymptotic diversity index Div:

$$Div = \lim_{t\to\infty} \gamma\text{-}Div(t) = \lim_{t\to\infty} \alpha\text{-}Div(t) = \left(\sum_{i=1}^{I} (p_i^*)^2\right)^{-1} \tag{8}$$

where p_i^* is the asymptotic proportion given by Theorem 1 associated to the fraction i with initial density $\mathbf{n}_i(0)$. Since the asymptotic proportions p_i^* depend on the habitat quality, we are able to investigate the effect of the habitat quality r_i on the asymptotic neutral genetic diversity Div.

Scenario 1: habitat quality may promote neutral genetic diversity.

We first investigate a metapopulation over an heterogeneous environment composed of two favorable habitats which may have different qualities r_i and different carrying capacities K_i. We also assume that in both habitats, the per capita growth rate f_i decreases with respect to the population density in each habitat:

$$f_i' < 0 \quad \text{on} \quad [0, \infty). \tag{H3}$$

To investigate the effect of habitat quality r_i on diversity Div, we assume that initially, the metapopulation is composed of only two neutral fractions $\mathbf{n}_1$ and $\mathbf{n}_2$. Since the metapopulation is at equilibrium $\mathbf{N}^*$, we have, for any time t, $\mathbf{n}_1(t) + \mathbf{n}_2(t) = \mathbf{N}^*$. As a consequence, the asymptotic diversity only depends on the asymptotic proportion p^* of one of the two fractions for instance $\mathbf{n}_1$ which is given by:

$$p^* = \frac{p_1(0)\varepsilon_{12} + p_2(0)\varepsilon_{21}(P^*)^2}{\varepsilon_{12} + \varepsilon_{21}(P^*)^2}, \quad \text{with} \quad p_1(0) = \frac{n_{11}(0)}{N_1^*},\ p_2(0) = \frac{n_{12}(0)}{N_2^*} \quad \text{and } P^* = \frac{N_2^*}{N_1^*}.$$

Using the qualitative properties of the asymptotic proportion stated in Appendix A.1, we provide the following result of the effect of the quality of one habitat on diversity Div. Since the habitats are both favorable, we look at the effect of habitat quality r_2 of the second habitat, without loss of generality.

Proposition 2 (Growth rate may promote diversity)**.** *Let us consider a fraction* $\mathbf{n}$ *solving equation* (2) *starting from* $\mathbf{n}(0) = (n_1(0), n_2(0))$*, inside a spatially-structured metapopulation at equilibrium* $\mathbf{N}^*$ *satisfying* (1) *with hypothesis* (H1)-(H3)*. Then the asymptotic diversity Div defined by* (8) *satisfies the following properties with respect to the quality of the habitat* 2*. Let* $p_k(0)$ *be the initial proportion of the fraction* $\mathbf{n}$ *inside each habitat* k*,* $p_k(0) = n_k(0)/N_k^*$*. Then we have:*

(a) Div decreases with respect to r_2*, if* $(\varepsilon_{12} - \varepsilon_{22})(\varepsilon_{21}K_2 - \varepsilon_{12}K_1)(p_1(0) - p_2(0)) > 0$*;*

(b) Div increases with respect to r_2*, if* $(\varepsilon_{21}K_2 - \varepsilon_{12}K_1)(\sqrt{\varepsilon_{21}}K_2 - \sqrt{\varepsilon_{12}}K_1)(p_1(0) - p_2(0)) < 0$*;*

(c) otherwise, Div reaches its maximum on $\bar{r}_2$ such that $p^*(\bar{r}_2) = 1/2$ and Div increases on $(0, \bar{r}_2)$ and decreases on $[\bar{r}_2, +\infty)$.

Figure 4(a) gives a schematic representation of Proposition 2 with respect to the two parameters ratio K_2/K_1 and $\varepsilon_{12}/\varepsilon_{21}$. The effect of habitat quality crucially depends on migration rate, as well as the carrying capacity of the environment. The carrying capacity will play a particular role in shaping neutral genetic diversity as we will see in the sequel. In addition, we see that habitat quality might have three different impacts on diversity: (1) a detrimental effect, (2) a beneficial effect or (3) a mixed effect.

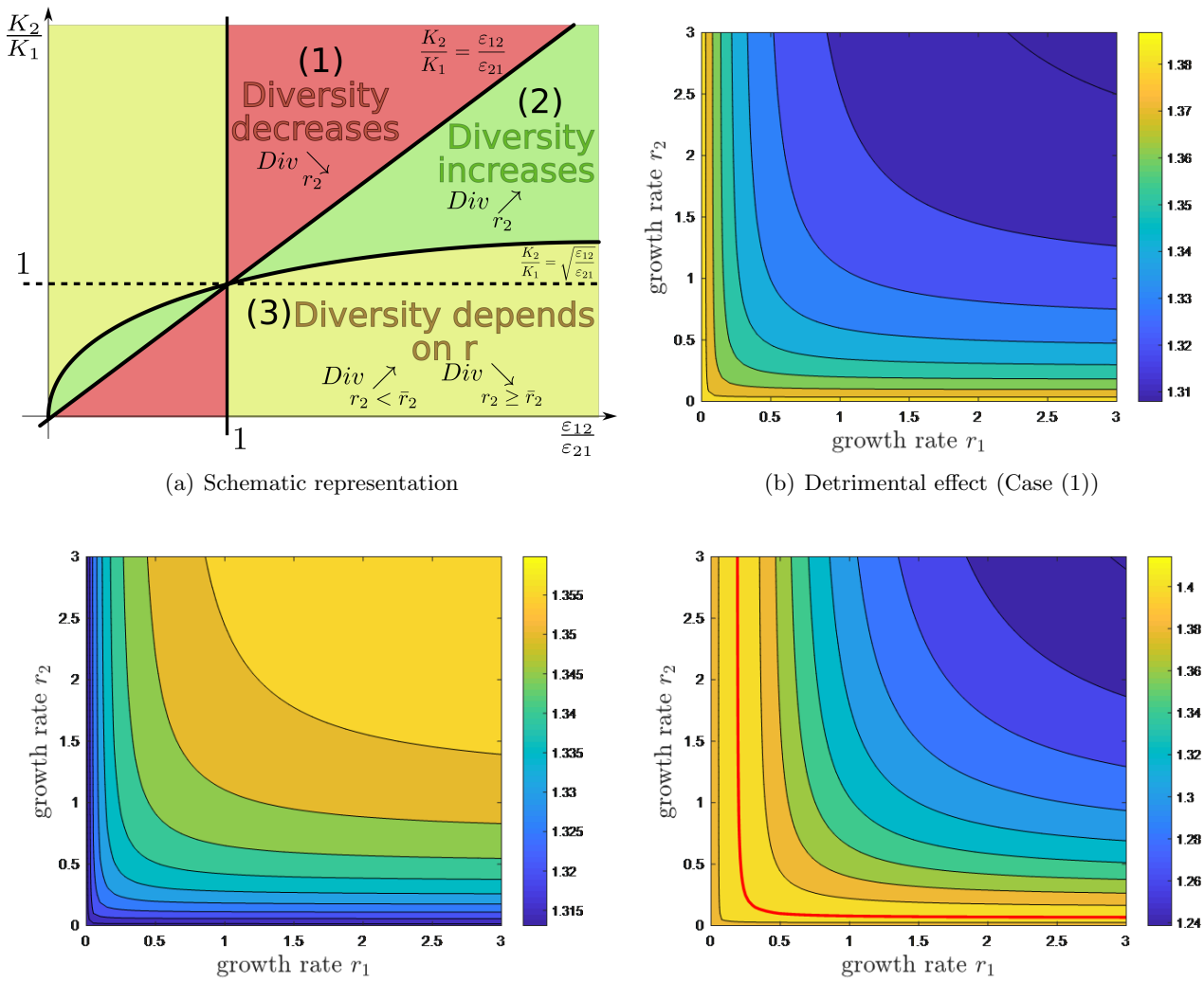
Growth rate r_2 always has a detrimental effect on diversity when migration from the largest habitat is smaller than migration from the smallest habitat (if $K_2 > K_1$ it corresponds to $\varepsilon_{12}/\varepsilon_{21} > 1$ and $\varepsilon_{21}K_2 > \varepsilon_{12}K_1$, see Fig.. 4(a) case (1) and Fig. 4(b)). In this scenario, the effect does not depend on the relative suitability of the habitats.

Conversely, growth rate r_2 always has a beneficial effect when the flux of individuals from the largest habitat is less than the one from the smallest; and the flux from the smallest is not too large. In particular if $K_2 > K_1$, the beneficial effect of the growth rate r_2 occurs when $\varepsilon_{21}K_2 > \varepsilon_{12}K_1$ and $\sqrt{\varepsilon_{21}}K_2 > \sqrt{\varepsilon_{12}}K_1$ (see Fig. 4(a) case (2) and Fig. 4(c)). As in the previous case, the effect of the quality of habitat 2 does not depend on the quality of habitat 1.

However, in many situations, the effect of habitat quality on diversity truly depends on the relative suitability of the habitats (see case (3) in Fig. 4(d)). In this particular situation, diversity increases as soon as one habitat is significantly less favorable than the other one or when they both have a low suitability in the sense that $r_2 < \bar{r}_2$. Conversely, when both habitats are of sufficient quality, the growth rates have a detrimental effect on diversity (see Fig. 4(d)).

Scenario 2: Detrimental sinks erode diversity.

We now turn to the source–sink model. In this case we aim to understand how the presence of a source might help to preserve the diversity of the sink. As above, we assume that the metapopulation is at equilibrium $\mathbf{N}^*$. We also assume that the metapopulation is initially composed of one fraction in the source $\mathbf{n}_1$, $\mathbf{n}_1(0) = (N_1^*, 0)$, and I different fractions in the sink, $\mathbf{n}_i$, initially equally distributed in the sink, $\mathbf{n}_i(0) = (0, N_2^*/I)$. Since the metapopulation is at equilibrium, we get that $\mathbf{n}_i(t) = (\mathbf{N}^* - \mathbf{n}_1(t))/I$ for any time t_0. Thus, the asymptotic diversity index Div only depends on the asymptotic proportion



(a) Schematic representation

(b) Detrimental effect (Case (1))

(c) Beneficial effect (Case (2))

(d) Mixed effect (Case (3))

Figure 4: Asymptotic diversity Div with respect to growth rates (r_1,r_2) in the case of scenario 1. (a) Summary of three possible cases of Proposition 2 according to the ratio of carrying capacities K_2/K_1 and the ratio of migration rates $\varepsilon_{12}/\varepsilon_{21}$. Initially $p_1(0) = 1$ and $p_2(0) = 0$, the carrying capacities are fixed, $K_1 = 100$ and $K_2 = 200$ and the migration rate from habitat 1 is $\varepsilon_{12} = 0.4$. (b) Detrimental effect: $\varepsilon_{21} = 2/3\varepsilon_{12} \approx 0.233$; (c) Beneficial effect $\varepsilon_{21} = 3/7\varepsilon_{12} \approx 0.17$ (d) Mixed effect: $\varepsilon_{21} = 3/2\varepsilon_{12} = 0.6$. The red line in (d) corresponds to the threshold $r_2 = \bar{(r_2)}$.

of the fraction $\mathbf{n}_1$ given from Theorem 1 by:

$$p^* = \frac{1}{1 + \frac{\varepsilon_{12}\varepsilon_{21}}{(r_2 + \varepsilon_{21})^2}}.$$

From this explicit formula, we can deduce the following properties of the asymptotic diversity Div.

Proposition 3 (A detrimental sink erodes diversity)**.** *Let us consider a source–sink metapopulation composed of one fraction* $\mathbf{n}_1$ *initially in the source* ($\mathbf{n}_1(0) = (N_1^*, 0)$) *and* $I \geq 1$ *fractions,* $\mathbf{n}_i$*, initially equally distributed in the sink,* $\mathbf{n}_i(0) = (0, N_2^*/I)$*. Then the asymptotic diversity* Div *satisfies the following properties:*

(a) Div decreases with respect to r_2*, if* $(\varepsilon_{12} - I\varepsilon_{21}) < 0$*;*

(b) otherwise, Div reaches its maximum on $\bar{r}_2 = \sqrt{\varepsilon_{12}\varepsilon_{21}}/\sqrt{I} - \varepsilon_{21}$ *and Div increases on* $(0, \bar{r}_2)$ *and decreases on* $[\bar{r}_2, +\infty)$*.*

Our result shows that in general, the deterioration of the sink tends to erode the genetic diversity of the metapopulation. This is especially true if the migration from the source is smaller than the migration from the sink, a decrease in the growth rate of the sink will always result in the erosion of diversity (see Fig. 5). Thus, it is more difficult to restore the diversity of a sink when the migration from the source is insufficient when compared to the migration from the sink. However, when the migration from the source is sufficient when compared to the migration from the sink, the diversity from the sink can be preserved if the quality of the sink is not too deteriorated (see Fig. 5). We note that when the quality of the sink initially starts to deteriorate, the diversity may even increase because the metapopulation size increases (see Holt (1985)). When the sink deteriorates, the erosion of diversity eventually occurs.

Moreover, let us stress that the genetic diversity of a sourcesink metapopulation does not depend on the habitat quality of the source r_1 neither on its carrying capacity K_1.

3.3 Migration may promote neutral genetic diversity at local and global scale.

Next we focus on the effect of migration on diversity, both for a spatially–structured metapopulation and a source–sink metapopulation.

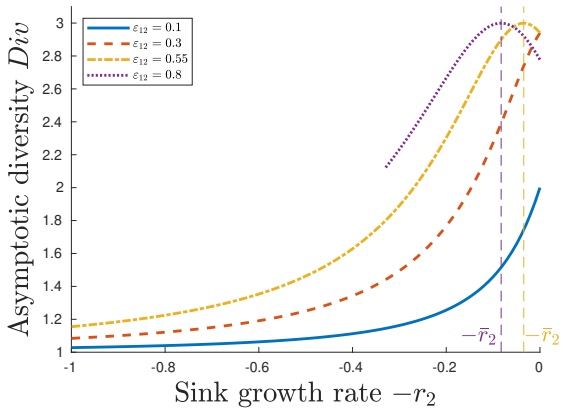


Figure 5: Behavior of the asymptotic diversity Div with respect to the growth rate $-r_2$ of the sink, for different values of the migration rate from the source ε_{12}: $\varepsilon_{12} = 0.1$ (blue plain curve), $\varepsilon_{12} = 0.3$ (red dashed curve), $\varepsilon_{12} = 0.55$ (orange dot-dashed curve) and $\varepsilon_{12} = 0.8$ (purple dotted curve). The migration from the sink is constant $\varepsilon_{21} = 0.2$ and the source has characteristics: $r_1 = 0.5$ $K_1 = 2000$. The maximum of diversity is reached for $-\bar{r}_2$.

Scenario 1: migration promotes genetic diversity.

We first investigate the metapopulation within two favorable habitats with different carrying capacities. The two habitats are connected through symmetric migration $\varepsilon_{12} = \varepsilon_{21} = \varepsilon > 0$. As in the previous section, we look at two neutral fractions but now, the first fraction $\mathbf{n}_1$ is initially in habitat 1 ($\mathbf{n}_1(0) = (N_1^*, 0)$) and the second fraction nb_2 is initially in habitat 2, ($\mathbf{n}_2(0) = (0, N_2^*)$). Since the metapopulation is at equilibrium, the asymptotic diversity Div defined by (8) only depends on the asymptotic proportion p^* of one of the two fractions defined by (7) .

We can deduce from qualitative properties of $p*$ (see Appendix A.2) the following properties on the diversity.

Proposition 4 (Migration increases diversity)**.** *Let us consider a metapopulation composed initially of two fractions:* $\mathbf{n}_1$ *initially in habitat* 1, $\mathbf{n}_1(0) = (N_1^*, 0)$, *and* $\mathbf{n}_2$ *initially in habitat* 2, $\mathbf{n}_2(0) = (0, N_2^*)$. *Then the asymptotic diversity* Div *increases with the migration rates* ε.

This result shows that migration promotes genetic diversity in metapopulations within globally favorable habitats. It emphasizes the fact that migration homogenizes the asymptotic proportion of the different fractions (see Appendix A.1).

Moreover, we can observe from Figure 6 that diversity is always higher when the ratio K_1/K_2 is close to 1. In other words, the closer the two habitat carrying capacities are, the higher the diversity is. However, since the per capita growth rates r_i are different in different habitats, the behavior of diversity is not completely symmetric with respect to K_1/K_2. We see that if K_2 is larger than K_1 ,

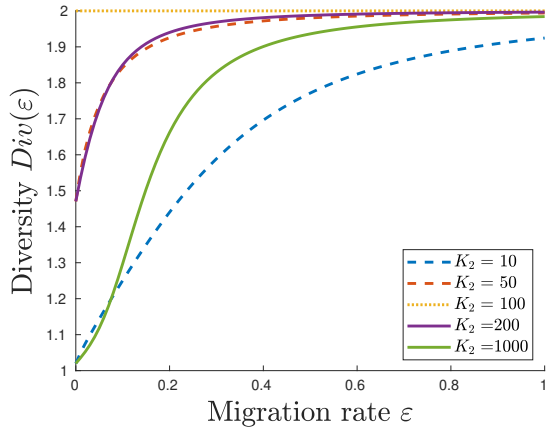


Figure 6: Behavior of the asymptotic diversity Div with respect of the migration rate ε for different values of the carrying capacity K_2 of habitat 2. The habitat 1 has higher intrinsic growth rate than habitat 2 ($r_1 = 0.3 > r_2 = 0.1$) and the carrying capacity of habitat 1 is stated to $K_1 = 100$.

then diversity is globally higher than if K_2 is smaller than K_1. So, if the first habitat is much better than the second habitat in the sense that $r_1 > r_2$ and $K_1 > K_2$ then diversity is promoted when habitats have similar quality, in the sense that $r_1 > r_2$ but $K_1 < K_2$. The tradeoff between the per capita growth rates and the carrying capacities promote diversity.

Scenario 2: High migration from the source acts as a "diversity rescue".

We now focus on the ability of migration to preserve genetic diversity from the sink for a sourcesink metapopulation. We assume that the metapopulation is initially composed of one fraction in the source $\mathbf{n}_1$, $\mathbf{n}_1(0) = (N_1^*, 0)$, and I fractions in the sink, $\mathbf{n}_i$, initially equally distributed in the sink, $\mathbf{n}_i(0) = (0, N_2^*/I)$. We already know that the asymptotic diversity is given by:

$$p^* = \frac{1}{1 + \dfrac{\varepsilon_{12}\varepsilon_{21}}{(r_2 + \varepsilon_{21})^2}}.$$

From this explicit formula, we can deduce some qualitative properties about the effect of migration on asymptotic diversity Div defined by (8).

Proposition 5 (Diversity rescue only up to a certain point)**.** *Let us consider a source–sink metapopulation at equilibrium, composed initially of one fraction* $\mathbf{n}_1$ *initially in the source,* $\mathbf{n}_1(0) = (N_1^*, 0)$ *and* $I \geq 1$ *fractions,* $\mathbf{n}_i$*, initially equally distributed in the sink,* $\mathbf{n}_i(0) = (0, N_2^*/I)$*. Then the asymptotic diversity satisfies the following properties:*

Migration from the source ε_{12}**:** *Div reaches a maximum when* $\varepsilon_{12} = I(r_2 + \varepsilon_{21})^2/\varepsilon_{21}$ *and*

- *Div increases with* ε_{12} *if* $\varepsilon_{12} < I(r_2+\varepsilon_{21})^2/\varepsilon_{21}$*;*
- *Div decreases with* ε_{12} *if* $\varepsilon_{12} \geq I(r_2+\varepsilon_{21})^2/\varepsilon_{21}$*;*

Migration from the sink ε_{21}**:** *its effect depends on the quality of the sink*

- *Div decreases with* ε_{21} *if* $(r_2-\varepsilon_{21})\big(\varepsilon_{12}-I(r_2+\varepsilon_{21})^2/\varepsilon_{21}\big) > 0$*;*
- *Div increases with* ε_{21} *if* $(r_2-\varepsilon_{21})\big(\varepsilon_{12}-I(r_2+\varepsilon_{21})^2/\varepsilon_{21}\big) < 0$*;*

Our results show that neutral diversity crucially depends on migration from, as well as the quality, of the sink whereas it does not depend on the quality of the source. If the migration from the sink is low ($\varepsilon_{21} < r_2$), then the migration from the source or the sink has the same effect. When migration from the source is small, then migration tends to increase diversity (see case (1) Fig. 7(a)) while if the migration from the source is large, they both erode diversity (see case (2) Fig. 7(a)). Conversely, when the migration from the sink is large ($\varepsilon_{21} > r_2$), there is a trade–off between the migration from the sink and from the source (see case (3) and (4) in Fig. 7(a)).

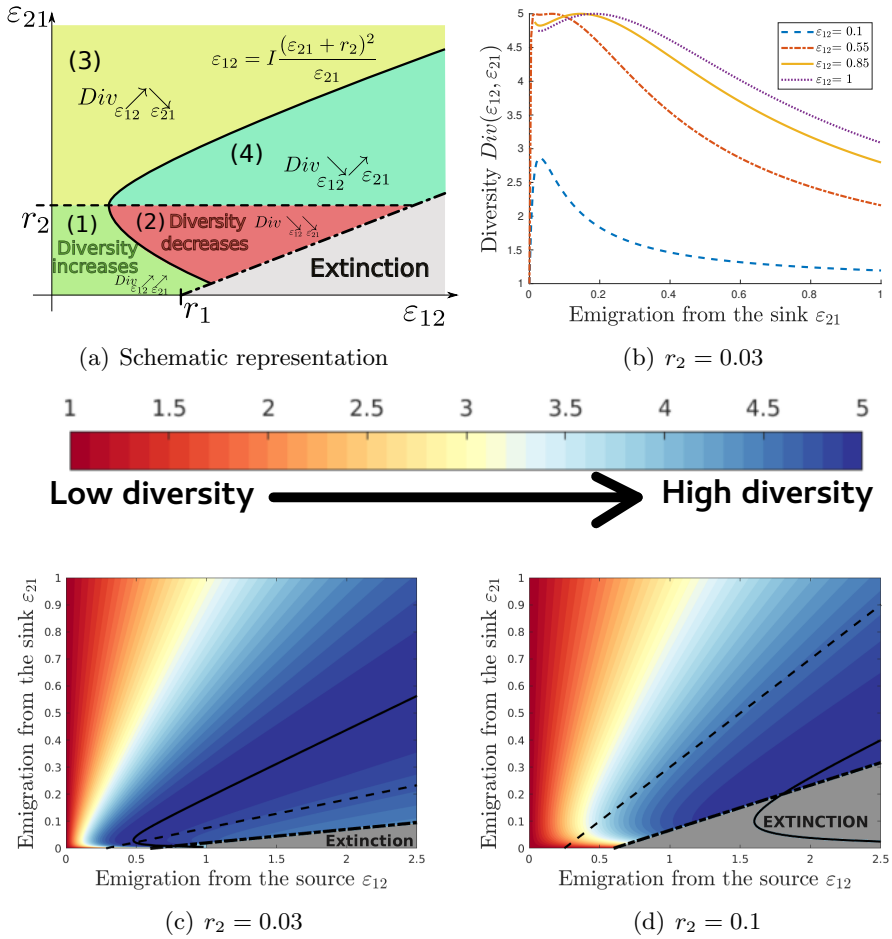
However, we can observe that diversity is higher for large migration from the source and intermediate migration from the sink. More precisely, we analytically show that maximum diversity is reached when

$$\varepsilon_{12} = I\frac{(\varepsilon_{21}+r_2)^2}{\varepsilon_{21}}.$$

This relation describes the balance between emigration from the source and the sink needed to preserve a large amount of diversity. We see that this formula also depends on the quality of the sink r_2. In particular, we deduce that emigration should be higher if the quality of the sink deteriorates (if r_2 increases). That means that you need massive emigration from the source to preserve the diversity of a poor sink. Moreover, the optimal curve reaches a minimum equal to $4Ir_2$ as $\varepsilon_{21} = r_2$. Thus, if $2Ir_2 > r_1$, maximal diversity cannot be reached. So we only keep a number of fractions from the sink which should be less or equal to $I_{max} = \lceil r_1/(2r_2)\rceil$ where $\lceil\cdot\rceil$ corresponds to the ceil function.

We also wonder whether the parameters that maximize genetic diversity also maximize the size of the metapopulation. We know from the work of Holt (1985), that dispersal might enhance the metapopulation size $N_T = N_1 + N_2$. More precisely, the metapopulation size is greater than K_1 if

$$\varepsilon_{12} \leq \frac{(r_1-r_2)}{r_2}(\varepsilon_{21}+r_2).$$



(a) Schematic representation (b) $r_2 = 0.03$

(c) $r_2 = 0.03$ (d) $r_2 = 0.1$

Figure 7: Behavior of the asymptotic diversity Div as a function of dispersal parameters ε_{12} and ε_{21} for various value of the intrinsic growth rate of the second habitat r_2: (b)-(c) $r_2 = 0.03$ and (d) $r_2 = 0.1$. In any simulations, the metapopulation is initially composed of 1 fraction in the source ($r_1 = 0.6$) and $I = 4$ fractions in the sink.The black plain line corresponds to the maximum of diversity. The black dashed line corresponds to the parameters value where the metapopulation size $N_1^* + N_2^*$ is maximal and the black dash-dotted line represents the critical migration rate from the source as the function of the migration from the sink so that extinction occurs (see hypothesis (H2) and Fig. 2) .

and reaches a maximum value when

$$\varepsilon_{12} = \frac{1}{2}\frac{(r_1 - r_2)}{r_2}(\varepsilon_{21} + r_2).$$

(see (Holt, 1985, section 2.2) for the details of computations). From our results, we show that this region mainly corresponds to a region where diversity is high (see black-dashed line on Figure 7(c)-(d)). Thus, dispersal parameters that enhance metapopulation size also promote neutral genetic diversity in the metapopulation. However, they do not coincide. The major difference is that metapopulation size depends on the quality of the source whereas genetic diversity does not.

4 From isolated habitats to connected habitats: effect on diversity.

In this section we aim to understand the effect of connecting two isolated populations with regards to their genetic diversity. More precisely, we assume that the metapopulation is composed of two populations N_1 and N_2 which are initially isolated. At time $t > 0$, we connect these populations and they start exchanging individuals. Their dynamics $N = (N_1, N_2)$ are described by equation (1). In this scenario, the metapopulation is no longer at equilibrium. In addition, we assume that the two populations are genetically different because they were isolated. We therefore assume that the metapopulation is composed of $I = 6$ neutral genetic fractions with densities $\mathbf{n}_i$ (see Fig. 8 and Fig. 10). The dynamics of these fractions are described by equation (2). Our aim is to decipher whether the connection of the two populations will decrease or increase the diversity at a local and global scale over time. To do so, we will look at the ratio between the initial α or γ–diversity and the α or γ–diversity at infinite time which are given respectively by equation and :

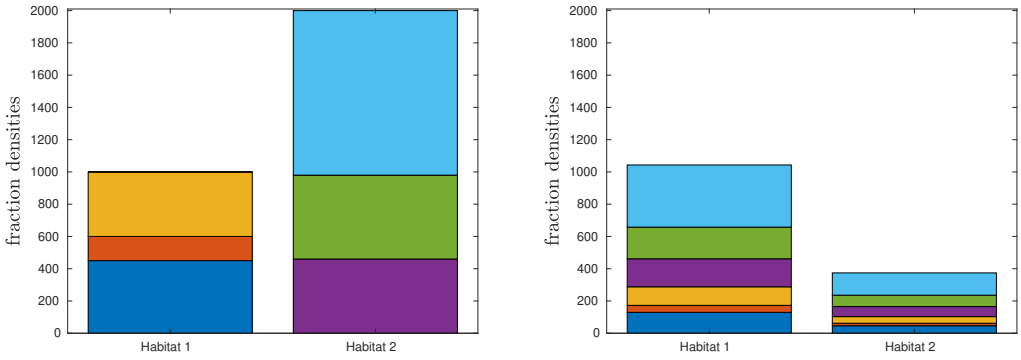
$$\frac{\gamma\text{-}Div(\infty)}{\gamma\text{-}Div(0)} \quad \text{and} \quad \frac{\alpha\text{-}Div(\infty)}{\alpha\text{-}Div(0)}. \tag{9}$$

If this ratio is larger than 1, the migration tends to promote diversity whereas if it is smaller than 1, the migration will tend to erode diversity.

Scenario 1: Migration promotes local genetic diversity. In the case of favorable habitats, we assume that initially, the populations are at carrying capacity, that is $N_1(0) = K_1$ and $N_2(0) = K_2$ and each population is composed of 3 different fractions (see Fig. 8). For the numerical computations, we describe the dynamics of each habitat using the logistic functions described by (5). In the sequel, we always assume that $r_1 > r_2$.

First, we can observe from Fig. 8 that migration strongly modifies the population size in each habitat (the population size in habitat 2 is divided by 5 over time). However, the fractions from habitat 2 remain higher in proportion than the fractions from habitat 1. Thus, even if habitat 2 is less favorable than habitat 1, these fractions contribute more to the diversity than the fractions from habitat 1 because the carrying capacity of habitat 2 is higher than the carrying capacity of habitat 1. This result enhances the importance of the carrying capacities on diversity.

More precisely, if we look at the ratio of α–diversity (see Fig. 9(b)), we see that local diversity does not change if carrying capacities are different (low or high ratio K_2/K_1). That means that local diversity at infinite time corresponds to the local diversity of the initial habitat with higher carrying



(a) Initial time

(b) Time $t = 20$

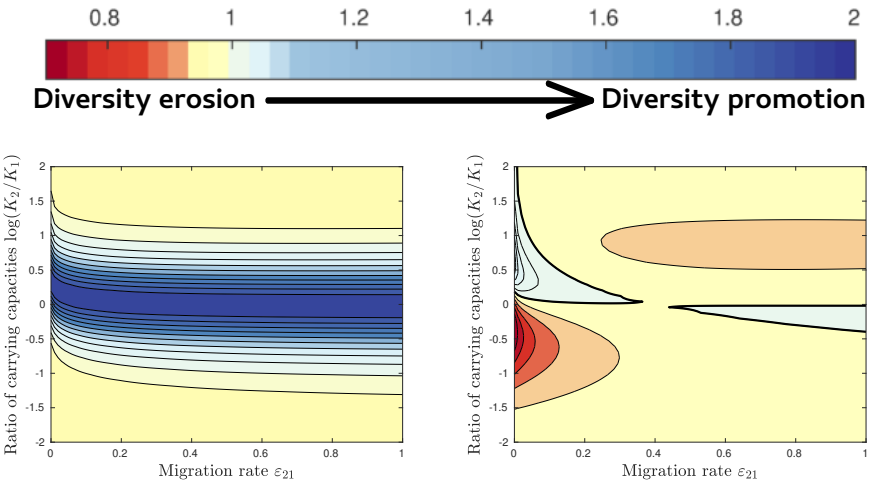
Figure 8: Evolution of $I = 6$ fractions in heterogeneous favorable environment: (a) 3 fractions (orange, red and blue) start in habitat 1 ($r_1 = 0.3$ and $K_1 = 1000$) and 3 fractions start (light blue, green and purple) in habitat 2 ($r_2 = 0.01$ and $K_2 = 2000$). The habitats are connected through asymmetric migration $\varepsilon_{12} = 0.1$ and $\varepsilon_{21} = 0.3$. (b) distribution of the fractions in the two habitats at time $t = 20$.

capacity. However, when the carrying capacities are similar (the ratio $K_2/K_1 \approx 1$), local diversity is always enhanced. That means that the fractions mix well. This pattern does not really depend on the migration rate. So, local diversity change mainly depends on the difference between carrying capacities.

However, global diversity is strongly modified by both migration and the differences between carrying capacities. (see Fig. 9(b)). Indeed, when migration is large, global diversity does not significantly change with respect to either carrying capacity or migration. However, when one of the migrations is low, it promotes diversity when the poorest habitat has a higher carrying capacity whereas it erodes diversity when the poorest habitat has a lower carrying capacity.

Scenario 2: Migration from the source helps to restore genetic diversity. In the source–sink model, we aim to understand if migration might help to rescue diversity from populations that have just become sink. This situation might occur due to climate change (see Jenouvrier et al. (2017) for the example of Emperor Penguins). To do so, we assume that the source has reached its carrying capacity K_1 and it is composed of only 1 neutral genetic fraction. Meanwhile, the sink is initially composed of 5 neutral genetic fractions with various densities.

As already mentioned in the previous section, migration helps to conserve all of the fractions in the metapopulation (see Fig. 10). Whats more, the diversity in each habitat is enhanced, especially that of the source which has gained all the fractions from the sink. More generally, the mean local diversity is always enhanced when we connect a source and a sink (see Fig. 11). We can observe that the



(a) Ratio of $\alpha-$diversity (b) Ratio of $\gamma-$diversity

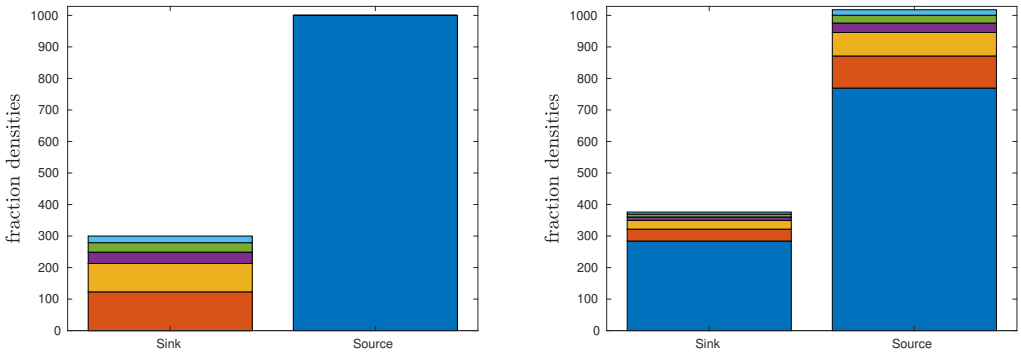
Figure 9: Effect of migration rate ε_{21} and the ratio of carrying capacities K_2/K_1 on the ratio of γ and $\alpha-$diversities. The carrying capacity of habitat 1 is fixed to $K_1 = 100$ while the carrying capacity K_2 varies from 1 to 10^4. The per capita growth rates are fixed to $r_1 = 0.3$ and $r_2 = 0.1$ and the migration rate from habitat 1 to 2 is $\varepsilon_{12} = 0.4$. The black line corresponds to the level set when the ratio equals to 1.

diversity index is doubled when migration is low, while it generally increases by 1/5 when it is large. At a global scale, diversity is mainly enhanced, except when migration from the sink is larger than migration from the source. Thus, if individuals flee from the sink and remain in the source habitat, then the diversity from the sink cannot be maintained and we observe an erosion of γ–diversity. This is mainly due to a strong competition between fractions in the source.

5 Conclusion and discussion.

We investigate the intertwined effect of dispersal and habitat quality on the neutral genetic diversity of a metapopulation, using a classical deterministic mathematical model, recognized as a robust descriptor of population dynamics over heterogeneous and discrete habitat patches (Holt, 1985). Our approach allows us to describe the dynamics of each neutral genetic fraction of which the metapopulation is composed, either at equilibrium or evolving in time. In particular, we have captured the transient dynamics of the neutral genetic diversity as well as its equilibrium. Our analytic characterization of the proportion of each neutral fraction at equilibrium provides us quantitative insights on the effect of dispersal and habitat quality on the diversity of metapopulation at local and global scale. Moreover, we have shown that our analytical results provide good approximations of the dynamics of individual–based models.

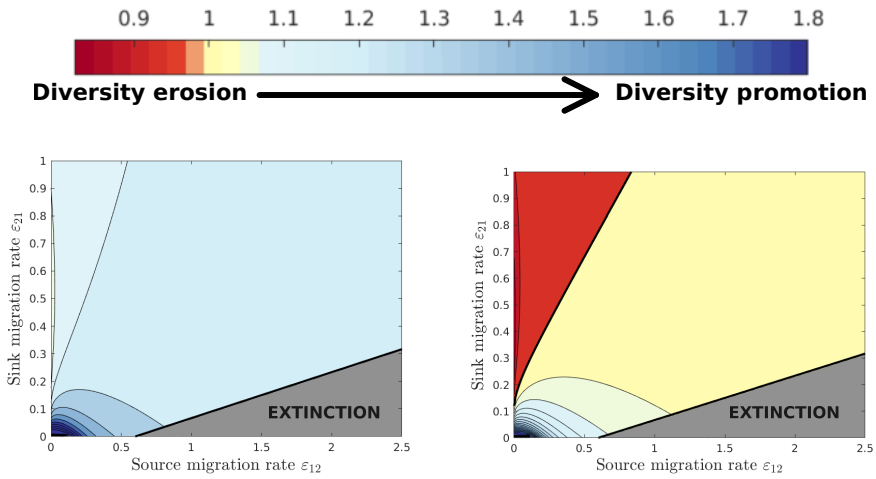
We have first shown that the conservation of the neutral genetic fractions in a metapopulation



(a) Initial time

(b) time $t = 20$

Figure 10: Evolution of $I = 6$ fractions in source–sink metapopulation: (a) 5 fractions (light blue, green, purple, orange and red) start in the sink ($r_2 = 0.03$) and 1 fraction starts in the source ($r_1 = 0.6$ and $K_1 = 1000$). The habitats are connected through asymmetric migration $\varepsilon_{12} = 0.1$ and $\varepsilon_{21} = 0.3$. (b) distribution of the fractions in the source and the sink at time $t = 20$.



(a) Ratio of $\alpha-$diversity

(b) Ratio of $\gamma-$diversity

Figure 11: Effect of migration on the ratio of γ and $\alpha-$diversities. The carrying capacity of habitat 1 is fixed to $K_1 = 1000$ and the sink starts with a population size $N_{02} = 300$. The per capita growth rates are fixed to $r_1 = 0.6$ for the source and $r_2 = -0.1$ for the sink. The black line corresponds to the level set when the ratio equals to 1.

is mainly due to the connections between habitat patches through dispersal. In any fully connected environment, all the fractions of the metapopulation are preserved in their initial habitat, even though the proportions may change. Thus the global richness of the metapopulation, corresponding to its number of living fractions, is preserved thanks to dispersal. Conversely, in an environment where a habitat patch cannot be reached, the fractions initially found in this habitat will go extinct, therefore eroding the richness of the metapopulation. Moreover, we showed that all of the fractions of a metapopulation will colonize all of the habitat patches with asymptotically the same proportion in each habitat. Accordingly, dispersal also enhances the local richness of each habitat.

In addition, we have shown that the growth rate of the habitat is directly influenced by its quality, and as a result has an important impact on diversity. Several empirical studies have already pointed out that environmental circumstances influence the genetic structure of metapopulations (Watts et al., 2015; Souza et al., 2002). In the source–sink scenario (scenario 2), we showed that a lower sink quality generally erodes diversity, especially when the sink becomes really deteriorated. However, when the sink quality is not too bad (r_2 close to 0), a reduction of sink quality might increase diversity because the exchange with the source enhances the size of the metapopulation. The detrimental effect of bad habitat quality on diversity is similar to the effect of the extinction process in stochastic framework (Slatkin, 1977; Maruyama and Kimura, 1980; Whitlock and Barton, 1997; Pannell and Charlesworth, 1999), even if these processes are ecologically different (in our model there are no extinction/recolonisation events). In addition, we show that the quality of the source has no influence on the diversity of the metapopulation even though it plays a crucial role in the survival of the metapopulation as well as the size of the populations in the source and the sink. In the scenario with a good quality habitat (scenario 1), the quality of the habitat always influences diversity. Moreover, its influence crucially depends on the relative carrying capacities of the habitats as well as the relative migration rates between habitats. In particular, when migration is symmetric, we have shown that improving the habitat quality of one patch tends to reduce diversity, because one habitat is favored over another, thus breaking the balance among the proportions of neutral fractions.

Moreover, we have shown that the neutral genetic dynamics crucially depends on the dispersal rate between habitats, as well as the dissimilarity of habitat quality. For a metapopulation composed of favorable habitats (scenario 1), an increase in the difference of carrying capacities tends to erode diversity at local and global scale. Similarly, for a source-sink metapopulation (scenario 2), a decrease of population growth rate in the sink also results in an erosion of diversity. However, in both scenarios, the intensity of erosion crucially depends on the ratio between emigration from one habitat to the

other. Using diversity indices, we showed that a metapopulation living within favorable habitats (scenario 1) and whose emigration from the habitat with smaller carrying capacity is higher than the emigration from the other habitat, can maintain a high level of diversity. The importance of the population size in each habitat is often ignored in metapopulation models, even if theoretical as well as empirical works report diversity change in small habitats (Ingvarsson, 1997; van Heerwaarden et al., 2010).

With the same mathematical framework, we have shown that source-sink metapopulation (scenario 2), whose emigration from the source is higher than emigration from the sink but not too much greater, can avoid both extinction and the erosion of diversity. However, even if the recolonization from the source is a critical process leading to diversity recovery, the escape from the unsuitable habitat is needed to be able to preserve the diversity of the sink. Moreover, our result shows that a massive migration from the sink, might result in the extinction of almost all of the fraction initially present in the sink. In this situation, a large number of individuals from the neutral fractions in the sink migrate to the source. Due to intraspecific competition, they are unable to survive thus reducing the proportion of these fractions inside the metapopulation. As a result, diversity will decrease if they cannot escape from the source quickly enough (large migration rate from the source). This extreme scenario which prevents the extinction of the metapopulation, does not allow the rescue of genetic diversity. In conclusion, the escape rate must be reasonable in order to preserve a high level of diversity in the sink. Whats more, the restoration of diversity can only come from the ability of the source to rescue fractions from the sink and help them to recolonize the sink.

diversity

We also numerically investigate the effect of connecting two isolated habitats. We show that local diversity is always promoted by this exchange. When habitats are both favorable, the increase is higher than when habitats are similar. When the habitats are source–sink, an increase of diversity is more significant when migration is small. The phenomenon occurs in this case because the total population increases significantly. The connection between habitats also generally promotes global diversity because the exchanges contribute to the mixing of the neutral genetic fractions. This mixing tends to balance the proportion of the different fractions in the habitats housing the metapopulation. However, in some situations, the global diversity might be reduced significantly. This occurs when habitats are favourable but dissimilar, and migration is low. If the flux of individuals from the habitat with the best quality (maximal growth rate) is larger than the flux from the other habitat, then diversity is eroded due to the connections between the habitats. This situation occurs because the

best quality habitat increases its population size when it is connected to other habitats. Similar situations can occur in sourcesink metapopulations when the migration from the sink is too large compared to the migration from the source. In this case, a large proportion of the neutral fractions from the sink is able to escape to the source. But due to the competition, they cannot survive which reduces their proportion in the metapopulation. As a consequence, global diversity is reduced. So in metapopulations composed of many sources and sinks, we may expect a reduction of diversity if individuals massively escape from the sinks.

In our deterministic model, we do not explicitly model genetic drift and mutations, which is an important difference with previous studies based on stochastic models (Lande, 1992; Lynch, 1988; Slatkin, 1985; Bohrer et al., 2005). However, our deterministic model is a good approximation of the population density of individual-based models when the number of individuals is large (Fournier and Méléard, 2004; Bansaye and Méléard, 2015). Thus, our model describes metapopulation with a large number of individuals in the different local populations. In this case, genetic drift is extremely rare because of large local population size (Bohrer et al., 2005). In addition, we look at an ecological time scale during which stochastic extinction is unlikely to occur because the number of individuals remains large. So our model truly differs from the classic model with extinction/recolonisation processes (Slatkin, 1977; Maruyama and Kimura, 1980; Whitlock and Barton, 1997; Pannell and Charlesworth, 1999). Finally, we assume that at our ecological time scale the mutation is rare so we can neglect them.

Our analytical formula links the demographic and dispersal characteristics of the metapopulation to neutral genetic diversity indices. These results are useful because they suggest that migration rates might be obtained from an estimate of local α–diversity indices. Roques et al. (2016) investigated the recovery of dispersal characteristics from genetic data in the context of a species in a heterogeneous landscape. They combine a mechanistic and a statistical model, describing the dynamics of the species and the data collection, to infer the parameters of population dynamics model from neutral genetic data. Our goal is to use the combination of these models to infer the dispersal behavior of Emperor penguins in Antarctica based on neutral genetic sampling Jenouvrier et al. (2017).

From a mathematical standpoint, our study provides new insight into the extensively studied topic of stationary solutions of dynamical systems. Subsequent to the recent approach developed by Garnier et al. (2012) to characterize traveling wave solutions of reactiondiffusion equations, we focus on the inside dynamics of a stationary solution within a dynamical system. Conversely, we work away from classical approaches that analyze the stability of stationary solutions. Our result characterizes the

dynamical balance that leads to stationary states and generalizes the concept of inside dynamics to systems of equations. These flexible and intuitive mathematical techniques could also be integrated into more complex models that are not necessarily compatible with stationary solutions (Garnier and Lewis, 2016). For instance, if climate conditions change through time, habitat quality will no doubt vary. Consequently, the metapopulation may not reach an equilibrium, but the mathematical model for the neutral genetic fraction should still be valid. Another example of nonstationary state is periodic-steady state. It may result from periodically changing environments or demographic systems that generates periodic steady states (discrete time stage structured models generate periodic steady state once they reach the first Hopf bifurcation) The stage–structured model will be investigated in a future paper.

6 Proof of results

6.1 Proof of Theorem 1.

Let ε_{12}, ε_{21} in $[0,1]$ and $\mathbf{n}(t)$ satisfies (2) with $\mathbf{n}(0) < \mathbf{N}^*$, $\mathbf{n}(0) \neq 0$ and $\mathbf{N}^*$ satisfies $0 = F[\mathbf{N}^*]\mathbf{N}^* + \mathbf{D}\mathbf{N}^*$, that is

$$\begin{cases} 0 = f_1(N_1^*)N_1^* - \varepsilon_{12}N_1^* + \varepsilon_{21}N_2^* \\ 0 = f_2(N_2^*)N_2^* + \varepsilon_{12}N_1^* - \varepsilon_{21}N_2^* \end{cases}$$

Using the ratio $P^* = N_2^*/N_1^* > 0$, we can rewrite the matrix $F[\mathbf{N}^*] + \mathbf{D}$ as follows:

$$\mathbf{M} = F[\mathbf{N}^*] + \mathbf{D} = \begin{pmatrix} -\varepsilon_{21}P^* & \varepsilon_{21} \\ \varepsilon_{12} & -\dfrac{\varepsilon_{12}}{P^*} \end{pmatrix}.$$

Then $\mathbf{n}$ satisfies $\mathbf{n}'(t) = \mathbf{M}\mathbf{n}(t)$. From the properties of $\mathbf{N}^*$, the matrix $\mathbf{M}$ has two eigenvalues, $\lambda = 0$ associated to eigenvector $\mathbf{N}^*$ and $\lambda_- = -\varepsilon_{21}P^* - \varepsilon_{12}/P^* < 0$ associated to an eigenvector $\mathbf{N}^*_-$. Thus, we can decompose the solution $\mathbf{n}(t)$ on the basis $(\mathbf{N}^*, \mathbf{N}^*_-)$ as follows:

$$\mathbf{n}(t) = p^*\mathbf{N}^* + e^{\lambda_- t}c_-\mathbf{N}^*_- \quad \text{where} \quad p^* = \frac{{}^t\mathbf{V}^*\mathbf{n}(0)}{{}^t\mathbf{V}^*\mathbf{N}^*} \quad \text{with} \quad {}^t\mathbf{V}^*\mathbf{M} = 0 \quad \text{and} \quad c_- \in \mathbb{R}.$$

A simple computation shows that

$$V^* = \begin{pmatrix} \varepsilon_{12} & 0 \\ 0 & \varepsilon_{21} \end{pmatrix} \mathbf{N}^*.$$

Since λ_- is negative, we conclude that:

$$\mathbf{n}(t) \to p^* \mathbf{N}^* \quad \text{as} \quad t \to \infty \quad \text{and} \quad p^* = \frac{n_1(0)\varepsilon_{12}N_1^* + n_2(0)\varepsilon_{21}N_2^*}{\varepsilon_{12}(N_1^*)^2 + \varepsilon_{21}(N_2^*)^2}.$$

6.2 Proof of Proposition 2.

Let us remind that α-$Div = \gamma$-$Div = Div(r_2)$ with

$$Div(r_2) = \frac{1}{(p^*(r_2))^2 + (1 - p^*(r_2))^2}.$$

A direct computation shows that the derivative of Div with respect to r_2 is

$$\partial_{r_2} Div(r_2) = \partial_{r_2}(p^*)(r_2)(1 - 2p^*(r_2))(Div(r_2))^2.$$

So, the sign of $\partial_{r_2} Div(r_2)$ is given by the sign of $\partial_{r_2}(p^*)(r_2)(1 - 2p^*(r_2))$.

Without loss of generality, we can assume that $p_1(0) = 1$ and $p_2(0) = 0$ and $\sqrt{\varepsilon_{21}}K_2 - \sqrt{\varepsilon_{12}}K_1 > 0$. Then we deduce the sign of $\partial_{r_2} Div$ from the Proposition 6 describing the monotonicity of p^* and Proposition 7 describing the position of p^* with respect to $1/2$ (see Appendix A.1 for the statements and the proofs of Propositions 6 and 7).

First, if $(\varepsilon_{21} - \varepsilon_{12}) > 0$ then $\varepsilon_{21}K_2 - \varepsilon_{12}K_1 > 0$ because $\sqrt{\varepsilon_{21}}K_2 - \sqrt{\varepsilon_{12}}K_1 > 0$ and according to Proposition 6, we know that p^* is decreasing with respect to r_2. In addition, from Proposition 7, we know that there exists $\bar{r}_2 > 0$ such that $p^*(r_2) \leq 1/2$ if $r_2 \geq \bar{r}_2$ and $p^*(r_2) > 1/2$ if $r_2 < \bar{r}_2$. Then we conclude that $Div(r_2)$ is increasing if $r_2 < \bar{r}_2$ and $Div(r_2)$ is decreasing if $r_2 \geq \bar{r}_2$.

Secondly, let us assume that $(\varepsilon_{21} - \varepsilon_{12}) < 0$ and $\varepsilon_{21}K_2 - \varepsilon_{12}K_1 > 0$. From Proposition 6, we know that p^* is decreasing with respect to r_2 and from Proposition 7, $p^*(r_2) \leq 1/2$ for any $r_2 > 0$. Then, we conclude that $Div(r_2)$ is decreasing.

Finally, let us assume that $(\varepsilon_{21} - \varepsilon_{12}) < 0$ and $\varepsilon_{21}K_2 - \varepsilon_{12}K_1 < 0$. Then, from Proposition 6, we know that p^* is increasing with respect to r_2. In addition, the Proposition 7 implies that $p^*(r_2) \leq 1/2$ for any $r_2 > 0$. In conclusion, the function $Div(r_2)$ is increasing with respect to r_2.

Similar arguments allow to conclude for the case $\sqrt{\varepsilon_{21}}K_2 - \sqrt{\varepsilon_{12}}K_1 \leq 0$.

6.3 Proof of Proposition 3.

Let us now turn to the source-sink metapopulation composed initially of 1 fraction in the source and $I > 0$ fractions in the sink. In this situation we know that the asymptotic proportion of the fraction initially in the source is given by $p^* = 1/(1 + \varepsilon_{12}\varepsilon_{21}/(r_2 + \varepsilon_{21})^2)$. And thus the diversity is given by $Div(r_2) = ((p^*)^2 + (1-p^*)^2/I)^{-1}$. A direct computation show that the derivative of Div with respect to r_2 only depends on the sign of $(p^*)'(1-(1+I)p^*)$. We can directly see from the formula of p^* that $(p^*)'$ is always positive. Then, we can show that $(1-(1+I)p^*)$ is positive if and only if $r_2 < \bar{r}_2$ where

$$\bar{r}_2 = \sqrt{\frac{\varepsilon_{12}\varepsilon_{21}}{I}} - \varepsilon_{21}.$$

We can observe that if $\varepsilon_{12} - I\varepsilon_{21} < 0$ then $\bar{r}_2$ is negative and since r_2 is positive, we always have $r_2 > \bar{r}_2$, which concludes the proof of Proposition 3.

6.4 Proof of Proposition 4.

Let us assume that the growth function satisfies hypotheses (H1) and (H3). We consider the asymptotic diversity of a metapopulation $\mathbf{N}^*$ at equilibrium, composed initially of two subgroups, $\mathbf{n}_1$ in habitat 1 ($\mathbf{n}_1(0) = (N_1^*, 0)$) and $\mathbf{n}_2$ in habitat 2 $\mathbf{n}_2(0) = (0, N_2^*)$. For any $\varepsilon > 0$, let us define p^* the asymptotic proportion of $\mathbf{n}_1$ defined by (7), then the asymptotic proportion of $\mathbf{n}_2$ is $(1-p^*)$. We thus define the asymptotic diversity indices $Div(\varepsilon)$ as follows:

$$Div(\varepsilon) = \left((p^*)^2 + (1-p^*)^2\right)^{-1}$$

Differentiate the diversity index Div with respect to ε, we get

$$\partial_\varepsilon Div(\varepsilon) = 2\partial_\varepsilon p^* \left(1 - 2p^*\right) Div(\varepsilon)^2$$

From the properties of the asymptotic proportion p^* stated in Appendix A.1 (see Proposition 9 and 10), we know that if $K_1 \geq K_2$ then $\partial_\varepsilon p^* \leq 0$ and $p^* \leq 1/2$ for all $\varepsilon \geq 0$. Then $1 - 2p^* \geq 0$ and the function $Div(\varepsilon)$ is nonincreasing with respect to ε. Similarly, if $K_1 < K_2$, then $\partial_\varepsilon p^* > 0$ and $p^* > 1/2$ for all $\varepsilon \geq 0$ which also implies that ${}^qDiv(\varepsilon)$ is nonincreasing with respect to ε. This concludes the proof of Proposition 4.

6.5 Proof of Proposition 5.

Let us assume that the growth function satisfies hypothesis (H1) and (H2). We consider the asymptotic diversity of a metapopulation $\mathbf{N}^*$ at equilibrium, composed initially of $I+1$ subgroups, one subgroup $\mathbf{n}_1$ in the source ($\mathbf{n}_1(0) = (N_1^*, 0)$) and I subgroups $\mathbf{n}_i$ initially identically distributed in the sink $\mathbf{n}_i(0) = (0, N_2^*/I)$. For any ε_{12}, ε_{21} in $[0, \infty)$, let us define from Theorem 1, $p^*(\varepsilon_{12}, \varepsilon_{21})$, the asymptotic proportion of $\mathbf{n}_1$, then the asymptotic proportion of $\mathbf{n}_i$ is $(1 - p^*(\varepsilon_{12}, \varepsilon_{21}))/I$. We thus define the asymptotic diversity indices $Div(\varepsilon_{12}, \varepsilon_{21})$ as follows

$$Div(\varepsilon_{12}, \varepsilon_{21}) = \left(p^*(\varepsilon_{12}, \varepsilon_{21})^2 + \frac{1}{I}\big(1 - p^*(\varepsilon_{12}, \varepsilon_{21})\big)^2 \right)^{-1}$$

We first look at the behavior of $Div(\varepsilon_{12}, \varepsilon_{21})$ with respect to ε_{12}. For the sequel, we will omit the variables $(\varepsilon_{12}, \varepsilon_{21})$. We differentiate with respect to ε_{12} and we get

$$\partial_{\varepsilon_{12}} Div = \frac{2}{I} \partial_{\varepsilon_{12}} p^* \big(1 - (1+I)p^*\big) Div^2.$$

From the properties of p^* stated in Appendix A.2 (see Proposition 12 and 13), we know that $\partial_{\varepsilon_{12}} p^*(\varepsilon_{12,\varepsilon_{21}}) \geq 0$ for all $\varepsilon_{12}, \varepsilon_{21}$ in $[0, \infty)$. Moreover, a similar argument as in the proof of Proposition 12 shows that $p^* > 1/(1+I)$ if and only if $\varepsilon_{12} < I(r_2 + \varepsilon_{21})^2/\varepsilon_{21}$. Combining those two inequalities, we conclude that Div is increasing if $\varepsilon_{12} < I(r_2 + \varepsilon_{21})^2/\varepsilon_{21}$ while it is non increasing if $\varepsilon_{12} \geq I(r_2 + \varepsilon_{21})^2/\varepsilon_{21}$.

Now let us look at the behavior of $Div(\varepsilon_{12}, \varepsilon_{21})$ with respect to ε_{21}. The derivative of Div with respect to ε_{21} is similar as the derivative with respect to ε_{12}, however, the behavior of $\partial_{\varepsilon_{21}} p^*$ is truly different from the behavior of $\partial_{\varepsilon_{12}} p^*$. As above, we obtain that for all $\varepsilon_{12}, \varepsilon_{21}$

$$\partial_{\varepsilon_{21}} Div = \frac{2}{I} \partial_{\varepsilon_{21}} p^* \big(1 - (1+I)p^*\big) Div^2$$

Since $p_1(0) = 1 > 0 = p_2(0)$, we know from Propositions 12 and 13 that $\partial_{\varepsilon_{21}} p^*(\varepsilon_{12,\varepsilon_{21}}) \geq 0$ if $(r_2 - \varepsilon_{21}) < 0$. Thus combining this estimates with the fact that $p^* > 1/(1+I)$ if and only if $\varepsilon_{12} < I(r_2 + \varepsilon_{21})^2/\varepsilon_{21}$, we conclude that Div is decreasing with respect to ε_{21} if $(r_2 - \varepsilon_{21})(\varepsilon_{12} > -I(r_2 + \varepsilon_{21})^2/\varepsilon_{21}) > 0$ while it is increasing if $(r_2 - \varepsilon_{21})(\varepsilon_{12} > -I(r_2 + \varepsilon_{21})^2/\varepsilon_{21}) < 0$. This concludes the proof of Proposition 5.

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A Properties of the asymptotic proportion p^*.

In this section we are interested in the qualitative properties of the asymptotic proportion of a fraction in a metapopulation at equilibrium. More precisely, we either consider a metapopulation in a spatially-structured favorable environment or a source–sink metapopulation at equilibrium $\mathbf{N}^*$. And we consider a fraction with density $\mathbf{n}$ inside this metapopulation which satisfies equation (2). We know from our previous result that the fraction will converge to an asymptotic proportion of the metapopulation p^* defined by (7). We investigate the effects of the quality of the habitats, that is its growth rate r_i, and the migration rates ε_{ij} on the asymptotic proportion p^*. These properties will give us insight on the behaviour of the diversity which is explain in the main text.

A.1 Scenario 1: Metapopulation in spatially-structured favorable environment

We consider a metapopulation over two good habitats at equilibrium. Using the notation of Theorem 1, the asymptotic proportion of the fraction with initial density $\mathbf{n}(0) = (n_1(0), n_2(0))$ is

$$p^* = \frac{n_1(0)\varepsilon_{12}N_1^* + n_2(0)\varepsilon_{21}N_2^*}{\varepsilon_{12}(N_1^*)^2 + \varepsilon_{21}(N_2^*)^2}. \tag{10}$$

A.1.1 Effect of the growth rate on asymptotic proportion.

We first look at the effect of the habitat quality defined by the growth rate of the habitat r_i on the asymptotic proportion p^*.

Proposition 6 (Monotonicity of p^* with respect to r_2)**.** *For any initial condition* $\mathbf{n}(0)$*, the asymptotic proportion* p^* *associated to the fraction* $\mathbf{n}$ *solving* (6)*, is monotonic with respect to the growth rate* r_2*. More precisely, the function* $r_2 \mapsto p^*(r_2)$ *is*

- *decreasing with respect to* r_2 *if* $(\varepsilon_{21}K_2 - \varepsilon_{12}K_1)\big(p_2(0) - p_1(0)\big) \leq 0$,
- *increasing with respect to* r_2 *if* $(\varepsilon_{21}K_2 - \varepsilon_{12}K_1)\big(p_2(0) - p_1(0)\big) \geq 0$.

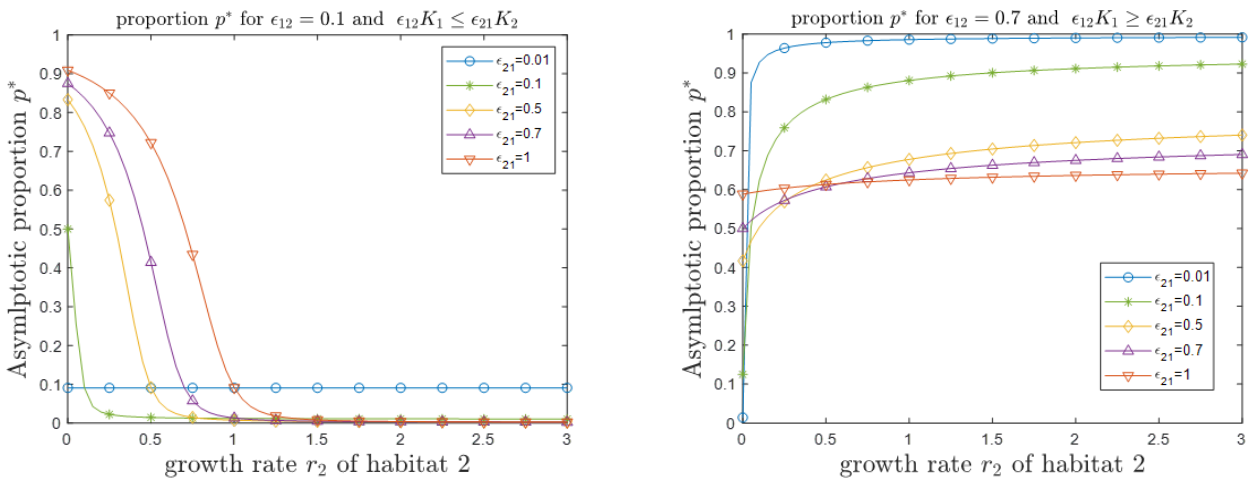
Our result shows that for a given fraction v , the impact of the growth rate of one habitat on the asymptotic contribution of this habitat mainly depends on the flux of individuals between the habitats. In particular, enhancing the quality of habitat 2 will promote contribution of habitat 2 if the flux of individuals from habitat 2 is higher than the one of habitat 1 (it corresponds to the case $\varepsilon_{21}K_2 \geq \varepsilon_{12}K_1$). Conversely, if the mean individuals flux from habitat 2 is smaller than the one from habitat 1, then the contribution of a poor quality habitat 2 is better than the contribution of a good quality habitat.

Let us now look at the relative contribution of the two habitats. More precisely, we assume that the fraction v is only present in one habitat, that is either $p_1(0) = 1$ and $p_2(0) = 0$ or $p_1(0) = 0$ and $p_2(0) = 1$. In this case we compare the asymptotic proportion p^* with respect to $1/2$ which corresponds to an equal contribution from each habitat.

Proposition 7 (Contribution of each habitat)**.** *Let us consider a fraction that fully occupied only one habitat, either* $p_1(0) = 1$ *and* $p_2(0) = 0$ *or* $p_1(0) = 0$ *and* $p_2(0) = 1$*. Then the asymptotic proportion satisfies the following conditions:*

- *If* $(\sqrt{\varepsilon_{21}}K_2 - \sqrt{\varepsilon_{12}}K_1)(\varepsilon_{21} - \varepsilon_{12}) \leq 0$ *then the sign of* $(p^*(r_2) - 1/2)$ *does not depend on* r_2*. In addition,* $p^*(r_2) \leq 1/2$ *if* $\big(p_2(0) - p_1(0)\big)(\varepsilon_{21} - \varepsilon_{12}) > 0$ *and* $p^*(r_2) \geq 1/2$ *if* $\big(p_2(0) - p_1(0)\big)(\varepsilon_{21} - \varepsilon_{12}) < 0$.
- *If* $(\sqrt{\varepsilon_{21}}K_2 - \sqrt{\varepsilon_{12}}K_1)(\varepsilon_{21} - \varepsilon_{12}) > 0$ *then there exists* $\bar{r}_2 > 0$ *such that* $p^*(\bar{r}_2) = 1/2$ *where*

$$\bar{r}_2 = \frac{\sqrt{\varepsilon_{21}}\big[\sqrt{\varepsilon_{21}} - \sqrt{\varepsilon_{12}}\big]}{1 - \dfrac{\varepsilon_{12}K_1}{\varepsilon_{21}K_2}\sqrt{\dfrac{\varepsilon_{21}}{\varepsilon_{12}}}\left[1 + \dfrac{\sqrt{\varepsilon_{12}}\big[\sqrt{\varepsilon_{21}} - \sqrt{\varepsilon_{12}}\big]}{r_1}\right]} \tag{11}$$



(a) (b)

Figure 12: Proportion of the subgroup of gene 1 in the case of scenario 1 ; In figure (a) first habitat: carrying capacity $K_1 = 100$);growth rate $r_1 = 1$,migration rate from habitat1 to habitat2 $\varepsilon_{12} = 0.1$; second habitat: carrying capacity $K_2 = 1000$, migration rate from habitat2 to habitat1 $\varepsilon_{21} \in \{0.01\,, 0.1\,, 0.5\,, 0.7\,, 1\}$. In figure (b) first habitat: carrying capacity $K_1 = 500$);growth rate $r_1 = 1$,migration rate from habitat1 to habitat2 $\varepsilon_{12} = 0.7$; second habitat :carrying capacity $K_2 = 300$, migration rate from habitat2 to habitat1 $\varepsilon_{21} \in \{0.01\,, 0.1\,, 0.5\,, 0.7\,, 1\}$.

In addition, we get

- $p^*(r_2) \geq \dfrac{1}{2}$ *if* $(r_2 - \bar{r}_2)\big(p_2(0) - p_1(0)\big)(\varepsilon_{21} - \varepsilon_{12}) > 0$;
- $p^*(r_2) \leq \dfrac{1}{2}$ *if* $(r_2 - \bar{r}_2)\big(p_2(0) - p_1(0)\big)(\varepsilon_{21} - \varepsilon_{12}) < 0$.

Our result shows that the relative contribution of each habitat may depend on the relative quality of the habitat. In particular, in an environment with a large habitat and a small habitat with smaller migration from the largest habitat than from the smallest habitat, the contribution of the large habitat is larger than the contribution of the smallest habitat whatever the quality of the habitats is.

Moreover, if we assume that habitat 1 is larger than habitat 2 ($K_1 > K_2$) then our result shows that the relative quality of the habitats may have influence on the relative contribution if the flux of individuals are either really high or low. More precisely, if migration from habitat 1 is really smaller than the migration from habitat 2 ($\sqrt{\varepsilon_{21}}K_2 > \sqrt{\varepsilon_{12}}K_1$) then its relative contribution is large only if the the quality of habitat 2 is really poor ($p^*(r_2) > 1/2$ if $r_2 \leq \bar{r}_2$). Conversely, if the migration from habitat 1 is larger than migration from habitat 2 ($\varepsilon_{12} > \varepsilon_{21}$), its relative contribution is large as long as the quality of habitat 2 is good enough ($p^*(r_2) > 1/2$ if $r_2 \geq \bar{r}_2$). However, when the fluxes between the habitats are similar ($\sqrt{\varepsilon_{21}}K_2 < \sqrt{\varepsilon_{12}}K_1$ and $\varepsilon_{12} < \varepsilon_{21}$) then the contribution of habitat 1 is always larger than the one of habitat 2 whatever the quality of the habitats.

Proof of Proposition 6.

Let ε_{12} and ε_{21} be in $(0,1]$, $\mathbf{F}$ satisfy hypothesis of Proposition 10, $p_1(0)$ and $p_2(0)$ be in $[0,1]$ and $\mathbf{N}^* = (N_1^*, N_2^*)$ be a stationary state of (1). We begin to study the variation of p^* with respect to r_2. Using Theorem 1, we have:

$$p^*(r_2) = \frac{p_1(0)\varepsilon_{12} + p_2(0)\varepsilon_{21}(P^*)^2}{\varepsilon_{12} + \varepsilon_{21}(P^*)^2} \quad \text{where} \quad P^* = \frac{N_2^*}{N_1^*}.$$

Differentiating the expression with respect to r_2, we obtain:

$$\partial_{r_2} p^*(r_2) = 2\frac{(p_2(0) - p_1(0))\varepsilon_{12}\varepsilon_{21}}{(\varepsilon_{12} + \varepsilon_{21}(P^*)^2)^2} P^* \partial_{r_2} P^*.$$

The variations of $p^*(r_2)$ only depend on the sign of $(p_2(0) - p_1(0))\partial_{r_2} P^*$. From the definition of P^*, we have

$$\partial_{r_2} P^* = \frac{\partial_{r_2} N_2^*}{N_1^*} - \frac{\partial_{r_2} N_1^*}{N_1^*} P^* \tag{12}$$

First, we study the variations of N_1^* and N_2^* according to r_2. From the definition of $\mathbf{N}^*$, we have:

$$\begin{cases} 0 = f_1(N_1^*)N_1^* - \varepsilon_{12}N_1^* + \varepsilon_{21}N_2^* \\ 0 = f_2(N_2^*)N_2^* - \varepsilon_{21}N_2^* + \varepsilon_{12}N_1^* \end{cases}. \tag{13}$$

Let us denote $g_1(u) = f_1(u)u$ and $g_2(u) = f_2(u)u$. We deduce from equation (13) that $g_1(N_1^*) = -g_2(N_2^*)$. Thus, differentiating this expression with respect to r_2, we have $\partial_{r_2} N_1^* \partial_u g_1(N_1^*) = -\partial_{r_2} N_2^* \partial_u g_2(N_2^*)$. Moreover, differentiating the system (13) with respect to r_2, we obtain:

$$\begin{cases} 0 = \partial_{r_2} N_1^* \partial_u g_1(N_1^*) - \varepsilon_{12}\partial_{r_2} N_1^* + \varepsilon_{21}\partial_{r_2} N_2^* \\ 0 = \partial_{r_2} N_2^* \partial_u g_2(N_2^*) - \varepsilon_{21}\partial_{r_2} N_2^* + \varepsilon_{12}\partial_{r_2} N_1^* + N_2^*\left(1 - \frac{N_2^*}{K_2}\right) \end{cases} \tag{14}$$

Dividing by N_1^* , we obtain:

$$\begin{cases} 0 = \frac{\partial_{r_2} N_1^*}{N_1^*}(\partial_u g_1(N_1^*) - \varepsilon_{12}) + \varepsilon_{21}\frac{\partial_\varepsilon N_2^*}{N_1^*} \\ 0 = \frac{\partial_{r_2} N_2^*}{N_1^*}(\partial_u g_2(N_2^*) - \varepsilon_{21}) + \varepsilon_{12}\frac{\partial_{r_2} N_1^*}{N_1^*} + \frac{N_2^*}{N_1^*}\left(1 - \frac{N_2^*}{K_2}\right) \end{cases}$$

From system (13), we obtain

$$f_2(N_2^*)N_2^* = \varepsilon_{21}N_2^* + \varepsilon_{12}N_1^*$$

and so we have: $r_2 N_2^* \left(1 - \frac{N_2^*}{K_2}\right) = \varepsilon_{21} N_2^* - \varepsilon_{12} N_1^*$ and using $P^* = \frac{N_1^*}{N_2^*}$,we obtain:

$$P^* \left(1 - \frac{N_2^*}{K_2}\right) = \frac{\varepsilon_{21}}{r_2} P^* - \frac{\varepsilon_{12}}{r_2}.$$

Then we have :

$$\begin{cases} 0 = \frac{\partial_{r_2} N_1^*}{N_1^*} (\partial_u g_1(N_1^*) - \varepsilon_{12}) + \varepsilon_{21} \frac{\partial_\varepsilon N_2^*}{N_1^*} \\ 0 = \frac{\partial_{r_2} N_2^*}{N_1^*} (\partial_u g_2(N_2^*) - \varepsilon_{21}) + \varepsilon_{12} \frac{\partial_{r_2} N_1^*}{N_1^*} + \frac{\varepsilon_{21}}{r_2} P^* - \frac{\varepsilon_{12}}{r_2} \end{cases}.$$

We solve this linear system to get:

$$\begin{cases} \frac{\partial_{r_2} N_1^*}{N_1^*} = \frac{-\frac{\varepsilon_{21}^2}{r_2} \left(\frac{\varepsilon_{12}}{\varepsilon_{21}} - P^*\right)}{(\partial_u g_1(N_1^*) - \varepsilon_{12})(\partial_u g_2(N_2^*) - \varepsilon_{21}) - \varepsilon_{12}\varepsilon_{21}} \\ \frac{\partial_\varepsilon N_2^*}{N_1^*} = \frac{\frac{\varepsilon_{21}}{r_2} \left(\frac{\varepsilon_{12}}{\varepsilon_{21}} - P^*\right) (\partial_u g_1(N_1^*) - \varepsilon_{12})}{(\partial_u g_1(N_1^*) - \varepsilon_{12})(\partial_u g_2(N_2^*) - \varepsilon_{21}) - \varepsilon_{12}\varepsilon_{21}} \end{cases}.$$

We deduce from equation (12) that

$$\partial_{r_2} P^* = \frac{\frac{\varepsilon_{21}}{r_2} \left(\frac{\varepsilon_{12}}{\varepsilon_{21}} - P^*\right) (\partial_u g_1(N_1^*) - \varepsilon_{12} + \varepsilon_{21} P^*)}{(\partial_u g_1(N_1^*) - \varepsilon_{12})(\partial_u g_2(N_2^*) - \varepsilon_{21}) - \varepsilon_{12}\varepsilon_{21}}. \tag{15}$$

To decipher the sign of $\partial_{r_2} P^*$, we first look at the sign of the denominator $(\partial_u g_1(N_1^*) - \varepsilon_{12})(\partial_u g_2(N_2^*) - \varepsilon_{21}) - \varepsilon_{12}\varepsilon_{21}$

From hypothesis (H1) and (H3), we know that $\partial_u g_i(N_i^*) \leq g_i(N_i^*)/N_i^*$. Moreover, we know from (13) that

$$\begin{cases} 0 = \frac{g_1(N_1^*)}{N_1^*} - \varepsilon_{12} + \varepsilon_{21} P^* \\ 0 = \frac{g_2(N_2^*)}{N_2^*} - \varepsilon_{21} + \varepsilon_{12} \frac{1}{P^*} \end{cases}. \tag{16}$$

Combining the two equations, we obtain that

$$\partial_u g_1(N_1^*) - \varepsilon_{12} \leq -\varepsilon_{21} P^* < 0 \quad \text{and} \quad \partial_u g_2(N_2^*) - \varepsilon_{21} \leq -\varepsilon_{12} \frac{1}{P^*} < 0. \tag{17}$$

Finally, we have:

$$(\partial_u g_1(N_1^*) - \varepsilon_{12})(\partial_u g_2(N_2^*) - \varepsilon_{21}) - \varepsilon_{12}\varepsilon_{21} \geq 0. \tag{18}$$

More precisely, we have $(\partial_u g_1(N_1^*) - \varepsilon_{12})(\partial_u g_2(N_2^*) - \varepsilon_{21}) - \varepsilon_{12}\varepsilon_{21} > 0$ because the equality case corresponds to either $N_1^* = 0$ or $N_2^* = 0$ and we know that $N_1^* > 0$ and $N_2^* > 0$.

Let us now look at the sign of the numerator of $\partial_{r_2} P^*$.

We first consider the following part $(\partial_u g_1(N_1^*) - \varepsilon_{12} + \varepsilon_{21} P^*)$. From hypothesis (H1) and (H3) combined with equation (16), we can say that $\partial_u g_i(N_i^*) - \varepsilon_{12} \leq g_i(N_i^*)/N_i^* - \varepsilon_{12} \leq -\varepsilon_{21} P^*$ and then

$$(\partial_u g_1(N_1^*) - \varepsilon_{12} + \varepsilon_{21} P^*) \leq 0. \tag{19}$$

It remains to look at the sign of $\left(\dfrac{\varepsilon_{12}}{\varepsilon_{21}} - P^*\right)$ We prove the following lemma

Lemma 8 (Property of P^* as a function of r_2)**.** *Let* $\mathbf{N}^*$ *be the solution of* (13) *under hypothesis* (H1) *and* (H3)*. Then, the ratio* $P^* = N_2^*/N_1^*$ *satisfies the following properties*

- *If* $\varepsilon_{21} K_2 \geq \varepsilon_{12} K_1$ *then* $\varepsilon_{12}/\varepsilon_{21} \leq P^*$ *and* P^* *is increasing with respect to* r_2*.*
- *If* $\varepsilon_{21} K_2 \leq \varepsilon_{12} K_1$ *then* $\varepsilon_{12}/\varepsilon_{21} \geq P^*$ *and* P^* *is decreasing with respect to* r_2*.*

Before stating of the proof of Lemma 8, we conclude the proof of Proposition 6.

The estimates of Lemma 8 combined with the previous inequalities (15)–(19) show that the sign of $\partial_{r_2} p^*(r_2)$ only depends on the sign of $(\varepsilon_{21} K_2 - \varepsilon_{12} K_1)\,(p_2(0) - p_1(0))$ which concludes the proof of proposition 6.

Proof of lemma 8.

We can first show from (15)–(18)–(19) that the monoticity of P^* depends only on the sign of $\left(\dfrac{\varepsilon_{12}}{\varepsilon_{21}} - P^*\right)$. Moreover, from equation (17), we know that the sign of $\left(\dfrac{\varepsilon_{12}}{\varepsilon_{21}} - P^*\right)$ is equal of the sign of $\dfrac{g_1(N_1^*)}{N_1^*}$ and therefore depends of the position of N_1^* relative to K_1.

We first start with the following changes of variables $Y_1^* = \varepsilon_{12} N_1^*$ and $Y_2^* = \varepsilon_{21} N_2^*$. Moreover, if we denote $\tilde{K}_1 = \varepsilon_{12} K_1$ and $\tilde{K}_2 = \varepsilon_{21} K_2$ then the system (16) becomes:

$$\begin{cases} 0 = \dfrac{\tilde{g}_1(Y_1^*)}{Y_1^*} - \varepsilon_{12}(1 - \tilde{P}^*) \\ 0 = \dfrac{\tilde{g}_2(Y_2^*)}{Y_2^*} - \varepsilon_{21}\left(1 - \dfrac{1}{\tilde{P}^*}\right) \end{cases}. \tag{20}$$

where $\tilde{g}_1(u) = u\tilde{f}_1(u)$ with $\tilde{f}_1(u) = r_1\left(1 - \dfrac{u}{\tilde{K}_1}\right)$, $\tilde{g}_2(u) = u\tilde{f}_2(u)$ with $\tilde{f}_2(u) = r_2\left(1 - \dfrac{u}{\tilde{K}_2}\right)$ and $\tilde{P}^* = \dfrac{Y_2^*}{Y_1^*}$.

Our aim is to show that if $\tilde{K}_2 > \tilde{K}_1$ then $\tilde{P}^* > 1$. This is equivalent to show that $Y_1^* > \tilde{K}_1$ if $\tilde{K}_2 > \tilde{K}_1$. The equilibrium point $Y^* = (Y_1^*, Y_2^*)$ of the model (20) satisfies $\tilde{G}_1(Y_1^*) = Y_2^*$ and

$\tilde{G}_2(Y_2^*) = Y_1^*$ where :

$$\tilde{G}_1(u) = -\frac{1}{\varepsilon_{12}}\left(\tilde{g}_1(u) - \varepsilon_{12}u\right) = -\frac{u}{\varepsilon_{12}}(\tilde{f}_1(u) - \varepsilon_{12})$$

$$\tilde{G}_2(u) = -\frac{1}{\varepsilon_{12}}\left(\tilde{g}_2(u) - \varepsilon_{21}u\right) = -\frac{u}{\varepsilon_{21}}(\tilde{f}_2(u) - \varepsilon_{21}).$$

First let us notice that from the hypothesis (H1), we know that $\tilde{G}_1(\tilde{K}_1) = \tilde{K}_1$ and $\tilde{G}_2(\tilde{K}_2) = \tilde{K}_2$. Moreover since $\tilde{K}_2 > \tilde{K}_1$, we can deduce from hypothesis (H3) that

$$\tilde{G}_1(\tilde{K}_2) = -\frac{\tilde{K}_2}{\varepsilon_{12}}(\tilde{f}_1(\tilde{K}_2) - \varepsilon_{12}) = \tilde{K}_2 - \frac{\tilde{K}_2}{\varepsilon_{12}}\tilde{f}_1(\tilde{K}_2) > \tilde{K}_2,$$

$$\tilde{G}_2(\tilde{K}_1) = -\frac{\tilde{K}_1}{\varepsilon_{21}}(\tilde{f}_2(\tilde{K}_1) - \varepsilon_{21}) = \tilde{K}_1 - \frac{\tilde{K}_1}{\varepsilon_{21}}\tilde{f}_2(\tilde{K}_1) < \tilde{K}_1.$$

Let us study the variation of $\tilde{G}_1$ on $(\tilde{K}_1, +\infty)$. The derivative of $\tilde{G}_1$ satisfies $\tilde{G}_1'(u) = 1 - \frac{r_1}{\varepsilon_{12}}\left(1 - \frac{2u}{\tilde{K}_1}\right) > 0$ if $u > \tilde{K}_1$ thus $\tilde{G}_1$ is increasing on $(\tilde{K}_1, +\infty)$.

Let us study the variation of $\tilde{G}_2$ on $(\tilde{K}_1, +\infty)$. As above we have: $\tilde{G}_2'(u) = 1 - \frac{r_2}{\varepsilon_{21}}\left(1 - \frac{2u}{\tilde{K}_2}\right) > 0$ if $u > \frac{\tilde{K}_2}{2}\left(1 - \frac{\varepsilon_{21}}{r_2}\right)$. So, we can say that

- If $\frac{\tilde{K}_2}{2}\left(1 - \frac{\varepsilon_{21}}{r_2}\right) < \tilde{K}_1$ then $\tilde{G}_2$ is increasing on $(\tilde{K}_1, +\infty)$.
- If $\frac{\tilde{K}_2}{2}\left(1 - \frac{\varepsilon_{21}}{r_2}\right) > \tilde{K}_1$ then $\tilde{G}_2$ is decreasing on $\left(\tilde{K}_1, \frac{\tilde{K}_2}{2}\left(1 - \frac{\varepsilon_{21}}{r_2}\right)\right)$ and increasing on $\left(\frac{\tilde{K}_2}{2}\left(1 - \frac{\varepsilon_{21}}{r_2}\right), +\infty\right)$.

From the definition of Y_1^* and Y_2^*, we know that Y_1^* is a fixed point of the function $h = \tilde{G}_2 \circ \tilde{G}_1$. Let us prove that Y_1^* belongs to $(\tilde{K}_1, \infty)$.

To conclude we need to consider two cases depending on the position of $\tilde{K}_1$ with respect to $\tilde{K}_2/2\,(1 - \varepsilon_{21}/r_2)$.

On the one hand, let us assume that $\tilde{K}_2/2\,(1 - \varepsilon_{21}/r_2) < \tilde{K}_1$. Then the function h is increasing on $(\tilde{K}_1, +\infty)$. Moreover, we have $h(\tilde{K}_1) = \tilde{G}_2(\tilde{K}_1) < \tilde{K}_1$ and $h(\tilde{K}_2) = \tilde{G}_2(\tilde{G}_1(\tilde{K}_2)) > \tilde{G}_2(\tilde{K}_2) = \tilde{K}_2)$ because $\tilde{G}_2$ is increasing on $(\tilde{K}_1, \infty)$. So, applying the intermediate value theorem to the monotone function h on $(\tilde{K}_1, +\infty)$, there exists an unique positive real Y_1^* such that $h(Y_1^*) = Y_1^*$ and $Y_1^* > \tilde{K}_1$.

On the other hand, if $\tilde{K}_2/2\,(1 - \varepsilon_{21}/r_2) \geq \tilde{K}_1$,then the function h is decreasing on $(\tilde{K}_1, \tilde{K}_2/2\,(1 - \varepsilon_{21}/r_2))$ and increasing on $(\tilde{K}_2/2\,(1 - \varepsilon_{21}/r_2), \infty)$. So $h(u) < h(\tilde{K}_1) < \tilde{K}_1$ on $(\tilde{K}_1, \tilde{K}_2/2\,(1 - \varepsilon_{21}/r_2))$. More-

over, we still have $h(\tilde{K}_2) > \tilde{K}_2$. Thus there exists a unique fixed point Y_1^* on $(\tilde{K}_1, \infty)$. We can then conclude that if $\tilde{K}_2 > \tilde{K}_1$ then $Y_1^* > \tilde{K}_1$ and $1 - \tilde{P}^* = \frac{r_1}{\varepsilon_{12}}\left(1 - \frac{Y_1^*}{\tilde{K}_1}\right) < 0$ and P^* is increasing with respect to r_2.

Proof of Proposition 7.

Let ε_{12}, $\varepsilon_{21} \in (0, 1]$ and $\mathbf{N}^* = (N_1^*, N_2^*)$ be the equilibrium of (1). We know from Theorem 1 that for any $p_1(0)$, $p_2(0)$ in $[0, 1]$, the asymptotic proportion p^* satisfies:

$$p^*(r_2) = \frac{p_1(0) + p_2(0)\left(\frac{\varepsilon_{21}}{\varepsilon_{12}}(P^*)^2\right)}{1 + \left(\frac{\varepsilon_{21}}{\varepsilon_{12}}(P^*)^2\right)} \quad \text{with} \quad P^* = \frac{N_2^*}{N_1^*}. \tag{21}$$

For the sake of simplicity,, we only look at the case where $p_1(0) = 1$ and $p_2(0) = 0$. The alternative case can be deduced by symmetry of the problem. Thus, we get

$$p^*(r_2) = \frac{1}{1 + \left(\frac{\varepsilon_{21}}{\varepsilon_{12}}(P^*)^2\right)}.$$

We can see that $p^*(r_2) = \frac{1}{2}$ if and only if $P^* = \sqrt{\varepsilon_{12}/\varepsilon_{21}}$ and p^* is decreasing with respect to P^*. Thus, in order to compare $p^*(r_2)$ with $1/2$, we just need to compare P^* with $\sqrt{\varepsilon_{12}/\varepsilon_{21}}$.

First let assume that $\varepsilon_{21}K_2 > \varepsilon_{12}K_1$. Then from the estimates of Lemma 8 we know that $P^* \geq \varepsilon_{12}/\varepsilon_{21}$.

On the one hand, if $\varepsilon_{12} \geq \varepsilon_{21}$ then for any $r_2 > 0$ we have

$$P^* \geq \frac{\varepsilon_{12}}{\varepsilon_{21}} \geq \sqrt{\frac{\varepsilon_{12}}{\varepsilon_{21}}}$$

and $p^*(r_2) \leq 1/2$ for any $r_2 > 0$.

On the other hand, if $\varepsilon_{12} < \varepsilon_{21}$ then we have $P^*(0) = \varepsilon_{12}/\varepsilon_{21} < \sqrt{\varepsilon_{12}/\varepsilon_{21}}$. Since P^* is increasing with respect to r_2, it may exist $\bar{r}_2 > 0$ such that $P^*(\bar{r}_2) = \sqrt{\varepsilon_{12}/\varepsilon_{21}}$ (eventually $\bar{r}_2 = \infty$ if $P^*(r_2) < \sqrt{\varepsilon_{12}/\varepsilon_{21}}$ for any $r_2 > 0$). Then,we can conclude that:

- $P^*(r_2) < \sqrt{\frac{\varepsilon_{12}}{\varepsilon_{21}}}$ and $p^*(r_2) > \frac{1}{2}$, for $r_2 < \bar{r}_2$;
- $P^*(r_2) = \sqrt{\frac{\varepsilon_{12}}{\varepsilon_{21}}}$ and $p^*(r_2) = \frac{1}{2}$, for $r_2 = \bar{r}_2$;

- $P^*(r_2) > \sqrt{\dfrac{\varepsilon_{12}}{\varepsilon_{21}}}$ and $p^*(r_2) < \dfrac{1}{2}$, for $r_2 > \bar{r}_2$.

Let us now determine the value $\bar{r}_2$. If $r_2 = \bar{r}_2$, then $P^* = \sqrt{\varepsilon_{12}/\varepsilon_{21}}$ and we get the following system:

$$\begin{cases} 0 = r_1\left(1 - \dfrac{N_1^*}{K_1}\right) - \varepsilon_{12} + \sqrt{\varepsilon_{21}\varepsilon_{12}} \\ 0 = \bar{r}_2\left(1 - \dfrac{N_2^*}{K_2}\right) - \varepsilon_{21} + \sqrt{\varepsilon_{21}\varepsilon_{12}} \end{cases} . \tag{22}$$

Solving this system, we obtain:

$$N_1^* = K_1\left[1 - \frac{\varepsilon_{12} - \sqrt{\varepsilon_{21}\varepsilon_{12}}}{r_1}\right] \text{ and } N_2^* = K_2\left[1 - \frac{\varepsilon_{21} - \sqrt{\varepsilon_{21}\varepsilon_{12}}}{\bar{r}_2}\right] \tag{23}$$

Since we are in the case where $\varepsilon_{21} < \varepsilon_{12}$, we can deduce that $N_1^* > K_1$ and $N_2^* < K_2$ and therefore $P^*(\bar{r}_2) < \dfrac{K_2}{K_1}$. So if $\dfrac{K_2}{K_1} < \sqrt{\dfrac{\varepsilon_{12}}{\varepsilon_{21}}}$ we should have $\bar{r}_2 = +\infty$. In addition, using the definition of $\bar{r}_2$ we obtain:

$$\bar{r}_2 = \begin{cases} \dfrac{\sqrt{\varepsilon_{21}}[\sqrt{\varepsilon_{21}} - \sqrt{\varepsilon_{12}}]}{1 - \dfrac{\varepsilon_{12}K_1}{\varepsilon_{21}K_2}\sqrt{\dfrac{\varepsilon_{21}}{\varepsilon_{12}}}\left[1 + \dfrac{\sqrt{\varepsilon_{12}}[\sqrt{\varepsilon_{21}} - \sqrt{\varepsilon_{12}}]}{r_1}\right]} & \text{if } \dfrac{K_2}{K_1} \geq \sqrt{\dfrac{\varepsilon_{12}}{\varepsilon_{21}}} \\ \infty & \text{if } \dfrac{K_2}{K_1} < \sqrt{\dfrac{\varepsilon_{12}}{\varepsilon_{21}}} \end{cases}$$

Similar arguments allow to conclude for the case $\varepsilon_{21}K_2 \leq \varepsilon_{12}K_1$.

A.1.2 Carrying capacities crucially determine the habitat contributions.

We now look at the effect of the migration rates on the asymptotic proportion of the fraction. In this section, we assume that the migration is symmetric:

$$\varepsilon_{12} = \varepsilon_{21} = \varepsilon \quad \text{with} \quad \varepsilon \in [0, 1].$$

Under these assumptions, the asymptotic proportion of the fraction $\mathbf{n}$ is given by the following formula:

$$p^* = \frac{p_1(0) + p_2(0)(P^*)^2}{1 + (P^*)^2},$$

where $p_i(0)$ corresponds to the initial proportion of the fraction in each habitat i, $p_i(0) = n_i(0)/N_i^*$ and the quantity P^* is the ratio between the density of population in habitat 2 and the one in habitat 1, $P^* = N_2^*/N_1^*$. From this formula, we observe that the dependency of p^* according to the migration rate ε only occurs through the ratio of equilibrium densities P^*.

Using this particular formula, we deduce results concerning the effect of passive migration ε on

the asymptotic contribution p^* of a fraction $\mathbf{n}$ satisfying (6).

Proposition 9 (Monotonicity of p^* with respect to ε)**.** *For any initial condition* $\mathbf{n}(0)$*, the asymptotic proportion* p^* *associated to the fraction* $\mathbf{n}$ *solving* (6)*, is monotonic with respect to the migration rate* ε*. More precisely, the function* $\varepsilon \mapsto p^*$ *is*

- *nondecreasing if* $(K_1 - K_2)\big(p_1(0) - p_2(0)\big) < 0$*;*
- *constant equal to* $p^* = \dfrac{p_1(0) + p_2(0)}{2}$ *if* $K_1 = K_2$*;*
- *nonincreasing if* $(K_1 - K_2)\big(p_1(0) - p_2(0)\big) > 0$*.*

Our result shows that the asymptotic proportion of a given fraction v is monotonic with respect to the migration rate ε. In addition, we have proved that this monotonicity only depends on the relative repartition of the fraction inside the metapopulation patches and the carrying capacities of the habitats. We can notice that the intrinsic growth rate r_i of the habitat does not play any role in the behavior of p^* with respect to ε. In particular, even if the habitat 2 is not as good as the habitat 1, that is $r_2 < r_1$, when its carrying capacity is higher than the one of habitat 1, that is $K_2 > K_1$, then the migration enhances the contribution from the habitat 2 which corresponds to the case where $0 = p_1(0) < p_2(0) = 1$. Thus the migration may promote the diversity from poor habitat quality if those habitats have a large carrying capacity.

To go further, we now look at the precise contribution of each habitat. More precisely, we assume that the fraction is only present in one habitat, that is either $n_1(0) = N_1^*$ and $n_2(0) = 0$ or $n_1(0) = 0$ and $n_2(0) = N_2^*$. In this case we quantify the asymptotic proportion p^* with respect to $1/2$ which corresponds to an equal contribution from each habitat.

Proposition 10 (Contribution of each habitat)**.** *Let us consider a fraction that fully occupies only one habitat, either* $p_1(0) = 1$ *and* $p_2(0) = 0$ *or* $p_1(0) = 0$ *and* $p_2(0) = 1$*. Then the asymptotic proportion satisfies:*

- $p^* < 1/2$ *if* $(K_1 - K_2)\big(p_1(0) - p_2(0)\big) < 0$*;*
- $p^* = \dfrac{1}{2}$ *if* $K_1 = K_2$*;*
- $p^* > 1/2$ *if* $(K_1 - K_2)\big(p_1(0) - p_2(0)\big) > 0$*.*

Our result first shows that the contribution of each habitat does not depend on the quality of the habitat r_i but only on the carrying capacity of this habitat. An habitat that can support more

individuals will have a higher contribution than the other. If $K_2 > K_1$ then the contribution from the habitat 2 is always larger than $1/2$ even if $r_2 < r_1$. In this case, the contribution from the habitat 2 is larger than the contribution from the habitat 1. In this case the habitat 2 dominates and its genetic diversity partially replaces the one from the habitat 1.

In addition, the migration cannot reverse the domination of one habitat on the other. More precisely, if $K_2 > K_1$, the contribution from habitat 2 is always higher than the one of habitat 1: $p^* - 1/2$ does not change sign when ε varies. However, the migration tends to balance the contribution from both habitats. Indeed the proposition (10) shows that when $K_2 > K_1$, the contribution from habitat 2 tends to decrease while the one from habitat 1 tends to increase. But in this case the contribution from habitat 2 is always higher than $1/2$ while the one from habitat 1 is smaller than $1/2$.

Proof of Proposition 9.

Let ε be in $(0, 1]$, $\mathbf{F}$ satisfying hypothesis of Proposition 10, $p_1(0)$ and $p_2(0)$ in $[0, 1]$ and $\mathbf{N}^* = (N_1^*, N_2^*)$ solves (13). We begin to study the variation of $p^*(\varepsilon)$ with respect to ε. Using Theorem 1, we have:

$$p^*(\varepsilon) = \frac{p_1(0) + p_2(0)(P^*)^2}{1 + (P^*)^2} \quad \text{where} \quad P^* = \frac{N_1^*}{N_2^*}$$

Differentiating the expression with respect to ε, we obtain:

$$\partial_\varepsilon p^*(\varepsilon) = 2\frac{(p_2(0) - p_1(0))}{(1 + (P^*)^2)^2} P^* \partial_\varepsilon P^*.$$

The variations of $p^*(\varepsilon)$ only depend on the sign of $(p_2(0) - p_1(0))\partial_\varepsilon P^*$. From the definition of P^*, we have

$$\partial_\varepsilon P^* = \frac{\partial_\varepsilon N_2^*}{N_1^*} - \frac{\partial_\varepsilon N_1^*}{N_1^*} P^*. \tag{24}$$

Let us now study the variations of N_1^* and N_2^* according to ε. From the definition of $\mathbf{N}^*$, we have:

$$\begin{cases} 0 = f_1(N_1^*)N_1^* - \varepsilon N_1^* + \varepsilon N_2^* \\ 0 = f_2(N_2^*)N_2^* - \varepsilon N_2^* + \varepsilon N_1^* \end{cases} \tag{25}$$

Let us denote $g_1(u) = f_1(u)u$ and $g_2(u) = f_2(u)u$. We deduce from equation (13) that $g_1(N_1^*) = \varepsilon(N_1^* - N_2^*) = -g_2(N_2^*)$. Thus, differentiating this expression with respect to ε, we have $\partial_\varepsilon N_1^* \partial_u g_1(N_1^*) =$

$-\partial_\varepsilon N_2^* \partial_u g_2(N_2^*)$. Moreover, differentiating the system (13) with respect to ε, we obtain

$$\begin{cases} 0 = \partial_\varepsilon N_1^* \partial_u g_1(N_1^*) - \varepsilon \partial_\varepsilon N_1^* + \varepsilon \partial_\varepsilon N_2^* + (N_2^* - N_1^*) \\ 0 = \partial_\varepsilon N_2^* \partial_u g_2(N_2^*) - \varepsilon \partial_\varepsilon N_2^* + \varepsilon \partial_\varepsilon N_1^* + (N_1^* - N_2^*) \end{cases} \tag{26}$$

Dividing by N_1^* and using $P^* = N_2^*/N_1^*$, we obtain

$$\begin{cases} 0 = \dfrac{\partial_\varepsilon N_1^*}{N_1^*}(\partial_u g_1(N_1^*) - \varepsilon) + \varepsilon \dfrac{\partial_\varepsilon N_2^*}{N_1^*} + (P^* - 1) \\ 0 = \varepsilon \dfrac{\partial_\varepsilon N_1^*}{N_1^*} + \dfrac{\partial_\varepsilon N_2^*}{N_1^*}(\partial_u g_2(N_2^*) - \varepsilon) + (1 - P^*) \end{cases}.$$

We solve this linear system to get:

$$\begin{cases} \dfrac{\partial_\varepsilon N_1^*}{N_1^*} = \dfrac{(1 - P^*)\partial_u g_2(N_2^*)}{(\partial_u g_1(N_1^*) - \varepsilon)(\partial_u g_2(N_2^*) - \varepsilon) - \varepsilon^2} \\ \dfrac{\partial_\varepsilon N_2^*}{N_1^*} = \dfrac{(P^* - 1)\partial_u g_1(N_1^*)}{(\partial_u g_1(N_1^*) - \varepsilon)(\partial_u g_2(N_2^*) - \varepsilon) - \varepsilon^2} \end{cases}.$$

We deduce from equation (24) that

$$\partial_\varepsilon P^* = \frac{(P^* - 1)(\partial_u g_1(N_1^*) + \partial_u g_2(N_2^*)P^*)}{(\partial_u g_1(N_1^*) - \varepsilon)(\partial_u g_2(N_2^*) - \varepsilon) - \varepsilon^2}. \tag{27}$$

To decipher the sign of $\partial_\varepsilon P^*$, we first look at the sign of the denominator $(\partial_u g_1(N_1^*) - \varepsilon)(\partial_u g_2(N_2^*) - \varepsilon) - \varepsilon^2$.

From hypothesis (H1) and (H3), we know that $\partial_u g_i(N_i^*) \leq g_i(N_i^*)/N_i^*$. Moreover, we know from (13) that

$$\begin{cases} 0 = \dfrac{g_1(N_1^*)}{N_1^*} + \varepsilon(P^* - 1) \\ 0 = \dfrac{g_2(N_2^*)}{N_2^*} + \varepsilon\left(\dfrac{1}{P^*} - 1\right) \end{cases}. \tag{28}$$

Combining the two equations, we obtain that

$$\partial_u g_1(N_1^*) - \varepsilon \leq -\varepsilon P^* < 0 \quad \text{and} \quad \partial_u g_2(N_2^*) - \varepsilon \leq -\varepsilon \frac{1}{P^*} < 0. \tag{29}$$

Finally, we have:

$$(\partial_u g_1(N_1^*) - \varepsilon)(\partial_u g_2(N_2^*) - \varepsilon) - \varepsilon^2 \geq 0. \tag{30}$$

More precisely, we have $(\partial_u g_1(N_1^*) - \varepsilon)(\partial_u g_2(N_2^*) - \varepsilon) - \varepsilon^2 > 0$ because the equality case corresponds to either N_1^* or $N_2^* = 0$ and we know that $N_1^* > 0$ and $N_2^* > 0$.

Let us now look at the sign of the numerator. We first consider the following part $(\partial_u g_1(N_1^*) + \partial_u g_2(N_2^*)P^*)$. Combining the two equations on (29), we get that:

$$(\partial_u g_1(N_1^*) + \partial_u g_2(N_2^*)P^*) \leq 0. \tag{31}$$

It remains to look at the sign of $(P^* - 1)$. We prove the following lemma.

Lemma 11 (Property of P^*)**.** *Let* $\mathbf{N}^*$ *be the solution of* (13) *with satisfying hypothesis* (H1) *and* (H3)*. Then, the ratio* P^* *satisfies the following properties:*

- $P^* < 1$ *and* P^* *is increasing if* $K_1 > K_2$*.*
- $P^* > 1$ *and* P^* *is increasing if* $K_1 < K_2$*.*

Before stating the proof of Lemma 11, we conclude the proof of Proposition 9. The estimates of Lemma 11 combine with the previous inequalities (29)-(30)-(31) show that the sign of $\partial_\varepsilon p^*$ only depends on the sign of $(K_2 - K_1)(p_1(0) - p_2(0))$ which concludes the proof of Proposition 9.

Proof of Lemma 11.

We can first show from (27)-(30)-(31) that the monotonicity of P^* only depends on the sign of $(P^* - 1)$. Moreover, from equation (28), we know that the sign of $(P^* - 1)$ is equal to the sign of $-g_1(N_1^*)/N_1^*$ and therefore depends on the position of N_1^* relative to K_1. Without loss of generality we can assume that $r_2 < r_1$.

In addition, we first consider the case $K_2 > K_1$. Our aim is to show that $N_1^* > K_1$. The equilibrium point $\mathbf{N}^*$ of the model satisfies $G_1(N_1^*) = N_2^*$ and $G_2(N_2^*) = N_1^*$ where

$$\begin{aligned} G_1(u) &= -\frac{1}{\varepsilon}(g_1(u) - \varepsilon u) = -\frac{u}{\varepsilon}(f_1(u) - \varepsilon) \\ G_2(u) &= -\frac{1}{\varepsilon}(g_2(u) - \varepsilon u) = -\frac{u}{\varepsilon}(f_2(u) - \varepsilon). \end{aligned}$$

First let us notice that from the hypothesis (H1), we know that $G_1(K_1) = K_1$ and $G_2(K_2) = K_2$. Moreover, since $K_2 > K_1$, we can deduce from hypothesis (H3) that

$$\begin{aligned} G_1(K_2) &= -\frac{K_2}{\varepsilon}(f_1(K_2) - \varepsilon) = K_2 - \frac{K_2}{\varepsilon} f_1(K_2) > K_2 \\ G_2(K_1) &= -\frac{K_1}{\varepsilon}(f_2(K_1) - \varepsilon) = K_1 - \frac{K_1}{\varepsilon} f_2(K_1) < K_1. \end{aligned}$$

Then, since f_1 and f_2 are bounded above by r_1 respectively r_2, we need to discuss with respect to the relative position of ε from r_1 and r_2.

Let us first assume that $\varepsilon < r_2 < r_1$. We know from hypothesis H1 and H3 that fi are decreasing on $(0, \infty)$. With the assumption on ε, we know that $f_i(0) - \varepsilon = r_i - \varepsilon > 0$ and $f_i(K_i) - \varepsilon < 0$. So applying the intermediate value theorem to the monotone functions f_i, there exist unique positive real $K_{i,\varepsilon}$ in $(0, K_i)$ such that $f_i(K_{i,\varepsilon}) = \varepsilon$. Thus, we obtain that $G_i(u) < 0$ on $(0, K_{i,\varepsilon})$ and $G_i(u) > 0$ on $(K_{i,\varepsilon}, \infty)$. Moreover, we can deduce, from the definition of $K_{i,\varepsilon}$ and the assumption on f_i that G_i is increasing on $(K_{i,\varepsilon}, \infty)$. We now prove that $N_1^* > K_1$. We can first observe that

$$G_1(K_2) = \frac{K_2}{\varepsilon}(\varepsilon - f_1(K_2)) > K_2 = G_2^{-1}(K_2).$$

Then, let us first assume that $K_{2,\varepsilon} > K_1$. Since G_2 is only positive on $(K_{2,\varepsilon}, \infty)$ and increasing on $(K_{2,\varepsilon}, \infty)$, we can deduce that G_2^{-1} is increasing over $(0, K_2)$ and

$$G_2^{-1}(K_1) > G_2^{-1}(0) = K_{2,\varepsilon} > K_1 = G_1(K_1).$$

Since G_1 and G_2^{-1} are increasing on (K_1, K_2), we deduce from the intermediate value theorem that N_1^* solving $G_1(N_1^*) = G_2^{-1}(N_1^*)$ belongs to (K_1, K_2).

Let us now assume that $K_{2,\varepsilon} < K_1$, then we have:

$$0 < G_2(K_1) = \frac{K_1}{\varepsilon}(\varepsilon - f_2(K_1)) < K_1.$$

Since G_2^{-1} is increasing on $(0, \infty)$, we deduce that

$$G_2^{-1}(K_1) > K_1 = G_1(K_1).$$

The same argument as above implies that $N_1^* > K_1$.

Let us now assume that $r_2 < \varepsilon < r_1$. In this case, G_2 is positive and increasing on $[0, K_2]$. And we have that

$$0 < G_2(K_1) = \frac{K_1}{\varepsilon}(\varepsilon - f_2(K_1)) < K_1.$$

We deduce that

$$G_2^{-1}(K_1) > K_1 = G_1(K_1). \tag{32}$$

Moreover, as in the previous case, there exists $K_{1,\varepsilon} < K_1$, such that $G_1(K_{1,\varepsilon}) = 0$ and G_1 is negative on $(0, K_{1,\varepsilon})$, G_1 is position on $(K_{1,\varepsilon}, \infty)$. Moreover, we have:

$$G_1(K_2) = \frac{K_2}{\varepsilon}(\varepsilon - f_1(K_2)) > K_2 = G_2^{-1}(K_2). \tag{33}$$

The intermediate value theorem and the definition of N_1^* imply that $N_1^* > K_1$.

Finally, let us assume that $r_2 < r_1 < \varepsilon$. In this case G_1 and G_2 are positive and increasing on $(0, K_2)$. The previous estimates (32) and (33) hold true and we deduce that $N_1^* > K_1$.

In conclusion, if $K_2 > K_1$ then $N_1^* > K_1$. then, We deduce from equation (28) that $P^* > 1$. Conversely if $K_2 < K_1$ the same proof implies that $P^* < 1$ which concludes the proof of Lemma 11.

Proof of Proposition 10.

Let $\varepsilon \in (0, 1]$ and $\mathbf{N}^* = (N_1^*, N_2^*)$ equilibrium of (1). We know from Theorem 1 that for any $p_1(0)$, $p_2(0)$ in $[0, 1]$, the asymptotic proportion p_ε^* satisfies

$$p^* = \frac{p_1(0) + p_2(0)(P^*)^2}{1 + (P^*)^2} \quad \text{with} \quad P^* = \frac{N_2^*}{N_1^*}. \tag{34}$$

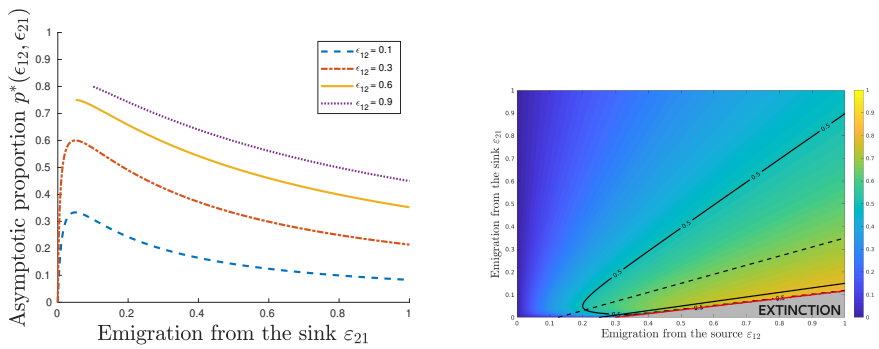
We first study the case where $p_1(0) = 1$ and $p_2(0) = 0$. From equation (34) we see that p^* is a decreasing function with respect to P^*. We thus deduce from Lemma 11 that $p^* < 1/2$ if $K_1 < K_2$ and $p^* > 1/2$ if $K_1 > K_2$.

Conversely, if $p_1(0) = 0$ and $p_2(0) = 1.$, from equation (34) we see that p^* is an increasing function with respect to P^*. We thus deduce from Lemma 11 that $p^* > 1/2$ if $K_1 < K_2$ and $p^* < 1/2$ if $K_1 > K_2$.

Finally, if $K_1 = K_2$ then $P^* = 1$ and $p^* = (p_1(0) + p_2(0))/2$ which concludes the proof of Proposition 10.

A.2 Scenario 2: Source–sink metapopulation

We now turn to the source–sink model with possibly different migration rates between habitats. Let us remind from Theorem 1 and the equilibrium of the model that in this scenario, the asymptotic



(a) $\varepsilon_{21} \mapsto p^*(\varepsilon_{12}, \varepsilon_{21})$ (b) Asymptotic proportion $p^*(\varepsilon_{12}, \varepsilon_{21})$

Figure 13: Behavior of the asymptotic proportion p^* as the function of the dispersal parameters ε_{12} and ε_{21}: (a) behavior of p^* with respect to migration from the sink ε_{21} with various values of the migration rate from the source ε_{12} (dashed blue curve $\varepsilon_{12} = 0.1$, dotted-dashed red curve $\varepsilon_{12} = 0.3$, plain yellow curve $\varepsilon_{12} = 0.6$ and dotted purple curve $\varepsilon_{12} = 0.9$; (b) behavior of p^* with respect to both parameters ε_{12} and ε_{12}. The plain black line describes the level set $p^* = 1/2$, while the red curve corresponds to the extinction limit. The black dashed line corresponds to the parameters value where the metapopulation size $N_1^* + N_2^*$ is maximal.

proportion of a neutral fraction with initial proportion $p_i(0)$ in each patch, is given by the following formula:

$$p^* = \frac{p_1(0) + p_2(0)\dfrac{\varepsilon_{12}\varepsilon_{21}}{(r_2+\varepsilon_{21})^2}}{1 + \dfrac{\varepsilon_{12}\varepsilon_{21}}{(r_2+\varepsilon_{21})^2}}.$$

A.2.1 High migration from the source acts as a "diversity rescue".

From this formula, we can deduce the following properties

Proposition 12 (Trade off between the migration rates ε_{ij})**.** *For any initial condition* $\mathbf{n}(0)$*, the asymptotic proportion* p^* *associated to the fraction* $\mathbf{n}$ *solving* (6)*, is monotonic with respect to migration rate from the source* ε_{12} *while there exists a trade off according to the migration from the sink* ε_{21}*. More precisely, for any* $\varepsilon_{21} \in (0,1)$*, the function* $\varepsilon_{12} \mapsto p^*(\varepsilon_{12}, \varepsilon_{21})$ *is*

- *increasing if* $p_1(0) < p_2(0)$*;*
- *decreasing if* $p_1(0) > p_2(0)$*;*

Moreover, for any $\varepsilon_{12} \in (0,1)$*, the function* $\varepsilon_{21} \mapsto p^*(\varepsilon_{12}, \varepsilon_{21})$ *satisfies the following properties:*

- *it is decreasing if* $(p_1(0) - p_2(0))(r_2 - \varepsilon_{21}) > 0$*;*
- *it is increasing if* $(p_1(0) - p_2(0))(r_2 - \varepsilon_{21}) < 0$*.*

Our results show that migration from the source always acts in the same way. It always increases the contribution from the sink while it reduces the contribution from the source. Indeed, if the fraction

is mainly in the sink that is $p_2(0) > p_1(0)$ then the migration from the source ε_{12} increases the asymptotic proportion p^*. Conversely, if the fraction is mainly in the source that is $p_1(0) > p_2(0)$ then the migration from the source ε_{12} decreases the asymptotic proportion p^*. As in the above scenario, the migration from the good habitat tends to balance the contribution from the two habitats. However, the effect of the migration from the sink ε_{21} is nonlinear and a trade off occurs. We see that the trade off only depends on the quality of the sink and it do not depend on the migration from the source ε_{12} neither on the quality of the source characterized by the per capita growth rate r_1 and the carrying capacity K_1 of the source. For instance if the fraction is mainly in the sink, the migration starts to increase the asymptotic proportion of the fraction from the sink. But when the migration rate reaches the threshold r_2 then its effect reverses and it starts to decrease this asymptotic proportion. Thus, small migration from the sink helps fraction from the sink to contribute to the metapopulation while a large migration from the sink reduces this contribution.

As already done in the previous scenario, we now look at the precise contribution of each habitat. More precisely, we assume that the fraction is only present in one habitat, that is either $n_1(0) = N_1^*$ and $n_2(0) = 0$ or $n_1(0) = 0$ and $n_2(0) = N_2^*$. In this case we quantify the asymptotic proportion p^* by comparing it to $1/2$ which corresponds to an equal contribution from each habitat.

Proposition 13 (Low migration from the source preserved source diversity)**.** *Let us consider a fraction that fully occupied only one habitat, either $p_1(0) = 1$ and $p_2(0) = 0$ or $p_1(0) = 0$ and $p_2(0) = 1$. Then the asymptotic proportion satisfies:*

- $p^* < 1/2$ *if* $\left(\varepsilon_{12} - \dfrac{(r_2+\varepsilon_{21})^2}{\varepsilon_{21}}\right)\big(p_1(0) - p_2(0)\big) < 0$;
- $p^* = \dfrac{1}{2}$ *if* $\varepsilon_{12} = \dfrac{(r_2+\varepsilon_{21})^2}{\varepsilon_{21}}$;
- $p^* > 1/2$ *if* $\left(\varepsilon_{12} - \dfrac{(r_2+\varepsilon_{21})^2}{\varepsilon_{21}}\right)\big(p_1(0) - p_2(0)\big) > 0$.

As we could expect, the contribution of each habitat crucially depends on the migration rates ε_{12} and ε_{21}, and the quality of the death rate in the source r_2. Conversely, the quality of the source do not play any role in the contribution.

We can first notice that the migration from the source plays a crucial role in the preservation of the fraction from the source. Indeed, let us compare the contribution from the sink p^*_{sink}, corresponding to initial condition with $p_1(0) = 0$ and $p_2(0) = 1$ and the the contribution from the source $p^*_{source} = 1 - p^*_{sink}$. From results of Proposition 13, if the migration rate from the source ε_{12} is above a threshold

ε_c equal to $\varepsilon_c = 4r_2$, then, the contribution from the sink is always smaller than the contribution from the source because $p^*_{sink} < 1/2$ (see Figure 13).

On top of that, our result shows that if the migration from the source is high compare to the migration from the sink, that is $\varepsilon_{12} > (r_2 + \varepsilon_{21})^2/\varepsilon_{21}$ then, the contribution from the sink is higher than the contribution from the source ($p^*_{sink} > 1/2$). So we need large migration from the source to preserve diversity from the sink.

Proof of Proposition 12.

Let $p_1(0)$, $p_2(0)$ be in $[0,1]$. We know from Theorem 1, that if the metapopulation is composed of a source and a sink, that is f_i satisfies hypothesis (H1) and (H2), the asymptotic proportion p^* associated to $p_1(0)$ and $p_2(0)$ is given for any $(\varepsilon_{12}, \varepsilon_{21}) \in (0,1]^2$ by:

$$p^*(\varepsilon_{12}, \varepsilon_{21}) = \frac{p_1(0) + p_2(0)\dfrac{\varepsilon_{12}\varepsilon_{21}}{(r_2+\varepsilon_{21})^2}}{1 + \dfrac{\varepsilon_{12}\varepsilon_{21}}{(r_2+\varepsilon_{21})^2}}. \tag{35}$$

We first look at the behavior of p^* with respect to ε_{12}. Differentiating the expression (35) with respect to ε_{12}, we obtain:

$$\partial_{\varepsilon_{12}} p^*(\varepsilon_{12}, \varepsilon_{21}) = \frac{(p_2(0) - p_1(0))\dfrac{\varepsilon_{21}}{(r_2+\varepsilon_{21})^2}}{\left(1 + \dfrac{\varepsilon_{12}\varepsilon_{21}}{(r_2+\varepsilon_{21})^2}\right)^2}. \tag{36}$$

Thus, if $p_1(0)) > p_2(0)$ then $\partial_{\varepsilon_{12}} p^*(\varepsilon_{12}, \varepsilon_{21}) < 0$ and p^* is decreasing with respect to ε_{12}.

Let us now look at the behavior of p^* with respect to ε_{21}. Differentiating the expression (35) with respect to ε_{21}, we obtain

$$\partial_{\varepsilon_{21}} p^*(\varepsilon_{12}, \varepsilon_{21}) = \frac{(p_2(0) - p_1(0))\dfrac{\varepsilon_{12}(r_2+\varepsilon_{21})(r_2-\varepsilon_{21})}{(r_2+\varepsilon_{21})^2}}{\left(1 + \dfrac{\varepsilon_{12}\varepsilon_{21}}{(r_2+\varepsilon_{21})^2}\right)^2}. \tag{37}$$

If $p_1(0) > p_2(0)$, then we have $\partial_{\varepsilon_{21}} p^*(\varepsilon_{12}, \varepsilon_{21}) < 0$ if $\varepsilon_{21} > r_2$ while $\partial_{\varepsilon_{21}} p^*(\varepsilon_{12}, \varepsilon_{21}) > 0$ if $\varepsilon_{21} < r_2$. This concludes the proof of Proposition 12.

Proof of Proposition 13.

Let $p_1(0) = 1$ and $p_2(0) = 0$,then we know from Theorem 1, that if the metapopulation is composed of a source and a sink, that is f_i satisfies hypothesis (H1) and (H2), the asymptotic proportion p^*

associated to $p_1(0)$ and $p_2(0)$ is given for any $(\varepsilon_{12}, \varepsilon_{21}) \in (0,1]^2$ by:

$$p^*(\varepsilon_{12}, \varepsilon_{21}) = \frac{1}{1 + \frac{\varepsilon_{12}\varepsilon_{21}}{(r_2 + \varepsilon_{21})^2}}.$$

A direct computation shows that $p^* \leq 1/2$ is equivalent to $\varepsilon_{12} \leq (r_2 + \varepsilon_{21})^2/\varepsilon_{21}$. Conversely, $p^* > /2$ if and only if we have $\varepsilon_{12} > (r_2 + \varepsilon_{21})^2/\varepsilon_{21}$ which concludes the proof of Proposition 13.

B The individual–based model of neutral genetic fractions.

We aim to compare our deterministic model with the following stochastic individual-based model. We assume that our metapopulation is composed of several individuals located in two types of habitat. Thus, we consider the spacial domain $\{0,1\}$ where 0 corresponds to the first habitat and 1 to the second habitat. Each individual i is described over time t through its location $X_i(t) \in \{0,1\}$. On top of that, we assume that our metapopulation is composed of J neutral fractions. For each subgroup $j \in \{1, \ldots, J\}$, we denote by $\mathbf{X}^j(t) = \left\{X_1^j(t), \cdots, X_{N_t^j}^j(t)\right\}$ the locations at time t of individuals belonging to the subgroup j, where N_t^j is the number of individuals at time t in the subgroup j.

Then, the location of all the individuals of the metapopulation $\mathbf{X}$ at time t is $\mathbf{X}(t) = \left\{\mathbf{X}^1(t), \ldots, \mathbf{X}^J(t)\right\} = \left\{X_1^1(t), \ldots, X_{N_t^1}^1(t), \ldots, X_1^J(t), \ldots, X_{N_t^J}^J(t)\right\}$. We use the set of all finite point measures $\mathcal{M}$ defined by

$$\mathcal{M} = \left\{\sum_{i=1}^{N} \delta_{x_i}\ , N \geq 0\ , x_1, x_2, \cdots, x_N \in \{0,1\}\right\}$$

. to describe the empirical density of the metapopulation given by the stochastic process:

$$\nu_t^n = \frac{1}{n} \sum_{j=1}^{J} \sum_{i=1}^{N_t^j} \delta_{X_i^j(t)}$$

where N_t^j is the number of individuals of subgroup j alive at time t, and $X_i^j(t)$ are their location at time t. The parameter n is the typical size of the population which eventually tends toward ∞. The dynamics of the metapopulation is described by the following process:

(a) The initial distribution $\nu_0^n \in \mathcal{M}$ is given by $\nu_0^n = \frac{1}{n} \sum_{j=1}^{J} \sum_{i=1}^{N_0^j} \delta_{X_i^j(0)}$ where $\sum_{j=1}^{J} N_0^j(0) = n$.

(b) For each individual located at $x \in \{0,1\}$, we define three independent exponential clocks as follows:

- reproduction rate $b(x)$
- natural death rate $d(x)$
- competition mortality rate $\dfrac{b(x)-d(x)}{nK(x)}\sum_{j=1}^{J}\sum_{i=1}^{N_t^j}\delta_x(X_j^i(t))$ where $K(x)$ is the carrying capacity in location x and $U(x,y)=0$ if $x\neq y$ and $U(x,x)=1$.

(c) If an individual dies, it disappears definitively.

(d) Each individual generates descendants that either remain in the parent location x or move to an other location y with a probability $\varepsilon(x,y)$ which depends on the parent location x and its new location y.

In our model, we see that the process ν_t^n is the sum of J processes $\nu_t^{j,n}$ corresponding to each subgroup and defined by $\nu_t^{j,n}=\dfrac{1}{n}\sum_{i=1}^{N_j(t)}\delta_{X_i^j(t)}$, starting from $\nu_0^{j,n}=\dfrac{1}{n}\sum_{i=1}^{N_j(0)}\delta_{X_i^j(0)}$.

We can deduce the infinitesimal generator L^n for the entire population process ν_t^n defined for a large class of functions ϕ from $\mathcal{M}$ into $\mathbb{R}$ by:

$$\begin{aligned}L^n\phi(\nu)=\;& n\sum_{x=0}^{1}\nu(x)\sum_{z=0}^{1}\varepsilon(x,z)\left[\phi\left(\nu+\frac{1}{n}\delta_{x+z}\right)-\phi(\nu)\right]b(x)\\ &+n\sum_{x=0}^{1}\nu(x)\left[\phi\left(\nu-\frac{1}{n}\delta_x\right)-\phi(\nu)\right]\left\{d(x)+\frac{b(x)-d(x)}{K(x)}\nu(x)\right\}.\end{aligned}$$

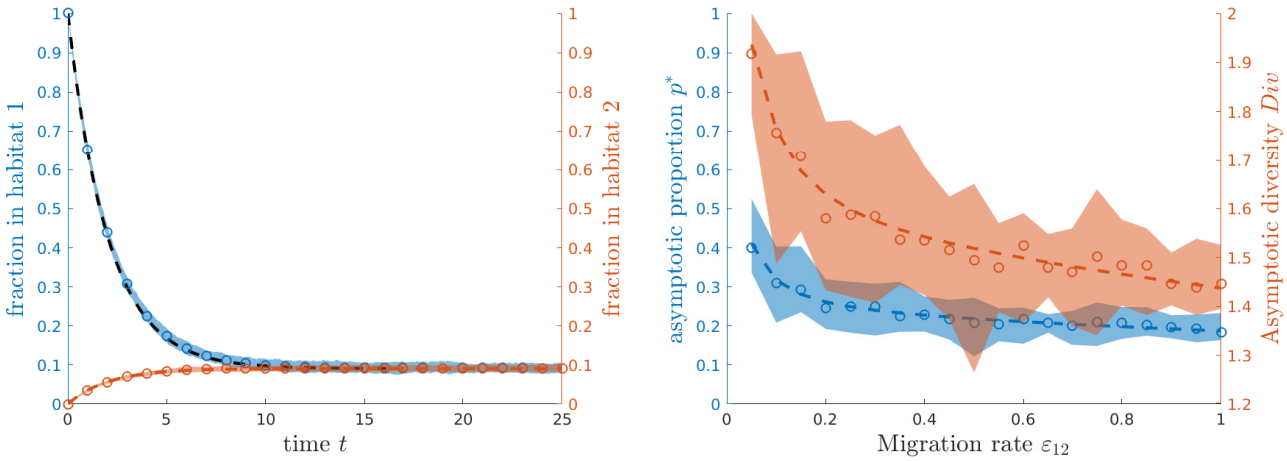
Then using classical results on stochastic process (Bansaye and Méléard, 2015), we can deduce that the process (ν_t^n) converges in law to the deterministic continuous functions $\mathbf{N}(t)=(N_1(t),N_2(t))$ solution of the following ODE systems:

$$\begin{cases}N_1'=r_1N_1\left(1-\dfrac{N_1}{K_1}\right)-b_1\varepsilon_{12}N_1+b_2\varepsilon_{21}N_2\\ N_2'=r_2N_2\left(1-\dfrac{N_2}{K_2}\right)-b_2\varepsilon_{21}N_2+b_1\varepsilon_{12}N_1\end{cases}.$$

Knowing the process ν_t^n, we can define the infinitesimal generator $L_t^{j,n}$ for each subgroup process $\nu_t^{j,n}$ as follows:

$$\begin{aligned}L_t^{j,n}\phi(\mu)=\;& n\sum_{x=0}^{1}\mu(x)\sum_{z=0}^{1}\varepsilon(x,z)\left[\phi\left(\mu+\frac{1}{n}\delta_{x+z}\right)-\phi(\mu)\right]b(x)\\ &+n\sum_{x=0}^{1}\mu(x)\left[\phi\left(\mu-\frac{1}{n}\delta_x\right)-\phi(\mu)\right]\left\{d(x)+\frac{b(x)-d(x)}{K(x)}{}^{1}\nu_t^n(x)\right\}.\end{aligned}$$

We deduce that each process $(\nu_t^{j,n})$ whose infinitesimal generator depends on ν_t^n, converges in law to



(a) Proportion in each habitat

(b) Asymptotic proportion and diversity

Figure 14: Stochastic and deterministic asymptotic proportion p^* (a) and diversity Div (b) of a metapopulation composed of 2 fractions. The dotted lines corresponds to our analytical formulas (10) (a) and (8) (b). The circles correspond to the median of respectively the asymptotic proportion (a) and the asymptotic diversity (b) of the IBM model averaged over 10^3 replicates ($n = 10$ individuals). Shading envelope is interval between 0.01 and 0.99 quantiles of respectively the asymptotic proportion and diversity obtained from the individual-based model.

the deterministic continuous functions $\mathbf{n}_t^j$ where $\mathbf{n}_t^j = (n_1^j(t), n_2^j(t))$ solves the ODEs system

$$\begin{cases} n_1' = r_1 n_1 \left(1 - \dfrac{N_1}{K_1}\right) - b_1 \varepsilon_{12} n_1 + b_2 \varepsilon_{21} n_2 \\ n_2' = r_2 n_2 \left(1 - \dfrac{N_2}{K_2}\right) - b_2 \varepsilon_{21} n_2 + b_1 \varepsilon_{12} n_1 \end{cases} . \tag{38}$$

Numerical simulations. We compare our analytical result associated to the ODE model (38) with two of the individual-based model: the asymptotic proportion p^* of fractions in each habitat and the asymptotic diversity index Div. We assume that the metapopulation is composed of $J = 2$ fractions initially located respectively in habitat 1 and 2. We observe that our analytical results fit well with both the temporal dynamics of the proportions and the dependence to parameters to asymptotic proportion and diversity even if the typical number of individuals in the individual-based model is relatively small $n = 10$.

C Numerical simulations for initially isolated population.

C.1 Symmetric migration always promotes diversity.

We first assume that the migrations between habitats are identical $\varepsilon_{12} = \varepsilon_{21} = \varepsilon$ with ε in $[0, 1]$. We investigate two cases: 1) where $K_1 > K_2$ and 2) where $K_1 < K_2$. In the first case, habitat 1 is better

than habitat 2 because both the per capita growth rate and the carrying capacity of habitat 1 are larger than that of habitat 2. Conversely, in the second case, habitat 1 has a higher per capita growth rate but habitat 2 has a larger carrying capacity.

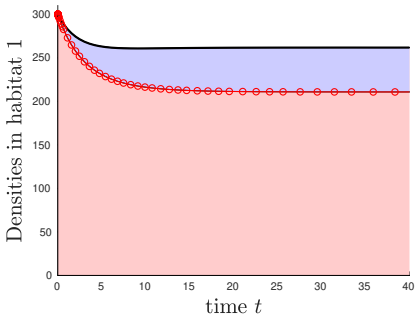
We first observe that even if the two subpopulations are not initially at equilibrium, the fractions spread and persist in all the habitats. For instance, fraction 1 is not present initially in habitat 2 but its density will rapidly grow to a positive equilibrium (see Figure 15(a)-(b) and Figure 15(d)-(e). So, even if the metapopulation is not at equilibrium, the richness of the genetic fraction is preserved at global scale as well as the local scale. Moreover, we can see from Figure 15(c) and Figure 15(f) that in both cases the proportions of each fraction in each habitat will converge to a proportion which is the same over the habitats. As in the equilibrium case, we observe that the asymptotic proportion of each fraction crucially depends on the ratio between the two carrying capacities.

C.2 Directional migration ($\varepsilon_{12} \neq \varepsilon_{21}$)

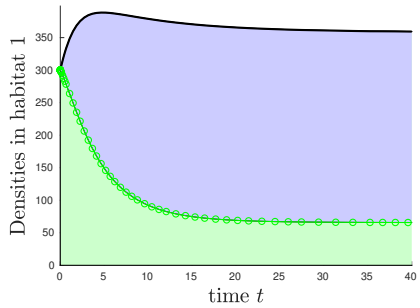
We now look at the effect of a directional migration on the dynamics of neutral genetic diversity. We may assume that migration ε_{12} from habitat 1 might be different from migration ε_{21} from habitat 2. As above, we first show that the proportion of each fraction $\mathbf{p}_1$ and $\mathbf{p}_2$ converges to asymptotic quantities p_1^* respectively p_2^* which are the same in both habitats (see Fig. 16). We can first notice that the qualitative behavior of the asymptotic proportion p^* does not truly depend on the carrying capacities. Indeed, we observe from Fig. 16 that the migration from the lower quality habitat 2 tends to decrease the contribution from the better quality habitat 1 while migration from the better habitat 1 reinforces its contribution.

However, the strength of the contribution of the habitat depends on the relative difference of carrying capacities K_1 and K_2 . More precisely, if $K_1 > K_2$ which means that habitat 1 is bigger than habitat 2, then if the migration from habitat 2 is not so high enough then the contribution from habitat 1 is always bigger than the one from habitat 2. Indeed, we can see from Fig. 16 that $p^* > 1/2$ for $\varepsilon_{21} < 0.2$ and any ε_{12}. Conversely, if $K_1 < K_2$, a low migration from habitat 1 ($\varepsilon_{12} < 0.1$) implies that contribution from habitat 2 is higher than the one from habitat 1. Even if the qualitative behavior seems symmetric with respect to K_1 and K_2, the thresholds are different.

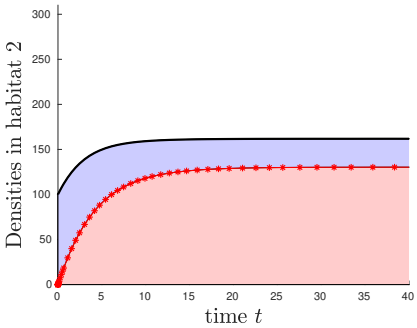
We now look at the effect of migration on the local and global genetic diversity indices. We can first notice that the behavior of the diversity with respect to the dispersal parameters is no more monotonic. We can observe from Figure 17 that for any carrying capacities, the diversity first increases with respect to either migration from the habitat 1 or 2 until a threshold which corresponds to the



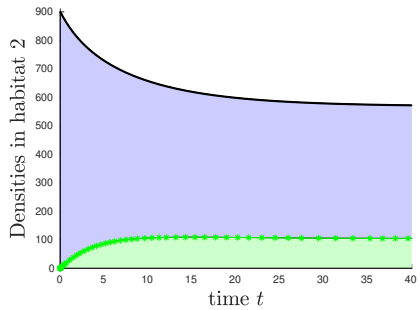
(a) Habitat 1 with $K_1 > K_2$



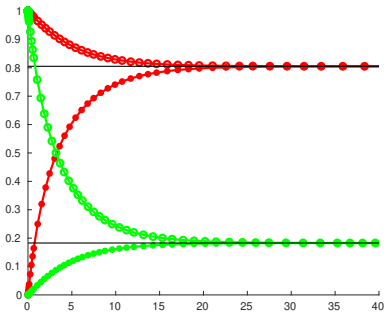
(b) Habitat 1 with $K_1 > K_2$



(c) Habitat 2 with $K_1 > K_2$

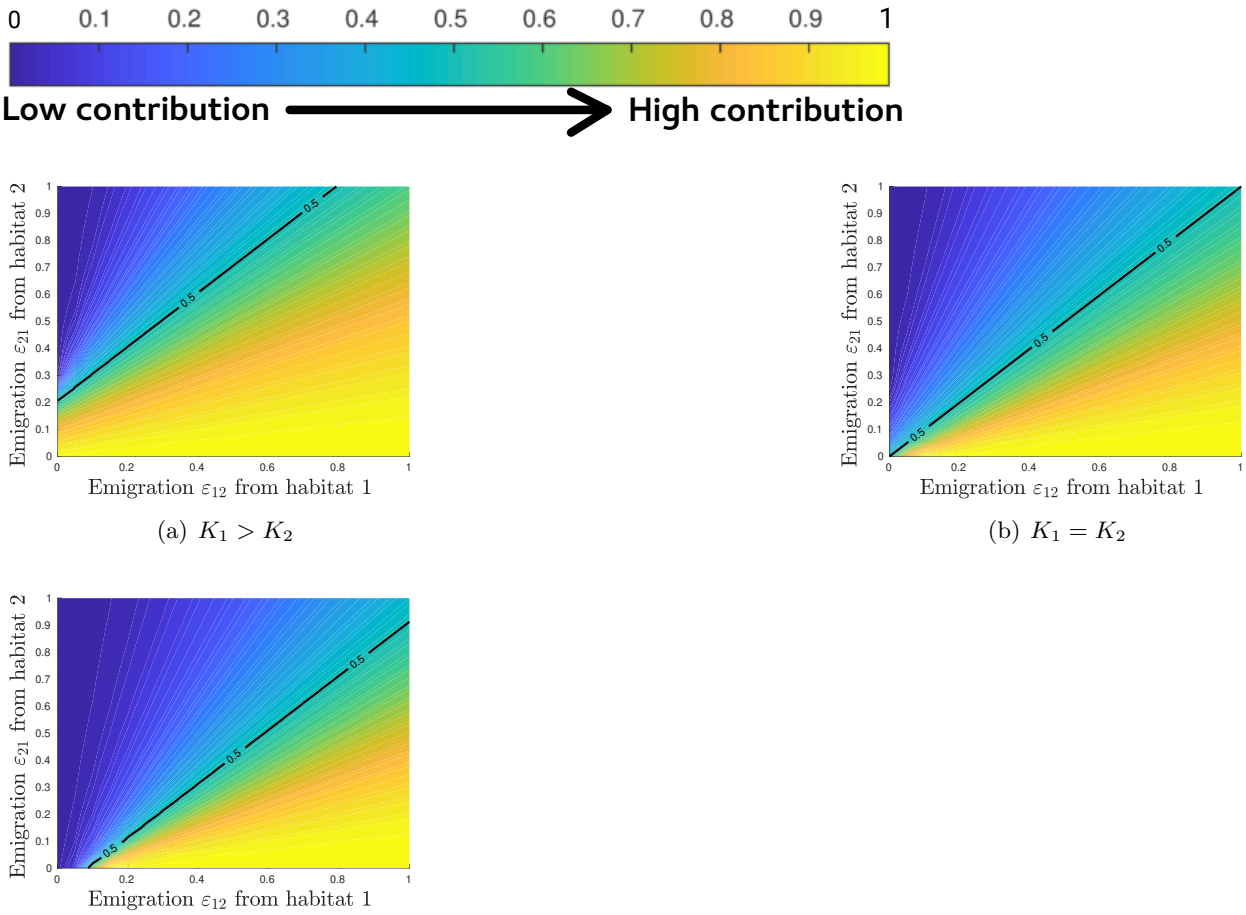


(d) Habitat 2 with $K_1 < K_2$



(e) Proportions $\mathbf{p}_1$ in the 2 habitats

Figure 15: Evolution of the two fractions $\mathbf{n}_1$ and $\mathbf{n}_2$ inside the metapopulation $\mathbf{N} = (N_1, N_2)$ composed of two favorable habitats ($r_1 = 0.3$ and $r_2 = 0.1$) with various carrying capacities: (a)-(c) $K_1 = 300$ and $K_2 = 100$; (d)-(f) $K_1 = 300$ and $K_2 = 900$.

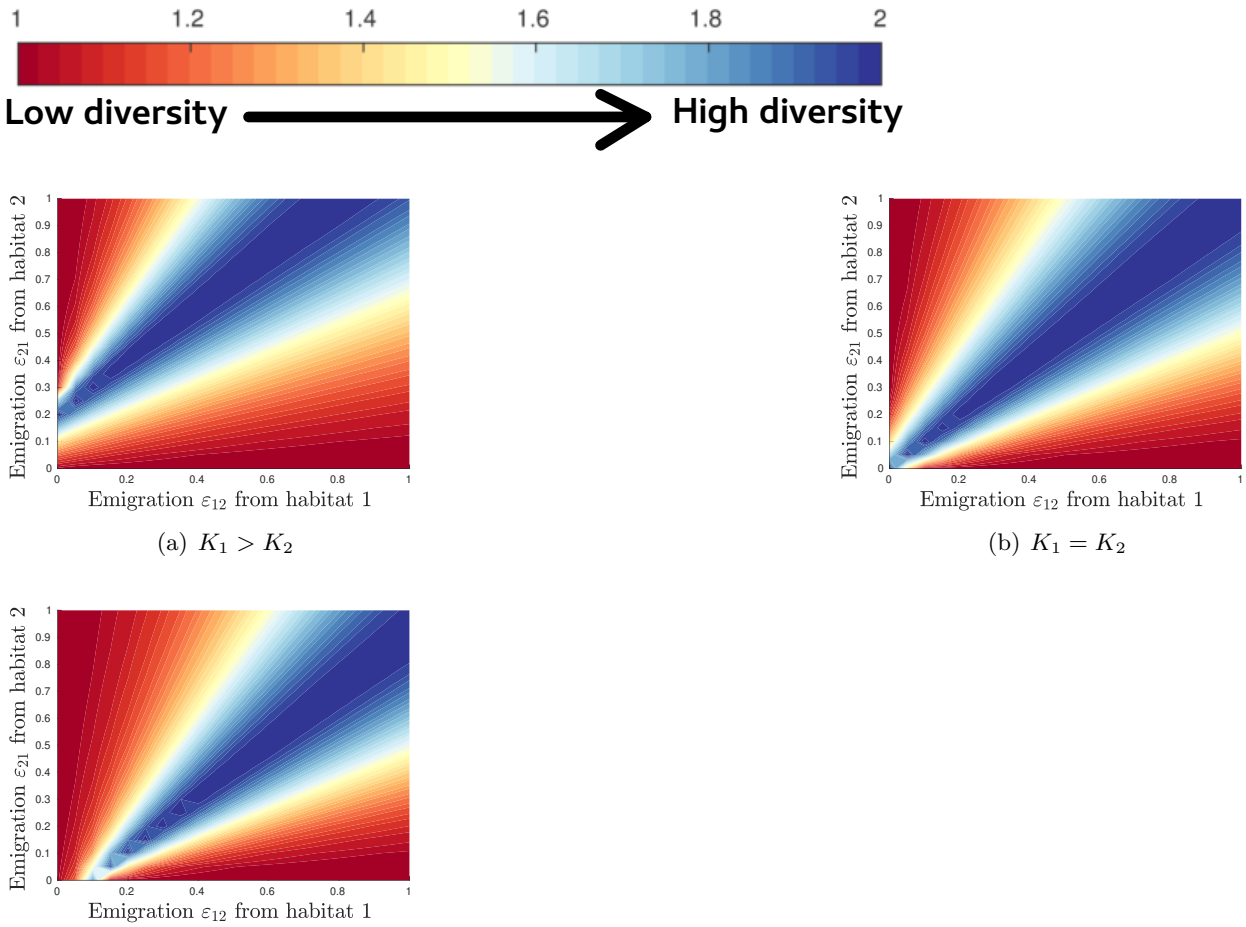


(a) $K_1 > K_2$

(b) $K_1 = K_2$

(c) $K_1 < K_2$

Figure 16: Behavior of the asymptotic proportion of the fraction 1 $\mathbf{p}_1$ with respect to migration rate ε_{12} and ε_{21} for different quality habitats: (a) $K_1 = 1000$; $K_2 = 100$ (b) $K_1 = K_2 = 500$ and (c) $K_1 = 100$; $K_2 = 1000$. The black line corresponds to the level set $p_1 = 0.5$. The fraction is initially in habitat 1 and $r_1 = 0.3$, $r_2 = 0.1$.



(a) $K_1 > K_2$

(b) $K_1 = K_2$

(c) $K_1 < K_2$

Figure 17: Behavior of the $\gamma-$diversity as a function of the migrations rates ε_{12} and ε_{21} for various carrying capacities: (a) $K_1 = 1000$, $K_2 = 100$, (b) $K_1 = K_2 = 500$ and (c) $K_1 = 100$, $K_2 = 1000$. Metapopulation is initially composed of 2 fractions, one in habitat 1 and the other in habitat 2. Habitat qualities are stated to $r_1 = 0.3$, $r_2 = 0.1$. The plain black line corresponds to the case where the proportion of the fraction 1 is equal to 0.5.

value $p^* = 1/2$ and then it may decrease. We can observe that the high level of diversity is reached when migration rates are of the same order, conversely to the case of source–sink model where the asymmetry of habitats forces an asymmetry in the migration. However, a small asymmetry occurs if we look closely to the maximum of diversity.