Effects of colonization asymmetries on metapopulation persistence

Séverine Vuilleumier a,∗, Benjamin M. Bolker b,1, Olivier Lévêque c

a Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne, Switzerland
b Biology Department, University of Florida, Box 118525, Gainesville, FL 32611-8525, USA
c Laboratoire de Théorie de l’Information (LTHI), École Polytechnique Fédérale de Lausanne (EPFL), Bâtiment INR, Station 14, 1015 Lausanne, Switzerland

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A B S T R A C T
Ocean currents, prevailing winds, and the hierarchical structures of river networks are known to create asymmetries in re-colonization between habitat patches. The impacts of such asymmetries on metapopulation persistence are seldom considered, especially rarely in theoretical studies. Considering three classical models (the island, the stepping stone and the distance-dependent model), we explore how metapopulation persistence is affected by (i) asymmetry in dispersal strength, in which the colonization rate between two patches differs in direction, and (ii) asymmetry in connectivity, in which the overall colonization pattern displays asymmetry (circularizing or dendritic networks). Viability can be drastically reduced when directional bias in dispersal strength is higher than 25%. Re-colonization patterns that allow for strong local connectivity provide the highest persistence compared to systems that allow circulation. Finally, asymmetry has relatively weak effects when metapopulations maintain strong general connectivity.

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1. Introduction

Most models of metapopulation dynamics assume that dispersal between patches is symmetric—i.e., that for any pair of patches, the probability of interpatch dispersal and hence the re-colonization probability is the same in both directions. Most of the literature on dispersal asymmetry focuses on source–sink metapopulation dynamics, which arise from variation in productivity of populations (Pulliam, 1988; Morris, 1991; Kawecki and Stearns, 1993; Kawecki, 1995; Holt, 1996; Saether et al., 1999; Kawecki and Holt, 2002). Directional dispersal resulting from heterogeneity (due to environmental gradients such as prevailing winds, ocean and river currents) is also well known to affect the symmetry of colonization processes between populations (Largier, 2003; Schooley and Wiens, 2003; Levin, 2006; Thorrold, 2006; Cheal et al., 2007; Bay et al., 2008). In particular, ecologists have documented asymmetric dispersal patterns for freshwater fish populations (Bolnick et al., 2008), for marine and riverine invertebrates (Lutscher et al., 2007; Bay et al., 2008; Young et al., 2008), and for various plant species (Friedman and Stein, 1980; Keddy, 1981; Watkinson, 1985; Gornall et al., 1998; Imbert and Lefèvre, 2003). Spatial heterogeneity can also create asymmetric patterns in the spatial distribution of connectivity among populations, as well as asymmetries in re-colonization rates between pairs of patches. For example, the fractal and hierarchical structure of river networks creates sub-structures (tributaries) that are strongly locally connected through river segments that allow colonization only in a particular direction. Such dendritic networks are found in watersheds and cave ecosystems as well as in river networks (Fagan, 2002; Benda et al., 2004; Finn et al., 2006; Labonne et al., 2008). Similarly, marine species are expected to disperse under the influence of ocean currents or depending on current bifurcations and large scale movement of water (Caley et al., 1996). Studies of a variety of empirical systems have shown that island and isolation-by-distance metapopulation models with homogeneous re-colonization patterns cannot capture the dynamics, nor the genetic structure, of such metapopulations (Gaines et al., 2003; Bode et al., 2006; Bay et al., 2008; Labonne et al., 2008; Muneepeerakul et al., 2008; Chaput-Bardy et al., 2009; Hughes et al., 2009). Although there is considerable evidence for various forms of asymmetry in re-colonization, the properties of metapopulation persistence under these conditions have been poorly explored. The few models that have considered an asymmetric re-colonization pattern make the simplifying assumption that the number of patches is very small, usually two (Pulliam and Danielson, 1991; Kawecki and Holt, 2002; Amarasekare, 2004), or that the asymmetry is either very weak (Ovaskainen, 2003) or complete (Vuilleumier and Possingham, 2006).

We consider here two types of asymmetries: asymmetry in dispersal strength and asymmetry in connectivity. Asymmetry in dis-
persistence describes the situation where the colonization rate, from patch $i$ to patch $j$, and the colonization rate in the reverse direction, from patch $j$ to patch $i$, differ in strength. These differences could be due to environmental gradients (e.g., wind, ocean currents) that favor dispersal in one direction. We define an asymmetry factor $0 \leq d \leq 1/2$ that characterizes the fraction of colonization that occurs in the unfavored direction. Under asymmetry in connectivity, the re-colonization rate in either direction between any two connected patches is either identical or perfectly asymmetric, but the global arrangement of connections has a directional bias that ranges from 0 (all asymmetric connections are oriented in the same direction, “downwind”) to 1/2 (asymmetric connections are oriented at random).

These two variants of re-colonization asymmetries are applied to three classical models: the island model, where re-colonization probabilities are identical between any two given habitat patches; the stepping stone model, where empty habitat patches can only be re-colonized by neighboring occupied patches; and the distance-dependent model, where re-colonization probabilities are assumed to decay exponentially with the inter-patch distance.

We first define the connectivity matrix resulting from the various colonization models considered. Second, following Ovaskainen and Hanski (2001), we estimate the metapopulation capacity, which corresponds to the leading eigenvalue of the connectivity matrix, for each case considered. Analytical solutions are presented when possible (for most cases of asymmetry in dispersal strength); otherwise we compute the eigenvalues numerically. We then run stochastic simulations in order to estimate extinction probabilities and to explore the relationship between metapopulation capacity and extinction when the number of habitat patches is finite and environmental stochasticity affects the rate of extinction and colonization.

We demonstrate that asymmetries can drastically affect metapopulation capacity and persistence, and provide recommendations on the use of metapopulation models to estimate persistence when asymmetry in the recolonization pattern is expected.

2. Methods

2.1. Metapopulation models


Metapopulation persistence depends on the balance between the probability of local population extinction and the re-colonization of empty habitat patches (Levins, 1969; Hanski, 1999). The dynamics of a metapopulation were first described by Levins (1969, 1970) in a continuous-time, deterministic island model, which considers $n$ equivalent patches having an equal probability of colonizing any of the $n-1$ other patches. The change in the expected fraction of occupied patches $p$ is determined by the local extinction rate ($e$) and the colonization rate ($c$). It follows that

$$\frac{dp}{dt} = cp(1-p) - ep,$$

which has a globally stable fixed point when

$$p^* = 1 - \frac{e}{c} > 0.$$

(1)

This model assumes a uniform re-colonization pattern in which each habitat patch has the same probability of re-colonization. A variant of the Levins model proposed by Hanski and Gyllenberg (1997) considers the re-colonization pattern as the product of $M$, where $c$ is the colonization rate of the focal species and the matrix $M$ describes the re-colonization pattern. In this $n \times n$ matrix, the element $m_{ij}$ characterizes the probability of colonization from habitat patch $i$ to habitat patch $j$. Under the island model, $m_{ii} = 1$ for all $i \neq j$. If we instead assume that colonization can only occur to and from neighboring patches, we obtain a stepping stone model (Kimura and Weiss, 1964) and the element of the matrix $M$, $m_{ij}$ will be different from zero only if $|i-j| = 1$. In this case, a metapopulation can persist if

$$1 - e Rc > e,$$

(Durrett and Levin, 1994), where $R$ is the number of neighboring populations. This condition also applies to a two-dimensional lattice model (Durrett and Levin, 1994).

Considering spatially distributed populations in which colonization decreases exponentially with distance, we have (Hanski, 1999):

$$m_{ij} = \begin{cases} \exp(-\alpha d) & \text{if } i \neq j \\ 0 & \text{if } i = j \end{cases}$$

where $d_{ij}$ is the distance between the habitat patches and $\alpha = 1/h$ sets the migration range of the focal species with $h$ being its mean dispersal distance. As $\alpha$ increases, the species dispersal range decreases.

The deterministic equation describing the evolution of the state of the system is given in Ovaskainen and Hanski (2001) for a discrete-time model:

$$p_j(t+1) - p_j(t) = c \sum_i m_{ij} p_i(t)(1 - p_j(t)) - ep_j(t)$$

where $p_j(t)$ denotes the probability that patch $j$ is occupied at time $t$. Note that Eq. (5) is only accurate if the occupancy probabilities in different patches are temporally uncorrelated. For a system with a large number of patches, in which each habitat patch contributes equally to the dynamics of the system, Eq. (1) provides a good approximation to Eq. (5).

Ovaskainen and Hanski (2001) show that in the case where the matrix $M$ is irreducible, an equilibrium solution $p^* > 0$ to the above equation exists if and only if

$$\lambda_M > \frac{e}{c},$$

where $\lambda_M$ is the largest eigenvalue of the matrix $M$.

Our main object of investigation in the following is twofold. First, we will study in detail, for the various models considered, the behavior of the largest eigenvalue of the landscape matrix $M$. Second, we will compare the viability threshold (6), obtained with the deterministic model of Ovaskainen and Hanski (2001), to that obtained numerically with a simple stochastic model of extinctions and colonizations.

2.2. Defining patterns of asymmetry

2.2.1. Asymmetry in dispersal strength

We characterize the asymmetry in dispersal strength by a factor $d$, varying from 0 (complete asymmetry) to 1/2 (complete symmetry). If $c$ is the total colonization rate from a given patch, then $c(1 - d)$ represents the total colonization rate in the main direction of colonization and $cd$ represents the total colonization rate in the other direction.

To allow comparison of the impact of asymmetry in the island model, the stepping stone model and the distance-dependent model, we normalize the largest eigenvalue of the adjacency matrix $M$. Thus, we assume that the largest row-sum of the matrix $M$ approaches 1 for large system size (and also that $m_{ii} = 0$ for all $i$). Under this normalization condition, the largest eigenvalue of $M$ also approaches 1 in the symmetric case. In practically all the situations considered in this section, the matrix $M$ is irreducible, so condition (6) applies. The only exception arises in extreme cases where the matrix $M$ is completely asymmetric (i.e. there is no cycle in the graph of patch connections), in which case extinction occurs with probability one, regardless of the system parameters.

In the remainder of this section (except for the grid stepping stone model) we assume that the landscape matrix $M$ has a Toeplitz structure, that is, $m_{ij} = f(i-j)$ for some function $f$ (see Gray, 2006).
The choice of the function \( f \) depends on the model considered (stepping stone, island or distance-dependent model) and the asymmetry introduced in the model. In order to investigate the impact of asymmetry, we further assume that

\[
m_{ij} = \begin{cases} f_+(|i-j|) & \text{if } j > i \\ 0 & \text{if } i = j \\ f_-(|i-j|) & \text{if } i > j \end{cases}
\]  
(7)

where \( f_+ \) and \( f_- \) are non-negative and decreasing functions on the set of positive integers obeying the following normalization conditions:

\[
\lim_{n \to \infty} \sum_{k=1}^{n/2} f_+(k) = d \quad \text{and} \quad \lim_{n \to \infty} \sum_{k=1}^{n/2} f_-(k) = 1 - d
\]

(8)

where \( d \) is the asymmetry factor of the model. Notice that as \( d \in [0, 1/2] \), the main direction of colonization under this model is the direction associated with the decay function \( f_- \). Condition (8) ensures that the largest row-sum of the matrix \( M \) for large system size \( n \) tends to 1.

**Island model.** In the island model, assuming that all habitat patches can be re-colonized from any other occupied habitat patch, we set \( f_+(k) = d/Z \forall k \geq 1 \) and \( f_-(k) = (1-d)/Z \forall k \geq 1 \)

(9)

where the normalization constant \( Z \) is taken to be \( Z = n/2 \), which ensures that condition (8) is satisfied. This leads to the matrix model

\[
m_{ij} = \begin{cases} \frac{d}{Z} & \text{if } j > i \\ 0 & \text{if } i = j \\ \frac{(1-d)}{Z} & \text{if } i > j \end{cases}
\]

(10)

**Stepping stone model.** In the stepping stone model, assuming that only neighboring habitat patches can be re-colonized, we have

\[
f_+(k) = d \quad \text{if } k = 1 \quad \text{and} \quad f_+(k) = 0 \quad \text{otherwise}
\]

(11)

and

\[
f_-(k) = 1-d \quad \text{if } k = 1 \quad \text{and} \quad f_-(k) = 0 \quad \text{otherwise}
\]

(12)

which leads to the matrix model

\[
m_{ij} = \begin{cases} d & \text{if } j = i + 1 \\ 1-d & \text{if } j = i + 1 \\ 0 & \text{otherwise} \end{cases}
\]

(13)

**Distance-dependent models.** To investigate the distance-dependent model, we focus on a model in which the colonization rate decreases exponentially with the ratio of the distance between habitat patches \(|i-j|\) normalized by the average colonization distance \( h \) of the species in focus, as suggested by Hanski (1999).

Additionally, for this model, we apply two forms of asymmetry: weak and strong asymmetry, which differ in the following sense: while the first model only favors the dispersal strength in one direction, the second one also creates a bias in the average colonization distances (see Fig. 1).

Under the **weakly asymmetric distance-dependent model**, the asymmetry factor \( d \) only enters into the matrix \( M \) as a weighting factor, as in the previously studied models. Asymmetry translates into a shift in the strength of colonization in one direction compared to the other. More precisely, we have

\[
f_+(k) = d \exp(-\alpha k)/Z \quad \forall k \geq 1 \quad \text{and} \quad f_-(k) = (1-d)\exp(-\alpha k)/Z \quad \forall k \geq 1
\]

(14)

where \( \alpha = 1/h > 0 \) and the normalization constant \( Z \) is given by

\[
Z = \sum_{k=1}^{\infty} \exp(-\alpha k) = \frac{1}{1 - e^{-\alpha}}
\]

(15)

in order to ensure that condition (8) is satisfied. This leads to the following matrix model

\[
m_{ij} = \begin{cases} d \exp(-\alpha|i-j|)/Z & \text{if } j > i \\ 0 & \text{if } i = j \\ (1-d)\exp(-\alpha|i-j|)/Z & \text{if } i > j \end{cases}
\]

(16)

In this case, it should be noted that the average colonization distance \( h \) is the same in both directions; only the strength of the dispersal changes from one direction to the other.

Under the **strongly asymmetric distance-dependent model**, the asymmetry is much stronger in the sense that the asymmetry factor \( d \) enters into the exponential decay of the colonization rate. Asymmetry mirrors a weighting of the strength of colonization in one direction compared to the other, as well as an asymmetry in the average colonization distance. This creates a much stronger bias than in the previous case, as illustrated on Fig. 1. More precisely, we have

\[
f_+(k) = d^\kappa/k! Z_+ \quad \forall k \geq 1 \quad \text{and} \quad f_-(k) = (1-d)^\kappa/k! Z_- \quad \forall k \geq 1
\]

(17)

Now, the two normalization constants \( Z_+ \) and \( Z_- \) depend on \( d \) and are given respectively by

\[
Z_+ = 1/(d(d-1) - 1)) \quad \text{and} \quad Z_- = 1/((1-d)((1-d)-1) - 1)
\]

(18)

in order to meet condition (8). This leads to the following matrix model:

\[
m_{ij} = \begin{cases} d^{j-i}/Z_+ & \text{if } j > i \\ 0 & \text{if } i = j \\ (1-d)^{j-i}/Z_- & \text{if } i > j \end{cases}
\]

(19)

Notice that in this case, the average colonization distances are

\[
h_+ = \frac{1}{\alpha \log(1/(1-d))}, \quad \text{in the main direction of colonization}
\]

(20)

and

\[
h_- = \frac{1}{\alpha \log(1/d)}, \quad \text{in the opposite direction}
\]

(21)

Therefore, \( h_- > h_+ \) and the difference increases as \( d \) approaches zero.

**Grid stepping stone models.** We now consider models where the habitat patches are located on a regular two-dimensional grid. The asymmetry factor \( d \) has to be interpreted with some caution.
in this case; we will focus our attention on the simple situation where only the four nearest neighbors of a given habitat patch can be re-colonized (i.e., assuming a von Neumann neighborhood of range 1). Thus, four directions of colonization are allowed: north, south, east and west. In this context, habitat patches are indexed by two numbers that indicate their positions, \( ik \), so we index the matrix elements of \( M \) so that element \( m_{ik,j} \) characterizes the re-colonization probability from a patch at coordinate \( ik \), to a patch at coordinate \( jl \). As above, the asymmetry factor \( d \in [0, 1/2] \) may be interpreted as follows: \( c (1 - d) \) is the total colonization rate in the main direction of colonization and \( cd \) is the total colonization rate in the opposite direction. We consider then two forms of asymmetry, diagonal and horizontal. The first case characterizes a situation where an environmental gradient (such as wind, altitude, or ocean current) favors two directions of dispersal (in this case, south and west) equally with respect to the other two (north and east). The second case differs from the first in assuming that dispersal in two directions (south and north) is unaffected by the environmental gradient.

For the diagonal asymmetry, we assume that the main direction of the impact of asymmetry points toward the south–west, i.e. that the south and west directions of colonization are characterized by a colonization rate of \((1 - d)/2\), and the north and east directions each have a colonization rate of \(d/2\). The matrix \( M \) therefore reads

\[
\begin{align*}
m_{ik,j} &= \begin{cases} 
  d/2 & \text{if } j = i + 1, \; k = l \text{ or } j = i, \; l = k + 1 \\
  (1 - d)/2 & \text{if } i = j + 1, \; k = l \text{ or } j = i, \; l = k + 1 \\
  0 & \text{otherwise.}
\end{cases}
\end{align*}
\]

For the horizontal asymmetry, we assume that the main direction of colonization points toward the east; from a given habitat patch, colonization occurs to the west with a rate \(d/2\), to the east with a rate \((1 - d)/2\), while colonization in the north and south directions is unaffected by asymmetry and occurs at a rate \(1/4\). Thus, the matrix \( M \) is given by

\[
\begin{align*}
m_{ik,j} &= \begin{cases} 
  d/2 & \text{if } j = i + 1, \; k = l \\
  1/4 & \text{if } i = j, \; |k - l| = 1 \\
  (1 - d)/2 & \text{if } i = j + 1, \; k = l \\
  0 & \text{otherwise.}
\end{cases}
\end{align*}
\]

We could consider other patterns of dispersal, but we will restrict our analysis to these two cases. They will allow us to differentiate the situation where only two (opposite) directions are affected by asymmetry from the situation where all directions are affected.

### 2.2.2. Asymmetry in connectivity

In our second set of analyses, we consider two types of global asymmetry in connectivity. The first case, called *circular* asymmetry, allows only asymmetrically connected pairs of patches (colonization probability proportional to \( c \) from \( i \) to \( j \) and 0 from \( j \) to \( i \)). The second case, called *bidirectional* asymmetry, allows symmetric re-colonization between some fraction of the pairs of patches (colonization probability proportional to \( c \) in each direction). Starting from the so-called *cascade model* where all asymmetries point towards the same direction, we gradually reverse the direction of connections in a symmetric or asymmetric way. This procedure leads either to a circulating re-colonization pattern within the metapopulation, as observed for example in ocean systems, or mimics the pattern observed in river networks, where bidirectional movement is possible along some segments. We introduce the following parameters to characterize the asymmetry of the model: \( T_C = \sum_{i,j} m_{ij} \) denotes the total number of connections in the system, \( T_S = \sum_{i,j,m} m_{ij} m_{ji} \) denotes the total number of symmetric (or bidirectional) connections and \( L_D = \sum_{ij} \) denotes the level of directionality, that is, the number of connections in the upper triangular part of the matrix \( M \) (i.e., in the direction opposite to the main direction of colonization).

We characterize the level of circulating asymmetry via the ratio \( a_c = L_D/T_C \), which is 0 for the cascade model and increases to 1/2 when asymmetric connections are randomly distributed. Here, we only consider values of \( a_c < 1/2 \); if \( a_c > 1/2 \), we can get identical results by setting the asymmetry parameter to \( 1 - a_c \) and reversing the orientation of the whole system. Bidirectional asymmetry is characterized via the parameter \( a_b = T_S/T_C \), which is zero for the cascade model and can be as large as 1/2 in the bidirectional model. In either case (circular or bidirectional asymmetry), we start from the cascade model, either based on an island model \((m_{ij} = 1 \text{ for } i < j \text{ and } 0 \text{ otherwise}); T_C = n(n - 1)/2\), or on a two-dimensional grid model (pattern of connections as in (22), with \( d = 1/2; T_C = 2(n - \sqrt{n}) \)). We then sample \( f = a_T T_C \) (or \( f = a_T T_C \)) connections, without replacement, from these connections, and reassign them as follows.

#### Circulating model: keep the connections asymmetric but switch their direction:

\[
\{m_{ij} = 1, m_{ji} = 0\} \rightarrow \{m_{ij} = 0, m_{ji} = 1\}.
\]

#### Bidirectional model: break \( f \) asymmetric connections and create \( f \) bidirectional connections elsewhere in the system, thus, sample \( f \) connections without replacement and break them, then sample \( f \) connections that were not chosen in the first sample and make them bidirectional:

\[
\{m_{ij} = 1, m_{ji} = 0\} \rightarrow \{m_{ij} = 0, m_{ji} = 1\}.
\]

Fig. 2 shows these two models.

Finally, we rescale the connectivity matrix so that the average per-patch connectivity is \( c \) (by dividing the binary connection matrix by the average number of neighbors, \( n/2 \) in the island case and \( 2 \) in the stepping-stone case). Asymmetry in connectivity is investigated only under the island and the stepping stone model, as in the distance-dependent model, connections have a weight that depends on their position and thus do not have conservative properties when permuted through the processes described above.

### 2.3. Computing metapopulation capacity and extinction probability

#### 2.3.1. Metapopulation capacity (\( \lambda_M \))

In the case where the matrix \( M \) is symmetric (i.e. when \( d = 1/2 \) and \( f_s = f_\cdot \)), it is a direct consequence of the spectral theory of large Toeplitz matrices (Gray, 2006) that \( \lambda_M \) approaches the largest row-sum of the matrix \( M \) for large system size, i.e. that

\[
\lambda_M \simeq \sum_{k=1}^{n/2} f_s(k) + \sum_{k=1}^{n/2} f_\cdot(\cdot-k) \quad \text{as } n \rightarrow \infty \quad d + (1 - d) = 1.
\]

Many methods are known in the mathematical literature for analyzing the largest eigenvalue (and more generally the whole spectrum) of large symmetric Toeplitz matrices (see Gray (2006) for a detailed account on this subject). Nevertheless, no general method is known for analyzing the largest eigenvalue of asymmetric Toeplitz matrices, which are encountered here.

In the asymmetric dispersal strength case, we can usually compute the metapopulation capacity \( \lambda_M \) analytically, either for particular values of system size \( n \) or in the limit of large system size. Indeed, when \( d < 1/2 \), the Perron–Frobenius theorem implies that \( \lambda_M \) is non-negative and smaller than or equal to the largest row-sum of the matrix, i.e. smaller than 1 for large system size. Furthermore, \( \lambda_M \) approaches 0 when \( d \) approaches 0. When no analytical formula can be provided, we compute the largest eigenvalue \( \lambda_M \) numerically.

In the asymmetric connectivity case, there is no analytical expression for the largest eigenvalue \( \lambda_M \), so we estimate it by numerical simulation. Note also that in this situation, unlike in the asymmetric dispersal strength case, the irreducibility condition of
Fig. 2. Patterns of asymmetry in colonization. Connection matrices for island model, 16 x 16 system. Top row, circulating: for $a_c = 1/2$ (top right), the system is fully asymmetric ($m_{ij} = 1 - m_{ji}$ for all $i, j$). Bottom row, bidirectional: for $a_c = 1/2$ (bottom right), the system is symmetric.

Ovaskainen and Hanski (2001) is not guaranteed, as random reconnections do not necessarily create full connectivity in the network. This is particularly true when the number of reconnections is small, as well as when the grid stepping stone model is considered. In the latter case, we consider only real leading eigenvalues $\lambda_M$.

2.3.2. Extinction probability ($p_E$)

In order to contrast the theoretical results on metapopulation capacity obtained with the deterministic model, we use numerical simulations to study the corresponding stochastic model. The model is a Markovian stochastic model that describes the evolution of habitat patch occupancy, using Monte Carlo simulation methods. We are interested in the behavior of the extinction probability $p_E$ of the whole system with respect to the main parameters of the model, namely $c, d$ and $e$. But now we consider a finite number of patches, $n = 100$, evolving according to the following stochastic process. At the beginning, all patches are occupied. Each time step is divided into an extinction phase, during which extinction occurs independently at each patch with probability $e$, and a colonization phase, during which each empty patch $i$ is recolonized with probability $c m_{ij}$ from patch $j$, given that this patch is occupied. We then evaluate the extinction probability $p_E$ as the average proportion of empty habitat patches after $g = 1000$ generations. We say that the system is stable if its survival probability is larger than 0. The average is taken over $s = 1000$ independent simulations. Contrasting the relationship between the time and the extinction probability in stochastic and deterministic metapopulation models appears to be strongly sensitive to the way the process is truncated (Cairns and Pollett, 2005). Indeed, if one were to let $g$ grow arbitrarily large, while maintaining $n$ fixed, then the extinction probability would tend to 1, independently of the system parameters. On the contrary, letting $g$ be fixed while increasing $n$ arbitrarily leads to a strictly positive survival probability in all cases. The arbitrary values of the number of patches $n$ and the number of generations $g$ considered here allow us to disentangle the impact of various asymmetric patterns under similar conditions.

We consider four different models for the asymmetric dispersal strength case (the island model, the strongly asymmetric distance-dependent model with $\alpha = 1$, the linear stepping stone model and the grid stepping stone model with horizontal asymmetry) and four different models for the asymmetric connectivity case (island and grid stepping stone models with circulating and bidirectional asymmetry).

Ovaskainen and Hanski (2001) show that this system is well approximated by the system given in (5). According to (6), the latter system is stable if and only if $\lambda_M(d) > e/c$. Below, we explore the validity of this condition for the simulated system, in the context of metapopulations with asymmetric dispersal strength.

3. Results

3.1. Metapopulation capacity $\lambda_M$

3.1.1. Asymmetry in dispersal strength

Fig. 3(a) shows the behavior of the metapopulation capacity $\lambda_M$ with respect to the asymmetry parameter $d$ for the island model and for the stepping stone model. For the island model the slope of the curve is infinite at $d = 0$, and $\lambda_M$ converges quickly to the value 1 as $d$ approaches 1/2 (i.e., the symmetric case). Remembering condition (6), this translates into a stabilization of the system, as soon as the colonization rate in the direction opposite to the main direction of colonization is greater than 0. Fitting a curve to the results in Fig. 3(a) gives
\( \lambda_M(d) \approx (4d(1-d))^{0.3} \) for large system size \( n \).

Under the stepping stone model, the metapopulation capacity \( \lambda_M \) is shown to behave as

\( \lambda_M(d) \approx \sqrt{4d(1-d)} \) for large system size \( n \) (this result is proved analytically in Appendix A.1). The results from this model are similar to those from the island model above (slope +\( \infty \) in \( d = 0 \), rapid convergence to 1 as \( d \) approaches 1/2), although the stability region where \( \lambda_M(d) > c/e \) is smaller than in the previous case, as Fig. 3(a) shows.

The value of \( \lambda_M \) remains relatively constant and displays the same value under both the island and the stepping stone model when \( d \) is above 0.36. However, below this value, the trajectories differentiate between the island and the stepping stone model. Following (6), viability is therefore predicted to decrease and to be most affected by the asymmetry factor \( d \) under the stepping stone model. As expected, when the asymmetry is complete, both models predict extinction.

For the case of weak asymmetry and distance-dependent colonization (Eq. (16)), whether dispersal range is restricted (\( \alpha = 10 \)) or not (\( \alpha = 1 \) (Fig. 3(b)), the behavior of \( \lambda_M \) resembles that of the stepping stone model in Fig. 3(a) for large values of \( \alpha \) (i.e. when the average colonization distance \( h \) is small). When \( \alpha \) is small (i.e. when the average colonization distance \( h \) is large), the behavior of \( \lambda_M \) resembles that of the island model in Fig. 3(a). Small changes occur for \( \lambda_M \) when the asymmetry factor \( d \) is above 0.36. Similar to the results shown in Fig. 3(a), viability increases with dispersal ability.

Under strong asymmetry, viability quickly decreases with the asymmetry factor \( d \) (Fig. 1(c)). A decrease in dispersal ability buffers this effect for intermediate values of \( d \). Interestingly, the shape of the relationship between \( d \) and \( \lambda_M \) differs from the previously studied cases (Fig. 3(a) and (b)) and depends on dispersal range \( \alpha \). When the asymmetry is strong (i.e. \( d \) is close to zero), the metapopulation capacity converges linearly to zero, at a rate increasing with a decrease in the dispersal range \( \alpha \). In the particular case where \( \alpha = 1 \), fitting a curve to the data points on Fig. 3(c) gives

\[ \lambda_M(d) \approx 2 \left( 1 - \sqrt{1 - 3d(1-d)} \right) \]  

(29)

This result implies in particular that \( \lambda_M \) has finite slope at \( d = 0 \). More precisely, it follows from (29) that \( \lambda_M'(0) = 3 \). Appendix A.2 gives a proof that

\[ \lambda_M'(0) \leq 3 \]  

(30)

for all values of \( n \) (when \( \alpha = 1 \)).

For other values of \( \alpha \), it can be inferred from Fig. 3(c) that the slope of \( \lambda_M \) in \( d = 0 \) also remains finite. This result therefore contrasts with the results obtained for the other models. Finally, Fig. 3(c) shows that the size of the stability region delimited by the condition \( \lambda_M(d) > c/e \) increases significantly with \( \alpha \) under the present model.

When colonization takes place on a grid and the main direction of colonization is along a diagonal of the grid, the behavior of the metapopulation capacity \( \lambda_M \) differs little from the corresponding linear stepping stone model, as Fig. 3(d) shows. This comes from the fact that the second dimension of the model does not enhance the survival probability of the metapopulation in this case.
Fig. 4. The minimum, median, and maximum value of the metapopulation capacity $\lambda_M$ as a function of the asymmetry parameters $a_b$ and $a_c$ for the island model and for the stepping stone model considering either bidirectional connection or a circulation system (see method for details). Only real leading eigenvalues were considered for the grid2D case; excluding 733/21,000 complex leading eigenvalues for the bidirectional case, and 20/21,000 pure-imaginary and 753/21,000 complex leading eigenvalues for the circulating case.

However, if only one direction displays an asymmetric pattern, i.e. the asymmetry is horizontal, then the metapopulation capacity is greatly enhanced, because of the possibility of persisting through re-colonizations in the direction perpendicular to the main direction of colonization. More precisely, the largest eigenvalue of the matrix $M$ is shown to behave for large system size as

$$\lambda_M^{2D}(d) \approx \frac{1 + \lambda_{1D}^{2D}(d)}{2},$$

where $\lambda_{1D}^{2D}(d)$ is the metapopulation capacity under the linear stepping stone model, given by (28). The result is illustrated in Fig. 3(d) and proved in Appendix A.3. As expected, when $d$ tends to 0, $\lambda_M^{2D}(d)$ tends to 1/2 and not to 0, which arises from the fact that the asymmetry affects only one direction. Even so, the slope of $\lambda_M^{2D}(d)$ is still infinite at $d = 0$, as in the linear model.

Therefore, when two directions of colonization are affected by the asymmetry factor $d$ (Fig. 3(d)) and a grid stepping stone model of colonization is assumed, the shape of the relationship between $\lambda_M$ and $d$ resembles that of the linear stepping stone model. However, removing a direction where the asymmetry factor $d$ applies qualitatively changes the prediction of viability. The value of $\lambda_M$ remains at relatively high values over the range of $d$ values and the stability region nearly doubles in size (Fig. 3(d)).

3.1.2. Asymmetry in connectivity

The metapopulation capacities $\lambda_M$ obtained for different values of asymmetry in connectivity, $a_b$ and $a_c$, considering respectively a circulating and a bidirectional model, are presented in Fig. 4 for both the island model and the stepping stone model. For the island model, the relationships between the metapopulation capacity and the asymmetry in connectivity are nearly identical in the bidirectional and circulating cases and are similar to the results from systems with asymmetry in dispersal strength (Fig. 3). In contrast, in the grid stepping stone model, the metapopulation capacity is highly variable, even when the model is symmetric ($a_b$ or $a_c = 1/2$). As the fraction of symmetric connections decreases (from 1/2 to zero), the metapopulation capacity becomes even more variable, and the patterns differ according to the type of asymmetry.

For the circulating model, the metapopulation capacity is strongly variable below an $a_c$ value of 0.25 (Fig. 4). This variability reflects the diversity of connectivity patterns that can be generated by displacing connections. Indeed, changing the direction of connections can lead to systems that are either stable or highly unstable. If this process generates numerous habitat patches with only connections going out or going in (source and sink habitat patches) the system is expected to be strongly prone to extinction. The presence of source and sink habitat patches is reflected by the fact that the metapopulation capacity remains below 1 over the range of $a_c$ values considered.

For the bidirectional model, values of metapopulation capacity can be larger than 1 (Fig. 4). The process of creating bi-directional connections generates systems in which connection density becomes strongly heterogeneous. This leads to the creation of isolated habitats and strongly connected substructures weakly connected to each other. Increasing the number of bi-directional connections quickly increases the metapopulation capacity. However, the variability of the values obtained remains high, corresponding to the diversity of the connectivity patterns obtained.
Finally, in both cases, thresholds occur for the minimum metapopulation capacity, the first at $\lambda_M = 1/2$. This phenomenon occurs because of the formation of cycles in the graph through the reconnection process. Indeed, it can be checked that the largest eigenvalue of a submatrix of $M$ corresponding to a cycle in the graph is equal to $1/2$ (as the adjacency matrix of a cycle is a circulating matrix and the non-zero coefficients of $M$ are all equal to $1/2$ in the grid stepping stone model). In the circulating model, these cycles appear only after a significant amount of link-flipping ($a_c > 0.2$ in the present sample), whereas they appear for any $a_b > 0$ in the bidirectional model (as a cycle of length 2 is automatically created after one reconnection in this case). One observes the formation of further thresholds for the bidirectional model, corresponding to the appearance of new structures in the graph (e.g., the next threshold is at $\lambda_M = 1/\sqrt{2} \approx 0.707$, which corresponds to the formation of adjacent cycles of length 2).

3.2. Extinction probability $p_E$ versus $\lambda_M$

3.2.1. Asymmetry in dispersal strength

The results are illustrated in Fig. 5, where both the metapopulation capacity $\lambda_M$ and the extinction probability $p_E$ are represented as functions of the asymmetry factor $d$, for various values of the colonization rate $c$ (the local extinction rate $e$ is kept constant at 0.1, as only the ratio $e/c$ matters in (6)). Four different models are considered: the island model (Fig. 5(a)), the strongly asymmetric distance-dependent model with $\alpha = 1$ (Fig. 5(b)), the linear stepping stone model (Fig. 5(c)) and the grid stepping stone model with horizontal asymmetry (Fig. 5(d)).

Under the island model, Fig. 3(a) suggests that for the parameters considered, the metapopulation can persist (the extinction probability predicted from the metapopulation capacity drops below 1) as soon as $d$ increases slightly above zero. This result matches the numerical results shown in Fig. 5; the thresholds values of the three colonization rates along the range of values of $d$ are relatively constant. Their behavior is relatively similar: they quickly level off to $e/c$, the value predicted for a symmetric metapopulation (6). Those results are reflected by the behavior of the metapopulation capacity $\lambda_M$: it stays close to 1 for a wide range of values of $d$ (from $d = 0.5$) before finally dropping to 0 when $d$ reaches 0.

Under the strongly asymmetric distance-dependent model, assuming large dispersal ability ($\alpha = 1$ (Fig. 5(b))), the extinction probability stays equal to 1 for a large range of $d$ values. The extinction probability reaches a threshold value at quite high values of $d$, which depend on the value of $c$ considered. The transition from maximal to minimal extinction probabilities is more gradual than in the previous case (Fig. 5(a)).

Under the stepping stone model (Fig. 5(c)), a similar phenomenon occurs: the extinction probability slowly decreases with increasing symmetry, but the decrease starts immediately when $d$ is slightly larger than 0. On the other hand, the threshold values reached for $d = 1/2$ are higher in this case. This is explained by the inherent low connectivity of the stepping stone model, whose extinction probability is therefore larger than that of other models. The parameter range over which extinction decreases as
Fig. 6. Probability of metapopulation extinction, $p_E$, as a function of the asymmetry parameter $a_{bc}$ and $a_{ac}$ for the island model and for the stepping stone with locale extinction rate $e = 0.1$ and the colonization rate $c = 0.1, 0.2, 0.3, 0.4, 0.5, 0.6$. Dynamics is simulated for 1000 time steps.

$(e/c)$ increases. Under this model, the predictions of extinction according to the metapopulation capacity $\lambda_M$ tend to disagree with the simulation results.

Finally, the behavior of the extinction probability is illustrated for the grid stepping stone model with horizontal asymmetry (Fig. 5(d)). Similar to the results for the island model (Fig. 5(a)), a quick decrease of the extinction probability when $d$ is slightly larger than zero is predicted. Expected extinction probabilities $(e/c)$ are reached for relatively low values of $d$ and converge more rapidly when colonization is high.

### 3.2.2. Asymmetry in connectivity

In the island model, the extinction probability reaches 1 under both the bidirectional and the circulating models, for all values of colonization rates, as the system becomes completely asymmetric (Fig. 6). As asymmetry in connectivity decreases, the extinction probability drops extremely rapidly when $c \geq 0.3$; when $c = 0.2$ it drops for $a_{bc}$ or $a_{ac} > 0.1$, and for $c = 0.1$ the metapopulation never persists.

Overall, persistence is very low in the grid stepping stone model and the behavior of the metapopulation capacity over the range of asymmetric values $a_{bc}$ and $a_{ac}$ differentiates between the bidirectional and circulating models. The extinction probability decreases faster with increased $a_{bc}$ than with increased $a_{ac}$ (Fig. 6). For a given level of asymmetry, the values of the colonization rate $c$ required for metapopulation viability are higher for the circulating case than for the bidirectional case. Under the circulating model, the proportion of permuted connections, $a_c$, needed to provide a viable network of habitat patches is high (30%–50%); whatever colonization rate is considered, all the connections have to be shuffled in order to reach the lowest extinction probability. Under the bidirectional model, a surprisingly low proportion of bidirectional connections, $a_{bc} (15%–20\%)$ is sufficient to drastically reduce the extinction probability of the metapopulation (Fig. 6). Extinction rapidly declines as the number of symmetric connections increases. When the number of reversed connections reaches 40%, the extinction probability stabilizes at a low value. These results might be predicted from the considerably lower average metapopulation capacities in the circulating case. However, because the connection matrices are not irreducible in this case, it is unclear whether the metapopulation capacity can be interpreted in the same way. Indeed, for a given level of asymmetry $a_c$, the mean metapopulation capacities are higher in the grid stepping stone model than in the island model, but the extinction probabilities are also higher, indicating that the standard comparisons based on metapopulation capacities do break down in this case.

### 4. Discussion

#### 4.1. Asymmetry in dispersal strength

Overall, persistence is relatively well maintained when asymmetry in dispersal strength is less than 25%. Below this level of
asymmetry, extinction probabilities resemble those from a completely symmetric system. Above this value, extinction predictions are highly sensitive to the migration model assumed and to the shape of asymmetry in the dispersal pattern. When a bias in re-colonization direction exceeds 35%, viability predictions quickly drop under both the stepping stone model and the distance-dependent model of migration. The worst situation for species viability is a pattern of re-colonization in which both direction and range of re-colonization are biased in one direction, under a distance-dependent migration model, when the species has a large dispersal ability ($\alpha = 1$) (Fig. 5[b]). Indeed, under those conditions, a small bias in the colonization pattern has the strongest impact on viability predictions, while for other models, the impact remains weak. Ultimately, when no limitation in distance is considered (island model) or when re-colonization is symmetric in some direction (such as e.g. for the stepping stone with horizontal asymmetry) viability predictions remain stable until asymmetry becomes extreme (more than 80% of re-colonization bias in one direction).

Interestingly, the two patterns of re-colonization that provide the lowest extinction probability appear to be common in ecosystems subject to environmental gradients. For example, in dynamic marine environments, where advection by currents carries individuals far from natal populations (Caley et al., 1996), such dynamics might provide a higher re-colonization potential between distant populations. Such patterns appear to be frequently associated with a local strong connectivity. Several recent studies have showed strong evidence that individuals can remain close to their natal habitats by exploiting local circulation patterns (Swearer et al., 2002; Warner and Cowen, 2002; Cowen et al., 2006; Becker et al., 2007; Cowen and Sponaugle, 2009; Morgan et al., 2009). In particular, Morgan et al. (2009) demonstrate that in conditions of wind-driven offshore transport and strong upwelling regions, marine larvae are more likely to recruit close to natal populations than previously thought. Although dispersal ability certainly affects the viability of metapopulations, a dispersal pattern that allows either some local symmetry or/and long distance dispersal might simply be an evolution into a heterogeneous environment to avoid extinction.

### 4.2. Asymmetry in connectivity

For asymmetry in connectivity, when dispersal distance is unlimited (the island model), viability does not differ between the two main patterns investigated. A small proportion of reverse connections quickly leads to viability, because the matrix has high connectance and because the initial configuration (before permutation of connections) follows a cascade model. Even though a pure cascade model is unviable, it provides a structure that allows full connectivity between all habitat patches. Under an island model, gradually permuting connections leads to a situation where re-colonization is allowed through the entire system. However, when re-colonization is limited in distance (as in the grid stepping stone model) and the number of connections is reduced, viability is much harder to achieve. To generate a configuration in which re-colonization process is possible across the entire network, the number of connection permutations must be fairly high. However, this global connectivity is achieved faster in the bi-directional model than in the circulating model. Even with a high colonization rate, a very small proportion of asymmetry in connectivity quickly increases the extinction probability under the circulating model, while under the bidirectional model, extinction predictions remain similar to those expected under symmetry when 10%–20% of asymmetry is considered (i.e., when $\alpha_1$ decreases to $\approx 0.3–0.5$). In the circulating model, the permutation process gradually creates large networks of habitat patches which increase the average length of successive connections to allow re-colonization, while the bidirectional model reinforces the local re-colonization potential of sub-networks of habitat patches. The resulting local sub-structure provides sources of colonizers for the habitats that might be more prone to extinction.

Our results agree with those of Vuilleumier and Possingham (2006). They contrast the prediction of metapopulation extinction under a symmetric (only bidirectional connections) and asymmetric (only one-directional connections) connectivity matrix, given any random number of connections. They show that the viability under an asymmetric colonization pattern is much lower than under a symmetric one. Our approach refines their study and differs in four aspects: the starting condition is a cascade model, intermediate forms of asymmetry are considered ($\alpha_0$, factor), specific numbers of connections are considered (grid stepping stone vs island model) and the generation of the connectivity matrix is performed under strong constraints which allow the creation of large loops or strong local connectivity in the system.

The connectivity matrices generated here are neither precisely one-dimensional nor two-dimensional and share some properties of dendritic networks (Tarboton, 1996; Campbell Grant et al., 2007). Some authors have shown that such structures affect metapopulation dynamics, inducing source–sink dynamics (Hannfling and Weetman, 2006; Labonne et al., 2008) and affecting the patterns of community diversity (Economos and Keitt, 2008; Rodriguez-Iturbe et al., 2009) as well as genetic relatedness (Woford et al., 2005; Labonne et al., 2008), diversity (Jansson et al., 2005; Morrissey and de Kerckhove, 2009), and species range distribution (Gaylord and Gaines, 2000; Leyer, 2006; Gurnell et al., 2008). Such networks are a longstanding object of study for hydrologists (e.g. Horton, 1945), who differentiate river networks that are structured in a few poorly interconnected groups of patches (Hortonian) from networks that have a better balance between local and long-distance connectivity (non-Hortonian). In this context, Labonne et al. (2008) showed that in Hortonian networks, extinction probability is enhanced, as root patches often go extinct, splitting the metapopulation into disconnected components with shorter persistence times. Speirs and Gurney (2001) and Lutscher et al. (2005) demonstrate that this effect is enhanced when dendritic structures are associated with a directional bias of re-colonization. Our bidirectional and circulating asymmetry cases are similar to non-Hortonian and Hortonian networks, but we allow for a large range of spatial configurations in which local and global clustering is allowed. We also confirm that this effect strongly depends on the ability of the species to disperse: when long range dispersal is allowed, as in the island model, there is little difference in extinction probability among the networks considered.

### 4.3. Predicted and actual threshold values for extinction

Predicted and actual threshold values in asymmetry in dispersal strength show a clear correspondence between the predicted threshold value $d^*$ computed from the equation $\lambda_M(d^*) = e/c$ and the value for which the probability $p_d$ drops below the value 1, when the island model and the two stepping stone models are considered. However, a careful observation of the results shows that, for the distance-dependent model, the predicted threshold value $d^*$ computed from the equation $\lambda_M(d^*) = e/c$ does not occur exactly where the probability $p_d$ drops below the value 1 (Fig. 3[b)]. The observed discrepancies can be explained in various ways.

First of all, the predicted threshold value $d^*$ is computed in the framework of the model (5), a deterministic model which does not a priori fully match with our stochastic simulations of the actual extinction probability.

We also expect differences because of differences in the underlying assumptions of the models. The deterministic and stochastic
models considered here would lead to identical predictions only for a large number of habitat patches that are equally connected to other habitat patches. Looking at a system where re-colonization from an habitat patch is restricted to a small number of habitat patches (such as the stepping-stone model) violates such an assumption and leads to deviations from the stochastic system. In addition, boundary effects cannot be neglected in a system with a relatively small number of patches.

Moreover, the stochastic model is evaluated at quasi-stationary equilibrium (that is, after a given number of generations). As shown by Cairns and Pollett (2005), the relationship between the time and the extinction probability in stochastic and deterministic metapopulation models can be strongly sensitive to the way the process is truncated. As the number of generations increases, so does the extinction probability and this independently of the system parameters. Similarly, extinction probability in the stochastic model decreases with the size of the system. Some of the discrepancies observed between the stochastic and deterministic predictions are expected from the chosen metapopulation size and the cut-off used. A detailed analysis of the impact of these parameters for each of the models investigated here could have been of interest but goes beyond the purpose of this study.

Finally, as mentioned above, the asymmetric connectivity model does not guarantee irreducibility of the landscape matrix $M$. When $M$ is reducible, the metapopulation is divided into groups of patches which are disconnected from each other and the condition $\lambda_M \geq e/c$ established by Ovaskainen and Hanski (2001) is not applicable. There is still much to say about the profile of surviving metapopulations (that is, the probability of persistence of a patch given its position). Given the theoretical result of Ovaskainen and Hanski (2001), it is known that when the reconolonization matrix $M$ is irreducible, the limit profile vector $\mathbf{p}^*$ is positive everywhere. Lutscher et al. (2007) refine this picture and show that in an environment with unidirectional flow there is an upstream limit above which a patch survival probability is close to zero, while a linear and strictly positive profile seems to emerge below this limit. Studying further this profile under our model is a promising future research track.

4.4. Robustness of our model

Our stochastic simulations are performed in discrete time: at each time step, we let all the extinctions occur first, and then simulate the colonizations. Reversing the order of events does not modify the behavior of the system during simulations, as we start with the situation where all habitat patches are occupied. However, if persistence is evaluated after the extinction events instead of the colonization events, viability predictions are lower, as shown in Fig. 7. Nevertheless, the general behavior of the extinction probability in relationship to asymmetry is not affected.

Continuous- and discrete-time colonization–extinction models of metapopulations can also differ in their predictions of extinction (Frank, 2005). In continuous-time models, extinctions and colonizations are not ordered. Extinctions occur at rate $e$, while colonizations between habitat patches $i$ and $j$ occur at rate $cm_{ij}$, and the time intervals between these events are assumed to be independent and exponentially distributed. As Fig. 8 shows, our results are robust to this change of model: simulations performed in discrete time or continuous time lead to similar behavior of the extinction probability with respect to the asymmetry factor $d$.

5. Conclusion

In heterogeneous environments, populations are fragmented and form metapopulations which persist through processes of extinction and re-colonization. Due to environmental heterogeneity, those fragmented populations form complex networks of habitat patches that can display asymmetry in dispersal. Such networks have dynamic, ecological and genetic properties that strongly differ from those observed in homogeneous systems and suffer from a general lack of theoretical exploration. Vuilleumier and Possingham, 2006; Campbell Grant et al., 2007; Labonne et al., 2008; Morrissey and de Kerckhove, 2009). Given fixed values of standard metapopulation parameters, such as overall colonization rate, extinction rate, and connectivity, we explored how the level and pattern of re-colonization asymmetry affect the metapopulation capacity and persistence.

We found that a directional bias in dispersal strength smaller than 25% does not affect metapopulation persistence; this threshold value reaches 80% when metapopulation benefits from a strong general connectivity (the island model) or with strong local connectivity (local horizontal symmetry). However, when the connectivity is generally weak (stepping stone model), a bias of as little as 35% drastically reduces viability. This effect is even stronger when the re-colonization bias affects both the strength and the average distance of dispersal. Networks that allow for a balance between local and global (long-distance) connectivity provide higher persistence than networks that allow for global connectivity and large circulating re-colonization patterns (island model).
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Appendix. Proofs

A.1. Linear stepping stone model

We prove here (28). Under the stepping stone model (13), the matrix $M$ may be rewritten as

$$M = \begin{pmatrix}
0 & d & 0 & 0 \\
1 - d & 0 & d & 0 \\
1 - d & 0 & \ddots & \ddots \\
0 & 1 - d & 0 & 0
\end{pmatrix}$$

$$= \sqrt{d(1-d)} \begin{pmatrix}
0 & x & 0 & 0 \\
1/x & 0 & x & 0 \\
1/x & 0 & \ddots & \ddots \\
0 & 1/x & 0 & x
\end{pmatrix}$$

where $x = \sqrt{d/(1-d)}$. Let us now write

$$D_n(\lambda) = \det \begin{pmatrix}
-\lambda & x & 0 & 0 \\
1/x & -\lambda & x & 0 \\
1/x & 0 & -\lambda & \ddots \\
0 & 1/x & 0 & -\lambda
\end{pmatrix}$$

It follows that $D_1(\lambda) = -\lambda, D_2(\lambda) = \lambda^2 - x(1/x) = \lambda^2 - 1$ and expanding the determinant along the last column for general $n$ gives

$$D_n(\lambda) = -\lambda D_{n-1}(\lambda) - x(1/x)D_{n-2}(\lambda) = -\lambda D_{n-1}(\lambda) - D_{n-2}(\lambda).$$

By induction, this shows that $D_n(\lambda)$ does actually not depend on $x$, so the eigenvalues of the matrices

$$\begin{pmatrix}
0 & x & 0 & 0 \\
1/x & 0 & x & 0 \\
1/x & 0 & \ddots & \ddots \\
0 & 1/x & 0 & x
\end{pmatrix}$$

and

$$\begin{pmatrix}
0 & 1 & 0 & 0 \\
1 & 0 & 1 & 0 \\
1 & 0 & \ddots & \ddots \\
0 & 1 & 0 & 1
\end{pmatrix}$$

are the same. It is now a well know fact that as $n \to \infty$, the largest eigenvalue of the latter matrix converges to 2 (Gray, 2006). So as $n \to \infty$, the largest eigenvalue of $M$ converges to

$$\lambda_E(d) = 2\sqrt{d(1-d)}.$$  

(A.5)

A.2. Strongly asymmetric distance-dependent model

We prove here (30). Under the distance-dependent model (19) and when $\alpha = 1$, the matrix $M$ may be rewritten as $M = d(1-d)X$, where

$$x_{ij} = \begin{cases}
d^{i-j-1} & \text{if } i < j \\
(1-d)^{j-i} & \text{if } i > j.
\end{cases}$$

(A.6)

Now, for any fixed $n$ and as $d$ tends to 0, the matrix $X$ tends to

$$X_0 = \begin{pmatrix}1 & 0 & 0 & \cdots & 0 \\
1 & 0 & 1 & \cdots & 0 \\
0 & 1 & 1 & \cdots & 0 \\
\vdots & \ddots & \ddots & \ddots & \ddots \\
0 & \cdots & 1 & \cdots & 1
\end{pmatrix}.$$  

(A.7)

In the following, we prove that for any $n$, the largest eigenvalue $\lambda_{X_0}$ of $X_0$ cannot be greater than 3, thus proving that as $d$ tends to 0,

$$\lim_{d \to 0} \frac{\lambda_{X_0}(d)}{d} = \lim_{d \to 0} \frac{d(1-d)\lambda_{X_0}}{d} \leq \lim_{d \to 0} \frac{3d(1-d)}{d} \leq 3$$

(A.8)

or in other words, that $\lambda_{X_0}(0) \leq 3$, which is (30).

The fact that $\lambda_{X_0} \leq 3$ is proven as follows. Let $D_n(\lambda)$ and $E_n(\lambda)$ be defined as

$$D_n(\lambda) = \det \begin{pmatrix}1 & -\lambda & \cdots & 0 \\
-\lambda & 1 & -\lambda & \cdots \\
\ddots & \ddots & \ddots & \ddots \\
0 & \cdots & 1 & -\lambda
\end{pmatrix}$$

and

$$E_n(\lambda) = \det \begin{pmatrix}1 & -\lambda & \cdots & 0 \\
-\lambda & 1 & -\lambda & \cdots \\
\ddots & \ddots & \ddots & \ddots \\
0 & \cdots & 1 & -\lambda
\end{pmatrix}.$$  

(A.9)

By expanding the determinant along the last column, the following recurrence relations are obtained:

$$D_{n+1}(\lambda) = -\lambda D_n(\lambda) - E_n(\lambda)$$

and

$$E_{n+1}(\lambda) = D_n(\lambda) - E_n(\lambda).$$

(A.10)

We now make the following claim: if $\lambda$ is real and $> 3$, then for all values of $n$, $|D_n(\lambda)| \geq |E_n(\lambda)|$ and $D_n(\lambda) E_n(\lambda) < 0$. This implies in particular that if $\lambda$ is real and $> 3$, then for all values of $n$, $D_n(\lambda) \neq 0$, so $\lambda$ cannot be an eigenvalue of $X_0$ and therefore $\lambda_{X_0} \leq 3$.

Proof of the claim. We proceed by induction. Since $D_1(\lambda) = -\lambda$ and $E_1(\lambda) = 1$, it is clear by assumption that $|D_1(\lambda)| \geq |E_1(\lambda)|$ and $D_1(\lambda) E_1(\lambda) < 0$. Assume now that $|D_n(\lambda)| \geq |E_n(\lambda)|$ and $D_n(\lambda) E_n(\lambda) < 0$. Then,

$$D_{n+1}(\lambda)E_{n+1}(\lambda) = -\lambda D_n(\lambda)^2 + E_n(\lambda)^2 + (\lambda - 1)D_n(\lambda)E_n(\lambda) < 0.$$  

(A.11)

Besides,

$$|E_{n+1}(\lambda)| = |D_n(\lambda) - E_n(\lambda)| = |D_n(\lambda)| + |E_n(\lambda)|$$

(A.12)

and
$$|D_{n+1}(\lambda)| = |\Delta D_n(\lambda) + E_n(\lambda)|$$

$$= |(\lambda + 1)D_n(\lambda) + E_n(\lambda) - D_n(\lambda)|. \tag{A.13}$$

As $|(\lambda + 1)D_n(\lambda)| \geq |E_n(\lambda) - D_n(\lambda)|$, it is still true by assumption that

$$|D_{n+1}(\lambda)| = |(\lambda + 1)D_n(\lambda) - |E_n(\lambda) - D_n(\lambda)|$$

$$\geq 4|D_n(\lambda)| - |E_n(\lambda) - D_n(\lambda)| \tag{A.14}$$

$$\geq 2(|D_n(\lambda)| + |E_n(\lambda)| - |E_n(\lambda) - D_n(\lambda)|)$$

$$= 2|E_n(\lambda)| - |E_n(\lambda) - D_n(\lambda)| = |E_n(\lambda)| \tag{A.15}$$

so the claim is proved. □

### A.3. Grid stepping stone model

We prove here (31). In the grid case, the matrix $M$ of the stepping stone model has the following structure:

$$M = \frac{1}{2} \begin{pmatrix}
M' & D & 0 \\
D' & D & D \\
0 & D & 0
\end{pmatrix} \tag{A.16}$$

where $M'$ is the matrix of the linear stepping stone model and $D = \text{diag}(1/2, \ldots, 1/2)$. The eigenvalue decomposition of each matrix $M'$ reads $M' = S\Lambda S^{-1}$, where $S$ is an invertible matrix and $\Lambda'$ is the diagonal matrix of eigenvalues of $M'$. Therefore,

$$M = \frac{1}{2} \begin{pmatrix}
\Lambda' & D & 0 \\
D' & \Lambda' & D \\
0 & D & \Lambda'
\end{pmatrix} \tag{A.17}$$

and the eigenvalues of $M$ are the same as those of

$$\Lambda = \frac{1}{2} \begin{pmatrix}
\Lambda' & D & 0 \\
D' & \Lambda' & D \\
0 & D & \Lambda'
\end{pmatrix}. \tag{A.18}$$

Let us denote by $\lambda_1^{D_M}(d)$ the largest eigenvalue of $M$ (that is, of $\Lambda$) and by $\lambda_1^{10}(d)$ the largest eigenvalue of $M'$ (that is, of $\Lambda'$). By Geršgorin's discs' argument, we know that

$$\lambda_1^{D_M}(d) \leq \frac{1}{2} (\lambda_1^{10}(d) + 1) \tag{A.19}$$

which proves half of the claim. This upper bound is achieved for large system size $n$: indeed, if $\lambda$ is an eigenvalue of the reduced size matrix

$$\bar{\Lambda} = \frac{1}{2} \begin{pmatrix}
\lambda_1^{10}(d) & 0 \\
1/2 & \lambda_1^{10}(d) & 1/2 \\
0 & 1/2 & \lambda_1^{10}(d) & 1/2 \\
0 & 1/2 & \lambda_1^{10}(d) & \lambda_1^{10}(d)
\end{pmatrix} \tag{A.20}$$

then it is easily seen that $\lambda$ is also an eigenvalue of the matrix $\Lambda$. As the largest eigenvalue of $\bar{\Lambda}$ is known to converge to $\frac{1}{2} (\lambda_1^{10}(d) + 1)$ for large $n$ (Gray, 2006), the claim is proved.


