Assessing mutualistic metacommunity capacity by integrating spatial and interaction networks

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Statement of authorship: MO originally developed the general idea and the framework, further enriched by FMunoz, FMassol and WT. MO finalised the framework, run all analyses, and wrote the first draft of the paper together with WT. All authors then contributed to the manuscript.

Keywords: Network, mutualism, metacommunity, threshold, theoretical ecology

Data accessibility statement: This manuscript did not use any real data, except the simulations. All scripts necessary to generate the simulated data and figures are accessible on gitlab (https:

21 //gitlab.com/marcohlmann/metacommunity_theory).

Abstract

We develop a spatially realistic model of mutualistic metacommunities that exploits the joint structure of spatial and interaction networks. Assuming that all species have the same colonisation and extinction parameters, this model exhibits a sharp transition between stable non-null equilibrium states and a global extinction state. This behaviour allows defining a threshold on colonisation/extinction parameters for the long-term metacommunity persistence. This threshold, the 'metacommunity capacity', extends the metapopulation capacity concept and can be calculated from the spatial and interaction networks without needing to simulate the whole dynamics. In several applications we illustrate how the joint structure of the spatial and the interaction networks affects metacommunity capacity. It results that a weakly modular spatial network and a power-law degree distribution of the interaction network provide the most favourable configuration for the long-term persistence of a mutualistic metacommunity. Our model that encodes several explicit ecological assumptions should pave the way for a larger exploration of spatially realistic metacommunity models involving multiple interaction types.

1 Introduction

A fundamental goal of predictive ecology is to forecast the dynamics of interacting species in a given region (Thuiller *et al.* 2013, Mouquet *et al.* 2015). Reaching such a goal has direct implications for biodiversity management and conservation and to anticipate or mitigate the effects of habitat destruction and global change on biodiversity.

Metapopulation models have long been used to characterise the dynamics of populations that can colonise, persist or go extinct in a given landscape configuration (Hanski & Ovaskainen 2003). This configuration is often summarised by a spatial network of suitable patches (Dale & Fortin 2010; Hagen *et al.* 2012) that best represents habitat patchiness in both natural and human-altered ecosystems (Haddad *et al.* 2015). Levins (1969) devised a seminal model of species occupancy *i.e.*, the probability of presence of species populations across a landscape. In this model, a mean-field, deterministic differential equation model represented the population dynamics in fully connected patches, so that equilibrium occupancy depended on both a colonisation and an extinction parameter. More than 30 years later, Etienne & Nagelkerke (2002) proposed a stochastic analogue of Levins' model and studied the links between the properties of the two models. Two sources of spatial heterogeneity can be embedded in metapopulation models: the heterogeneity on colonisation/extinction parameters among species (functional connectivity) and on the spatial network structure (structural connectivity) (Tischendorf & Fahrig 2000). The impact of structural connectivity on stationary occupancy (*e.g.*, Gilarranz & Bascompte 2012) underlines the influence of fragmentation on metapopulation persistence (Fahrig 2003, Fletcher Jr *et al.* 2018). Subsequent deterministic, spatially realistic models acknowledged variation of connectivity among nodes, and allowed quantifying analytically the viability of a metapopulation that depends on the mere structural properties of the spatial network (Ovaskainen & Hanski 2001, Hanski & Ovaskainen 2003). The viability is defined through the metapopulation capacity, *i.e.*, a threshold on colonisation and extinction parameters above which the metapopulation can survive. This threshold is thus of prime importance in biological conservation (Groffman *et al.* 2006).

However, populations of a species are likely to interact with many other species within habitat

patches. These interactions should also affect the spatial coexistence of multiple metapopulations and their respective capacities (Thuiller *et al.* 2013). Metacommunity models are designed to assess the joint dynamics of multiple species in a habitat network (Leibold *et al.* 2004). While the structure of interaction networks is known to strongly influence biodiversity dynamics (Sole & Bascompte 2007), most existing deterministic metacommunity models generally focused on global competition and competition-colonisation trade-off in fully connected patches (Tilman *et al.* 1997, Calcagno *et al.* 2006), or sometimes in evenly connected patches (*e.g.*, lattice Amarasekare *et al.* 2004, Mouquet *et al.* 2011). Models focusing on other interaction types (e.g. facilitation, mutualistic and trophic) were developed for species-poor communities, homogeneous or lattice space (*i.e.* for few species Nee *et al.* 1997, Gravel & Massol 2020, homogeneous space Astegiano *et al.* 2015, lattice space Kéfi *et al.* 2007), preventing the study of complex networks and further generalisations.

Yet, stochastic models of interactions where species are either present or absent can encode mechanisms through specific rules, like having at least one prey to survive in the Trophic Theory of Island Biogeography (Gravel *et al.* 2011, Massol *et al.* 2017), or through increasing probability of presence depending on prey availability (Cazelles *et al.* 2016, Auclair *et al.* 2017). The latter model belongs to graphical models, a class of statistical models that represents conditional dependencies between species distributions using graphs. Using network-based metrics, these models can encode several mechanisms in terms of conditional probabilities of presence (Staniczenko *et al.* 2017). Nevertheless, these approaches still ignore the spatial structure of the environment.

So far, theoretical studies on the dynamics of metacommunities within a spatially explicit environment and with biotic interactions have rarely considered how the dynamics jointly depend on graph properties of both interaction and spatial networks (e.g., Amarasekare *et al.* 2004, but see Zhang *et al.* 2021), trophic interactions (Pillai *et al.* 2010, Brechtel *et al.* 2018, Gross *et al.* 2020 but see Wang *et al.* 2021) or mutualistic interactions on a lattice (Filotas *et al.* 2010, Sardanyés *et al.* 2019). These models often elude the question of existence of a non-null equilibrium, and the metacommunity persistence is often assessed through tedious dynamic simulations or using strong approximations (Wang *et al.* 2021). If this approach provides points in the parameter space where the metacommunity persists, it neither maps regions of this space leading to persistence,

nor it demonstrates the existence of critical thresholds acting on metacommunity persistence as in metapopulation theory.

Interestingly, thresholds between local community persistence and extinction have already been identified in the case of positive interactions (Callaway 1997, Kéfi *et al.* 2016). For instance, mutualistic interactions play a major role in natural systems by conditioning coexistence (Valdovinos 2019). Thébault & Fontaine (2010) showed that mutualistic networks generally have a nested architecture favouring persistence, and empirical surveys evidenced a truncated power-law of degree distribution (Bascompte & Jordano 2006, Vázquez *et al.* 2009, Bascompte 2009). Kéfi *et al.* 2007 studied a metacommunity model with facilitation on a lattice space. However, no network-based model of spatially realistic, mutualistic metacommunities has been proposed so far. Such model should allow to test the joint impact of the structure of the spatial and interaction networks on the viability of a metacommunity and, potentially, allow to exhibit thresholds acting at the mutualistic metacommunity level. It should also reconcile the ongoing debate on the impact of the structure of the spatial network on metapopulations (Fletcher Jr *et al.* 2018).

In this paper, we explicitly model mutualistic interactions in an heterogeneous space using dynamic Bayesian networks (Auclair *et al.* 2017). We derive then a deterministic approximation and exhibit a threshold in metacommunity persistence assuming that all species have the same colonisation and extinction parameters. It defines an abrupt transition between stable coexistence and global metacommunity extinction. Our approach extends the computation of metapopulation capacity *sensu* Ovaskainen & Hanski to the case of mutualistic metacommunities with specific assumptions on colonisation and extinction functions. Using numerical methods, we show how metacommunity capacity relies on the structure of both mutualistic and spatial networks. Importantly, specific submodels can be derived to encode key ecological assumptions on extinction and colonisation. For these different ecological assumptions, we represent how spatial proximity of sites and mutualistic interactions modulate colonisation and/or extinction probability, and we compute metacommunity capacities. We finally explore the relationship between the degrees of the nodes of both spatial and interaction networks and species' occupancy at equilibrium. This allows extracting ecological relevant quantities on species among the sites (*e.g.*, mean occupancy) or in sites among

species (*e.g.*, species diversity, interaction network diversity). We thus quantify how metacommunity capacity is shaped by the joint structure of spatial and interaction networks.

2 Stochastic models of metacommunity dynamics using dynamic Bayesian networks

We first present a formalism that unifies stochastic spatially realistic metapopulation models and mainland-island models of biotic interactions in discrete time using Dynamic Bayesian Networks (DBNs). DBNs describe dependencies between random variables at different time steps through a bipartite directed graph, and represent stochastic models in which parameters are networks (Lähdesmäki & Shmulevich 2008, Koller & Friedman 2009). The network represents the influences between species distributions between two time steps. Once the structure of causal influences is fixed, several distributions can be associated to a given network structure through different parameterisations. These parameterisations represent interaction mechanisms that describe the effect of neighbour species or sites on the probability of presence of a given species at time $t+1$. See Appendix for a more precise introduction on dynamic Bayesian networks and proof of the convergence of the different models.

The heterogeneous space is represented by a spatial network $G_s = (V_s, E_s)$, where V_s is the set of spatial vertices and E_s the set of spatial edges (linking unordered pairs of vertices). We assume that this network is undirected and connected, *i.e.*, considering two nodes u and v of G_s, there is always a path from u to v. Biotic interactions in the metacommunity are represented by an interaction network $G_b = (V_b, E_b)$, with V_b its set of vertices and E_b its set of edges, which we also assume undirected and connected. We note $n = |V_s|$ and $m = |V_b|$ (see Table 1 for notations).

Object	Name
G_s	Spatial network (n nodes)
G_b	Interaction network (m nodes)
G_s^0	Spatial network where edges have been deleted (n nodes)
G_b^0	Interaction network where edges have been deleted (m nodes)
$G_{s,b} = G_s \square G_b$	Cartesian product of the spatial and biotic interaction networks ($n * m$ nodes)
$\mathbf{A_s}$	Adjacency matrix of the spatial network
$\mathbf{A_b}$	Adjacency matrix of the biotic interaction network
$\mathbf{A_{s,b}} = \mathbf{A_s} \otimes \mathbf{I_m} + \mathbf{I_n} \otimes \mathbf{A_b}$	Adjacency matrix of the Cartesian product network)
G_c	Colonisation network ($n * m$ nodes)
G_e	Extinction network ($n * m$ nodes)
$\mathbf{A_c}$	Adjacency matrix of the colonisation network
$\mathbf{A_e}$	Adjacency matrix of the extinction network
λ_M	Metacommunity persistence capacity
λ_I	Metacommunity invasion capacity
Λ_s	Dominant eigenvalue of the adjacency matrix of the spatial network
Λ_b	Dominant eigenvalue of the adjacency matrix of the biotic interaction network
$\Lambda_{s,b} = \Lambda_s + \Lambda_b$	Dominant eigenvalue of the adjacency matrix of the Cartesian product network

Table 1: Notations

2.1 Spatially realistic metapopulation model

We start by defining, using DBNs, a spatially realistic metapopulation model where populations of a single species colonise the spatial network G_s. Let X_i^t be a random variable associated to the presence of a population in a site i (*i.e.* the node v_i of G_s) at time t ($1 \leq i \leq n$, $t \in \mathbb{N}^*$, where $\mathbb{N}^*$ is the set of positive integers). We depict the dependency structure between the X_i^t using a DBN built from G_s (Fig. 1a). Defining the neighbours of v_i in G_s as $N_s(i)$, the parents of X_i^{t+1} in the DBN are $\{X_i^t, \mathbf{X^t_{N_s(i)}}\}$. This means that the presence of a population at time $t+1$ is causally influenced by the presence of a population at time t in site i and in sites adjacent to i. In this first model, no other variables or species influence the presence of a population in site i at time $t+1$. Through conditional probabilities, the parameterisation encodes the way the presence or absence of a population in adjacent sites modulates the probability of presence of a population in the focal site. Here, we chose the same parameterisation as in Gilarranz & Bascompte 2012.

$$\mathbb{P}(X_i^{t+1} = 1 | X_i^t, \mathbf{X}^t_{N_s(i)}) = (1 - (1-c)^{\sum_{k \in N_s(i)} X_k^t})(1 - X_i^t) + (1-e)X_i^t \quad (1)$$

where c and e are the respective colonisation ($0 < c < 1$) and extinction ($0 < e < 1$) parameters. In Eq. 1, the probability of presence grows with the number of occupied adjacent sites. Specifically, the probability that node i includes a population at time $t + 1$ is $1 - e$ if it had one at time t, while the probability that node i is colonised between time t and time $t + 1$ is equal to 1 minus the probability that all occupied neighbouring sites do not colonise node i, which happens with probability $1 - c$ independently for each of these nodes.

2.2 A mainland-island model with biotic interactions

In this section, we present, using DBNs, a mainland-island model of species community where different species colonise an island without any spatial structure but with a biotic interaction network G_b.

Let X_j^t be the random variable associated to the presence of population of species j on the island. A DBN representing the dependency structure is built from G_b (Fig. 1a). Here, the DBN represents the network of species interactions as interactions affect colonisation and extinction probabilities on the island. Defining as $N_{G_b}(j)$ the neighbours of v_j in G_b , the parents of $X_j^{(t+1)}$ in the DBN are $\{X_j^t, \mathbf{X^t_{N_{G_b}(j)}}\}$, meaning that the presence of species v_j and species that interact with v_j at time t on the island, causally influences the presence of species v_j at time $t + 1$. Importantly, there is no other variables influencing the presence of a species v_j at time $t + 1$. We chose a parameterisation similar to Auclair *et al.* 2017:

$$\mathbb{P}(X_j^{t+1} = 1 | X_j^t, \mathbf{X}^t_{N_{G_b}(j)}) = c(1 - X_j^t) + (1 - e(1 - \frac{\sum_{k \in N_{G_b}(j)} X_k^t}{1 + deg_{G_b}(j)}))X_j^t \quad (2)$$

where $deg_{G_b}(j)$ is the degree of j in G_b. The probability of extinction (defined by Eq. 2) belongs to $]0, 1[$ (Appendix). Although the dependency between species occurrences can encode any kind of interactions, we here focus on the mutualistic case by imposing an extinction function. In this case, the probability of extinction of a given species decreases with the number of species present that interact with the focal species.

2.3 Spatially realistic models of mutualistic metacommunities

Integrating the models from Section 2.1 and 2.2, we built a spatially explicit metacommunity model. In this model, several species, interacting through G_b, are colonising the spatial network G_s. The colonisation and extinction probabilities of population of a given species in a site are affected by the presence of interacting species in the same site and presence of population of focal species in neighbour sites. To do so, we used the Cartesian product of graphs that builds a network from G_b and G_s (Imrich & Klavzar 2000).

Definition 1. *The Cartesian product of G_s and G_b, $G_{s,b} = G_s \square G_b$ is the graph in which the set of nodes is $V_s \times V_b$. A node of this graph is identified by a pair of nodes of G_s and G_b. Moreover, there is an edge between (u_s, u_b) and (v_s, v_b) if ($u_s = v_s$ and $(u_b, v_b) \in E_b$) or ($u_b = v_b$ and $(u_s, v_s) \in E_s$). The first condition corresponds to the case where the two species are present at the same location and interact with one another; the second condition, to the case where only one species is considered and the two locations are linked by a spatial edge.*

The adjacency matrix, $A_{s,b}$, of $G_{s,b}$ is

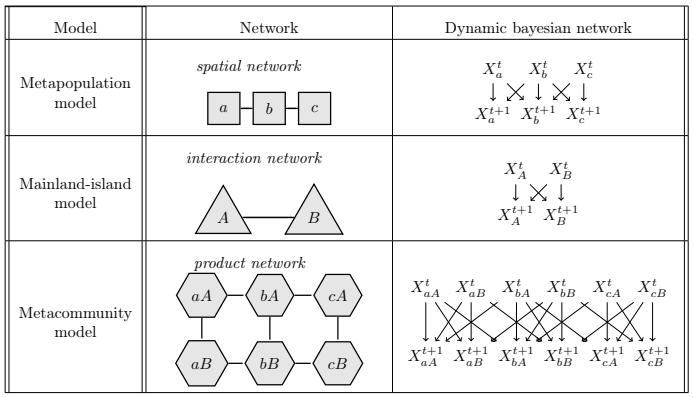
$$\mathbf{A_{s,b}} = \mathbf{A_s} \otimes \mathbf{I_m} + \mathbf{I_n} \otimes \mathbf{A_b} \tag{3}$$

where $\mathbf{I_m}$ and $\mathbf{I_n}$ denotes the identity matrices of dimension m and n and $\otimes$ denotes the Kronecker product of two matrices.

Let X_{ij}^t be the random variable associated to the presence of a population of species j in site i at time t. The dependency structure between the X_{ij}^t is depicted using a DBN that is built from $G_{s,b}$ (Fig. 1a). Defining as $N(i,j)$ the neighbours of (v_i, v_j) in $G_{s,b}$, the parents of X_{ij}^{t+1} in the DBN are $\{X_{ij}^t, \mathbf{X^t_{N(i,j)}}\}$. This means that the presence of a population of species j in site i at time $t+1$ is causally influenced by the presence of population of the same species in adjacent sites at time t and by the presence of populations of species that interact with j in the same site.

At this stage, it is crucial to define several submodels that formalise key ecological assumptions in

(a) The different models



(b) A temporal dynamic

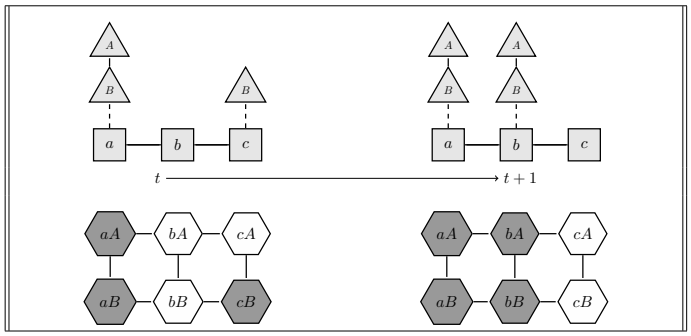


Figure 1: (a) Metapopulation model, mainland-island interaction model and metacommunity model. The second column represents the network associated to each model (spatial, interaction and product network). The third column represents the dynamic Bayesian network associated to each model that represents the causal influences of variables (presence of populations of a given species, species on the island, species in sites) at t on variables at $t + 1$
(b) Simulating a dynamic in the combined effect model between two time steps. The nodes of the product network are either empty or occupied (grey: occupied, white: empty). For the sake of simplicity, the model here is turned deterministic ($c = 1$, $e = 1$). To colonise a new node of the product network, species A and B must be both present in the same site and can colonise adjacent site only. The population of species B originally present in site c goes extinct since it does not co-occur with A at t whereas species A and B that co-occur in site a colonise the site b.

the product graph, using either the spatial network or the biotic interaction network to modulate colonisation and extinction probability.

Let G_s^0 be the network that has the same set of nodes as G_s but an empty set of edges, and let G_b^0 be the network that has the same set of nodes as G_b but an empty set of edges. We introduce then the colonisation network G_c ($\mathbf{A_c}$ is its adjacency matrix) and the extinction network G_e ($\mathbf{A_e}$ is its adjacency matrix). These networks modulate the colonisation and extinction probability in the different submodels. We build two submodels from a given product graph (Fig. 2) :

- a Levins type submodel, where both the spatial and biotic interaction networks modulate the colonisation probability ($G_c = G_s \square G_b$), while the extinction probability is constant ($G_e = G_s^0 \square G_b^0$)
- a combined effect submodel, where both the spatial and the biotic interaction networks modulate the colonisation probability ($G_c = G_s \square G_b$), and the biotic interaction network modulates the extinction probability ($G_e = G_s^0 \square G_b$)

For the two submodels, the conditional probabilities of colonisation and non-extinction are expressed as:

$$\mathbb{P}(X_{ij}^{t+1} = 1 | X_{ij}^t = 0, \sum_{(k,l)\in N_{G_c}(i,j)} X_{kl}^t) = \epsilon + (1-\epsilon)\left[1 - (1-c)^{\sum_{(k,l)\in N_{G_c}(i,j)} X_{kl}^t}\right] \quad (4)$$

$$\mathbb{P}(X_{ij}^{t+1} = 1 | X_{ij}^t = 1, \sum_{(k,l)\in N_{G_e}(i,j)} X_{kl}^t) = 1 - e\left(1 - \frac{\sum_{(k,l)\in N_{G_e}(i,j)} X_{kl}^t}{1 + deg_{G_e}((i,j))}\right) \quad (5)$$

where $\epsilon \in]0;1[$ is a constant that guarantees the convergence of the model. This constant allows colonisation from an external source, analogous to nodal self-infection in the epidemiology literature (Van Mieghem & Cator 2012). The proposed metacommunity model is analogous to the open Levins model, that better fits with data than the classic Levins model (Laroche *et al.* 2018). $deg_{G_e}((i,j))$ is the degree of (v_i, v_j) in G_e, and $N_{G_c}(i,j)$ (resp. $N_{G_e}(i,j)$) denotes the neighbours of (v_i, v_j) in G_c (resp. G_e). Fig. 1b shows a simplistic dynamics in the combined effect model. Computing the stationary distribution is also intractable in the general case (since transition matrix is of dimension 2^{nm}), but, it is however possible to simulate the dynamics of the metacommunity as Gilarranz &

Bascompte (2012) did for metapopulation model. The code to sample in the stochastic model is available on the gitlab repository (`https://gitlab.com/marcohlmann/metacommunity_theory`).

3 The nm-intertwined model

Since studying the stochastic model of Section 2.3 is intractable in the general case, we propose to study deterministic models that approximate the stochastic models, referred to as the intertwined model in the epidemiology literature (Van Mieghem 2011). We extended the spatially realistic Levins model to a metacommunity model based on the product of spatial and interaction network (Ovaskainen & Hanski 2001). The approximation is derived from Van Mieghem (2011) and Bianconi (2018). The aim is to study the dynamics of mean occupancy of each species j in each site i, *i.e.* $p_{ij}(t) = \mathbb{E}(X_{ij}^t) = \mathbb{P}(X_{ij}^t = 1)$ where $\mathbb{E}(.)$ denotes the expected value. For all i and j:

$$p_{ij}(t+1) = \mathbb{E}((1-X_{ij}^t)(\epsilon+(1-\epsilon)(1-(1-c)^{\sum_{(k,l)\in N_{G_c}(i,j)} X_{kl}^t}))) + \mathbb{E}((1-e(1-e)^{\sum_{(k,l)\in N_{G_e}(i,j)} X_{kl}^t})X_{ij}^t) \tag{6}$$

Eq. 6 leads to a hierarchy of equations that cannot be solved (*i.e.* we need to consider $\mathbb{E}(X_{1,1}^t, ..., X_{m,n}^t)$ to find a solution to the system). In order to get moment closure, we assume that site occupancies are independent. More precisely, for any sequence of indices $n(1), n'(1); ..., n(r), n'(r')$:

$$\mathbb{E}(X_{n(1),n'(1)}^t, ..., X_{n(r),n'(r')}^t) \simeq \mathbb{E}(X_{n(1),n'(1)}^t) ... \mathbb{E}(X_{n(r),n'(r')}^t) \tag{7}$$

After some algebra, introducing a new single index v for the nodes of the product network and assuming that $c << 1$,$e << 1$ and $\epsilon << c$ (see Appendix), it follows :

$$p_v(t+1) - p_v(t) = C_v(\mathbf{p}(\mathbf{t}))(1 - p_v(t))) - E_v(\mathbf{p}(\mathbf{t}))(p_v(t)) \tag{8}$$

where $C_v(\mathbf{p}(\mathbf{t})) = c\sum_u [A_c]_{v,u} p_u(t)$ and $E_v(\mathbf{p}(\mathbf{t})) = e(1 - \sum_u [A_e]_{v,u} p_u(t)/M_u)$ with $M_u = 1 + deg_{G_e}(u)$

This rewrites:

$$\mathbf{p(t+1)} - \mathbf{p(t)} = c(\mathbf{A_c p(t)}) \odot (\mathbf{1} - \mathbf{p(t)}) - e(\mathbf{1} - (\mathbf{D_e} + \mathbf{I}_{nm})^{-1}\mathbf{A_e p(t)}) \odot \mathbf{p(t)} \tag{9}$$

where $\odot$ denotes the element-wise product, $\mathbf{D_e}$ denotes the in-degree matrix of G_e and $\mathbf{I}_{nm}$ denotes the identity matrix of dimension nm.

Eq. 8 is analogous to master equation of Ovaskainen & Hanski (2001). Now, to assess the viability of a given mutualistic metacommunity, we need to determine the equilibrium states and evaluate their local stability in function of c and e parameters.

3.1 Metapopulation capacity

In these spatially realistic metapopulation models, equilibrium state is either stable coexistence (all sites have non-null occupancy) or global extinction (all patches have null occupancy). Metapopulation capacities have thus been derived to assess both the persistence and the stability of metapopulations at equilibrium (Hanski & Ovaskainen 2000, Ovaskainen & Hanski 2001). The metapopulation persistence capacity λ_M is a threshold between coexistence and global extinction (depending on the colonisation and extinction parameters), computable from the spatial network. Importantly, in spatially realistic metapopulation models, as soon as a population is present in a site, it can colonise gradually the entire spatial network.

More formally, in the metapopulation case, G_b is made of a single node, $(m = 1)$ and we assume that G_s is undirected and connected. We have:

$$\forall t \in \mathbb{N}^*,\ \mathbf{p(t)} \in \overline{\Omega} = \{x \in \mathbb{R}^n, \forall i,\ 0 \leq x_i \leq 1\} \tag{10}$$

with the following assumptions on the colonisation functions (per site i), $C_i(.)$, and extinction functions, $E_i(.)$:

- there is no external source of migrants

$$C_i(\mathbf{0}) = 0 \tag{11}$$

- the occupied sites make a positive contribution to the colonisation function of an empty site

$$\forall \mathbf{p} \in \Omega = \{x \in \mathbb{R}^n, \forall i,\ 0 < x_i < 1\}, C_i(\mathbf{p}) > 0 \tag{12}$$

$$\begin{cases} \frac{\partial C_i}{\partial p_j}(\mathbf{p}) \geq 0 \quad \text{for } i \neq j \\ \frac{\partial C_i}{\partial p_i}(\mathbf{p}) = 0 \end{cases} \tag{13}$$

- there is no mainland population, extinction rates are positive and, eventually, reduced by the presence of local populations

$$\forall p \in \overline{\Omega}, E_i(\mathbf{p}) > 0 \tag{14}$$

$$\begin{cases} \frac{\partial E_i}{\partial p_j} \leq 0 \quad \text{for } i \neq j \\ \frac{\partial E_i}{\partial p_i} = 0 \end{cases} \tag{15}$$

- Colonisation and extinction functions are smooth functions

$$C_i \in \mathcal{C}^1(\overline{\Omega}) \tag{16}$$

$$E_i \in \mathcal{C}^1(\overline{\Omega}) \tag{17}$$

Let:

$$g_i(\mathbf{p}) = \frac{eC_i(\mathbf{p})}{cE_i(\mathbf{p})} \tag{18}$$

The model is also assumed to be irreducible. Let $\mathbf{J}$ be the matrix of dimension $n \times n$ so that:

$$J_{ij} = \begin{cases} 1 & \text{if } \frac{\partial g_i}{\partial p_j}(\mathbf{p}) > 0, \mathbf{p} \in \overline{\Omega} \\ 0 & \text{otherwise} \end{cases} \tag{19}$$

We say that the model is irreducible if $\mathbf{J}$ is irreducible, i.e., the graph that has $\mathbf{J}$ as adjacency matrix is strongly connected.

In the case of the spatially realistic Levins model :

- $C_i(\mathbf{p}) = c(\mathbf{A_s p})_i$
- $E(\mathbf{p}) = e$

where $\mathbf{A_s}$ is the adjacency matrix of the spatial network. Then,

$$g_i(\mathbf{p}) = (\mathbf{A_s p})_i \tag{20}$$

and the model is irreducible since $\mathbf{A_s}$ is irreducible.

The metapopulation invasion capacity, λ_I, is defined as the dominant eigenvalue of the Jacobian matrix of g evaluated in $\mathbf{p} = 0$. It measures the stability of the equilibrium $\mathbf{p} = 0$ that is the ability of a single population to invade the spatial network.

Definition 2. *The metapopulation persistence capacity, λ_M, is defined as:*

$$\lambda_M = \sup_{\mathbf{p} \in \Omega} h(\mathbf{p})$$

where

$$h(\mathbf{p}) = \min_i h_i(\mathbf{p})$$

and

$$h_i(\mathbf{p}) = g_i(\mathbf{p}) \frac{1 - p_i}{p_i}$$

We now present a weak version of the main theorem of Ovaskainen & Hanski (2001).

Theorem 1. *(Ovaskainen & Hanski) The deterministic metapopulation model has a non-trivial non-negative equilibrium state if and only if the threshold condition* $\lambda_M > \frac{e}{c}$ *(if all the components of* $\mathbf{g}$ *are concave) or* $\lambda_M \geq \frac{e}{c}$ *(otherwise) is satisfied. Moreover, if the threshold condition is satisfied, the non-trivial non-negative equilibrium state is unique if all components of* g *are concave and equilibria are ordered otherwise.*

λ_M is a threshold on the colonisation/extinction parameters that allows the metapopulation to persist. Importantly, if the metapopulation persists, the equilibrium points are interior (they belong to Ω), meaning that all occupancies are strictly positive.
Moreover, if all the components of $\mathbf{g}$ are concave (it is the case for the spatially realistic Levins model), we have:

$$\lambda_M = \lambda_I = \Lambda_s \tag{21}$$

where Λ_s is the dominant eigenvalue of $\mathbf{A_s}$. If one component (or more) of $\mathbf{g}$ is not concave, then $\lambda_I < \lambda_M$

3.2 Extension to mutualistic metacommunity capacity

In order to extend the metapopulation concept to metacommunity concept, we first consider a case with no interaction. Assuming that all species have the same colonisation and extinction parameters, since they also share the same spatial network, they have then the same metapopulation capacity even if their have independent dynamics. However, in this case, we cannot define a metacommunity capacity since the different metapopulations have independent dynamics: if a species is initially absent from the metacommunity, it will never colonise it. In this section, we show that adding mutualistic interactions to the metacommunity tangle the dynamics of the different metapopulations and allows defining a single threshold controlling the extinction of the entire metacommunity. Importantly, we show that this metacommunity capacity is higher than individual metapopulation capacities.

3.2.1 The mutualistic metacommunity concept

We extend metapopulation capacities from Section 3.1 to mutualistic metacommunity capacities in the dynamical system defined by Eq. 9, using the product of the spatial network and the biotic interaction network and specific assumptions on colonisation and extinction functions. Importantly, in our spatially realistic mutualistic metacommunity model, as soon as a population of a given species is present in a site, it can colonise gradually the entire spatial network and populations of partner species will also colonise the spatial network thanks to this focal species. As a consequence, the proposed mutualistic metacommunity model presents a sharp transition between coexistence (all species have non-null occupancy in all sites) and global extinction (all species have null occupancy in all sites).

For this model, the state space is: $\Omega = \{x \in \mathbb{R}^{n*m}, \forall v \in \{1, ..., n*m\}\ 0 < x_v < 1\}$

We have:

$$C_v(\mathbf{p}(\mathbf{t})) = c \sum_u [A_c]_{v,u} p_u(t) \tag{22}$$

and

$$E_v(\mathbf{p}(\mathbf{t})) = e(1 - \sum_u [A_e]_{v,u} p_u(t)/M_u)) \tag{23}$$

In order to apply theorem 1 to the product network, we first verify assumptions on colonisation and extinction functions (notice that index v represents a combination of a site and a species index).

- there is no external source of migrants

$$C_v(\mathbf{0}) = 0 \tag{24}$$

  Notice that this assumption is only verified at order 1

- species occupying sites make a positive contribution to the colonisation function of an empty site

$$\forall \mathbf{p} \in \Omega, C_v(\mathbf{p}) > 0 \tag{25}$$

$$\begin{cases} \frac{\partial C_v}{\partial p_u}(\mathbf{p}) \geq 0 \quad \text{for } u \neq v \\ \frac{\partial C_v}{\partial p_v}(\mathbf{p}) = 0 \end{cases} \tag{26}$$

Importantly, in both Levins type and combined effect model, since $G_c = G_s \square G_b$, an empty site can be colonised by a given species if this species is present in neighbor sites or if species that interact with the focal species are present in this site. By doing so, even if a species is initially absent from the metacommunity, it can colonise it thanks to partner species.

- there is no mainland population, extinction rates are positive and reduced by the presence of others species

$$\forall p \in \overline{\Omega}, E_v(\mathbf{p}) > 0 \tag{27}$$

$$\begin{cases} \frac{\partial E_i}{\partial p_j} \leq 0 \quad \text{for } i \neq j \\ \frac{\partial E_i}{\partial p_i} = 0 \end{cases} \tag{28}$$

Notice that, due to this assumption, we stick to the modelling of mutualistic metacommunity.

- Colonisation and extinction are smooth functions

$$C_v \in \mathcal{C}^1(\overline{\Omega}) \tag{29}$$

$$E_v \in \mathcal{C}^1(\overline{\Omega}) \tag{30}$$

Additionally:

Proposition 1. *The Levins type model and the combined effect model are irreducible on* $\overline{\Omega}$

See proof in Appendix.

We then define metacommunity invasion capacity as the dominant eigenvalue of the jacobian matrix of g evaluated in $\mathbf{p} = 0$.

Definition 3. *The mutualistic metacommunity persistence capacity, λ_M, is defined as:*

$$\lambda_M = \sup_{\mathbf{p}\in\Omega} h(\mathbf{p})$$

where

$$h(\mathbf{p}) = \min_{v} h_v(\mathbf{p})$$

and

$$h_v(\mathbf{p}) = g_v(p)\frac{1-p_v}{p_v}$$

By applying theorem 1, a non-trivial equilibrium that the dynamical system has a non trivial equilibrium if and only if $\lambda_M > \frac{e}{c}$. λ_M is then a threshold on the colonisation/extinction parameters that allows the mutualistic metacommunity to persist. Importantly, a non-trivial equilibrium point is interior (it belongs to Ω), so each species in each site has a positive abundance at equilibirum.

Proposition 2. *For the Levins type model, $\lambda_M = \lambda_I = \Lambda_s + \Lambda_b$*

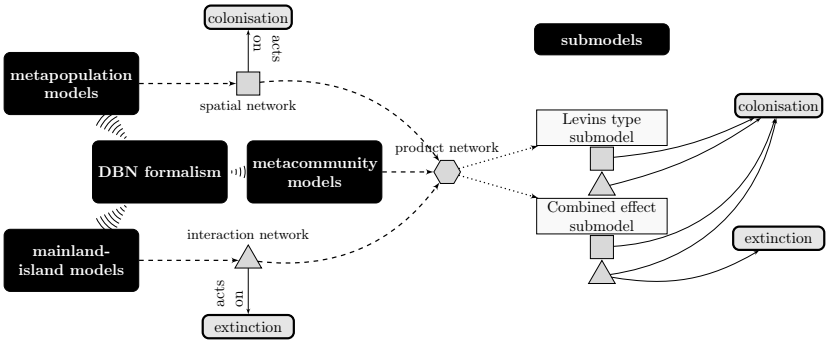
The Levins type model is actually the spatially realistic metapopulation model with $G_c = G_s \square G_b$ as spatial network (the extinction is constant equals to e). The dominant eigenvalue, Λ_c, of A_c is $\Lambda_s + \Lambda_b$. Consequently, for the Levins type submodel:

$$\lambda_M = \lambda_I = \Lambda_s + \Lambda_b \tag{31}$$

For the combined effect model, $\lambda_I = \Lambda_s + \Lambda_b$ (see Appendix for proof). Notice that in the Levins type model, both the biotic interaction and the spatial networks play interchangeable roles.

3.2.2 Computation of metacommunity capacity for the combined effect model

For the combined effect model, we computed the metacommunity capacity λ_M using Appendix D of Ovaskainen & Hanski 2001 and simulating annealing. We propose an implementation in R and Python available at: https://gitlab.com/marcohlmann/metacommunity_theory. Only the



Name of the submodel	Mechanisms and assumptions	Colonisation and extinction networks	Metacommunities capacities
Levins type	The spatial and the biotic network modulate the colonisation probability. The extinction probability is constant. The different sites and species acts independently on the probability of presence of a species.	$G_c = G_s \square G_b$ $G_e = G_s^0 \square G_b^0$	$\lambda_I = \lambda_M = \Lambda_s + \Lambda_b$
Combined effect	The spatial and the biotic network modulate the colonisation probability. The biotic interaction network modulates the extinction probability. The different sites and species acts independently on the probability of presence of a species.	$G_c = G_s \square G_b$ $G_e = G_s \square G_b^0$	$\lambda_I = \Lambda_s + \Lambda_b$ λ_M: to compute numerically

Figure 2: Top: Map of the different models, submodels and their parameters. Bottom: The four submodels associated to mutualistic metacommunity models, their assumptions, colonisation/extinction networks and metacommunity capacities

metapopulation or the metacommunity persistence capacity is really the focus for assessing viability. For the sake of simplicity, we will thus use metacommunity capacity as metacommunity persistence capacity in the rest of the text (unless specified otherwise)

4 Applications

4.1 Illustration

To illustrate the metacommunity capacity concept, we built a toy model (Fig. 3). We used a circular spatial network with 4 nodes (Fig. 3a) and a star shaped interaction network made of 4 nodes (Fig. 3b), which could represent a plant species and its mutualistic mycorrhizal fungi species. The Cartesian product is built from the spatial and the interaction networks (Fig. 3c). For the illustration, we derived the Levins type submodel dynamics. In this case, both metacommunity invasion capacity λ_I and persistence capacity λ_M are equal to the dominant eigenvalue of the product of the networks (3.73). λ_M defines the feasibility domain that is the portion of space where all species

have a non-null occupancy (see Song *et al.* (2018)) (Fig. 3d). We showed two possible outcomes of species occupancy dynamics (Fig. 3). One had a combination of colonisation and extinction values allowing metacommunity persistence, while the other had values outside the feasibility domain and yielded metacommunity extinction. Occupancies of persisting species converge toward two different values due to symmetries in the product network. Despite its simplicity, this toy model shows that we can predict the outcome of mutualistic metacommunity dynamics for any location of the parameter space, depending on the metacommunity capacity.

4.2 Structures of spatial and mutualistic interaction network jointly shape the metacommunity capacity

We applied our model to investigate how the structure of the spatial and interaction networks shape the metacommunity capacity of a bipartite mutualistic system. To simulate landscape fragmentation, we sampled two types of spatial networks while keeping constant the expected number of edges. We generated random spatial networks with 10 nodes in either Erdős-Renyi graphs (all edges are independent and identically distributed, with connectance $C = 0.25$) or modular graphs using a block model ($C = 0.25$, more details in Appendix). We only kept connected spatial networks and used 15 replicates for each type of spatial network. Concerning the mutualistic network, we sampled two types of bipartite networks while keeping constant the number of edges. We generated random interaction networks with 14 nodes and 16 edges in either Erdős-Renyi graphs or networks with degree distribution shaped as a power-law of scaling parameter equals to 2. We used the function *sample_fitness_pl* implemented in the R package *igraph* (Csardi & Nepusz 2006). We only kept connected interaction networks and used 15 replicates per type of interaction network. We then computed the colonisation and extinction networks for each combination of spatial and interaction networks, so generating $4 * 4 * 15 = 900$ different networks in total. This number of replicates was large enough to generate robust results (see Appendix). We first computed the metacommunity capacities for each combination of spatial and interaction networks to assess the viability range of the metapopulations. Then, we choose c and e parameters so that the mutualistic metacommunity persists and compared the stochastic model with its nm-intertwined deterministic approximation.

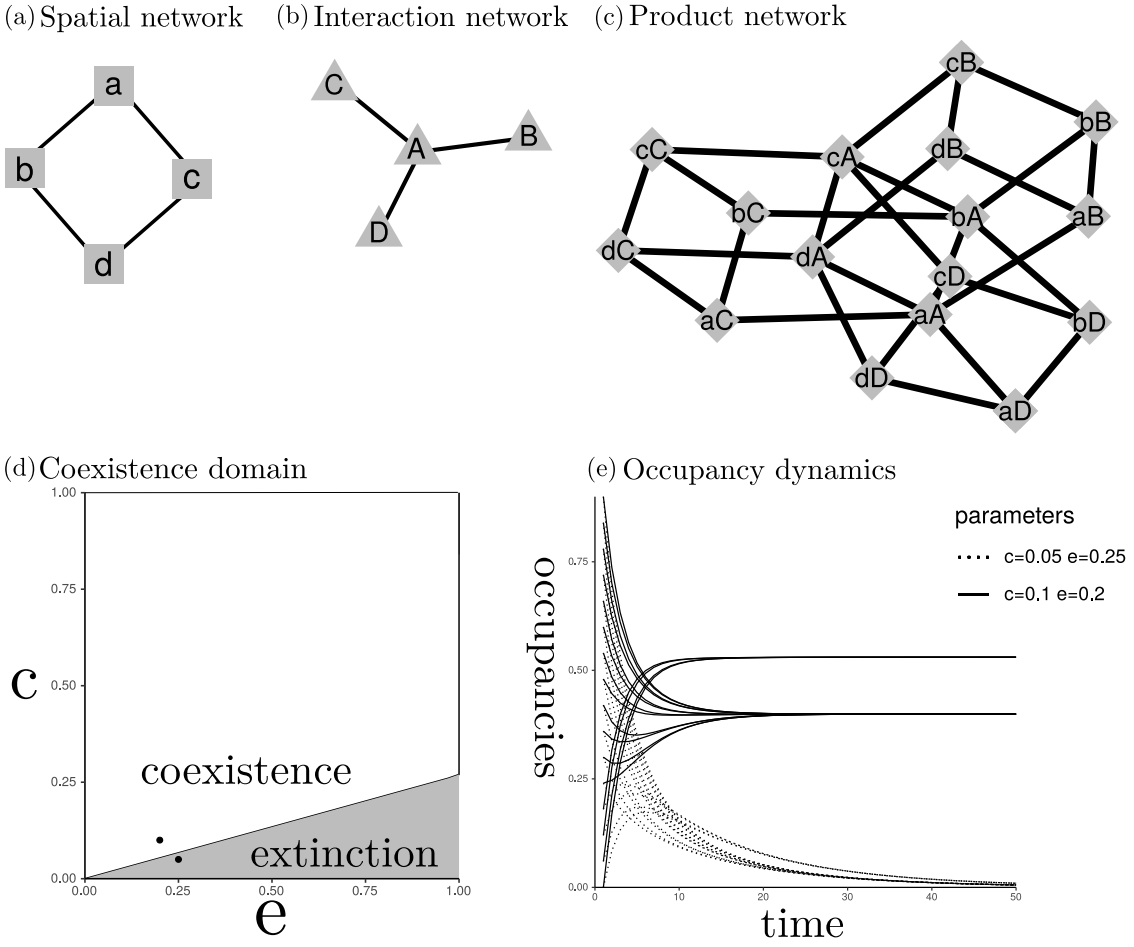


Figure 3: Toy model built from (a) a circular spatial network, (b) a star-shaped interaction network giving (c) the product network. The product network defines (d) the persistence and extinction domain. (e) Two trajectories sampled in and outside the persistence domain leading to persistence or extinction of the metacommunity

We also studied how species occupancy at equilibrium and aggregated quantities build from these occupancies (mean occupancy, species diversity) depend on node characteristics of both networks in the deterministic model.

4.2.1 Computing metacommunity capacities

We computed the metacommunity capacity λ_M for the Levins type and combined effect submodels with the four combinations of networks structure (Fig. 4, Fig. S3). Despite known concerns on the ability to fit power-laws on small networks (Clauset *et al.* 2009, Stumpf & Porter 2012), we were able to statistically distinguish estimation of metacommunity capacity for almost all sampled combinations of structures (cf. Appendix). For both the Levins type and combined effect submodel, the metacommunity capacity decreased when the spatial network was modular and when the degree distribution was not a power-law. In this case, the modularity of the spatial network had a stronger impact on the metacommunity capacity than the structure of the mutualistic interaction network. Metacommunity capacity values were similar for the combined effect and Levins type model.

4.2.2 Comparison between the stochastic model and the nm-intertwined model

We compared the output of the stochastic metacommunity models with the nm-intertwined model for a given network combination with colonisation and extinction parameters chosen so that the metacommunity persist. We set $c = e = 0.05$, $\epsilon = 0.0005$ and used a spatial network with modularity of 0.36 and a mutualistic network with a degree distribution sampled in a power-law with parameter 2. We sampled 1000 trajectories on 1500 time steps in the Levins type and the combined effect model and compared the mean stationary local occupancies and total occupancy with the prediction of the nm-intertwined model. For the combined effect model, the nm-intertwined model provides a accurate approximation of total occupancy (sum of occupancies of all species in all sites) at equilibrium (Fig. 5a). The deterministic model also provides a reasonible approximation of local occupancies (occupancy of each species in each site) compared to the mean values computed from the stationary distribution built from the stochastic simulations (Fig. 5b). We show this comparison for the Levins type model in Appendix (Fig. S4). Both the total occupancy and local occupancies

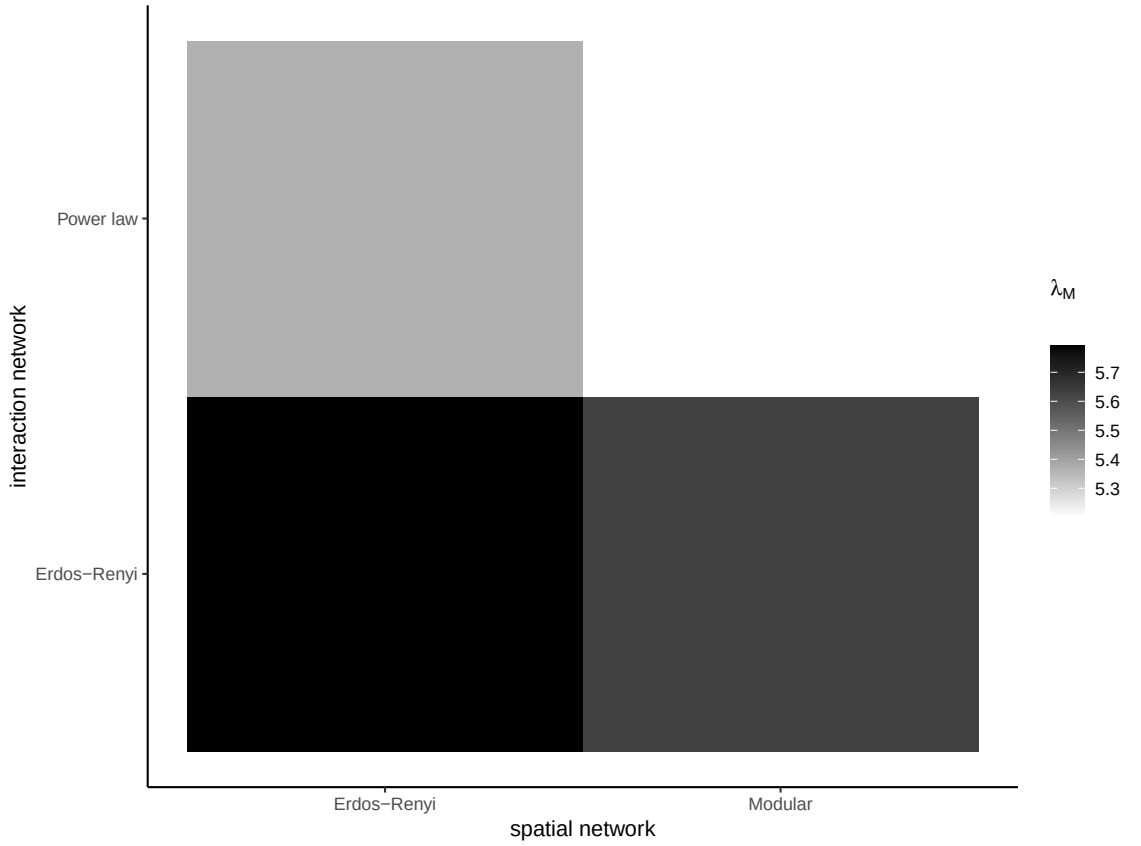


Figure 4: Assessing metacommunity persistence capacity in function of the structure of the spatial network (Erdős-Renyi/Modular) and the structure of the interaction network (Erdős-Renyi/Power law) for the combined effect model

are higher at equilibrium with the combined effect model compared to the Levins type model.

4.2.3 A focus on species occupancies at equilibrium for a given network combination

Using the same parameters than the previous section, we simulated metacommunity dynamics and studied how the occupancy at equilibrium of each node of the product network depends on its degree for the combined effect model (see Appendix for the Levins type model). Additionally, we studied the mean occupancy of species across sites, plus species and link diversity in each site.

We represented the occupancy of the nodes of the product network (that is the colonisation

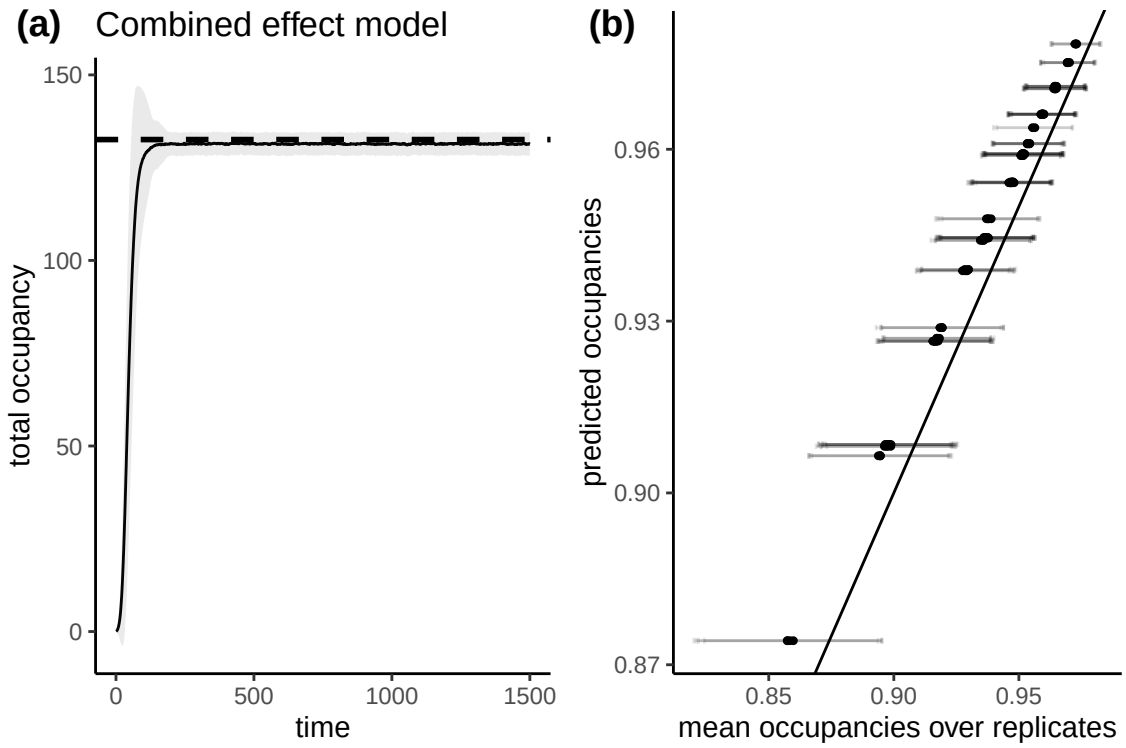


Figure 5: Comparison between the stochastic metacommunity model and the nm-intertwined model for the combined effect model. (a) Comparison of the mean total occupancy dynamics averaged over 1000 replicates (solid line, the standard deviation is represented in grey) with the prediction of the equilibrium by the nm-intertwined model (dashed line) (b) Comparison of the mean local occupancies in the stationary distribution of the stochastic metacommunity model with the predicted values by the nm-intertwined model

network in this combined effect model) in function of their degree (Fig. 6). The occupancy of the nodes of the product network (indexed by a species and a site) increased with the degree of the nodes. Moreover, in this submodel, at a fixed node degree of the product network, the occupancy decreased with the ratio of the degree of the site over the degree of the node of the product network. This means that nodes of the product network that combined a generalist species with a low-connected site have a higher occupancy at equilibrium compared to nodes that combined a specialist species with a highly connected site. We observed the same patterns for the Levins type model with lower occupancies (Appendix). From the occupancies at equilibrium, we then

computed, species α-diversities in each site using the framework developed in (Ohlmann *et al.*, 2019) with $\eta = 2$ (Fig. 6). We observed a positive relationship between species α-diversity and the degree of the nodes of the spatial network (Fig. 6). Mirroring the analysis on the spatial network, we represented the mean occupancy among the sites (Fig. 6) and observed a positive relationship between mean occupancy of a species and its degree in the biotic interaction network. For the Levins type model, we observed similar patterns except lower occupancies and mean occupancies per species (Fig. S5).

5 Discussion

In this paper, we proposed a stochastic spatially explicit model of mutualistic metacommunities that depends on the structure of spatial and biotic interaction networks, using Dynamic Bayesian Networks and graph products. Our stochastic model is built by integrating a metapopulation and a mainland-island interaction model (where species colonise an island influenced by a known meta-network). Spatial and interaction networks can modulate colonisation and extinction probabilities depending on the mechanisms that are encoded in the model. We proposed two sub-models but we encourage the implementation of other parameterisations or even interaction type since the stochastic model is highly flexible. The proposed mainland-island model is analogous to the trophic theory of island biogeography (TTIB, Gravel *et al.* 2011, Massol *et al.* 2017). However, in the TTIB, the interaction network must be a directed acyclic graph contrary to our mainland-island model where any network, even empty, can be used. The TTIB represents trophic interaction as energy flow from basal to non-basal species at a given time step whereas our stochastic interaction model represents population dynamics between two time steps, allowing feedback loops. The downside of this flexibility is the complexity and high-dimensionality of our stochastic model. However, network symmetries can be used to perform exact dimension reduction as in epidemics model (Simon *et al.* 2011).

In order to further investigate properties of our mutualistic metacommunity model, we did a deterministic approximation to obtain the nm-intertwined model, named in reference to epidemics

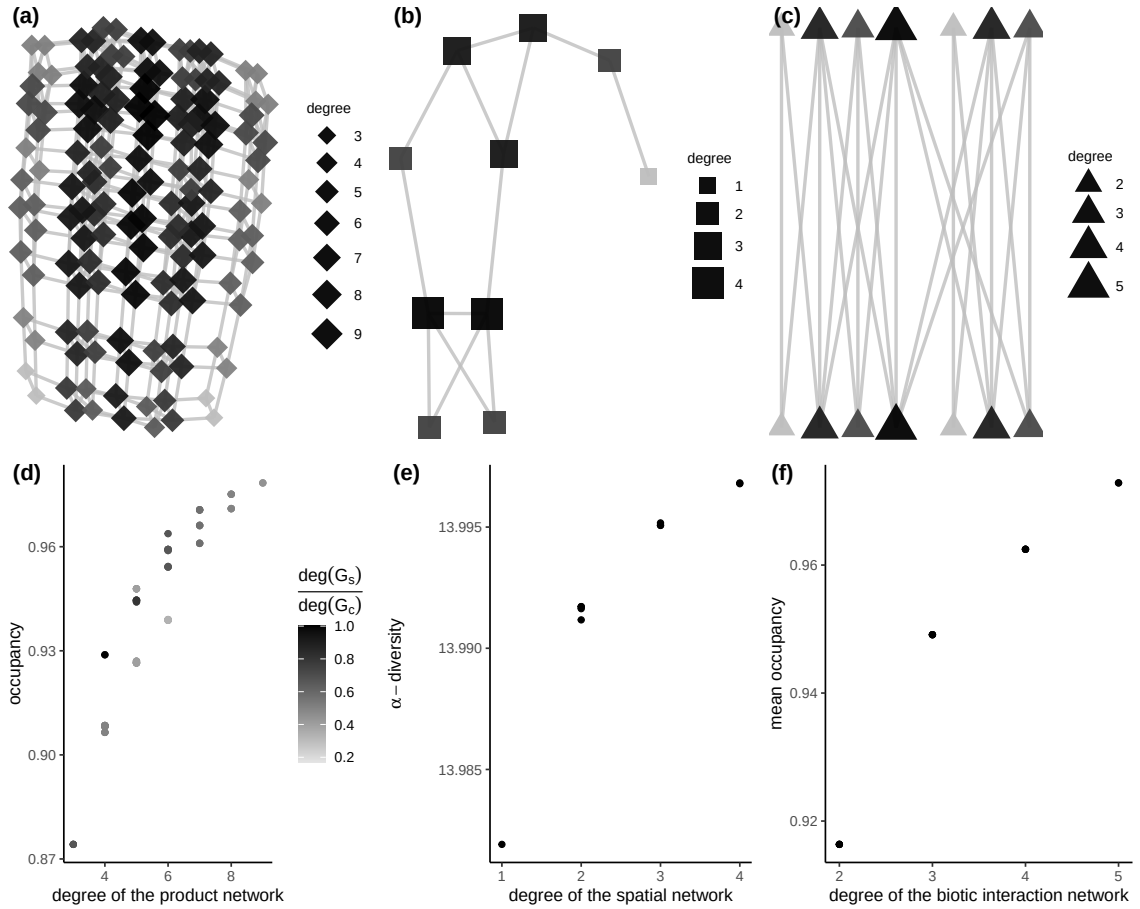


Figure 6: Simulating the dynamics for a given spatial and biotic interaction network with the combined effect model. (a) Colonisation network whose size of the nodes is proportional to their degree and colour indicates the occupancy at equilibrium (grey: low occupancy, black: high occupancy) (b) Spatial network whose size of the nodes is proportional to their degree and colour indicates the species α-diversity at equilibrium (grey: low α-diversity, black: high α-diversity) (c) Mutualistic interaction network whose size of the nodes is proportional to their degree and colour indicates the mean occupancy across the sites at equilibrium (grey: low mean occupancy, black: high mean occupancy) (d) Relationship between the occupancy at equilibrium and the degree of the node of the product network. Each point of the relationship (corresponding to a node of the product graph) is coloured according to the ratio of the degree of the site in the spatial network over the degree of the focal node in the colonisation network (e) Relationship between the species α-diversity at equilibrium and the degree of the sites in the spatial network (f) Relationship between the mean occupancy at equilibrium and the degree of the species in the biotic interaction network

model (Van Mieghem 2011). It allows to keep track of interaction and spatial network structure in the deterministic model, contrary to mean field approximation in lattice based metacommunity models (Kéfi *et al.* 2007). We assume that species occupancies vary independently and we showed, using simulations, that it provides a reasonable approximation of our metacommunity stochastic model (Fig. 5). However, this approximation holds as soon as the metacommunity is far from the extinction threshold. Otherwise, pairwise correlation between species occupancies must be considered (pair approximation, *e.g.*, Kéfi *et al.* 2007) or even higher order correlation structure (Hiebeler & Millett 2011, Wuyts & Sieber 2022).

Assuming that all species have the same colonisation and extinction parameters, our deterministic metacommunity model showed a sharp transition between states where the metacommunity persisted (*i.e.*, all species have non-null occupancy in all sites), and a state where the entire metacommunity went extinct (*i.e.*, all species have null occupancy in all sites). The transition depended on the structure of the interaction and spatial networks and on colonisation and extinction parameters. We defined the metacommunity capacity, a scalar quantity depending on the structure of both networks, as a threshold on colonisation/extinction parameters governing persistence of interacting species, thus extending the single-species concept of metapopulation capacity (Hanski & Ovaskainen 2000, Ovaskainen & Hanski 2001) to a metacommunity context. Importantly, strong assumptions on colonisation and extinction functions lead to the threshold behaviour of our model. We assume that both spatial and interaction networks contribute to species colonisation. By doing so, even if a species is absent from the metacommunity, populations of this species can colonise sites where partner species are present. This guarantees not to have prior invariant (except $\mathbf{0}$) in the model, as for deterministic metapopulation model and leads to the threshold behaviour of the metacommunity model. We consider that mutualistic interactions help implantation of new species. This assumption is supported by the existence of foundation species that helps the metacommunities to settle down (*e.g.*, cushion plants, Reid & Lortie 2012). In our mutualistic model, presence of a foundation species in the metacommunity will lead to colonisation of the metacommunity by partner species.

We extended the framework of metapopulation capacity to the case of a mutualistic meta-

community with a critical extinction threshold that is the same for all species belonging to the metacommunity. Importantly, in this model, even in the absence of biotic interactions, all species have the same metapopulation capacity (since they have the same spatial network and colonisation and extintion parameters) leading to a the same extinction threshold for all species (even if they have independant dynamics). Adding mutualistic interactions tangle the different metapopulation dynamics and increase metapopulation capacity (that becomes metacommunity capacity) thus strengthening the metacommunity in regard to extinction. This conclusion is specific to the deterministic model, while local extinctions are still possible in our stochastic model. We showed that spatial and interaction networks jointly determine the metacommunity capacity (Fig. 4, Fig. S3). In other words, any viability statement on a metacommunity (like classic metapopulation viability statements, *e.g.*, Bulman *et al.* 2007) should be done using both networks, although we should keep in mind that the perceived spatial grain (*i.e.* nodes of the spatial network) and colonisation/extinction parameters might differ among species. Metacommunity capacity has important implications for biodiversity management (*e.g.*, for metapopulations Groffman *et al.* 2006), since it helps conservationists to forecast and thus prevent crossing critical thresholds to metacommunity extinction when facing habitat destruction, pollution or other alteration. Despite appealing properties, our deterministic mutualistic metacommunity model is ecologically unrealistic since all species have stricly positive occupancies at equilibirum (in case of metacommunity persistence) ignoring so the possibility of local extinction due to environmental constrains or demographic stochasticity.

Our model of mutualistic metacommunity showed a sharp state-transition. Such abrupt transitions are known for community with positive interactions along environmental gradients (Callaway 1997, Kéfi *et al.* 2016). We somehow extended these known results for mutualistic metacommunities. Mutualistic interactions tangle individual metapopulation dynamics and strengthen metacommunity in regards of extinction and, thanks to the proposed framework, we are able to quantify the gain in viability. If we assume that species have different colonisation and extinction parameters (depending on the environment for example) or that new species cannot colonise the metacommunity thanks to mutualistic partners, we can no more apply Ovaskainen & Hanski (2001). We might expect intermediate equilibrium states (*i.e.*, states where only a subset of species goes extinct). Can

we extend the framework for other types of interactions? The assumptions on extinction functions in our model cannot represent non-mutualistic interactions and thus prevent its extension to competitive or multitrophic metacommunities. Regarding competition, competitive exclusion models in communities (Chesson 2000) and metacommunities (Calcagno *et al.* 2006) can lead to several intermediate states between coexistence and extinction of the entire metacommunity. However, competitive interactions along environmental gradients can induced dependencies between species, entailing alternative stable states (Liautaud *et al.* 2019). In the classic Lotka-Volterra deterministic model, conditions on trophic interaction network can lead to states where some of the species goes extinct but not the entire community (Takeuchi 1996; Bunin 2017). Wang *et al.* (2021) proposed a two species extension of metapopulation capacity with trophic interaction. They consider the metapopulation capacity for the prey and the predator separately. By approximating equilibrium prey occupancy, they compute predator metapopulation capacity. They extend the results to food chain in a hierarchical way. Contrary to the proposed framework, they do not propose a metacommunity capacity but rather a set of metapopulation capacity that depends on each other in hierarchical way. It could be extended towards a trophic metacommunity model in a more general framework in several ways (Gross *et al.* 2020). However, predicting the outcome of these models from parameters only still poses tough challenges (Gross *et al.* 2020). In particular, this makes it difficult to establish critical thresholds for conservation science for competitive and trophic metacommunities. Nevertheless, we doubt that a single threshold value governs the fate of many species engaged in several types of interaction with each others as we believe that threshold phenomena occur in multi-interactions metacommunity. Our model should pave the way for a better understanding of properties of spatially realistic trophic and competitive metacommunity models.

Acknowledgements

We dedicate this article to the memory of Marc Ohlmann, who tragically died in a mountain accident in June 2023. This was the last article of his thesis and one on which he spent the most energy. We thank Fabien Laroche for insightful comments and references on metapopulation and

metacommunity models. This research was funded by the French Agence Nationale de la Recherche (ANR) through the GlobNet (ANR-16-CE02-0009) and EcoNet (ANR-18-CE02-0010) projects and from 'Investissement d'Avenir' grants managed by the ANR (Montane: ANR-10-LAB-56).

A Appendix: details on the model and simulations and proofs

A.1 Stochastic models of metacommunity dynamics using dynamic Bayesian networks

A.1.1 Bayesian networks and dynamic Bayesian networks

Given a set of n random variables (X_1,...,X_n) (we note $\mathrm{I} = \{1, ..., n\}$),

Definition 4. *Two random variables X_i and X_j are independent conditionally given $\mathbf{X}_{\mathbf{I}\setminus\{\mathbf{i},\mathbf{j}\}}$ iff:*

$$\mathbb{P}(X_i, X_j|\mathbf{X}_{\mathbf{I}\setminus\{\mathbf{i},\mathbf{j}\}}) = \mathbb{P}(X_i|\mathbf{X}_{\mathbf{I}\setminus\{\mathbf{i},\mathbf{j}\}})\mathbb{P}(X_j|\mathbf{X}_{\mathbf{I}\setminus\{\mathbf{i},\mathbf{j}\}})$$

Bayesian networks aim to map conditional independence statements using a Directed Acyclic Graph G (DAG). For a given node u, we note $Pa_u(G)$ the set of nodes that are parents of u.

$$Pa_u(G) = \{v \in V, (v, u) \in E\} \tag{32}$$

The joint probability $\mathbb{P}(\mathbf{X})$ factorises over G as :

$$\mathbb{P}(X_1, ..., X_n) = \prod_i \mathbb{P}(X_i|\mathbf{X}_{Pa_i(G)}) \tag{33}$$

The factorisation gives the independence conditional statement according to the structure of the DAG.

A particular case of Bayesian network consists in Dynamic Bayesian Networks (DBNs). Indexing our previous n random variables by time t, a DBN describes the homogeneous dependencies between $\{X_1^t, ..., X_n^t\}$ and $\{X_1^{t+1}, ..., X_n^{t+1}\}$ using a directed bipartite network G_{bip} (we note $\mathbf{A_{bip}}$ its

adjacency matrix). Importantly, as the structure of G_{bip} does not depend on t, it can be built using an aggregated network G (we note $\mathbf{A}$ its adjacency matrix) and a graph P_2 (we note $\mathbf{A_2}$ its adjacency matrix) whose set of nodes is $\{t, t+1\}$ and set of edges is $\{(t, t+1)\}$. We have

$$\mathbf{A_{bip}} = \mathbf{A_2} \otimes (\mathbf{A} + \mathbf{I_n}) \tag{34}$$

where $\mathbf{I_n}$ denotes the identity matrices of dimension n. We set $\tilde{\mathbf{A}} = \mathbf{A} + \mathbf{I_n}$ and denotes $\tilde{G}$ the associated graph. The joint probability factorizes over G_{bip}:

$$\mathbb{P}(X_1^{t+1}, ..., X_n^{t+1} | X_1^t, ..., X_n^t) = \prod_i \mathbb{P}(X_i^{t+1} | \mathbf{X}_{Pa_i(\tilde{G})}) \tag{35}$$

A.1.2 Convergence properties of the stochastic models

The spatially realistic metapopulation model is a homogeneous Markov chain on $\chi = \{0, 1\}^n$. A state of the metapopulation is a binary vector of length n indicating whether each site is occupied or not. The dimension of the transition matrix is $2^n * 2^n$ and the probability of transition between a state $s_k = (x_1, ..., x_n)$ and $s_l = (\tilde{x_1}, ..., \tilde{x_n})$ is

$$P_{k,l} = \mathbb{P}(X_1^{t+1} = \tilde{x_1}, ..., X_n^{t+1} = \tilde{x_n} | X_1^t = x_1, ..., X_n^t = x_n) \tag{36}$$

By applying conditional independence statements, we get:

$$P_{k,l} = \prod_i \mathbb{P}(X_i^{t+1} = \tilde{x_i} | X_i^t = x_i, \mathbf{X^t_{N_s(i)}} = (x_{N_s(i)})) \tag{37}$$

$\mathbf{0}$ is an absorbing state of the model. However, the model will reach a quasi-stationary distribution (see Darroch & Seneta 1965) before extinction which gives a distribution of all possible states of the metapopulation among sites. Getting extinction time and quasi-stationary distribution require to compute eigenvectors and eigenvalues of $\mathbf{P}$ that are intractable in the general case since $\mathbf{P}$ is high-dimensional. Using the "sampling from the past" algorithm (Aldous *et al.*, 1988) is an alternative option to estimate the quasi-stationary distributions and associated eigenvalues, see e.g. Schreiber

et al. (2023) for an application of this technique in an ecological context.

The mainland-island model of species interaction is a homogeneous Markov chain on $\chi = \{0,1\}^m$ with no absorbing state. A state of the mainland-island model of species interaction is a binary vector of length m, representing the composition of the community. The dimension of the transition matrix is $2^m * 2^m$ and the probability of transition between a state $s_k = (x_1, ..., x_m)$ and $s_l = (\tilde{x_1}, ..., \tilde{x_m})$ is

$$P_{k,l} = \prod_j \mathbb{P}(X_j^{t+1} = \tilde{x_j} | X_j^t = x_j, X_{N_b(j)}^t = (x_{N_b(j)})) \tag{38}$$

The chain converges towards a unique stationary distribution, a distribution of probability over all possible species communities. However, as in the metapopulation case, computing the stationary distribution is intractable in the general case since $\mathbf{P}$ is high-dimensional. To summarise, in the metapopulation model, the spatial network acts on the probability of colonisation, whereas in the interaction model, the biotic network acts on the probability of extinction.

Proposition 3. *The stochastic spatially realistic metacommunity model converges towards a unique stationnary distribution*

In the stochastic spatially realistic models of mutualistic metacommunities, the transition matrix of the chain is of dimension $2^{mn} * 2^{mn}$, encoding the probability of transition between a state $\mathbf{s_k} = (x_{11}, ..., x_{mn})$ of the metacommunity and a state $\mathbf{s_l} = (\tilde{x_{11}}, ..., \tilde{x_{mn}})$, where $x_{ij} \in \{0,1\}$ describes the presence of a population of species i in site j. We note $\mathbf{P}$ the transition matrix, the probability of transition between $\mathbf{s_k}$ and $\mathbf{s_l}$ is :

$$P_{k,l} = \prod_{i,j} \mathbb{P}(X_{ij}^{t+1} = \tilde{x_{ij}} | X_{11}^t = x_{11}, ..., X_{mn}^t = x_{mn}) \tag{39}$$

Moreover, we have:

$$\mathbb{P}(X_{i,j}^{t+1} = 1 | X_{i,j}^t = 0, \sum_{(k,l) \in N_{G_c}(i,j)} X_{k,l}^t) = \epsilon + (1-\epsilon) * (1 - (1-c)^{\sum_{(k,l) \in N_{G_c}(i,j)} X_{k,l}^t}) \tag{40}$$

with $\epsilon \in]0;1[$ and $c \in]0;1[$. We have:

$$\mathbb{P}(\epsilon < \epsilon + (1-\epsilon) * (1-(1-c)^{\sum_{(k,l)\in N_{G_c}(i,j)} X^t_{k,l}}) < 1) = 1 \tag{41}$$

Moreover:

$$\mathbb{P}(X^{t+1}_{i,j} = 1 | X^t_{i,j} = 1, \sum_{(k,l)\in N_{G_e}(i,j)} X^t_{k,l}) = 1 - e(1 - \frac{\sum_{(k,l)\in N_{G_e}(i,j)} X^t_{k,l}}{1 + deg_{G_e}((i,j))}) \tag{42}$$

where $e \in]0;1[$. We have then:

$$\frac{e}{1 + deg_{G_e}((i,j))} < e(1 - \frac{\sum_{(k,l)\in N_{G_e}(i,j)} X^t_{k,l}}{1 + deg_{G_e}((i,j))}) < e \tag{43}$$

The probability of extinction is in $]0;1[$.

Consequently :

$$\forall i \in \{1,...,n\}, \forall j \in \{1,...,m\},\ \mathbb{P}(X^{t+1}_{i,j} = x_{i,j} | X^t_{1,1} = \tilde{x_{1,1}}, ..., X^t_{m,n} = \tilde{x_{m,n}}) > 0 \tag{44}$$

It follows that $\mathbf{P}$ is irreducible and aperiodic and $(\mathbf{X^t})^t$ converges towards a unique stationary distribution. Importantly, in the stationnary distribution, each species in each sites has a non-nul probability of presence.

A.2 The nm-intertwined model

The approximation is derived from Bianconi (2018) and Van Mieghem (2011). The aim is to study the dynamics of occupancy of each species j in each site i: $p_{ij}(t) = \mathbb{E}(X^t_{ij})$. For all i and j, we have

$$p_{i,j}(t+1) = \mathbb{E}((1-X^t_{i,j})(\epsilon+(1-\epsilon)(1-(1-c)^{\sum_{(k,l)\in N_{G_c}(i,j)} X^t_{k,l}}))) + \mathbb{E}(X^t_{i,j}(1-e(1-\frac{\sum_{(k,l)\in N_{G_e}(i,j)} X^t_{k,l}}{1 + deg_{G_e}((i,j))}))) \tag{45}$$

This approach leads to a hierarchy of equations that cannot be solved (i.e. we need to consider

$\mathbb{E}(X^t_{1,1},...,X^t_{m,n})$ to find a solution to the system). A drastic approximation consists in the mean field approximation, for any sequence of indices $n(1),n'(1);...,n(r),n'(r')$, we assume :

$$\mathbb{E}(X^t_{n(1),n'(1)},...,X^t_{n(r),n'(r')}) \simeq \mathbb{E}(X^t_{n(1),n'(1)})...\,\mathbb{E}(X^t_{n(r),n'(r')}) \tag{46}$$

$$p_{i,j}(t+1) = (1-p_{i,j}(t))(\epsilon+(1-\epsilon)(1-(1-c)^{\sum_{(k,l)\in N_{G_c}(i,j)} p_{kl}(t)})+(1-e(1-\frac{\sum_{(k,l)\in N_{G_e}(i,j)} p_{k,l}(t)}{1+deg_{G_e}((i,j))}))p_{i,j}(t) \tag{47}$$

We assume that $c=o(1)$, $e=o(1)$ and $\epsilon=o(c)$, a Taylor expansion at order 1 with set $M_{i,j} := 1+deg_{G_e}((i,j))$ leads to:

$$p_{i,j}(t+1) = (1-p_{i,j}(t))(\epsilon+(1-\epsilon)(c\sum_{(k,l)\in N_{G_c}(i,j)} p_{k,l}(t))+(1-e+e\sum_{(k,l)\in N_{G_e}(i,j)} p_{k,l}(t))/M_{i,j})p_{i,j}(t) \tag{48}$$

$$p_{i,j}(t+1) = (1-p_{i,j}(t))(c\sum_{(k,l)\in N_{G_c}(i,j)} p_{k,l}(t))+(1-e+e\sum_{(k,l)\in N_{G_e}(i,j)} p_{k,l}(t))/M_{i,j})p_{i,j}(t) \tag{49}$$

We introduce a single index v for the nodes of the product networks and get:

$$p_v(t+1) = (1-p_v(t))(c\sum_{u\in N_{G_c}(v)} p_u(t))+(1-e+e\sum_{u\in N_{G_e}(v)} p_u(t))/M_v)p_v(t) \tag{50}$$

$$p_v(t+1)-p_v(t) = (1-p_v(t))(c\sum_{u\in N_{G_c}(v)} p_u(t))-e(1-\sum_{u\in N_{G_e}(v)} p_u(t))/M_v)p_v(t) \tag{51}$$

$$p_v(t+1)-p_v(t) = C_v(\mathbf{p(t)})(1-p_v(t)))-E_v(\mathbf{p(t)})(p_v(t)) \tag{52}$$

where $C_v(\mathbf{p(t)}) = c\sum_u [A_c]_{v,u}p_u(t)$ and $E_v(\mathbf{p(t)}) = e(1-\sum_u [A_e]_{v,u}p_u(t)/M_v)$.

$$\mathbf{p(t+1)}-\mathbf{p(t)} = c(\mathbf{A_c p(t)})\odot(\mathbf{1}-\mathbf{p(t)})-e(\mathbf{1}-(\mathbf{D_e}+\mathbf{I}_{nm})^{-1}\mathbf{A_e p(t)})\odot\mathbf{p(t)} \tag{53}$$

where $\odot$ denotes the element-wise product, D_e denotes the indegree matrix of G_e and $\mathbf{I}_{nm}$ the identity matrix of dimension nm.

A.3 Proof of proposition 1

We need to show that the two submodels are irreducible. Let $\mathbf{J}$ be the matrix of dimension $n \times n$ so that:

$$J_{ij} = \begin{cases} 1 & \text{if } \frac{\partial g_i}{\partial p_j}(\mathbf{p}) > 0, \mathbf{p} \in \overline{\Omega} \\ 0 & \text{otherwise} \end{cases} \tag{54}$$

We say that the model is irreducible if $\mathbf{J}$ is irreducible, i.e., the graph that has $\mathbf{J}$ as adjacency matrix is strongly connected.

Importantly, as pointed out in Smith (2008), we need to show that the models are irreducible on $\overline{\Omega}$, that is the interior of the domain but also its boundary.

We have:

$$g_v(\mathbf{p}) = \frac{\sum_u [A_c]_{v,u} p_u}{1 - \sum_u [A_e]_{v,u} p_u / M_v} \tag{55}$$

We first note that g_v is defined on $\overline{\Omega}$ since:

$$|\sum_u [A_e]_{v,u} p_u / M_v| \leq |\sum_u [A_e]_{v,u} / M_v| < 1 \tag{56}$$

We have:

$$\frac{\partial g_v}{\partial p_u}(\mathbf{p}) = \frac{[A_c]_{v,u}(1 - \sum_k [A_e]_{v,k} p_k / M_v) + ([A_e]_{v,u}/M_v) \sum_k [A_c]_{v,k} p_k}{(1 - \sum_k [A_e]_{v,k} p_k / M_v)^2} \tag{57}$$

For the Levins type model:

$$\frac{\partial g_v}{\partial p_u}(\mathbf{p}) = [A_c]_{v,u} \tag{58}$$

And since, G_s and G_b are both strongly connected and $G_c = G_s \square G_b$, G_c is also strongly connected and $\mathbf{J}$ is irreducible on $\overline{\Omega}$.

For the combined effect model, we note that $E(G_e) \subset E(G_c)$. It follows that $[A^c]_{v,u} = 0 \implies$

$[A^e]_{v,u} = 0$ and $[A^e]_{v,u} = 1 \implies [A^c]_{v,u} = 1$. We have then:

$$\frac{\partial g_v}{\partial p_u}(\mathbf{p}) = \frac{[A_c]_{v,u} + (\sum_k [A_c]_{v,k}[A_e]_{v,u}p_k/M_v - [A_c]_{v,u}[A_e]_{v,k}p_k/M_v)}{(1 - \sum_k [A_e]_{v,k}p_k/M_v)^2} \tag{59}$$

- If $[A_c]_{v,u} = 0$, then $[A_e]_{v,u} = 0$ and, for all k, $[A_c]_{v,u}[A_e]_{v,k} - [A_c]_{v,k}[A_e]_{v,u} = 0$. It follows that $\frac{\partial g_v}{\partial p_u}(\mathbf{p}) = 0$

- If $[A_c]_{v,u} = 1$ and $[A_e]_{v,u} = 0$, then:

$$\frac{\partial g_v}{\partial p_u}(\mathbf{p}) = 1 - \sum_k [A_e]_{v,k}p_k/M_v \tag{60}$$

  and $\frac{\partial g_v}{\partial p_u}(\mathbf{p}) > 0$

- If $[A_c]_{v,u} = 1$ and $[A_e]_{v,u} = 1$, then:

$$\frac{\partial g_v}{\partial p_u}(\mathbf{p}) = \frac{1 + (\sum_k [A_c]_{v,k} - [A_e]_{v,k})/p_k M_v}{(1 - \sum_k [A_e]_{v,k}p_k/M_v)^2} \tag{61}$$

Since $E(G_e) \subset E(G_c)$, we have $(\sum_k [A_c]_{v,k} - [A_e]_{v,k}) > 0$ and $\frac{\partial g_v}{\partial p_u}(\mathbf{p}) > 0$.

Consequently, for the combined effect model, then non-zero elements of $\mathbf{J}$ are the non-zero elements of $\mathbf{A_c}$. Since $G_c = G_s \square G_b$ it follows that $\mathbf{J}$ is irreducible.

A.4 Computation of λ_I

As provided in the main text, for the Levins type submodel, $\lambda_I = \lambda_M = \Lambda_s + \Lambda_b$. We now compute the λ_I for the three other submodels.

We first compute the Jacobian matrix of $\mathbf{p} \mapsto g(\mathbf{p})$ evaluated in $\mathbf{p} = 0$. We have

$$\frac{\partial g_v}{\partial p_u}(\mathbf{0}) = [A_c]_{v,u} \tag{62}$$

λ_I is the dominant eigenvalue of $\left(\frac{\partial g_v}{\partial p_u}(\mathbf{0})\right)_{u,v}$

- Combined effect submodel

  For this submodel, $A_c = A_s \otimes I_m + I_n \otimes A_b$, it follows $\lambda_I = \Lambda_s$

A.5 Computation of λ_M

In order to compute λ_M for the combined effect submodel, the separated effect model and the rescue effect submodel where the components of $\mathbf{g}$ are not concave, we used a simulated annealing algorithm. We used the result of the iterative procedure described in Appendix D of Ovaskainen & Hanski 2001 as starting point.

The code to compute the metacommunity capacity in the different models is available at: `https://gitlab.com/marcohlmann/metacommunity_theory`.

We assessed the performance of the method on the Levins type model on the simulated data, since we know analytically the metacommunity capacity in this case. We used 20000 time steps on the 900 different networks for the two submodels. The maximum is not reached (Fig. S1a) but the there is a strong correlation (0.955) between the estimated metacommunity capacities and the theoretical metacommunity capacities (Fig. S1b), allowing so comparison of the metacommunity capacities among the different network structures.

B Appendix: detail on the simulation

B.1 Spatial networks

In order to mimic fragmentation of the landscape, we sampled spatial networks (10 nodes) using Erdős-Renyi model and a block model. For the Erdős-Renyi model, the probability of connection was $C = 0.25$ and we kept connected networks only. For the block model, we partitioned in two

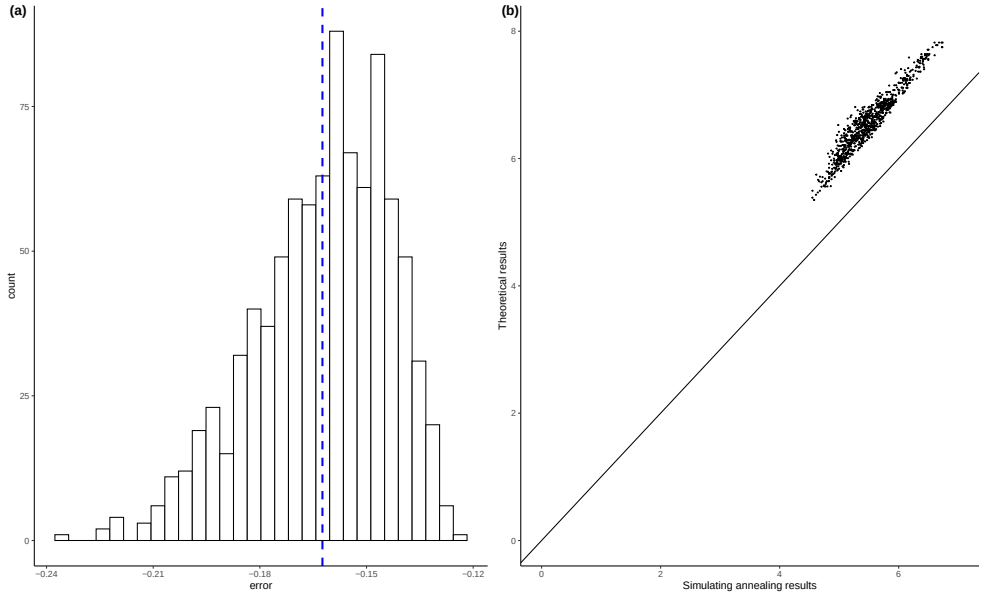


Figure S1: (a) Distribution of the relative error in the estimation of the metacommunity capacity (b) Relation between the metacommunity persistence capacity computing using a simulating annealing algorithm and the theoretical metacommunity capactity for the Levins type submodel

groups of equal sizes, p and q, with a matrix of probability of connection, $\mathbf{\Pi}$, given by:

$$\begin{array}{c} \begin{array}{cc} p & q \end{array} \\ \begin{pmatrix} \frac{7C}{4} & \frac{C}{4} \\ \frac{C}{4} & \frac{7C}{4} \end{pmatrix} \begin{array}{c} p \\ q \end{array} \end{array}$$

where $C = 0.25$.

The overall probability of connection in the network is :

$$\mathbb{P}(i \leftrightarrow j) = \sum_{k \in \{p,q\}, l \in \{p,q\}} Pr(i \leftrightarrow j | i \in k, j \in l) Pr(i \in k) Pr(j \in l) \tag{63}$$

$$\mathbb{P}(i \leftrightarrow j) = \frac{1}{4}(\frac{7C}{4} + \frac{C}{4} + \frac{C}{4} + \frac{7C}{4}) \tag{64}$$

$$\mathbb{P}(i \leftrightarrow j) = C \tag{65}$$

So the expected value of connectance for all spatial networks is the same despite different modularity values (Fig. S2).

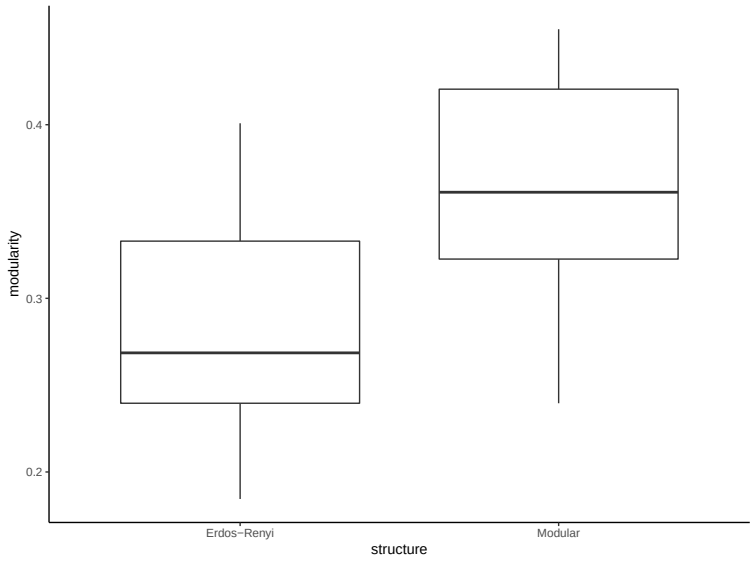


Figure S2: Distribution of the modularity of the spatial networks over the 15 replicates for the Erdős-Renyi strucutre and the modular structure

B.2 Biotic interaction networks

We first generated random undirected network with various shapes of the degree distribution using the function *sample_fitness_pl* implemented in the R package *igraph* (Csardi & Nepusz, 2006). We generated Erdős-Renyi networks and networks with a degree distribution given by a power-law. We only kept connected networks. On the random network G sampled ($\mathbf{A}$ is its adjacency matrix), we build a bipartite network G_{bip} with adjacenncy matrix $\mathbf{A_{bip}}$ as:

$$\mathbf{A_{bip}} = \mathbf{A_2} \otimes (\mathbf{A} + \mathbf{I_n}) \tag{66}$$

where $\mathbf{A_2}$ is the adjacency matrix of an undirected graph made of two nodes and a single edge between these two nodes. By doing so, all the sampled undirected bipartite networks are strongly connected.

B.3 Results

We simulated the dynamic (as presented in the main text for the combined effect submodel) for the Levins type model (Fig. S5, Fig. S6).

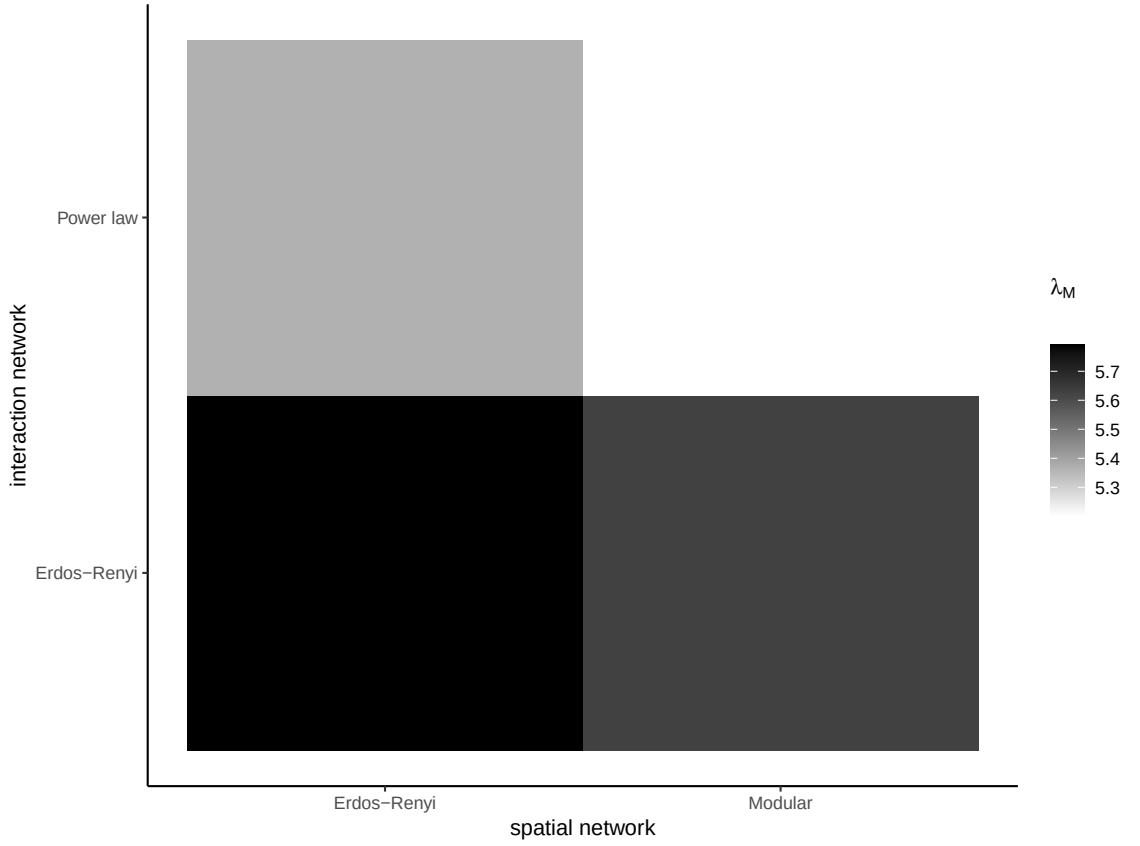


Figure S3: Assessing metacommunity persistence capacity in function of the structure of the spatial network (Erdős-Renyi/Modular) and the structure of the interaction network (Erdős-Renyi/Power law) for the Levins type model

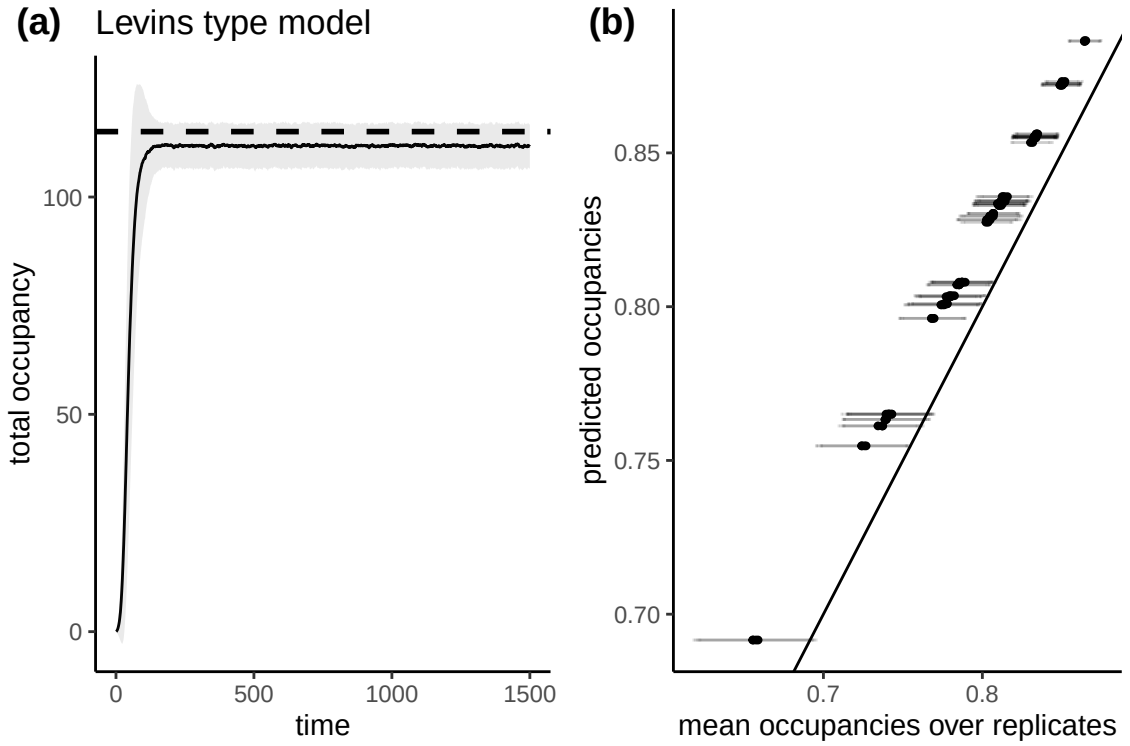


Figure S4: Comparison between the stochastic metacommunity model and the *nm*-intertwined model for the Levins type model. (a) Comparison of the mean total occupancy dynamics averaged over 1000 replicates (solid line, the standard deviation is represented in grey) with the prediction of the equilibrium by the *nm*-intertwined model (dashed line) (b) Comparison of the mean local occupancies in the stationary distribution of the stochastic metacommunity model with the predicted values by the *nm*-intertwined model

B.4 Robustness of metacommunity capacity estimation

We analysed the robustness of the estimation of λ_M for the four different structures for each submodel. We described the distribution of λ_M (225 samples per combination of structure for each model) using a boxplot (Fig. S7). Morever, we used a Tukey test to estimate the confidence intervals of the difference in mean metacommunity capacity per pairs of structures (Fig. S8). For the Levins type and combined effect model, all differences in mean λ_M were statistically different of 0. For the seperated effect and rescue effect model, difference in mean λ_M of PL/E-E/E (PL: Power-Law, E: Erdős-Renyi, M: Modular) and PL/M-E/M were statistically not different from 0.

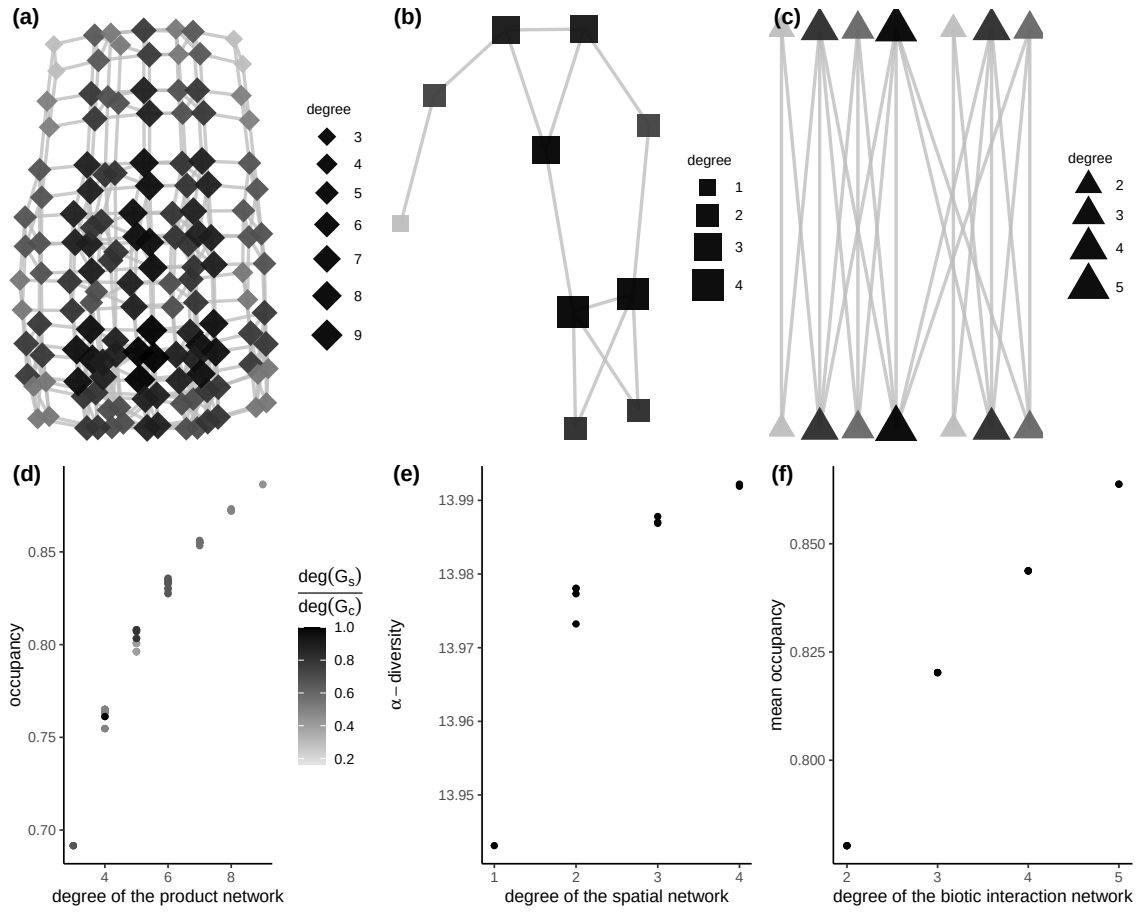


Figure S5: Simulating the dynamics for a given spatial and biotic interaction network with the Levins type model. (a) Colonisation network whose size of the nodes is proportional to their degree and colour indicates the occupancy at equilibrium (grey: low occupancy, black: high occupancy) (b) Spatial network whose size of the nodes is proportional to their degree and colour indicates the species α-diversity at equilibrium (grey: low α-diversity, black: high α-diversity) (c) Mutualistic interaction network whose size of the nodes is proportional to their degree and colour indicates the mean occupancy across the sites at equilibrium (grey: low mean occupancy, black: high mean occupancy) (d) Relationship between the occupancy at equilibrium and the degree of the node of the product network. Each point of the relationship (corresponding to a node of the product graph) is coloured according to the ratio of the degree of the site in the spatial network over the degree of the focal node in the colonisation network (e) Relationship between the species α-diversity at equilibrium and the degree of the sites in the spatial network (f) Relationship between the mean occupancy at equilibrium and the degree of the species in the biotic interaction network

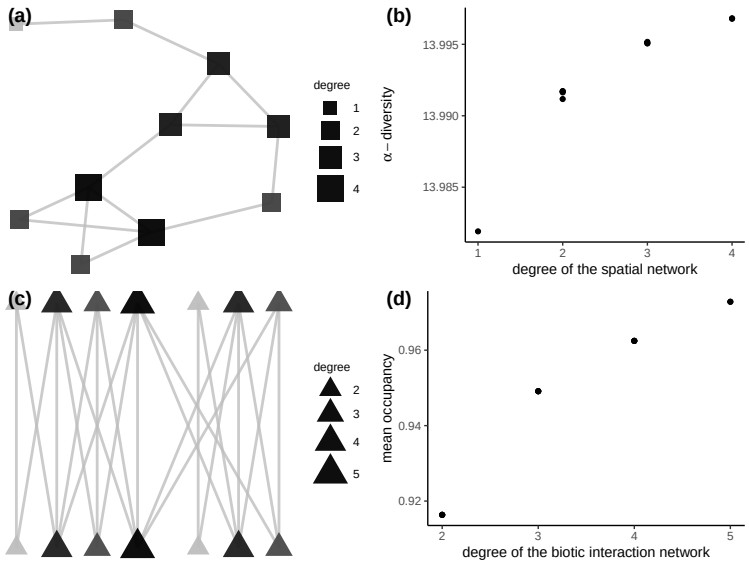


Figure S6: Aggregated statistics from occupancy at equilibrium for the combined effect submodel in the spatial network and the biotic interaction network. (a) Spatial network whose size of the nodes is proportional to their degree and colour indicates the α-diversity at equilibrium (grey: low α-diversity, black: high α-diversity). (b) Relationship between the α-diversity at equilibrium and the degree of the sites in the spatial network. (c) Biotic interaction network whose size of the nodes is proportional to their degree and colour indicates the mean occupancy across the sites at equilibrium (grey: low α-diversity, black: high α-diversity). (d) Relationship between the mean occupancy at equilibirum and the degree of the species in the biotic interaction network.

It means that, for these two models, whatever the structure of the spatial network (Modular or Erdős-Renyi), mean λ_M was comparable for a power-law or Erdős-Renyi biotic interaction network.

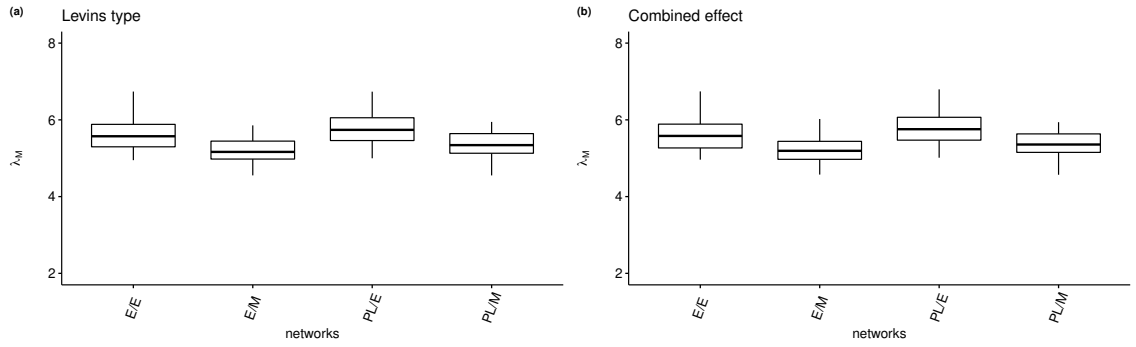


Figure S7: Boxplot representing distributions of λ_M for each combination of structure in the Levins type and the combined effect model. E: Erdős-Renyi, PL: Power-Law, M: Modular

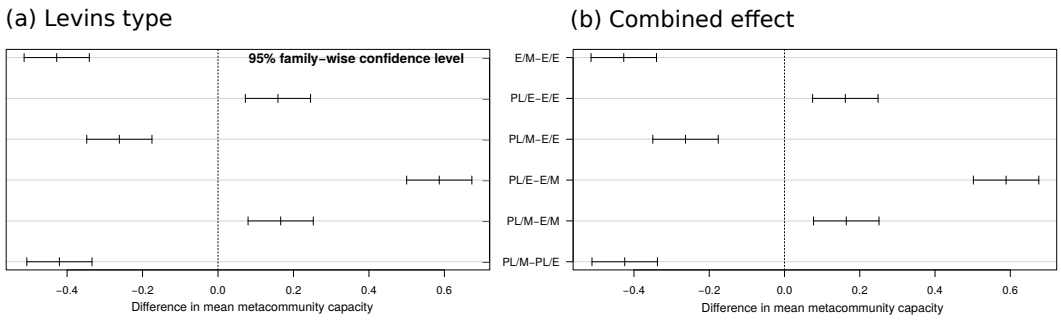


Figure S8: Tukey plot representing the confidence intervals of the difference in mean metacommunity capacity per pairs of structures. E: Erdős-Renyi, PL: Power-Law, M: Modular

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