Emergence of metacommunities in niches landscapes driven by self-recruitment segregation

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Complex interactions are at the root of the population dynamics of many natural systems, particularly for being responsible for the allocation of species and individuals across opposite ecological niches. On the other side, the randomness that unavoidably characterises complex systems has increasingly challenged the niche paradigm providing alternative neutral theoretical models. We introduce a network-inspired metapopulation individual-based model (IBM), hereby named self-recruitment segregation, where the density of individuals in the hosting nodes (niches) drives the individuals spatial assembling while still constrained by nodes’ saturation. In particular, we prove that the core-periphery structure of the networked landscape triggers the spontaneous emergence of empty nodes, which segregate the population in multistable patterns of metacommunities. Furthermore, a quantisation effect in the number of empty niches is observed once the total system mass varies continuously, emphasising thus a striking feature of the robustness of niche stationary density distributions. We argue that such spontaneous emergence of metacommunities separated by empty nodes supports the concept of the highly contentious vacant niches and suggests the configuration diversity of segregated niches.

The distinct feature of complex systems is their critical reliance on the interactions between the constituent entities. Such strong dependence has given birth to the discipline of network science [1][2]. From this perspective, nodes represent either single individuals or groups thereof, (i.e., metapopulations), and edges, the respective interactions among them. According to the positive, negative or neutral nature of such interactions, they can identify mutualism, competition, or commensalism, respectively [5][6]. There is a long tradition in population dynamics, further strengthened by complexity science, to attribute collective behaviors such as self-organisation or adaption, in biological or social systems, to interactions between entities (e.g., Lotka-Volterra models) [1][5][6]. In ecology, the coexistence of a large variety of species is thought to be possible because of their ability to occupy specific spatial niches, namely the habitat (resources, prey/predators, competitors, climate, etc.) where they live, as a consequence of a long and highly selective evolutionary process [7][8].

An alternative approach adopted in recent years to tackle the question of niche segregation is that of neutral theory, according to which organised patterns can occur exclusively due to the randomness of several factors that decisively condition species survivability [7][12]. Stochastic processes are the common ground around which the modern neutral theory of biodiversity is erected [8][10]. In this regard, individuals are considered indistinguishable from each other, and irrelevant interspecies interactions are discarded from the governing dynamics. Thus elementary processes such as births/deaths or random walks result crucial in describing the collective dynamics emerging from individual-based models (IBM). In the context of neutral theory, there have been several attempts to justify niche segregation in terms of the randomness of the decisive factors during the evolutionary process [9][9]. For instance, there is a consolidated debate whether the species fully occupy all the niches to overcome Gause’s law of competitive exclusion [5][8][10] or either vacant niches can exist due to an optimal fitness landscape [6]. According to the latter thesis, the fitness function that describes the adaption of the species to the niches domain, is rather rugged and multipeaked. This way, the randomness associated with the initial conditions will allow the individuals assembling around some (local) optima and eventually allow the emergence of vacant niches around the landscape minima. Niches landscapes found in nature are highly nested and are generally built on mutualistic interactions such as the generalist-specialist trophic networks [13][15]. The ubiquity of disassortativity in ecological networks gives valuable insight into the spatial distribution of animals, plants, and other living beings in their respective habitats.

Inspired by the framework described above, our aim in this Letter is to present a simple and stylised model capable to reproduce the emergence of empty niches and the resulting metacommunities, namely communities of populated, i.e., filled, nodes in the metapopulation framework, both triggered by the heterogeneity of the network support. Our approach is reminiscent of the celebrated Schelling’s model [16][18], according to which self-organised patterns of segregation spontaneously emerge due to the interactions between (at least) two antagonistic types of individuals. At variance with such paradigm, and in the spirit of neutral theory, we hereby consider a single species of individuals. We show that in the absence of inter-species interactions, the metacommunity formation is now exclusively due to the spatial disassortativity of the networked landscape, particularly the presence of multiple cores linked together through bridges (peripheral) nodes. In a simplified format, we consider a connected network, whose nodes are supposed to rep-
resent the existing niches. To assess the niches saturation (limited resources, competition, or predators), we assume that the nodes have a maximum carrying capacity of possible individuals to allocate. The displacement driving force in our model is set on the individuals affinity describing intra-species mutualistic play (the agents are indistinguishable), considered a universally accepted virtue in population dynamics. We will refer to the influence that the identical individuals exert on each other as self-recruitment. Hence, densely populated niches are more likely to attract new agents than less populated ones, provided the carrying capacity allows for them. The resulting collective behavior is the emergence of different configurations of metacommunities surrounded by vacant niches.

Mathematically speaking, we consider a simple (i.e., without self-loops or multi-edges) connected and undirected graph made of $\Omega$ nodes $\{v_i\}_{\Omega}$ whose structure is encoded in its adjacency matrix entries, $A_{ij} = 1$ if there is a link between nodes $v_i$ and $v_j$, and zero otherwise. A fundamental assumption of our model is that the network is characterised by a heterogeneous degree distribution $\{p(k_i)\}_{\Omega}$ where the degree of node $v_i$ is defined as $k_i = \sum_{j=1}^{\Omega} A_{ij}$. If we denote the state of the system at time $t$ by $\mathbf{n}(t) = (n_1(t), n_2(t), \ldots, n_\Omega)$ and the probability of observing such state by $P(n, t)$, then the mathematical formalism that governs the individuals dynamics is described by the master equation [19, 20]:

$$\frac{dP(\mathbf{n}, t)}{dt} = \sum_{\mathbf{n}'} \left[ T(\mathbf{n}|\mathbf{n}')P(\mathbf{n}', t) - T(\mathbf{n}'|\mathbf{n})P(\mathbf{n}, t) \right],$$

where $T(\mathbf{n}|\mathbf{n}')$ stands for the transition probability from state $\mathbf{n}$ to state $\mathbf{n}'$. Following the idea of the finite carrying capacity of the spatial niches (and similarly to [21, 22]), we impose to each node $v_i$ a maximum number of agents $1 \leq n_i \leq N$ that can be hosted. With a slight abuse of notation, the transition from node $v_i$ to node $v_j$ is written as:

$$T(n_i - 1, n_j + 1|n_i, n_j) = \frac{A_{ij} n_i}{k_i} \frac{n_j}{N}g\left(\frac{n_j}{N}\right),$$

where the function $g(\cdot)$ represents the probability for the agents to settle in the chosen host node and quantifies the mutualism among individuals while still considering the finite size of the nodes. A significant difference with other random processes, e.g., the biased random walks [23], is that the probability of choosing the host node is independent of the densities of individuals in the other neighbour nodes [24]. This subtle but crucial feature makes sense for the niche interpretation of the spatial support [11, 22]: the individual cannot a priori choose the most suitable node before first “testing the ground”. Said differently, the agents perceive the pressure of limited resources or numerous predators once they reside on a given niche, but not earlier. Throughout this Letter, we will make a straightforward assumption regarding the mutualism function $g(\cdot)$: the hosting node will recruit individuals proportionally to the density of agents already present therein, and at the same time, the probability for a recruited individual to settle in the selected node, is proportional to the available free space (capacity constraint). In formula we have

$$g\left(\frac{n_j}{N}\right) = \frac{n_j N - n_j}{N},$$

which constitutes the prominent logistic function and has plentiful applications in many areas of science and in particular in ecology [3]. Applying a standard procedure, we multiply both sides of Eq. (1) by $n_i$, and summing over $n_i$ for all $i$, we obtain the evolution equation for the average density $\langle n_i \rangle$ which in the thermodynamic limit $N \rightarrow +\infty$ yields the mean-field (MF) equations:

$$\dot{\rho}_i = \sum_j \mathcal{L}_{ij} \rho_i \rho_j \left[ 1 - \frac{\rho_i}{k_i} \left( 1 - \frac{\rho_j}{k_j} \right) \right], \forall i, \tag{3}$$

where $\rho_i = \lim_{N \rightarrow +\infty} \langle n_i \rangle / N$ is the node density and $\mathcal{L}_{ij} = A_{ij} / k_i - \delta_{ij}$ corresponds to the random walk (RW) Laplacian [1, 4]. Notice also that in the limit of large $N$ we drop any correlation among different nodes i.e., $\langle n_i n_j \rangle \sim \langle n_i \rangle \langle n_j \rangle$ based on the van Kampen ansatz [20].

Starting from the MF [3] we can determine the equilibrium states $\{\rho^*_i\}_{\Omega}$ and based on that we can afterwards perform a (linear) stability analysis. A straightforward computation (the interested reader can refer to the Supplemental Material (SM)) allows to obtain the node density in the $\gamma$-th metacommunity at the equilibrium to be given by

$$\rho^*_i = 0 \quad \text{or} \quad \rho^*_i = 1 - \frac{C_i}{k_i}, \forall i, \tag{4}$$

where $C_i = (1 - \beta_i) / (1/k_i)\Omega_i$ is a conservation constant that depends on the initial configuration $\{\rho^0_i\}_{\Omega}$ and $\beta_i = \sum_{j \in M_i} \rho^0_j / \Omega_i$ is the average stationary node density of the $\gamma$-th metacommunity $M_\gamma$ with size $\Omega_\gamma$. Eq. (4) results thus an implicit equation for the stationary nodes’ densities. In particular, in the case of a single metacommunity, $\beta_i$ is the global density, i.e., the total number of agents divided by the number of non empty nodes. Observe that the average $\langle 1/k \rangle_{\Omega_\gamma}$, has been performed over the $\Omega_\gamma$ nodes forming the metacommunity. From relation (4), it is straightforward that nodes resulting occupied at equilibrium should have a degree $k_i > C_\gamma$ or will be vacant otherwise. Because $C_\gamma$ decreases with the total mass, the last observation suggests that acting on the mass we can induce the agents to segregate at the nodes with higher degrees, possibly leaving the ones with a lower degree vacant. To elucidate the robustness of the metacommunities we will consider the case when a single empty node, adjacent to a given metacommunity, is slightly perturbed [20] and postpone a complete stability analysis to the SM. We start by assuming the system settles on some equilibrium and we focus on the $\gamma$-th metacommunity, whose nodes are characterised by $\rho^*_j = 1 - C_j / k_j > 0$. Suppose it exists an empty node $i$ connected exclusively to the metacommunity $\gamma$ to which
we allocate a small amount of mass, such that this new configuration still satisfies the same constraints ($\gamma$ and $\beta$ remain unchanged assuming $\Omega_\gamma$ is large enough to neglect the small amount of mass we have to remove from each node but the $i$-th one to satisfy the constraint), that is $\rho_i^* \rightarrow \delta$ and $\rho_j^* = 1 - C_\gamma / k_j$ for $j \neq i$. A direct computation allows to obtain the linearised dynamics that governs node $v_i$ at early time

$$
\dot{\delta} \approx \delta \left( 1 - C_\gamma / k_i \right) \sum_{j=1}^{\Omega_\gamma} L_{ij} \rho_j^*. 
$$

From here we can conclude that the $v_i$-th node will increase its mass (acquiring it from other $\Omega_\gamma$ nodes) if $C_\gamma < k_i$ and will transfer it to the other nodes of the metacommunity $\gamma$ otherwise. Similarly, if we add a small mass $\delta$ to an occupied node, the system is always stable. In fact, if we slightly perturb only the $i$-th node of the metacommunity $\gamma$, $\rho_i^* \rightarrow \rho_i^* + \delta$, with $\delta > 0$, a straightforward computation allows writing $\dot{\rho}_i^* \approx -\delta \rho_i^* \sum_{j=1}^{\Omega_\gamma} L_{ij} \rho_j^*$, thus proving the stability of the metacommunity. This is reasonable since the added mass to some pre-existing metacommunity cannot escape from it being surrounded by empty nodes.

The local analysis emphasises the role of the degree distribution heterogeneity in the existence of stable states with empty nodes. For instance, in a regular graph, the only possible (non-trivial) stable state is the one being uniformly occupied since $C_\gamma < k$ for all the nodes. Nevertheless, in the following, we will see that, for non-regular networks, a node can be either empty or occupied depending on the combination of a random choice of the initial conditions and the structural features of the network structure. The latter yields to stable configurations with different numbers of vacant nodes, a phenomenon we hereby refer to as multistability. To illustrate the outcomes of the self-recruitment dynamics, we refer to Fig. 1, where the system has been initialised with a uniform distribution of nodes’ densities for all the panels. From the previous analysis, if the average density is sufficiently large, i.e., $\beta > 1 - 1/\Omega$, all nodes are occupied at equilibrium, resulting in a single metacommunity. However, as $\beta$ is gradually reduced, some empty nodes (the least connected ones and those with the largest bridgeness centrality) start to emerge. Decreasing the total mass would result in increasing the constant $C_\gamma$, which in turn forces all the nodes for which $k_j > C_\gamma$ is no longer satisfied, to deplete. The mass accumulates on fewer nodes in such a way to satisfy the new equilibrium condition.

Notice that, in general, the interpretation of the system behavior depends on the knowledge of the conservation constant $C_\gamma$, which cannot be $a$ priory inferred. Also from Fig. 1, one can notice that for (sufficiently) small variations of the mass, the set of empty/occupied nodes remains the same, showing that the system is resilient in switching to a state with more (less) vacant nodes while the mass decreases (increases). Such “quantisation” phenomenon is exclusively due to the discrete distribution of the network support and can be understood starting from the conservation constant $C_\gamma = (1 - \beta_\gamma) / (1/k)\Omega$, which changes continuously with $\beta_\gamma$, if the number of metacommunities does not vary, that in turn depends on the total average density $\beta$. Since the degrees are discrete and the network is finite, density intervals, where $C_\gamma$ does not overtake the next lowest degree of occupied nodes, will certainly exist. Furthermore, the length of such intervals must decrease when the differences between the successive degrees become smaller, suggesting that a broader...
FIG. 2. (Upper panels) Number of empty nodes $f$ vs. the average density $\beta$. The shaded blue and red areas (in panels b) and c)) show the multistability phenomenon as measured by the min-max node occupancy resulting from several independent simulations. a) Erdos-Renyi networks with different network sizes and same probability to have a link among two nodes ($p = 1/3$). As the number of nodes increases, the quantisation becomes weaker while the multistability is almost absent. b) The London Tube network [28] (red curve) vs. a synthetic core-periphery one (blue curve). The shaded area corroborates the multistability claim, and the quantisation appears neatly manifested by the plateaus. (Inset) Number of metacommunities $N$ vs. the fraction of empty nodes $f$ showing that to the same fraction of empty nodes corresponds a different number of metacommunities. c) The disassortative plant-pollinator network [29]. Although the quantisation is still evident, no multistability is effectively present. (Lower panels) Metacommunities visualisation (shaded coloured areas) and empty nodes (white circles): d) and e) results for two different densities initialisations for the same value of $\beta = 0.15$ close to the abrupt transition in $f$ vs $\beta$ (see panel b)) in the London Tube network. f) the same result of panels d) and e) for the plant-pollinator network for $\beta = 0.15$.

degree distribution will show a less pronounced quantisation effect.

To better infer the role of network topology on both the metacommunities emergence and the quantisation of the fraction of vacancies, in Fig. 2 we analyse a set of both synthetic and real networks with different structural characteristics. In panel a), we show that as the size of the random networks increases, the quantisation effect in occupying, respectively depleting the nodes becomes more diluted, in line with our prediction. The importance of the heterogeneity of the degree distribution in the formation of metacommunities is further accentuated in disassortative networks where nodes are naturally arranged in interacting groups of highly and loosely connected entities. In panel b), we consider a synthetic and a real core-periphery network, where at variance with the Erdos-Renyi topology (of panel a)), besides quantisation, we observe the emergence of many different metacommunities (panels d) and e)). This scenario is a neat manifestation of multistability, i.e., different stable states for different initial conditions for the same system parameter $\beta$, as attested by the shaded area in panel b). In fact, for two initial nodes densities conditions, with same total mass, randomly chosen from a uniform distribution, we have two distinct configurations of metacommunities with a different fraction of vacant nodes. There is a clear difference between the synthetic and the empirical network since the latter is provided with “bridge” nodes that connect two or more cores, as explained in detail in the SM. This peculiarity makes the real core-periphery network prone to split in different metacommunities once the density $\beta$ starts to decrease, at variance with the synthetic network where multiple metacommunities appear only when the density takes low values. Nevertheless, the multistability seems to vanish when we consider a plant-pollinator network [29], panels c) and f). Such difference between the behaviors arising from the two networks can be justified due to the nestedness of the mutualistic networks where specific individuals connect to very few generalists species which on their side attach to many different specialist ones. The presence of bridge nodes allows a broader repartition of the mass $\beta$, for the core-periphery network. To further elucidate this assertion, in the SM, we have introduced a simple model of core-periphery network with a tunable fraction of bridge nodes, obtaining qualitatively identical results with the London Tube network [28]. Instead, in mutualistic networks, densely connected nodes surrounded, in
most cases, exclusively by leaf nodes, impede the accumulation of sufficient amounts of mass in disparate parts of the structure, discouraging the diversification of metacommunities configurations.

Summarising, the self-recruitment segregation process introduced in this Letter can induce the network to organise in metacommunities, separated by empty nodes. The stationary process reveals the role of the network degree heterogeneity in the emergence of vacant nodes as novel states whose fraction is quantised during the node filling process and exhibits multistable configurations. Such features are absent in other random processes such as random walks [21–23, 30–32] or Schelling’s segregation [16–18, 33–34]. From the ecological perspective, the outcomes of our model stress that rich patterns endowed with vacant niches can exist as a natural outcome of first principles such as mutualism and limited resources. In particular, the quantisation effect illustrates the robustness of the niche configurations to changes in the density of individuals. The emergence of multistable states demonstrates that niche segregation can be affected by the randomness of the process, in line with the paradigm of the fitness landscape [6]. On the other side, the high disassortativity of the nested trophic networks diminishes such multistability suggesting that mutualistic networks globally optimise their fitness in the niche occupation. The relevance of vacant niches can extend beyond the ecological perspective and help better understand how segregation in human dynamics that has energetically flourished in many post-industrialised societies can lead to the spontaneous creation of urban prairies [35].

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Appendix A: The stability analysis of the fixed points

We start by first emphasising that for the simple connected network made of $\Omega$ nodes the system of ODEs (3)

$$\dot{\rho}_i = \sum_{l=1}^{\Omega} L_{il} \rho_i \rho_l \left[ 1 - \rho_i - \frac{k_l}{k_i} (1 - \rho_i) \right], \forall i, \quad (A1)$$

of the main text generalises to:

$$\dot{\rho}_i = \sum_{l=1}^{\Omega} L_{il} \left[ \rho_l g(\rho_i) - \frac{k_l}{k_i} \rho_i g(\rho_l) \right] = \sum_{l=1}^{\Omega} A_{il} \left[ \frac{\rho_l g(\rho_i)}{k_l} - \frac{\rho_i g(\rho_l)}{k_i} \right], \forall i, \quad (A2)$$

where we have kept a general form for the function $g(\rho_i/N)$. We assume $g$ to be a $C^1$ concave function on the open interval $(0, 1)$ with $g(0) = 0 = g(1)$ and $g(x) > 0$ for all $x \in (0, 1)$. Consequently, the stationary density of node $i$ ($i = 1, \cdots, \Omega$) is either 0 or given by the unique non-zero solution (provided it exists) of the equation:

$$\frac{\rho_i^*}{C_\gamma k_i} = g(\rho_i^*), \quad (A3)$$

with the constant $C_\gamma$ such that $\sum_{i \in M_\gamma} \rho_i^* = \Omega_\gamma \beta_\gamma$ where the sum runs over the nodes belonging to the same community $M_\gamma$ as node $i$ and $\Omega_\gamma \beta_\gamma$ is the total mass in this community. Fig. 3 represents graphically the solution of Eq. (A3) with $\zeta = C_\gamma k$, for two distinct values of $k$. Theorem 1 establishes general results for the local stability of the fixed points.

![Graphical interpretation of the stationary densities solution](image)

**FIG. 3.** Geometrical interpretation of the stationary densities solution of Eq. (A3). We show the graph of a generic function $g(n_i/N)$. We assume $g$ to be a $C^1$ concave function on the open interval $(0, 1)$ with $g(0) = 0 = g(1)$ and $g(x) > 0$ for all $x \in (0, 1)$. Consequently, the stationary density of node $i$ ($i = 1, \cdots, \Omega$) is either 0 or given by the unique non-zero solution (provided it exists) of the equation:

**Theorem 1** Let $G$ be a simple connected and undirected network made of $\Omega$ nodes $v_1, v_2, \cdots, v_\Omega$ such that their corresponding degrees are sorted in increasing order, i.e. $k_1 \leq k_2 \leq \cdots \leq k_\Omega$. Consider the following dynamical system:

$$\dot{\rho}_i = \sum_{j=1}^{\Omega} L_{ij} \left[ \rho_j g(\rho_i) - \frac{k_j}{k_i} \rho_i g(\rho_j) \right], \quad (A4)$$

with initial conditions $\rho_i(0) = \rho_i^0$ and $\sum_{i=1}^{\Omega} \rho_i^0 = \beta \Omega$, for some $\beta \in (0, 1)$. Suppose that $g$ is a $C^1$ concave function on the open interval $(0, 1)$ with $g(0) = 0 = g(1)$ and $g(x) > 0 \forall x \in (0, 1)$. Assume moreover that all the non-empty nodes in the steady state form a single metacommunity. Then:
1. The following fixed point:

\[
\begin{dcases}
\rho_i^* = 0 & \forall i : k_i < \frac{1}{c g'(0)} \\
\rho_i^* > 0 & \forall i : k_i > \frac{1}{c g'(0)}
\end{dcases}
\]  

(A5)

with \( \rho_i^* > 0 \) the non-zero solution of \([A3]\) is a locally stable fixed point of the above dynamical system, with the constant \( c \) given by:

\[
c = \frac{\beta \Omega}{\sum_{j=1}^{\Omega} k_j g(\rho_j^*)},
\]

and it coincides with \( C_1 \) defined from \([A3]\).

2. Any fixed point with \( \rho_i^* = 0 \) for some \( k_i > \frac{1}{c g'(0)} \) is locally unstable.

The local stability analysis will be carried out by computing the jacobian matrix \( J \) associated to the previous system:

\[
J_{ij} = \frac{\partial}{\partial \rho_j}(\dot{\rho}_i) = \sum_{l=1}^{\Omega} \frac{A_{il}}{k_l} [\delta_{ij} g(\rho_i) + \rho_j g'(\rho_i) \delta_{ij}] - \sum_{l=1}^{\Omega} \frac{A_{il}}{k_l} [\delta_{ij} g(\rho_i) + \rho_i g'(\rho_i) \delta_{ij}]
\]

\[
= \frac{A_{ij}}{k_j} \left[ g(\rho_i) - \frac{\rho_j g'(\rho_i)}{k_i} \right] + \delta_{ij} \sum_{l}^{\Omega} \frac{A_{il}}{k_l} \left[ \frac{\rho_i g'(\rho_i)}{k_l} - g(\rho_i) \right].
\]

Let us remember that the nodes are ranked in increasing order of their degrees, i.e. \( k_1 \leq k_2 \leq k_\Omega \). Let \( s \in \{1, 2, \cdots, \Omega\} \) be such that:

\[
\begin{dcases}
 k_i c g'(0) < 1 & \text{for } i = 1, \cdots, s \\
 k_i c g'(0) > 1 & \text{for } i = s + 1, \cdots, \Omega.
\end{dcases}
\]

(A7)

Let us now evaluate the jacobian matrix at the fixed point given by Eq. \([A5]\). We will denote by \( M \) the jacobian matrix \( J \) evaluated at this fixed point. The fixed point will be locally stable if and only if all the eigenvalues of \( M \) are negative.

1. For \( i, j = 1, \cdots, s \), we have \( \rho_i^* = 0 \) and \( \rho_j^* = 0 \) and thus:

\[
M_{ij} = \delta_{ij} \sum_{l=s+1}^{\Omega} L_{il} \left[ \frac{\rho_i^* g'(0)}{k_l} - \frac{g(\rho_i^*)}{k_i} \right]
\]

\[
= \delta_{ij} \sum_{l=s+1}^{\Omega} \frac{A_{il}}{k_l} \left[ g'(0) - \frac{1}{c k_i} \right].
\]

(A8)

Since \( k_i c g'(0) < 1 \) for \( i = 1 \cdots, s \), we deduce that \( M_{ii} < 0 \) for \( i = 1, \cdots, s \). We also deduced that any fixed point with \( \rho_i^* = 0 \) and \( k_i c g'(0) > 1 \) will be unstable.

2. For \( i = 1, \cdots, s \) and \( j = s + 1, \cdots, \Omega \), we have \( M_{ij} = 0 \). Consequently \( M \) is a block matrix and it remains to investigate the stability of the submatrix \((M_{ij})_{ij}\) with \( i, j = s + 1 \cdots, \Omega \).

3. For \( i, j = s + 1, \cdots, \Omega \), we have:

\[
M_{ij} = \frac{A_{ij}}{k_i} \rho_i^* \left[ \frac{1}{c k_j} - g'(\rho_j^*) \right] + \delta_{ij} \sum_{l=s+1}^{\Omega} \frac{A_{il}}{k_l} \left[ g'(\rho_i^*) - \frac{1}{c k_i} \right].
\]

Let us observe that:

\[
\sum_{i=s+1}^{\Omega} M_{ij} = \sum_{i=s+1}^{\Omega} \frac{A_{ij}}{k_i} \rho_i^* \left[ \frac{1}{c k_j} - g'(\rho_j^*) \right] + \sum_{l=s+1}^{\Omega} \frac{A_{ij}}{k_l} \left[ g'(\rho_i^*) - \frac{1}{c k_j} \right] = 0,
\]

(A9)
since the network is undirected. Moreover, \( \sum_{i \neq j} M_{ij} = -M_{jj} \). Assuming \( g'(\rho_i^*) - \frac{1}{\kappa_i} < 0 \) \( \forall i = s + 1 \cdots, \Omega \), one can make use of the Gershgorin theorem to deduce the stability of the submatrix \( (M_{ij})_{ij=i=s+1}^{\Omega} \). Indeed, according to this theorem, the spectrum of this submatrix is contained in the set of disks

\[
\bigcup_{j=s+1}^{\Omega} D(M_{jj}, R_j)
\]

(A10)

centred in \( M_{jj} < 0 \) and with radius

\[
R_j = \sum_{i=s+1}^{\Omega} |M_{ij}| = -M_{jj}.
\]

(A11)

Consequently, we deduce that the spectrum of the submatrix \( (M_{ij})_{ij=i=s+1}^{\Omega} \) is contained in the left half plane, hence showing that all the eigenvalues of the matrix \( M \) have a negative real part.

**Appendix B: Detailed analysis of metacommunities emergence and features**

As emphasised in the main document, for a given degree sequence, the structure of the network along with the average nodes density \( \beta \), will determine whether empty nodes and metacommunities will emerge. In this appendix, we consider the dynamical process (3) evolving on top of several types of networks with \( g(x) = x(1-x) \):

\[
\dot{\rho}_i = \sum_{j=1}^{\Omega} L_{ij} \rho_i \rho_j \left[ 1 - \rho_i - \frac{k_j}{k_i} (1 - \rho_j) \right], \quad \forall i = 1, \cdots, \Omega.
\]

For sufficiently large values of the average density \( \beta \) and generic initial conditions without empty nodes, a single metacommunity will be in place, and there will be no asymptotically empty nodes, and the stationary nodes densities are given by

\[
\rho_i^* = 1 - \frac{1 - \beta}{k_i \langle 1/k \rangle},
\]

where \( \langle 1/k \rangle = \sum_{j=1}^{\Omega} \frac{1}{k_j} \). Empty nodes emerge as soon as there is at least a node of degree \( k_i \) such that \( k_i = \frac{1 - \beta}{\langle 1/k \rangle} \).

Hence, the first node(s) to become empty are the ones with the lowest degree \( k_{\min} \) and this happens when \( \beta = 1 - k_{\min} \langle 1/k \rangle \). As an example let us consider the network model of Fig. 1 in the main text that we here repose as Fig. 4 for which \( k_{\min} = 2 \). There are three nodes with degree 2 whose density could potentially vanish for some \( \beta \).

A simple computation returns \( \beta = 1 - \frac{24}{27} \sim 0.259 \).

**FIG. 4.** As the reaction-diffusion process takes place, the first node(s) to become empty is (are) the one(s) with the lowest degree, namely \( k_{\min} = 2 \), for the above graph.

In Fig. 5 we analyse the impact of the network modularity on the fraction of empty nodes \( f \). The red curve shows \( f \) vs. \( \beta \) for a disassortative modular network made of 20 densely connected subgraphs formed by a number of nodes comprised between 5 and 10, linked together through bridge nodes, i.e. nodes whose removal splits the network into disconnected subgraphs. Such networks can be obtained starting from a ring network and then replacing every two nodes by a densely connected subgraph. The corresponding adjacency matrix is shown in the inset on the lower left corner and confirms the modularity of the network (each pixel represents a connection between 2 nodes). As the average density \( \beta \) decreases, we observe that the mean fraction of empty nodes increases in a continuous way up to reaching a first plateau corresponding to the case where (almost all the) bridge nodes are empty and the network is
split into (almost) 20 metacommunities. For smaller values of $\beta$ the fraction of empty nodes increases again until it stabilises for low values of $\beta$, i.e. smaller than $\sim 10^{-2}$, when also nodes into the subgraphs are empty. The blue curve shows $f$ vs. $\beta$ for a network obtained using a rewiring degree preserving process on the former one. The new adjacency matrix is now represented in the inset on the upper right corner. Due to the rewiring procedure, the network now looks like a random network but the degree sequence is unchanged. The corresponding behaviour of $f$ vs. $\beta$ is now quite different and exhibits a step-like behaviour. In both cases, the results were averaged over 100 distinct network realisations. The min-max deviation in the resulting value of $f$ is represented by the dashed region.

![Image](image.png)

**FIG. 5.** Fraction of empty nodes $f$ vs. the average density $\beta$. The results were averaged over 100 distinct network realisations. The shaded area shows the multistability as measured by the min-max occupancy resulting from all the realisations.

To understand these different behaviours we analyse the number of metacommunities emerging in the modular network as well as in the rewired one (see Fig. 6). For a very large range of values of $\beta$ the rewired network exhibits one metacommunity (see the blue curve in Fig. 6), associated to a unique constant $C_1 \equiv C_1(\beta)$. Consequently, nodes densities are essentially constrained by their degree, as shown in Fig. 7 where we reported the stationary nodes densities $\rho^*_i$ vs. their degree (nodes densities were initialized randomly such that the average density satisfies $\beta = 0.15$). As a consequence, nodes with a degree larger than $C_1$ are filled while all the others become empty. Since the degree sequence is finite, this implies the observed jumps on the blue curve given in Fig. 5. On the other hand, for the diassortative modular network, the mass first distributes among the distinct modules (20 in this case) leaving the bridges nodes empty (see the red curve in Fig. 6). To each of these modules corresponds a constant $C_\gamma = (1 - \beta_\gamma)/(1/k_\Omega)$. Inside the $\gamma$-th module, all the nodes with a degree $k_i < C_\gamma$ will then become empty. As $C_\gamma$ is of order $C_1/l$, with $l$ the number of modules, nodes with smaller degree can also be filled, leading to a lower value of the fraction of empty nodes, except when $\beta$ is very large or very small (see Fig. 5). Moreover, as the constants $C_\gamma$ differ from each other, distinct stationary densities can be observed for nodes with the same degree (see Fig. 6). Since the way the mass distributes among the modules depends (in a highly non-trivial way) on the initial densities, averaging over sufficiently many configurations leads in fine to a smooth evolution of $f$ vs. $\beta$ (see the red curve in Fig. 5).
FIG. 6. Number $N$ of metacommunities vs. the fraction of empty nodes $f$. The shaded area shows the multistability as measured by the min-max deviation resulting from all the realisations.

FIG. 7. Stationary nodes densities $\rho_i^*$ as a function of their degree $k$, for the rewired version of the modular disassortative network used in Fig. 5. The initial conditions are given by $\rho_i(0) = 0.15$. Nodes densities were initialized randomly such that the average density satisfies $\beta = 0.15$.

FIG. 8. Stationary nodes densities $\rho_i^*$ as a function of their degree $k$, for the modular disassortative network used in Fig. 5. Nodes densities were initialized randomly such that the average density satisfies $\beta = 0.15$.

To highlight the impact of node bridgeness in the emergence of metacommunities, we show in Fig. 10 the results obtained using a small modular network with a varying fraction of bridge nodes of degree 2 between the modules and we computed the number of metacommunities $N$ vs. $\beta$. To construct such network, we first generate $m$ cliques of size $k$ ($k \geq 3$). We then connect the $i$-th clique to the $i+1$-th clique ($i = 1, \cdots, m-1$) by means of a path of length 1 or 2. The procedure is illustrated in Fig. 9 for $m = 4$ and $k = 4, 5$. As $\beta$ is reduced, the bridge nodes become empty, leaving the mass in the disconnected modules. The larger the number of bridge nodes, the larger the number of metacommunities.
FIG. 9. Modular network with cliques of size $k = 4, 5$ connected through paths of length 1 or 2. The removal of a (blue) node belonging to a path of length 2 breaks the connectivity of the network.

FIG. 10. Number of metacommunities $N$ as a function of the average node density $\beta$, for a modular network with a number $i$ of bridge nodes. The network was built using the procedure described in the text with 10 cliques of size $4 \leq k \leq 7$. For each value $i$, the data were averaged over 10 independent initial configurations.