The role of the spatial topology in trophic metacommunities: Species with reduced mobility and total population size

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ABSTRACT

A central question in ecology is understanding the influence of the spatial topology on the dynamics of a metacommunity. This is not an easy task, as most fragmented ecosystems have trophic interactions involving many species and patches. Recent attempts to solve this challenge have introduced certain simplifying assumptions or focused on a limited set of examples. These simplifications make the models mathematically tractable but keep away from real-world problems. In this paper, we provide a novel methodology to describe the influence of the spatial topology on the total population size of the species when the dispersal rates are small. The main conclusion is that the influence of the spatial topology is the result of the influence of each path in isolation. Here, a path refers to a pairwise connection between two patches. Our framework can be readily used with any metacommunity, and therefore represents a unification of biological insights. We also discuss several applications regarding the construction of ecological corridors.

1. Introduction

Habitat fragmentation is one of the major drivers of terrestrial biodiversity declines and, yet, the practice is predicted to intensify over the coming years (Fletcher et al., 2018). Promoting the movement of individuals among isolated regions has strongly emerged as a possible solution (Amarasekare, 2008; Leibold et al., 2004; Resasco et al., 2017). From an ecological point of view, the movement allows a species to colonize an unoccupied region or improve the search for resources. On the other hand, it may also increase the mortality rate due to predation, starvation, etc. Bonte et al. (2012). This double role of the movement constantly arises in many real problems, *e.g.*, the optimal location of a marine protected area or the construction of ecological corridors (Haddad et al., 2014; Rassweiler et al., 2012; Resasco et al., 2017). Today, understanding the precise influence of the movement and the spatial topology on the behavior of the species is of critical importance. Although significant progress has been made in a broad variety of situations, many important questions remain unsolved (Gross et al., 2020; Guzman et al., 2019).

One of the recurrent results in spatial ecology is that the population dynamics observed at the scale of local patches depends largely on the dynamics in other habitats through the movement of individuals (Abdala-Roberts et al., 2019; Gross et al., 2020; Guzman et al., 2019; Leibold et al., 2004; Zhang et al., 2021, 2022). Most fragmented ecosystems contain trophic interactions with a high number of species and patches (Gross et al., 2020; Guzman et al., 2019; Leibold et al., 2004), making the analysis of any model a challenging task. Due to these

difficulties, many biological insights and management guidelines have been derived from the metapopulation theory, *i.e.*, single species in fragmented landscapes (Franco and Ruiz-Herrera, 2015; Hastings and Botsford, 2006; Ruiz-Herrera, 2018; Zhang et al., 2015). However, care must be taken when applying them in real situations, especially if the population abundances of the interacting species are highly variable. Actually, there is growing evidence that community-level processes and spatial variables determine many ecological patterns (Gross et al., 2020; Guzman et al., 2019; Leibold et al., 2004; Zhang et al., 2022). For instance, Baiser et al. (2013) found that the species sorting and patch dynamics models accurately explain many ecological properties of the aquatic food web in the leaves of the northern pitcher plant *Sarracenia purpurea*. Another experiment (Zhang et al., 2017) with spatially diffusing laboratory populations of the heterotrophic budding yeast *Saccharomyces cerevesiae* limited by an essential nutrient revealed, among many other things, that in a system of five patches, the total population abundance was found to be higher in a homogeneous than heterogeneous environment with diffusion (with the same total resource level in both cases). In this experiment, Zhang et al. considered a particular spatial topology or spatial arrangement for the patches and made the transfer of individuals manually. The main results by Zhang et al. (2017) were rather unexpected because the reverse conclusion had been theoretically and experimentally deduced in previous works with metapopulations (DeAngelis et al., 2016; Franco and Ruiz-Herrera, 2015; Zhang et al., 2015).

In this paper, we propose a novel approach for describing the influence of the spatial topology on the population abundance of a species in general metacommunities when the dispersal rates are small. To this task, we will analyze a classical metacommunity model, (see (2.1) in the next section). There are thousand of papers analyzing the same question with the same type of model and parameters as we employ here, Hayes and Anderson (2018), Zhang et al. (2017), Wang et al. (2021), Ruiz-Herrera and Torres (2020), Amarasekare (2008), Sadykov and Farnsworth (2021), Zhang et al. (2021) and Suzuki and Economo (2021). The main difficulty lies in the huge number of parameters and combinations, (e.g. there are $2\,097\,152$ spatial topologies for a metacommunity made of five nodes and two species). Since such numbers are unmanageable, even with computer aid, the common practice is to focus on a reduced number of topologies. This practice could be highly problematic. In particular, it does not allow extrapolate a general property regarding the influence of the spatial topology on the fate of a metacommunity. The main contribution of the paper is that we deduce general properties that are valid for any topology and metacommunity. For example, one of the main messages is that the influence of the spatial topology is the sum of the influence of the paths in isolation. In other words, we must visualize the spatial topologies as a collection of paths and analyze each of the paths in an independent manner. Here, a path refers to a pairwise connection between two patches. Our results also identify certain patches and paths that play a disproportionately large role in maintaining the total population size of a target species (see Mouquet et al., 2013 and the concept of keystone communities/patches). As stressed in the paper, the assumption of small dispersal rates is crucial in our analysis.

2. Material and methods

2.1. Modeling framework and basic definitions

We study the dynamical behavior of n species that inhabit a fragmented ecosystem of m patches. A classical model for the metacommunity is

$$
\begin{cases}
x'_{1i}(t) = x_{1i}(t)\left(r_{1i} - r_{1i}\frac{x_{1i}(t)}{K_{1i}} + \sum_{\substack{j=1\\j\neq 1}}^{n} a_{1ji}x_{ji}(t)\right) + \sum_{j=1}^{m} b_{1ij}x_{1j}(t) \\
\quad\vdots \\
x'_{ni}(t) = x_{ni}(t)\left(r_{ni} - r_{ni}\frac{x_{ni}(t)}{K_{ni}} + \sum_{\substack{j=1\\j\neq n}}^{n} a_{nji}x_{ji}(t)\right) + \sum_{j=1}^{m} b_{nij}x_{nj}(t)
\end{cases}
$$

(2.1)

for $i = 1, \dots, m$. In this model, $x_{li}(t) \geq 0$ represents the density of the lth species in patch i and $x'_{li}(t)$ denotes the derivative with respect to t. The parameters r_{li} and K_{li} are strictly positive and denote the maximum per capita rate of increase and carrying capacity of the lth species in patch i, respectively. The different types of interaction among the species in patch i are determined by a_{lji}. For example, if $a_{lji} > 0$ and $a_{jli} < 0$, there is a predator–prey interaction between the lth species (predator) and the jth species (prey) in patch i. For a simple overview, we can write the model of the form

$$X'(t) = X(t)G(X(t)) + BX(t)$$

with $X(t)$ the population vector, organized by patch, $G(X)$ the growth rate matrix (a block diagonal matrix), and B the movement matrix (block matrix). In particular, the sub-matrix $B_l = (b_{lij})$ describes the movement of the lth species. We assume that $B_l = h_l C_l$ where $h_l \geq 0$ is a scale parameter which defines the magnitude of the migration or the degree of mobility of the lth species and $C_l = (c_{lij})$ is a matrix which codifies in the off-diagonal elements the spatial topology or the spatial arrangement of the patches for the lth species. For c_{lij}, a strictly positive value indicates that the lth species can move from patch j to patch i, whereas a "0" means that there is no such a path. We consider weighted matrices, which include rare and frequent dispersal events.

For instance, a large value $c_{lij} > 0$ indicates that the path is very likely to be used by the individuals of the lth species. The diagonal elements c_{lii} are the negative sum of off-diagonal elements for columns i, reflecting the total amount of emigration from patch i for the lth species. We observe that all patches are isolated for the lth species when the matrix C_l is identically zero. In our analysis, we do not impose that all species have the same spatial topology. In this manner, our approach treats the spatial topologies as a species-specific property, instead of a community-level trait.

System (2.1) is a classical model in spatial ecology. The reader can consult (Levin, 1974; Ruiz-Herrera and Torres, 2020; Holland and Hastings, 2008; Hayes and Anderson, 2018; Gross et al., 2020; Nishikawa and Motter, 2010; Sadykov and Farnsworth, 2021; Zhang et al., 2017) and the references therein for experimental/ theoretical works in which (2.1) is the modeling framework. For the sake of simplicity, we have analyzed a metacommunity with growth rates of the Lotka–Volterra type in the main text. Nevertheless, our methodology works for general growth rates, (see Section F in the SI).

In the figures presented in this paper, we adopt the network approach (Artzy-Randrup and Stone, 2010; Urban and Keitt, 2001) that describes landscapes as collections of habitat patches (nodes) linked by edges represented links between different patches. An arrow from node i to node j for the representation of the spatial topology of the lth species indicates the ability of the individuals of this species to disperse from patch i to patch j.

2.2. Methodology

The movement associated with demographic processes (e.g. emigration, immigration, colonization) operates on comparable or smaller timescales than local foodweb dynamics (Amarasekare, 2008). In other words, parameters $h_1, \dots, h_n$ are smaller than the interaction parameters in (2.1). This is the focus of the paper, dispersal phenomena, i.e, movement from birth site to distant reproducing sites. On the other hand, we restrict ourselves to metacommunities with a unique equilibrium $(p_{11}, \dots, p_{n1}, \dots, p_{1m}, \dots, p_{nm})$ with $p_{li} > 0$ for all l, i which is a global attractor for all non-zero solutions of (2.1). From this equilibrium, we then define $T_1(h_1, \dots, h_n), T_2(h_1, \dots, h_n), \dots, T_n(h_1, \dots, h_n)$ as the total number of individuals of species 1, species 2, …, species n, across all nodes in the steady state solution, respectively (see Definition 1 in SI for the precise expression of these functions). Notice that we are excluding local extinctions in the metacommunity. In our analysis, the parameters associated with the local dynamics, *i.e.*, r_{li}, K_{li}, a_{lji}, are always fixed. We make explicit the dependence of the degrees of mobility of the species on $T_1(h_1, \dots, h_n), \dots, T_n(h_1, \dots, h_n)$ because they are the key parameters to understand the influence of the spatial topologies.

Our methodology consists of exploring the effect of the spatial topologies on $T_1(h_1, \dots, h_n), T_2(h_1, \dots, h_n), \dots, T_n(h_1, \dots, h_n)$ by varying the matrices $C_1, \dots, C_n$. Specifically, we follow a perturbation approach, starting from no dispersal at all species and introducing a very small amount of dispersal.

There are two main ingredients in our arguments:

(M1) $T_1(0, \dots, 0), \dots, T_n(0, \dots, 0)$ are independent of the matrices $C_1, \dots, C_n$.

(M2) We have proved in SI (see Proposition 1) that $\frac{\partial T_l}{\partial h_s}(0, \dots, 0)$ depends on C_s but not on the other matrices. Moreover, if $C_s = 0$, that is, all patches are isolated for the sth species, then $\frac{\partial T_l}{\partial h_s}(0, \dots, 0) = 0$.

From an applied side, **(M2)** says that the influence of the movement of the sth species on the total population size of the lth species is independent of the movement of the other species. Using **(M1)** and **(M2)**, we can analyze $T_l(h_1, \dots, h_n)$ for small values of $h_1, \dots, h_n$. Specifically, if $\frac{\partial T_l}{\partial h_s}(0, \dots, 0) > 0$ (resp. < 0) for a matrix C_s, the movement of the

individuals of the sth species in the spatial topology associated with C_s increases (resp. decreases) the total population size of the lth species. Moreover, we can compare the influence of two different topologies. If C_s and $\widetilde{C}_s$ are two different matrices and $\frac{\partial T_l}{\partial h_s}(0, \ldots, 0)$ is greater for C_s than for $\widetilde{C}_s$, the value of $T_l(h_1, \ldots, h_n)$ is greater when the sth species moves in the first spatial topology than in the second topology.

For small values of $h_1, \ldots, h_n$, we have that

$$T_l(h_1, \ldots, h_n) \approx T_l(0, \ldots, 0) + h_1 \frac{\partial T_l}{\partial h_1}(0, \ldots, 0) + \cdots + h_n \frac{\partial T_l}{\partial h_n}(0, \ldots, 0). \quad (2.2)$$

Thus, the benefits/damages of the movement of a particular species within a spatial topology could be magnified/buffered by the movement of the other species. Moreover, we maximize (resp. minimize) $T_l(h_1, \ldots, h_n)$ for small values of $h_1, \ldots, h_n$ finding the topologies that maximize (resp. minimize) $\frac{\partial T_l}{\partial h_1}(0, \ldots, 0), \ldots, \frac{\partial T_l}{\partial h_n}(0, \ldots, 0)$. Observe that we can analyze the presence of some sedentary species with our framework. If, for example, the first l_0 species are mobile and the rest are sedentary in (2.1), the total population sizes are $T_1(h_1, \ldots, h_{l_0}, 0, \ldots, 0)$, $\ldots, T_n(h_1, \ldots, h_{l_0}, 0, \ldots, 0)$.

3. Results

3.1. A general property: The additive influence of the paths when the species have reduced mobility

The partial derivatives $\frac{\partial T_l}{\partial h_1}(0, \ldots, 0), \ldots, \frac{\partial T_l}{\partial h_n}(0, \ldots, 0)$ have very complex expressions but they can be always expressed as (see Proposition 1 in SI)

$$\frac{\partial T_l}{\partial h_s}(0, \ldots, 0) = \sum_{\substack{i,j=1 \\ j \neq i}}^{m} c_{sij} x_{sj}^* (\Delta_{lsi} - \Delta_{lsj}) \quad (3.3)$$

for, $l, s = 1, \ldots, n$ where Δ_{lsi} and Δ_{lsj} are quantities associated with the lth and sth species that depend on the local dynamics in patch i and j, respectively; and x_{sj}^* is the population density of the sth species in patch j at the equilibrium in the absence of movement, (following the notation in Section 2, $x_{sj}^* = p_{sj}(0, \ldots, 0)$). The manner of writing $\frac{\partial T_l}{\partial h_s}(0, \ldots, 0)$ in (3.3) is one of the main contributions of this paper because it allows us to deduce two general results. First, since (3.3) is a weighted sum of the off-diagonal elements of the matrix $C_s = (c_{sij})$, the influence of the spatial topology of the sth species on the total population size of the lth species is the result of the influence of the movement in each path in isolation. Thus, there are no global effects of the spatial topology itself. Notice that the influence of a concrete path is determined by the biological features of the departing and arriving patches. It is worth noting that common concepts in spatial ecology such as irreducibility or modularity (see Artzy-Randrup and Stone, 2010) are not crucial features for understanding the role of the spatial topologies when the species have reduced mobility. Second, if the movement of individuals of the sth species from patch i to patch j increases (resp. decreases) the total population size of the lth species, then the movement from patch j to patch i decreases (resp. increases) it. To justify this claim, we observe that the contribution of the movement of the sth species from patch j to patch i in (3.3) is $c_{sij} x_{sj}^* (\Delta_{sli} - \Delta_{slj})$. Particularly, since $c_{sij} x_{sj}^* \geq 0$, if $\Delta_{lsi} - \Delta_{lsj} < 0$, (resp. > 0) the movement of the sth species in this path reduces (resp. increases) the total population size of the lth species independently of c_{sij}. The analysis of the path from patch i to patch j involves the sign of $\Delta_{lsj} - \Delta_{lsi}$ which is the opposite of $\Delta_{lsi} - \Delta_{lsj}$.

To facilitate understanding, we study a metacommunity made of three competitors with reduced mobility in a landscape of 10 nodes, (see Fig. 1, first row). With the parameters given in Fig. 2, we collect the different values of Δ_{lsi} in Table 1. The influence of the spatial topology of species 1 on its total population size is the sum of the influence of the 10 paths, namely the path from patch 1 to 2, from 2 to 3, from 3 to 4,..., and from 10 to 1. In this particular case, the path

Table 1
Values of Δ_{lsi}. These parameters determine the influence of the different paths in the spatial topologies of Fig. 1. See SI Section B1.

j	Δ_{11j}	$\Delta_{12j} = \Delta_{13j}$
$j = 1$	1.211	−0.110
$j = 2$	1.325	−0.172
$j = 3$	1.448	−0.241
$j = 4$	1.578	−0.315
$j = 5$	1.719	−0.396
$j = 6$	1.869	−0.484
$j = 7$	2.032	−0.580
$j = 8$	2.208	−0.685
$j = 9$	2.4	−0.8
$j = 10$	2.838	−1.064

from patch 10 to patch 1 decreases its total population size, and the rest of the paths increases it. Therefore, if we remove these last paths in the spatial topology (see Fig. 1 second row), the total population size of species 1 decreases (see Fig. 2 red curve). Generally speaking, the movement of individuals of a species towards patches of lower biological quantities generally increases its total population size. In the metacommunity discussed in Fig. 1/Table 1, the path from patch 10 to patch 1 reduces total abundance because the individuals goes to a patch with lower competition. The analysis of the influence of the spatial topology of species 2 on the total population size of species 1 is analogous. Specifically, we have to analyze the contribution of the 10 paths in isolation. In this case, the path from patch 10 to patch 1 has a negative contribution on the total population size of the first species, and the rest of the paths have a positive contribution. In an analogous manner, we can analyze the influence of the third species on the total population size of the first species.

In summary, the total population size of a species in a metacommunity depends on two facts: the parameters associated with the local dynamics in all patches, and the spatial topologies. When the species have a reduced mobility, the influence of the spatial topologies is the result of the influence of each path in isolation. In turn, the analysis of the influence of a concrete path depends on the parameters associated with the local dynamics of the arriving and departing patches, via the quantities Δ_{sij} of (3.3).

3.2. Examples of applying the model to different metacommunities

The generality of the modeling framework in (2.1) masks many phenomena that depend on the type of metacommunity. To avoid this problem, we will apply our results to simple metacommunities made of two species in landscapes with a general number of patches, say m. The reduced number of species in the metacommunities allows us to re-write model (2.1) and formula (3.3) in a more friendly manner.

3.2.1. Predator–prey metacommunities

Consider the equations

$$\begin{cases} x_i'(t) &= x_i(t)(r_i - r_i \frac{x_i(t)}{K_i} - \alpha_i y_i(t)) + \sum_{j=1}^{m} c_{ij} h_1 x_j(t) \\ y_i'(t) &= y_i(t)(s_i - s_i \frac{y_i(t)}{Q_i} + \beta_i x_i(t)) + \sum_{j=1}^{m} \widetilde{c}_{ij} h_2 y_j(t) \end{cases} \quad (3.4)$$

for $i = 1, \ldots, m$ with $x_i(t)$ and $y_i(t)$ the population densities of a prey and a generalist predator in patch i, respectively. In (3.4), r_i is the maximum per capita rate of increase, K_i is the carrying capacity and α_i is the predation rate of the prey in patch i. The spatial topology of the prey is determined by the matrix $C = (c_{ij})$ and $h_1 \geq 0$ stands for its degree of mobility. In an analogous manner for the predator, we define s_i, Q_i, β_i, $\widetilde{C}$ and h_2. Model (3.4) has linear functional relationship and logistic growth of the predator without prey. Notice that the model fits in the modeling framework given in (2.1) but it is not the most common structure for predator–prey models. Although our results are applicable
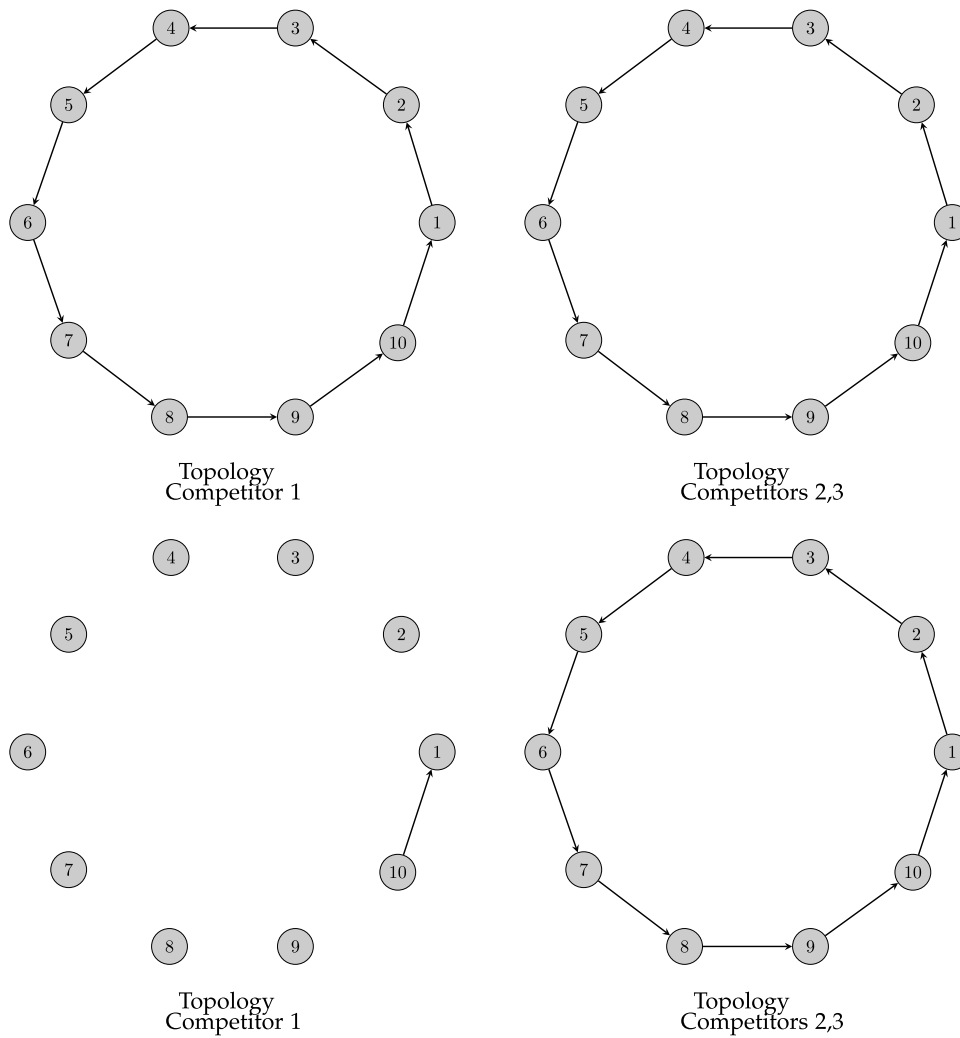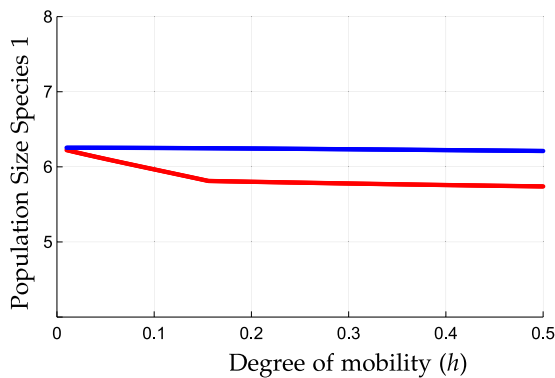
Fig. 1. Spatial topologies employed in Fig. 2.

Fig. 2. Representation of the total population size of the first competitor. Fixed parameters $r_{li} = K_{li} = 1$ and competition rates $a_{lj1} = -0.1$, $a_{lj2} = -0.15$, $a_{lj3} = -0.2$, $a_{lj4} = -0.25$, $a_{lj5} = -0.3$, $a_{lj6} = -0.35$, $a_{lj7} = -0.4$, $a_{lj8} = -0.45$, $a_{lj9} = -0.5$ and $a_{lj10} = -0.6$ for all $i = 1, \ldots, 10$; $l, j = 1, 2, 3$ with $l \neq j$. For simplicity, we assume that all competitors have the same degree of mobility, i.e., $h_1 = h_2 = h_3 = h$. The entries of the matrices C_l in both metacommunities are $c_{lij} = 0.2$ if the route from patch j to patch i exists for the lth species. The blue and red curves represent $T_1(h, h, h)$ in the topologies of the first and second rows in Fig. 1, respectively. See Table 1 for the values of Δ_{lji}.

for general models (see Section F in SI), we always impose the presence of a globally stable equilibrium.

The dynamics in patch i in the absence of movement, i.e., $h_1 = h_2 = 0$, is given by

$$\begin{cases} x'_i(t) & = & x_i(t)(r_i - r_i \frac{x_i(t)}{K_i} - \alpha_i y_i(t)) \\ y'_i(t) & = & y_i(t)(s_i - s_i \frac{y_i(t)}{Q_i} + \beta_i x_i(t)). \end{cases} \tag{3.5}$$

In this case, the (local) coexistence state is

$$x^*_i = \frac{K_i s_i (r_i - \alpha_i Q_i)}{r_i s_i + \alpha_i \beta_i K_i Q_i} \quad \text{and} \quad y^*_i = \frac{(s_i + \beta_i K_i) Q_i r_i}{r_i s_i + \alpha_i \beta_i K_i Q_i}.$$

The prey is excluded in (3.5) when

$$r_i - \alpha_i Q_i \leq 0.$$

Thus, to prevent the presence of local extinctions for the prey in the absence of movement, we suppose that $r_i - \alpha_i Q_i > 0$ for $i = 1, \ldots, m$. We denote by $T_1(h_1, h_2)$ and $T_2(h_1, h_2)$ the total population sizes of the prey and the predator in (3.4), respectively. In the SI (see Proposition 2), we have obtained that

$$\frac{\partial T_1}{\partial h_1}(0, 0) = \sum_{\substack{i,j=1 \\ j \neq i}}^{m} c_{ij} x^*_j \left(\frac{1}{r_i - \alpha_i Q_i} - \frac{1}{r_j - \alpha_j Q_j} \right), \tag{3.6}$$

$$\frac{\partial T_1}{\partial h_2}(0, 0) = \sum_{\substack{i,j=1 \\ i \neq j}}^{m} \widetilde{c}_{ij} y^*_j \left(\frac{-\alpha_i K_i}{r_i(s_i + \beta_i K_i)} + \frac{\alpha_j K_j}{r_j(s_j + \beta_j K_j)} \right), \tag{3.7}$$
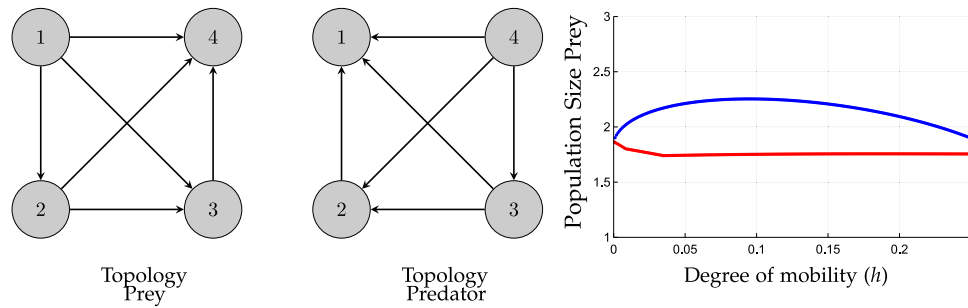
Fig. 3. Spatial topologies for the prey and predator (first columns) and representation of the total population size of the prey. We analyze model (3.4) with parameters $r_i = s_i = Q_i = K_i = 1$, $\alpha_1 = 0.1$, $\alpha_2 = 0.25$, $\alpha_3 = 0.9$, $\alpha_4 = 0.95$, $\beta_i = 0.1$ for $i = 1, 2, 3, 4$. We assume that both species have the same degree of mobility, i.e., $h_1 = h_2 = h$. The blue curve represents $T_1(h, h)$ in the represented topologies. Notice that with these parameters, the represented topologies maximize the overall population size of the prey. The red curve represents $T_1(h, h)$ in the topologies that minimize the total population size of the prey. Specifically, we change the sense of all the paths in the represented topologies. The entries of the matrices are $c_{ij} = 0.2$ or $\widetilde{c}_{ij} = 0.2$ if the route from the patch j to the patch i exists.

$$\frac{\partial T_2}{\partial h_1}(0,0) = \sum_{\substack{i,j=1 \\ j \neq i}}^{m} c_{ij} x_j^* \left(\frac{\beta_i Q_i}{s_i(r_i - \alpha_i Q_i)} - \frac{\beta_j Q_j}{s_j(r_j - \alpha_j Q_j)} \right), \qquad (3.8)$$

and

$$\frac{\partial T_2}{\partial h_2}(0,0) = \sum_{\substack{i,j=1 \\ i \neq j}}^{m} \widetilde{c}_{ij} y_j^* \left(\frac{1}{s_i + \beta_i K_i} - \frac{1}{s_j + \beta_j K_j} \right), \qquad (3.9)$$

with x_j^*, y_j^* the density of population of the prey and the predator in patch j at the equilibrium in the absence of movement, respectively.

When both species have reduced mobility, the movement of the prey from patch j to patch i increases its own total population size (see Expression (3.6)), provided

$$r_j - \alpha_j Q_j > r_i - \alpha_i Q_i, \qquad (3.10)$$

(see Remark 1 in SI). If the reverse inequality is satisfied, the movement decreases it. Note that the prey is close to being excluded in patch i when $r_i - \alpha_i Q_i \approx 0$. In light of (3.10), promoting the diffusion to those patches, i.e., sources close to becoming sinks, is highly recommended to enhance the total population size of the prey. Generally speaking, formula (3.6) suggests that the movement of the prey to "less quality" patches increases its own population density. The manner to measure the quality of the patch i is via the quantity $r_i - \alpha_i Q_i$, that depends on the intrinsic biological features of the patch and predation pressure. Following the same logic with expression (3.7), the movement of the predator from patch j to patch i contributes positively to the total population size of the prey, provided $\frac{\alpha_i K_i}{r_i(s_i + \beta_i K_i)} < \frac{\alpha_j K_j}{r_j(s_j + \beta_j K_j)}$. Intuitively, $\frac{\alpha_i K_i}{r_i(s_i + \beta_i K_i)}$ is a quantity that measures the predators' damages on the prey in patch i. Therefore, the recommendation to enhance the total population size of the prey is to promote the movement of the predator towards patches where they provoke less damages to the prey. The analysis of the influence of the spatial topologies on the total population size of the predator is analogous using expressions (3.8) and (3.9). With the previous discussion, we have the precise description of the role of any path in the metacommunity when the populations have a reduced mobility. The influence of the spatial topologies will be the sum of the influences mentioned above. In particular, if we want to describe the topologies that maximize the total population size of the prey when they have reduced mobility, we have to construct the topologies with only paths with positive contribution to the total population size of the prey. They are always directed graphs (see Fig. 3) because if a path has a positive (resp. negative) contribution, the path in the opposite sense, i.e., exchanging the departing and arriving patches, has a negative (resp. positive) contribution. Thus, directed movements are those with the highest influence of the total population size of the species in metacommunities.

3.2.2. A metacommunity with a mobile competitor and a sedentary competitor

Consider the system

$$\begin{cases} x_i'(t) = x_i(t)\left(r_i - r_i \frac{x_i(t)}{K_i} - \alpha_i y_i(t)\right) + \sum_{j=1}^{m} c_{ij} h_1 x_j(t) \\ y_i'(t) = y_i(t)\left(s_i - s_i \frac{y_i(t)}{Q_i} - \gamma_i x_i(t)\right) \end{cases} \qquad (3.11)$$

for all $i = 1, \ldots, m$. In this model, r_i, s_i and K_i, Q_i are the maximum per capita rates of increase and carrying capacities for the competitors in patch i, respectively. The parameters $\alpha_i, \gamma_i \geq 0$ represent the competition rates in patch i. In (3.11), we assume that the second competitor is sedentary, i.e., $h_2 = 0$. Analogously to the predator–prey metacommunity discussed above, we assume that

$$r_i - \alpha_i Q_i > 0$$

$$s_i - \gamma_i K_i > 0$$

for all $i = 1, \ldots, m$ to exclude the presence of local extinctions in the absence of movement. Notice that the (local) coexistence state is

$$x_i^* = \frac{K_i s_i (r_i - \alpha_i Q_i)}{r_i s_i + \alpha_i \gamma_i K_i Q_i} \quad \text{and} \quad y_i^* = \frac{(s_i - \gamma_i K_i) Q_i r_i}{r_i s_i + \alpha_i \gamma_i K_i Q_i}.$$

We denote the total population sizes of the competitors by $T_1(h_1, 0)$ and $T_2(h_1, 0)$. In the SI (see Section D), we have obtained that

$$\frac{\partial T_1}{\partial h_1}(0,0) = \sum_{\substack{i,j=1 \\ j \neq i}}^{m} c_{ij} x_j^* \left(\frac{1}{r_i - \alpha_i Q_i} - \frac{1}{r_j - \alpha_j Q_j} \right), \qquad (3.12)$$

$$\frac{\partial T_2}{\partial h_1}(0,0) = \sum_{\substack{i,j=1 \\ j \neq i}}^{m} c_{ij} x_j^* \left(\frac{-\gamma_i Q_i}{s_i(r_i - \alpha_i Q_i)} + \frac{\gamma_j Q_j}{s_j(r_j - \alpha_j Q_j)} \right). \qquad (3.13)$$

The analysis of the influence of the spatial topology on the total population size of the competitors when the mobility degree is reduced is similar to that in model (3.6). We underline the recommendation of promoting the diffusion of the mobile competitor towards regions where it is close to being excluded to enhance its own total population size.

4. Practical implications

The previous results provide new guidelines for managers who wish to maximize the total population size of a target species in metacommunities. We take advantage of the following insights:

(R1) The influence of the movement of a species within a spatial topology on the total population size of a target species is the result of the contribution of each path in isolation.

(R2) The movement of individual of a species towards patches of lower biological qualities generally increases its total population size.
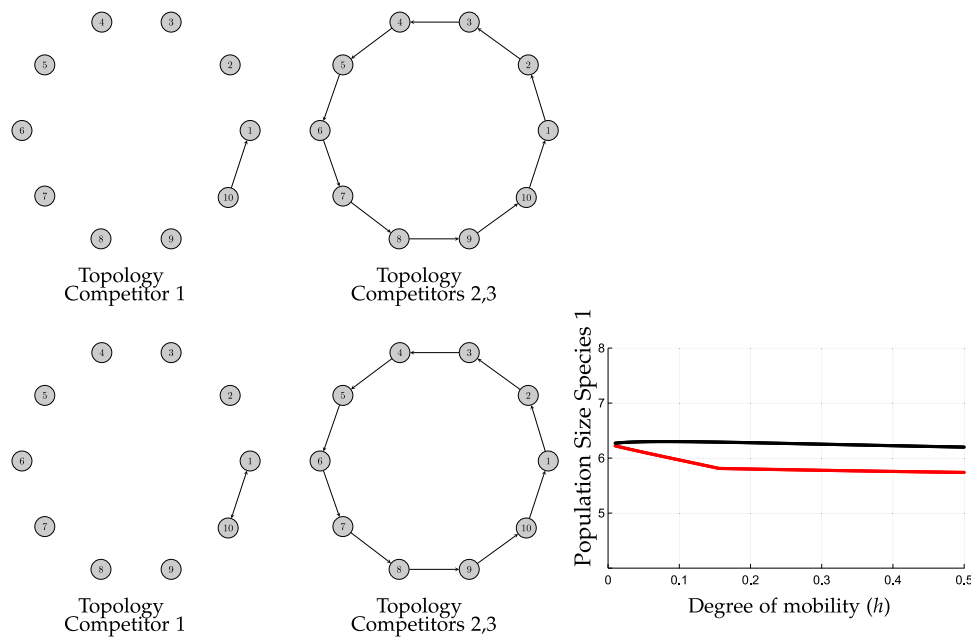
Fig. 4. Spatial topologies (left and center columns) and representation of the total population size of the first competitor. We analyze a metacommunity made of three competitors in a landscape of ten patches with the same parameters as those in Fig. 1. The red and black curves represent $T_1(h, h, h)$ in the topologies of the first and second rows, respectively. In other words, we add the path from patch 1 to patch 10 in the spatial topology of the first competitor. Notice that the benefit of this path is almost the same as the benefits of the paths from patches 1 to 2, 2 to 3 and so on, (see Fig. 2 blue curve).

4.1. Which is the additional path that maximizes the total population size of a target species?

The answer of this question depends on the ability of the rest of the species to use the additional path. If only the target species can use the corridor, managers should construct a path from the "strongest source" to the "weakest source". As emphasized in Fig. 4, the introduction of a single path in a spatial topology could produce a noticeable increment of the total population size. When other species can use the additional path as well, the result of the influence of the movement of the different species is hard to predict. However, if the arriving patch is close to becoming a sink for the target species, the benefits of the movement of that species normally prevail.

4.2. Consequences of the loss of dispersal routes

Given that some paths have negative influence on the total population size of some species, the loss of paths in the spatial topologies per se does not necessarily threaten the biodiversity. On the other hand, the influence of a path on the total population size of a species only depends on the biological features of the arriving and departing patches. Particularly, the influence of the loss of paths on the total population size of the species does not depend on the number of isolated cluster of the resulting landscapes. We illustrate this phenomenon in Fig. 5 with a predator–prey metacommunity of eight patches in which patches 3 and 5 have the same biological features. In this metacommunity, the bidirectional path joining patches 3 and 8 and the one joining patches 5 and 8 have the same influence because they involve patches with identical biological features.

5. Discussion

This paper offers a cohesive framework to study the influence of the spatial topology on the total population size of a species in trophic metacommunities. This is a long-outstanding question with deep repercussions in conservation and management, (see the open question (c) in Gross et al., 2020; Guzman et al., 2019; Zhang et al., 2021). We have analyzed a general model, moving beyond simple spatial topologies or a reduced number of patches. As stressed in Guzman et al. (2019), trophic metacommunities are not well understood and our knowledge is still under development. It is worth noting that the benefits/damages of the spatial topologies for diffusive movements can involve a considerable variation of the total population size of a species, magnifying or diluting any management strategy.

Our main contribution was to provide useful expressions of the partial derivatives of the total population size of a species with respect to their degrees of mobility. The key difficulty of this task comes from the high number of parameters involved in (2.1), obstructing even the use of any symbolic mathematical algorithm.

5.1. A unified perspective for the role of the spatial topologies

The movement of many species is associated with demographic processes, Amarasekare (2008, 2003), Guzman et al. (2019) and Strauss et al. (2019). When all species exhibit this type of movement, that is, low dispersal rates, the influence of the spatial topologies on the total population size of a species is the sum of the influence of each path in isolation. In other words, we have to visualize the spatial topologies as a collection of paths and analyze the contribution of each of them independently. The contribution of a specific path on the total population size of a species depends on the growth rates, carrying capacities, and the interaction among the species of the arriving and departing patches. Generally speaking, the movement of individuals from high-quality patches (i.e. low competition) to low-quality (high competition) ones leads to the increase of its own population size. This movement is a manner of releasing competitive pressure so that individuals that would have lost to competition in the source can still survive by emigrating to low-quality patches (see crowding effects mentioned in Debinski and Holt, 2000). Notice that competition strength is composed of both the competition rate and the abundance of the species. Thus, it is possible to have a case where moving to a patch with fewer individuals does release individuals from competition, even if the competition strength is higher. The movement of individuals from high quality patches to low quality ones also echoes the long-standing explorations of rescue effect and source–sink dynamics. Our results indicate that promoting rescue effects of a species, *i.e.,* the movement of individuals from
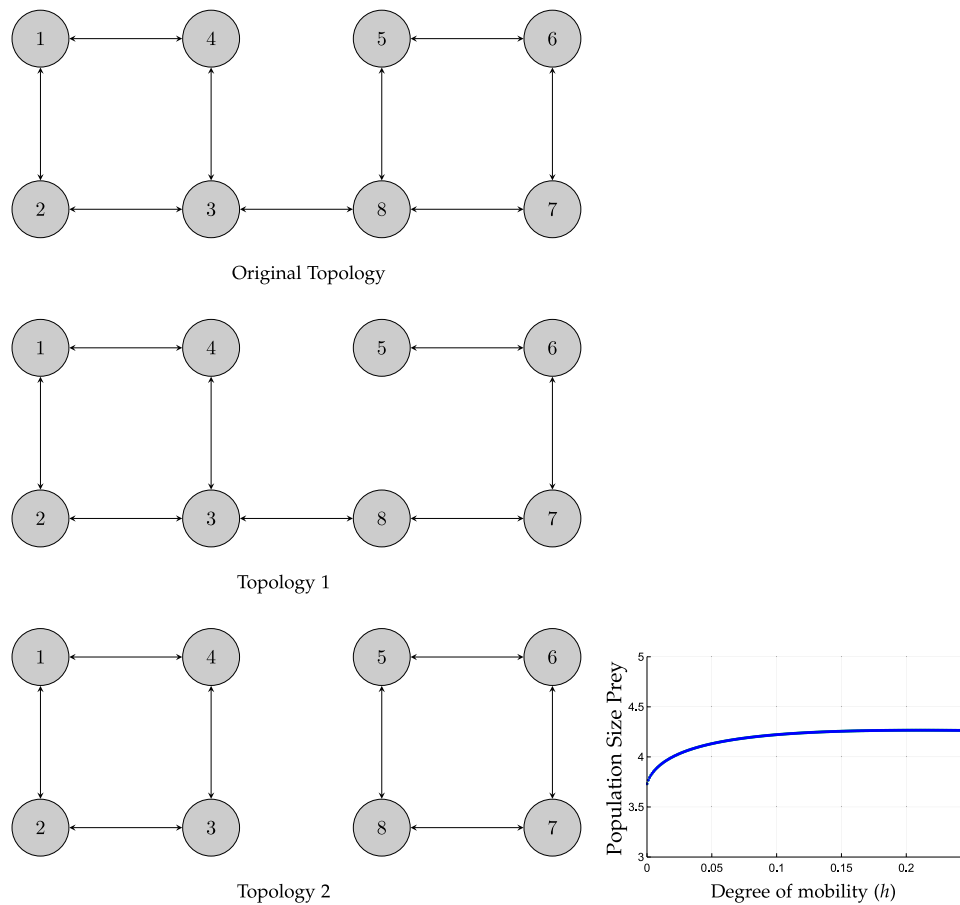
Fig. 5. Spatial topologies and representation of the total population size of the prey in both topologies. We analyze a predator–prey metacommunity (model (3.4)) in a landscape of eight patches. Fixed parameters $r_i = K_i = s_i = Q_i = 1$ and $\beta_i = 0.1$. $\alpha_1 = \alpha_7 = 0.15$, $\alpha_2 = \alpha_6 = 0.3$, $\alpha_3 = \alpha_5 = 0.9$, $\alpha_8 = \alpha_4 = 0.95$. For simplicity, we assume that both species have the same degree of mobility, i.e., $h_1 = h_2 = h$. The entries of the matrices C_l in both metacommunities are $c_{lij} = 0.2$ if the route from patch j to patch i exists, (we are assuming the same spatial topology for both species). Under these conditions, $T_1(h, h, h)$ coincides in both topologies. Since the biological features of patches 3 and 5 are the same, the influence of the bidirectional path joining patches 3 and 8 is the same as that of the bidirectional path joining patches 5 and 8. Both curves coincide by this reason. Notice that an individual has access to all patches in topology 1 but not in topology 2.

surrounding habitats to avoid local extinctions, leads to a considerable increment of its overall population size in metacommunities with low dispersal rates.

The analysis of the total population of a species has a long tradition in ecology, starting with the work by Freedman and Waltman (1977) for simple metapopulations of two patches, (see Ruiz-Herrera and Torres, 2018; Zhang et al., 2020, 2017 for recent results in this direction). A common conclusion of these papers is that the total population size of a species can exceed the sum of the carrying capacities of the isolated patches. Put differently, the movement of the species in a metacommunity can have a positive influence on a species. In comparison with those works, our main contribution is to extend the analysis to landscapes with complex spatial topologies and any number of species. Recently, Zhang et al. (2017) analyzed the total population abundance of a mobile consumer in a consumer-resource system with five patches. They hypothesized that a consumer population diffusing in a landscape with a heterogeneously distributed input of exploitable renewed limiting resource can reach a greater total biomass than a population diffusing in a space with the same total input of resources distributed homogeneously, (see Hypothesis 3). They rejected theoretically and experimentally this hypothesis. Nevertheless, this conclusion should be taken with caution because the spatial topology of the consumer did not enter in the game. According to our results, the spatial topologies generally play a negligible influence on the total population size of a species in homogeneous landscapes. However, the spatial topologies normally play a remarkable role in heterogeneous landscapes. Under the biological conditions in Zhang et al. (2017), it

seems that they considered a spatial topology with a negative influence on the consumer. However, this is not always true. In fact, we have provided a spatial topology in SI (see Fig. E1 in SI) with a positive influence on the consumer and for which the hypothesis stated by Zhang et al. holds.

In agreement with previous works Haddad et al. (2017), a general insight of this paper is that the total biomasses of the species chiefly depend on the spatial topologies. Neglecting these variables involve the lack of a key factor in any metacommunity. Most papers in spatial ecology focus on a reduced number of examples for the spatial topologies. Some popular options are the fully connected topology, where direct dispersal from one patch to another is possible, or the so-called Erdös–Rényi random graphs (Artzy-Randrup and Stone, 2010; Gross et al., 2020). We stress that these options never contain the most beneficial path structures for population abundances, because they introduce symmetric (bidirectional) dispersal paths. As mentioned in Section 3, if the movement of a species in a path from patch i to patch j increases (resp. decreases) its own total population size or the total population size of other species, the movement in the path from patch j to patch i decreases (resp. increases) it. This remark implies that symmetric spatial topologies normally have less influence on the total population sizes of the species than, for instance, the dendritic or directed graphs presented in riverine metacommunities. This result echoes recent theoretical and experimental findings, see Heino et al. (2015) and the references therein. From a conservation perspective, this paper has provided a strategy to increase the total population size of

a target species varying the spatial topology. However, in large, multi-species communities, structures that confer higher overall population sizes for some species could cause reduction in others. Thus, the alteration of spatial topologies should be employed for species specific objectives.

5.2. An alternative interpretation of some classical concepts in spatial ecology

The number of dispersal connections, or connectivity, and the evenness of their distribution among patches are usual measures in spatial ecology that overlook crucial information of the spatial topologies. The analysis of these variables alone can lead to apparently contradictory results. For example, there are theoretical and experimental results in which heterogeneous distributions of paths in the spatial topologies negatively/positively impact the abundance of a population (see Gross et al., 2020; Barter and Gross, 2016 and the references therein). Our results suggest there are paths with positive influence on the abundance of a species and paths with negative influence. Moreover, the influence of a path is determined by the biological features of the arriving and departing patches. Particularly, increasing the number of dispersal connections damages a target species when most introduced paths have a negative influence. On the other hand, different species of a meta-community normally have spatial topologies based on their dispersal traits (*e.g.* wind dispersed vs. bird dispersed seeds, walking vs. flying species). The common assumption of sharing the same spatial topology is oversimplifying, specially when there exist refuges of competitions within the landscape or great differences among the movement abilities of the populations. For example, the directional water flow and its influence on the movement of a population determine its spatial topology in river metacommunities. Assuming the same topology for all species would involve the introduction of fictitious paths for some species and the removal of real paths for other ones. We stress that the topologies are normally very different among the species in the most beneficial situation for a target species (see Fig. 3). Generally speaking, imposing the same topology for all species is a condition that dilutes the influence of the spatial variables on the total population size of the species.

Originally, a keystone species was defined as a species with a crucial role in community structure and/or ecosystem functioning, (see the classical work by Paine in the sixties on rocky intertidal communities Paine, 1966). There are many metacommunities in nature in which some habitats play a disproportional influence for species recruitment and species diversity. With these prototypical examples, Mouquet et al. (2013) extend the concept of keystone species to communities and ecosystems. Our results suggest that the concept of keystone community can be interpreted at the level of connections, not only habitats. Interestingly, these keystone elements are found at very dispersal rates, *i.e.*, when the communities are rather isolated. For example, in Fig. 3, the paths of the topology involves an increment of one third of its total abundance.

5.3. Limitations and future research directions

This paper has offered a number of biological insights for general metacommunities. Nevertheless, care must be taken when applying them in real situations. We have imposed two crucial assumptions: the absence of local extinctions and small dispersal rates. Local extinctions in metacommunities are rather common in nature (Amarasekare, 2008; Franco and Ruiz-Herrera, 2015; Leibold et al., 2004), but they were neglected in this paper. The first natural question will be to extend our analysis to metacommunities that allow local extinctions. The analysis of highly mobile species requires a different approach and new phenomena emerge. Note that the optimal spatial topology suggested in Section 3 is never recommended for populations with a high degree of mobility. If the flux of individuals is relatively high on a directed graph
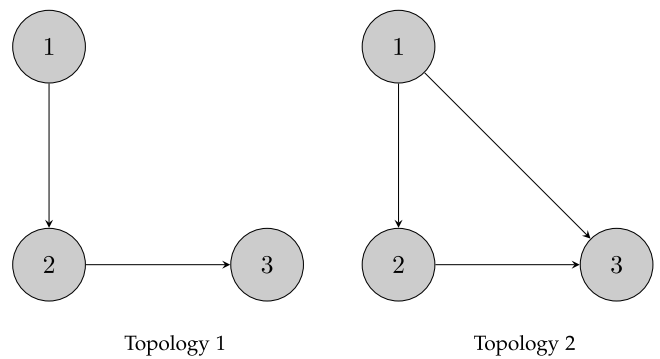

Fig. 6. Representation of two topologies in which the additive influence of the paths is not valid for highly mobile species.

like that in Fig. 3, the whole population tends to occupy a unique patch. Thus, the overall population size in that topology will be smaller than in the topology made of isolated nodes. We mention that the additive influence of the paths mentioned in Section 3 is not valid for highly mobile species either. For example, the introduction of a path from patches 1 and 3 in Fig. 6 does not have influence on a highly mobile species. Biologically, the benefit of this new path is reduced because the access to patch 1 to patch 3 passing through patch 2 is rather simple for a highly mobile individual.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.jtbi.2023.111479.

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