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An analytical approach to spatio-temporal dynamics of neutral community models

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Abstract   We propose a spatial version of the neutral community model on a network of interconnected patches. The dynamical equations for the abundances and higher order moments of the abundances are established. Due to the neutrality assumption these equations are autonomous, enabling an exact analysis of spatio-temporal dynamics. We compute local (i.e., inside a patch) and global (i.e., between patches) diversities, and illustrate our results with two examples: (1) a non-spatial community, for which we recover previous results, and (2) a model with a finite number of patches which are all connected to each other with equal migration intensity. We discuss the relevance of this model for experiments in microbial ecology.

1 Introduction

In community ecology the assumption of species neutrality states that all individuals, even if they belong to different species, are described by identical ecological parameters, such as growth, death and migration rates (Hubbell 2001; Alonso et al. 2006).

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Under the neutrality assumption, the species an individual belongs to is nothing more than a label, which is passed from one generation to the next. The ecological processes an individual undergoes are not affected by its species label.

The neutrality assumption reduces significantly the complexity of community models. Under deterministic dynamics, the neutrality assumption leads to rather trivial models. Stochastic neutral community models, on the other hand, can yield more interesting dynamics. These models combine birth–death processes for the different species, with higher-level processes such as competition, migration and speciation. This leads to abundance dynamics of all species present in the community.

Stochastic neutral models have a long tradition in community ecology (Caswell 1976), and have gained much popularity due to the works of Bell (2000) and Hubbell (2001). In this paper, we focus on Hubbell's neutral model. It describes the species abundance dynamics of a local community in contact with a much larger regional community. When an individual in the local community dies, it is replaced by the offspring of another local individual, or by an immigrant of the regional community. The parameters quantifying this replacement process do not depend on the species of either the dying or replacing individual, which is species neutrality.

As such, Hubbell (2001)'s neutral community model has no explicit spatial structure, although such a structure is implied by the connection of the local community to the regional community. This spatially implicit version has been studied extensively. For instance, an exact formula is available for the stationary distribution of species abundances, which in some cases matches empirical data amazingly well (Vallade and Houchmandzadeh 2003; Volkov et al. 2003; Etienne 2005).

Spatially explicit versions of Hubbell's neutral model have been proposed by taking into account the spatial position of individuals (Bell 2000; Hubbell 2001; Chave and Leigh 2002; Houchmandzadeh and Vallade 2003; Zillio et al. 2005; Rosindell and Cornell 2007). These models have been used to determine species–area relationships and clustering properties of species in (one-, two- and three-dimensional) space. Alternatively, a few studies have considered models of interconnected patches, every patch carrying a local comunity, and have computed measures of intra- and inter-patch diversity (Economo and Keitt 2008; Munoz et al. 2008).

In a previous paper (Vanpeteghem et al. 2008), we have introduced an analytical approach to the dynamics of non-spatial neutral community models. In the present paper, we extend this dynamical analysis to spatial neutral models. Our model is inspired by the interconnected patch communities of Economo and Keitt (2008). Whereas they computed the average diversity in the stationary state, we construct and solve the dynamical equations for species abundance moments of higher order, and quantify the variance of intra- and inter-patch diversity predictions.

2 Model description

The spatial structure of our neutral community model is shown in Fig. 1. We consider a metacommunity, i.e., a set of interconnected local communities. Each local community is located on a patch, and individuals from the metacommunity can migrate from one patch to another. The metacommunity is coupled to a much larger, regional
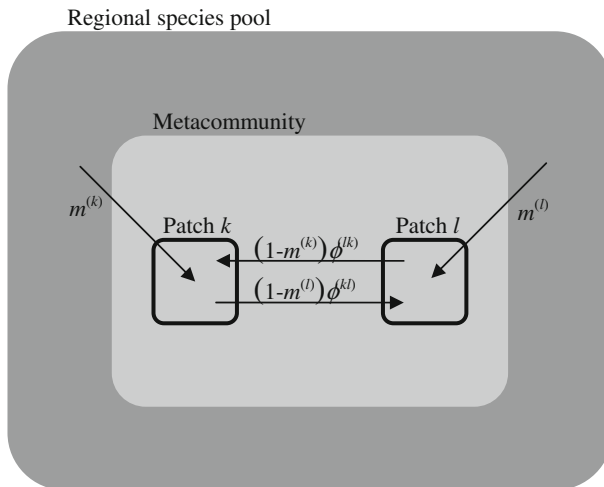
Fig. 1 The spatial model structure. The regional species pool has an effect on the metacommunity through immigration events [$m^{(k)}$ to patch k, and $m^{(l)}$ to patch l]. Patches in the metacommunity have an effect on other patches in the metacommunity through reproduction events [$(1 - m^{(k)})\phi^{(lk)}$ from patch l to patch k, and $(1 - m^{(l)})\phi^{(kl)}$ from patch k to patch l]

species pool. Individuals from the regional species pool can immigrate to the meta-community. Note that our use of the term "metacommunity" differs from Hubbell (2001) (in Hubbell's terminology the metacommunity denotes the regional species pool), but corresponds to common terminology in community ecology (Leibold et al. 2004).

2.1 Metacommunity composition

As in Hubbell (2001)'s neutral community model, we assume that on the timescale of the patchy metacommunity (which is the timescale we are interested in), the regional species pool does not evolve. Our metacommunity model is therefore parameterized by the composition of the regional species pool, whereas the composition of the meta-community as such is described by dynamical variables. We now introduce the model parameters and variables, summarized in Table 1, for the regional species pool and the metacommunity.

We assume that the regional species pool is so large that it can be described by relative abundances. The species pool consists of S species, each with a fixed (i.e., constant on the timescale of the metacommunity) abundance. We denote the relative abundance of species i in the regional species pool by p_i, for $i = 1, 2, \ldots, S$. We also introduce the relative abundance vector

$$\vec{p} = [p_1 \quad p_2 \quad \ldots \quad p_S],$$

whose components sum up to 1.

Table 1 Explanation of model variables and parameters. Bold-faced variables denote stochastic variables

Symbol	Explanation
Variables	
$N_i^{(k)}$	Absolute abundance of species i in patch k
$\vec{N}^{(k)}$	Vector of absolute species abundances in patch k
$\vec{N}_i$	Vector of absolute abundances of species i in metacommunity
$N_{uv}^{(ab)}, N_{uvw}^{(abc)}, \ldots$	Moments of absolute abundances, for patches a, b, … and species u, v, …, defined in (7)
$Z^{(kl)}$	Similarity index between local communities in patches k and l, defined in (10)
$Z^{(kk)}$	Simpson concentration index of local community in patch k
Z_{intra}	Intra-patch concentration index, i.e., concentration index averaged over patches, defined in (11)
Z_{inter}	Inter-patch concentration index, i.e., concentration index of metacommunity, defined in (12)
$C_\alpha^{(a)}, C_\alpha^{(ab)}, \ldots$	Summed moments of abundance (sum over one species index), for patches a, b, …, defined in (13)
$C_{\alpha;\beta}^{(a;c)}, C_{\alpha;\beta}^{(ab;c)}, \ldots$	Summed moments of abundance (sum over two species indices), for patches a, b, c, …, defined in (14)
Parameters	
S	Number of species in regional species pool
p_i	Relative abundance of species i in regional species pool
P	Number of patches in metacommunity
$J^{(k)}$	Size of local community in patch k
$\mu^{(k)}$	Total death rate in patch k
$m^{(k)}$	Relative intensity of individual migration from regional species pool to patch k of metacommunity
$\phi^{(kl)}$	Relative intensity of parent–offspring migration from patch k of metacommunity to patch l of metacommunity

The metacommunity consists of J individuals, and is divided into P patches. The local community in patch k consists of $J^{(k)}$ individuals. We introduce the vector

$$\vec{J} = \begin{bmatrix} J^{(1)} & J^{(2)} & \ldots & J^{(P)} \end{bmatrix},$$

whose components sum up to J. All community sizes, J for the metacommunity and $J^{(k)}$ for the local patch commnunities, are constant in time (the so-called zero-sum assumption of Hubbell 2001).

Each individual in the metacommunity belongs to one of the S species of the regional species pool. We denote the absolute abundance of species i in patch k by $N_i^{(k)}$. We define the abundance vectors

$$\vec{N}^{(k)} = \begin{bmatrix} N_1^{(k)} & N_2^{(k)} & \ldots & N_S^{(k)} \end{bmatrix},$$

whose components sum up to $J^{(k)}$;

$$\vec{N}_i = \begin{bmatrix} N_i^{(1)} & N_i^{(2)} & \cdots & N_i^{(P)} \end{bmatrix},$$

whose sum gives the total number of individuals of species i in the metacommunity;

$$\vec{N} = \begin{bmatrix} \vec{N}^{(1)} & \vec{N}^{(2)} & \cdots & \vec{N}^{(P)} \end{bmatrix},$$

whose components sum up to J.

2.2 Metacommunity dynamics

The metacommunity dynamics are triggered by death events. The site that was occupied by the dead individual, is immediately occupied by a new individual. This new individual is either an immigrant from the regional species pool, or the offspring of an individual in the metacommunity. We now describe the metacommunity dynamics in detail.

Consider patch k of the metacommunity. The total death rate in patch k is denoted by $\mu^{(k)}$. Thus, the probability that in the time interval $[t, t + \varepsilon]$ one of the $J^{(k)}$ individuals in patch k dies, is given by $\mu^{(k)}\varepsilon + o(\varepsilon)$ as $\varepsilon \to 0$. The per capita death rate in patch k is given by $\mu^{(k)}/J^{(k)}$.

A death event in patch k is compensated with probability $m^{(k)}$ by an immigration from the regional species pool, or with probability $1 - m^{(k)}$ by a reproduction in the metacommunity. In the latter case, the parent need not be located in patch k. To describe the spatial separation between parent and offspring, we introduce the probability that offspring in patch k has its parent in patch l, denoted by $\phi^{(lk)}$. The parameters $\phi^{(lk)}$ satisfy

$$\sum_{l=1}^{P} \phi^{(lk)} = 1. \tag{1}$$

Note that these dynamics define a double spatial structure (see Fig. 1). First, the regional species pool composition $\vec{p}$ has an effect on patch k in the metacommunity through immigration events, described by parameter $m^{(k)}$. Note that this spatial structure is also present in Hubbell (2001)'s model. Second, the metacommunity as such, e.g., the community composition $\vec{N}^{(l)}$ in patch l, has an effect on patch k of the metacommunity through reproduction events, described by the parameters $(1 - m^{(k)})\phi^{(lk)}$. This patchy structure is absent in Hubbell's model. The model of Munoz et al. (2008) considers perfectly isolated patches (i.e., $\phi^{(lk)} = 0$).

It is interesting to consider the limit of an extremely diverse regional species pool. To do so, we take the most even composition for a given number of species S,

$$\vec{p} = \begin{bmatrix} \frac{1}{S} & \frac{1}{S} & \cdots & \frac{1}{S} \end{bmatrix},$$

Fig. 2 An alternative model interpretation. When the regional species pool is highly diverse, any immigration event will bring a new species to the metacommunity. Hence, immigration can be considered as speciation
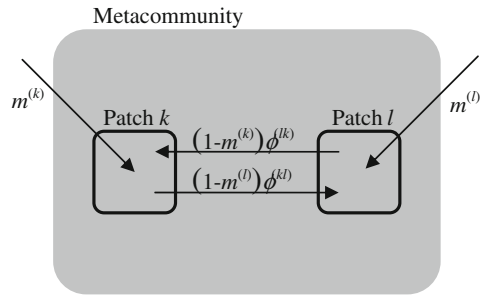
and take the limit for large amounts of species, $S \to \infty$. In that case, every immigration event from the regional species pool introduces a new species in the metacommunity. This can be interpreted as a speciation mechanism (Etienne et al. 2007). In that case, our model consists of P interconnected patches in which occasionally a new species appears. This metacommunity model with speciation, illustrated in Fig. 2, will be used in the examples of Sect. 5.

2.3 Markov process and transition rates

The model formulation leads to a continuous-time Markov process. Any event of this process consists in simultaneously decreasing by one the abundance of a species i in a patch k and increasing by one the abundance of a species j in the same patch k. The transition rate of such an event (we assume $i \neq j$) is given by

$$
R_{ij}^{(k)}\left(N_i^{(k)}; p_j, \vec{N}_j\right) = \mu^{(k)} \frac{N_i^{(k)}}{J^{(k)}} \left[m^{(k)} p_j + \left(1 - m^{(k)}\right) \right.
$$
$$
\left. \times \left(\phi^{(kk)} \frac{N_j^{(k)}}{J^{(k)} - 1} + \sum_{l,\, l \neq k} \phi^{(lk)} \frac{N_j^{(l)}}{J^{(l)}} \right) \right].
$$

or, including the case $i = j$,

$$
R_{ij}^{(k)}\left(N_i^{(k)}; p_j, \vec{N}_j\right) = \mu^{(k)} \frac{N_i^{(k)}}{J^{(k)}} \left[m^{(k)} p_j + \left(1 - m^{(k)}\right) \left(\sum_l \phi^{(lk)} \frac{N_j^{(l)} - \delta_{ij}\delta_{kl}}{J^{(l)} - \delta_{kl}} \right) \right].
$$

By summing over all possible events in patch k,

$$
\sum_{i,j} R_{ij}^{(k)}\left(N_i^{(k)}; p_j, \vec{N}_j\right) = \mu^{(k)}, \tag{2}
$$

we get the death rate $\mu^{(k)}$ in patch k, showing that the dynamics are triggered by death events. Note that some of these events do not have a net effect on the abundance vector $\vec{N}$, namely, when the species of the replacing individual is the same as that of the dead individual ($i = j$). Nevertheless, such events have a contribution in the sum (2).

As our model is stochastic, we need some notation to deal with randomness. Bold-faced symbols are used for random variables. For instance, the random variable corresponding to the abundance of species i in patch k is denoted by $\boldsymbol{N}_i^{(k)}$, and the vector containing the random abundances of the S species in the P patches by $\vec{\boldsymbol{N}}$. To simplify notation, we do not distinguish consistently a random variable from its realisation. For instance, we write the probability that $\vec{\boldsymbol{N}}$ takes the value $\vec{N}$ both as $\mathbb{P}(\vec{\boldsymbol{N}} = \vec{N})$ and as $\mathbb{P}(\vec{N})$. We denote expectations by $\mathbb{E}$ such as in the expression $\mathbb{E}\boldsymbol{N}_i^{(k)}$.

The transition rates $R_{ij}^{(k)}$ for species $i, j = 1, \ldots, S$ and patches $k = 1, \ldots, P$, define a matrix of transitions between states $\vec{N}$ of the Markov process. It is easy to verify that the number of states is finite, and that the transition matrix is irreducible. As a consequence, the Markov process has a unique stationary distribution (Van Kampen 1992). Any initial probability distribution $\mathbb{P}(\vec{N})$ will converge to the stationary distribution; these dynamics are described by the master equation (Van Kampen 1992),

$$
\frac{\mathrm{d}}{\mathrm{d}t}\mathbb{P}(\vec{N}) = \sum_{\substack{i,j,\,k \\ i \neq j}} R_{ij}^{(k)}\left(N_i^{(k)} + 1; p_j, \vec{N}_j - \vec{e}^{(k)}\right)\mathbb{P}\left(\vec{N} + \vec{e}_i^{(k)} - \vec{e}_j^{(k)}\right)
$$

$$
- \sum_{\substack{i,j,\,k \\ i \neq j}} R_{ij}^{(k)}\left(N_i^{(k)}; p_j, \vec{N}_j\right)\mathbb{P}(\vec{N}), \tag{3}
$$

where we used the SP-dimensional basis vectors $\vec{e}_i^{(k)}$ (all components 0 except component (k, i) which is 1) and the P-dimensional basis vectors $\vec{e}^{(k)}$ (all components 0 except component k which is 1).

3 Moment equations

The master equation (3) describes the spatio-temporal dynamics of our neutral community model. However, these equations cannot be solved directly due to the large number of dynamical variables. We perform two exact model reduction steps, reducing significantly the number of variables. In this section we derive moment equations from the master equation; in the next section, we derive diversity dynamics from the moment equations. It turns out that moments up to fourth order are required to compute mean and variance of diversity indices. Hence, we derive dynamical equations for the moments up to fourth order.

3.1 First model reduction

The master equation (3) is a set of linear differential equations in the variables $\mathbb{P}(\vec{N})$, and could in principle be solved by direct integration. However, this direct approach is not feasible, because the number of variable is too large. Indeed, there are as many variables as there are distributions of J individuals over S species and P patches. More precisely, if there are $J^{(k)}$ individuals in patch k, for $k = 1, 2, \ldots, P$, the number of variables $\mathbb{P}(\vec{N})$ is given by

$$\prod_{k=1}^{P} \binom{J^{(k)} + S - 1}{J^{(k)}}, \tag{4}$$

a product of binomial coefficients. E.g., for $S = 10$, $P = 10$ and $J^{(k)} = 100$ for all k, there are 3.5×10^{14} variables in the master equation (3). Obviously, any problem of such a huge dimension, even if it is linear, cannot be tackled directly.

We perform a first model reduction step, by considering the moments of the probability distribution $\mathbb{P}(\vec{N})$. Although the technique of moment equations is usually an approximation (Dieckmann et al. 2000), neutral community models are known to yield exact moment equations (Vallade and Houchmandzadeh 2003; Houchmandzadeh and Vallade 2003; Vanpeteghem et al. 2008). By restricting attention to lower-order moments (in our case, up to fourth order), a major reduction of the model complexity can be obtained.

3.2 Dynamics of generating function

We derive the moment equations using a generating function. To do so, we introduce auxiliary variables $z_i^{(k)}$ with $i = 1, \ldots, S$ and $k = 1, \ldots, P$, and group them together in the SP-dimensional vector $\vec{z}$. We define the generating function Φ of the SP variables $N_i^{(k)}$ by

$$\Phi(\vec{z}) = \mathbb{E}\left[\prod_{i,k} \left(z_i^{(k)}\right)^{N_i^{(k)}}\right] = \sum_{\vec{N}} \mathbb{P}(\vec{N}) \prod_{i,k} \left(z_i^{(k)}\right)^{N_i^{(k)}}. \tag{5}$$

The generating function Φ is of particular interest to us, because it satisfies a simple dynamical equation. As shown in Appendix A, the following equation can be obtained from the master equation (3):

$$\frac{d}{dt}\Phi(\vec{z}) = \sum_{\substack{i,j,k \\ i \neq j}} \left[\mu^{(k)} m^{(k)} p_j \frac{\left(z_j^{(k)} - z_i^{(k)}\right)}{J^{(k)}} \frac{\partial \Phi(\vec{z})}{\partial z_i^{(k)}} \right.$$
$$\left. + \mu^{(k)} \left(1 - m^{(k)}\right) \sum_l \phi^{(lk)} \frac{z_j^{(l)} \left(z_j^{(k)} - z_i^{(k)}\right)}{J^{(k)}(J^{(l)} - \delta_{kl})} \frac{\partial^2 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)}} \right]. \tag{6}$$

3.3 From generating function to moments

Partial derivates of the generating function Φ with respect to $z_i^{(k)}$ yield the moments of the abundances $N_i^{(k)}$. For instance, assuming $(a, u) \neq (b, v)$,

$$\frac{\partial^3 \Phi}{(\partial z_u^{(a)})^2 \partial z_v^{(b)}}\bigg|_E = \mathbb{E}\left[N_u^{(a)}(N_u^{(a)} - 1)N_v^{(b)}\right],$$

where evaluation in E stands for $z_i^{(k)} = 1$ for all i and k. As these moments play a crucial role in our computations, we introduce a separate notation:

$$N_{uv}^{(ab)} = N_u^{(a)}\left(N_v^{(b)} - \delta_{uv}^{(ab)}\right) \tag{7a}$$

$$N_{uvw}^{(abc)} = N_u^{(a)}\left(N_v^{(b)} - \delta_{uv}^{(ab)}\right)\left(N_w^{(c)} - \delta_{uw}^{(ac)} - \delta_{vw}^{(bc)}\right) \tag{7b}$$

$$N_{uvwx}^{(abcd)} = N_u^{(a)}\left(N_v^{(b)} - \delta_{uv}^{(ab)}\right)\left(N_w^{(c)} - \delta_{uw}^{(ac)} - \delta_{vw}^{(bc)}\right)\left(N_x^{(d)} - \delta_{ux}^{(ad)} - \delta_{vx}^{(bd)} - \delta_{wx}^{(cd)}\right), \tag{7c}$$

where $\delta_{uv}^{(ab)}$ stands for $\delta_{ab}\delta_{uv}$.

Note that the moments (7) count the number of ways of selecting individuals without replacement from the metacommunity for a given order of species (subscripts) and patches (superscripts). For instance, assuming $(a, u) \neq (b, v)$, the moment $N_{uuv}^{(aab)}$ equals the number of samples of three individuals, in which the first and second individual belong to species u and patch a, and the third individual belongs to species v and patch b.

Note also that the moments (7) are invariant for any permutation applied to both species (subscripts) and patches (superscripts). E.g., for the third-order moments,

$$N_{uvw}^{(abc)} = N_{vuw}^{(bac)} = N_{uwv}^{(acb)} = N_{vwu}^{(bca)} = N_{wuv}^{(cab)} = N_{wvu}^{(cba)}.$$

Using the moments (7), the derivatives of the generating function Φ are

$$\frac{\partial \Phi}{\partial z_u^{(a)}}\bigg|_E = \mathbb{E}N_u^{(a)}$$

$$\frac{\partial^2 \Phi}{\partial z_u^{(a)} \partial z_v^{(b)}}\bigg|_E = \mathbb{E}N_{uv}^{(ab)}$$

$$\frac{\partial^3 \Phi}{\partial z_u^{(a)} \partial z_v^{(b)} \partial z_w^{(c)}}\bigg|_E = \mathbb{E}N_{uvw}^{(abc)}$$

$$\frac{\partial^4 \Phi}{\partial z_u^{(a)} \partial z_v^{(b)} \partial z_w^{(c)} \partial z_x^{(d)}}\bigg|_E = \mathbb{E}N_{uvwx}^{(abcd)}.$$

3.4 Dynamics of moments

By taking partial derivatives of the dynamical equation (6) with respect to $z_i^{(k)}$, we get dynamical equations for the moments. Such a computation (the details are given in Appendix B) leads to the following results:

- For the first-order moments,

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}N_u^{(a)} = T_u^{(a)}, \tag{8a}$$

with

$$T_u^{(a)} = \frac{\mu^{(a)}}{J^{(a)}}\left[m^{(a)}\left(-\mathbb{E}N_u^{(a)} + p_u J^{(a)}\right)\right.$$

$$\left. + (1 - m^{(a)})\sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}}\left(-J^{(l)}\mathbb{E}N_u^{(a)} + J^{(a)}\mathbb{E}N_u^{(l)}\right)\right].$$

- For the second-order moments,

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}N_{uv}^{(ab)} = T_{u;v}^{(a;b)} + T_{v;u}^{(b;a)}, \tag{8b}$$

with

$$T_{u;v}^{(a;b)} = \frac{\mu^{(a)}}{J^{(a)}}\left[m^{(a)}\left(-\mathbb{E}N_{uv}^{(ab)} + p_u(J^{(a)} - \delta_{ab})\mathbb{E}N_v^{(b)}\right)\right.$$

$$+ (1 - m^{(a)})\sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}}\left(-J^{(l)}\mathbb{E}N_{uv}^{(ab)}\right.$$

$$\left.\left. + \left(J^{(a)} - \delta_{ab}\right)\left(\mathbb{E}N_{uv}^{(lb)} + \delta_{uv}^{(lb)}\mathbb{E}N_v^{(b)}\right)\right)\right]$$

- For the third-order moments,

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}N_{uvw}^{(abc)} = T_{u;vw}^{(a;bc)} + T_{v;uw}^{(b;ac)} + T_{w;uv}^{(c;ab)}, \tag{8c}$$

with

$$T_{u;vw}^{(a;bc)} = \frac{\mu^{(a)}}{J^{(a)}}\left[m^{(a)}\left(-\mathbb{E}N_{uvw}^{(abc)} + p_u(J^{(a)} - \delta_{ab} - \delta_{ac})\mathbb{E}N_{vw}^{(bc)}\right)\right.$$

$$+ (1 - m^{(a)})\sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}}\left(-J^{(l)}\mathbb{E}N_{uvw}^{(abc)}\right.$$

$$\left.\left. + \left(J^{(a)} - \delta_{ab} - \delta_{ac}\right)\left(\mathbb{E}N_{uvw}^{(lbc)} + (\delta_{uv}^{(lb)} + \delta_{uw}^{(lc)})\mathbb{E}N_{vw}^{(bc)}\right)\right)\right]$$

Note that $T^{(a;bc)}_{u;vw}$ is invariant for a simultaneous permutation of patch indices b, c and species indices v, w:

$$T^{(a;bc)}_{u;vw} = T^{(a;cb)}_{u;wv}$$

- For the fourth-order moments,

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}N^{(abcd)}_{uvwx} = T^{(a;bcd)}_{u;vwx} + T^{(b;acd)}_{v;uwx} + T^{(c;abd)}_{w;uvx} + T^{(d;abc)}_{x;uvw}, \qquad (8d)$$

with $T^{(a;bcd)}_{u;vwx}$ given by

$$
\begin{aligned}
T^{(a;bcd)}_{u;vwx} = \frac{\mu^{(a)}}{J^{(a)}} \Bigg[& m^{(a)} \left(-\mathbb{E}N^{(abcd)}_{uvwx} + p_u (J^{(a)} - \delta_{ab} - \delta_{ac} - \delta_{ad})\mathbb{E}N^{(bcd)}_{vwx} \right) \\
& + (1 - m^{(a)}) \sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}} \left(-J^{(l)}\mathbb{E}N^{(abcd)}_{uvwx} \right. \\
& + \left(J^{(a)} - \delta_{ab} - \delta_{ac} - \delta_{ad} \right) \\
& \left. \times \left(\mathbb{E}N^{(lbcd)}_{uvwx} + \left(\delta^{(lb)}_{uv} + \delta^{(lc)}_{uw} + \delta^{(ld)}_{ux} \right) \mathbb{E}N^{(bcd)}_{vwx} \right) \right) \Bigg]
\end{aligned}
$$

Again, $T^{(a;bcd)}_{u;vwx}$ is invariant for a simultaneous permutation of patch indices b, c, d and species indices v, w, x:

$$T^{(a;bcd)}_{u;vwx} = T^{(a;cbd)}_{u;wvx} = T^{(a;bdc)}_{u;vxw} = T^{(a;cdb)}_{u;wxv} = T^{(a;dbc)}_{u;xvw} = T^{(a;dcb)}_{u;xwv}.$$

Note that, e.g., the dynamical equation (8c) for the third-order moments is only determined by moments of order three and lower. Hence, these dynamics could be solved exactly without additional equations or assumptions. This is remarkable, because moment equations typically require higher-order moments (Dieckmann et al. 2000). The species neutrality assumption guarantees that the moment equations close.

Note also that the lower-order moment equations (8) strongly suggest the equations for moments of order higher than four. However, as we will see in the next section, we will only need the moment equations up to fourth order to derive mean and variance of diversity indices.

4 Diversity dynamics

The computations of the previous section have led to the set of exact moment equations (8). We argue that an additional model reduction step is needed, to further reduce the number of variables. To do so, we consider indices for the similarity between local patch communities. We write their dynamics in terms of a limited number of auxiliary variables.

4.1 Second model reduction

The moment equations (8) are linear differential equations in the moment variables $\mathbb{E}N_u^{(a)}$, $\mathbb{E}N_{uv}^{(ab)}$, $\mathbb{E}N_{uvw}^{(abc)}$ and $\mathbb{E}N_{uvwx}^{(abcd)}$. For a local community consisting of S species and P patches, the number of moment variables of order α is given by

$$\binom{\alpha + SP - 1}{\alpha}. \tag{9}$$

The dynamics of the moments of order α are determined by the moments of order α and lower. Hence, the moments of order α satisfy a system of linear differential equations of dimension $\mathcal{O}(S^\alpha P^\alpha)$. E.g., for $S = 10$ and $P = 10$, the dynamical system for the moments of order 1, 2, 3 and 4 is of dimension 100, 5.1×10^3, 1.7×10^5 and 4.4×10^6, respectively.

Although this is a considerable model reduction compared to the full master equation (compare 4.6×10^6 variables for the four moment equations, with 3.5×10^{14} variables for the master equation), the number of variables is still too large to be of practical use. We perform a second model reduction step, by considering similarity and diversity indices in the metacommunity.

4.2 Similarity and diversity indices

Standard quantities available from ecological studies are the diversity of a community at a certain location, or the similarity between communities at different locations (Legendre and Legendre 1998). We use the spatial neutral community model to generate predictions for these quantities. We introduce the similarity index $Z^{(kl)}$,

$$\mathbf{Z}^{(kl)} = \frac{1}{J^{(k)} J^{(l)}} \sum_{i=1}^{S} N_i^{(k)} N_i^{(l)}, \tag{10}$$

that can be interpreted as the probability that an individual drawn randomly from the community in patch k and an individual drawn randomly from the community in patch l belong to the same species. The larger $\mathbf{Z}^{(kl)}$, the more similar the communities in patch k and l.

Interestingly, the similarity index $\mathbf{Z}^{(kl)}$ can be used to measure the diversity of different communities. For instance, the index $\mathbf{Z}^{(kk)}$ equals the Simpson concentration index (Simpson 1949) of the community present in patch k. The smaller $\mathbf{Z}^{(kk)}$, the more diverse the community in patch k. Hence, a Simpson diversity index can be defined by applying a decreasing transformation to the Simpson concentration index. Common choices are $1 - \mathbf{Z}^{(kk)}$, $1/\mathbf{Z}^{(kk)}$ or $-\ln \mathbf{Z}^{(kk)}$.

We define the intra-patch concentration index as the patch concentration index averaged over all patches, i.e., over the entire metacommunity,

$$\mathbf{Z}_{\text{intra}} = \frac{1}{P} \sum_{k=1}^{P} \mathbf{Z}^{(kk)} = \frac{1}{P} \sum_{k=1}^{P} \frac{1}{J^2} \sum_{i=1}^{S} \mathbf{N}_i^{(k)} \mathbf{N}_i^{(k)}, \tag{11}$$

and the inter-patch concentration index as the concentration index of the metacommunity

$$\mathbf{Z}_{\text{inter}} = \frac{1}{P^2} \sum_{k,l=1}^{P} \mathbf{Z}^{(kl)} = \frac{1}{(PJ)^2} \sum_{i=1}^{S} \left(\sum_{k=1}^{P} \mathbf{N}_i^{(k)} \right) \left(\sum_{l=1}^{P} \mathbf{N}_i^{(l)} \right). \tag{12}$$

The intra-patch concentration index $\mathbf{Z}_{\text{intra}}$ is always larger or equal to the inter-patch concentration index $\mathbf{Z}_{\text{inter}}$. Hence, the intra-patch diversity is always smaller than the inter-patch diversity. There is thus extra diversity due to the spatial structure of the metacommunity.

4.3 Diversity dynamics

We compute the dynamics of mean and variance of $\mathbf{Z}^{(kl)}$, which we will use to study mean and variance of $\mathbf{Z}_{\text{intra}}$ and $\mathbf{Z}_{\text{inter}}$. First, we introduce notation for moments summed over one species index:

$$C_\alpha^{(\cdot)} = \sum_i p_i^\alpha \tag{13a}$$

$$C_\alpha^{(a)} = \sum_i p_i^\alpha \mathbb{E} \mathbf{N}_i^{(a)} \tag{13b}$$

$$C_\alpha^{(ab)} = \sum_i p_i^\alpha \mathbb{E} \mathbf{N}_{ii}^{(ab)} \tag{13c}$$

$$C_\alpha^{(abc)} = \sum_i p_i^\alpha \mathbb{E} \mathbf{N}_{iii}^{(abc)} \tag{13d}$$

$$C_\alpha^{(abcd)} = \sum_i p_i^\alpha \mathbb{E} \mathbf{N}_{iiii}^{(abcd)} \tag{13e}$$

Note that these quantities are invariant for permutations of patch indices a, b, c, d. It is also easily verified that $C_0^{(a)} = J^{(a)}$. Next, we introduce notation for moments summed over two species indices:

$$C_{\alpha;\beta}^{(a;\cdot)} = \sum_{\substack{i,j \\ i \neq j}} p_i^\alpha p_j^\beta \mathbb{E} \mathbf{N}_i^{(a)} \tag{14a}$$

$$C_{\alpha;\beta}^{(a;c)} = \sum_{\substack{i,j \\ i \neq j}} p_i^\alpha p_j^\beta \mathbb{E} \mathbf{N}_{ij}^{(ac)} \tag{14b}$$

$$C_{\alpha;\beta}^{(ab;c)} = \sum_{\substack{i,j \\ i \neq j}} p_i^\alpha p_j^\beta \mathbb{E}N_{i\,ij}^{(abc)} \tag{14c}$$

$$C_{\alpha;\beta}^{(ab;cd)} = \sum_{\substack{i,j \\ i \neq j}} p_i^\alpha p_j^\beta \mathbb{E}N_{i\,ijj}^{(abcd)} \tag{14d}$$

The latter quantities are invariant for interchanging indices a and b, interchanging c and d, and interchanging (a, b, α) and (c, d, β). We have the following identities:

$$C_{\alpha;\beta}^{(a;\cdot)} = C_\alpha^{(a)} C_\beta^{(\cdot)} - C_{\alpha+\beta}^{(a)}$$
$$C_{\alpha;\beta}^{(ab;\cdot)} = C_\alpha^{(ab)} C_\beta^{(\cdot)} - C_{\alpha+\beta}^{(ab)}$$
$$C_{\alpha;0}^{(a;c)} = (J^{(c)} - \delta_{ac})C_\alpha^{(a)} - C_\alpha^{(ac)}$$
$$C_{\alpha;0}^{(ab;c)} = (J^{(c)} - \delta_{ac} - \delta_{bc})C_\alpha^{(ab)} - C_\alpha^{(abc)}$$

Mean and variance of $\mathbf{Z}^{(kl)}$ can be expressed using the C-quantities:

$$\mathbb{E}\mathbf{Z}^{(kl)} = \frac{1}{J^{(k)} J^{(l)}} C_0^{(kl)}$$
$$\mathbb{E}\left[\left(\mathbf{Z}^{(kl)}\right)^2\right] = \frac{1}{(J^{(k)} J^{(l)})^2} \left(C_{0;0}^{(kl;kl)} + C_0^{(kkll)} + C_0^{(kkl)} + C_0^{(kll)} + C_0^{(kl)}\right)$$
$$\operatorname{Var} \mathbf{Z}^{(kl)} = \mathbb{E}\left[\left(\mathbf{Z}^{(kl)}\right)^2\right] - \left(\mathbb{E}\mathbf{Z}^{(kl)}\right)^2$$

for $k \neq l$, and

$$\mathbb{E}\mathbf{Z}^{(kk)} = \frac{1}{(J^{(k)})^2} \left(C_0^{(kk)} + J^{(k)}\right)$$
$$\mathbb{E}\left[\left(\mathbf{Z}^{(kk)}\right)^2\right] = \frac{1}{(J^{(k)})^4} \left(C_{0;0}^{(kk;kk)} + C_0^{(kkkk)} + 4C_0^{(kkk)} + 2(J^{(k)} + 1)C_0^{(kk)} + (J^{(k)})^2\right)$$
$$\operatorname{Var} \mathbf{Z}^{(kk)} = \mathbb{E}\left[\left(\mathbf{Z}^{(kk)}\right)^2\right] - \left(\mathbb{E}\mathbf{Z}^{(kk)}\right)^2$$

As a consequence, it suffices to compute the dynamics of the C-quantities to get the dynamics of $\mathbb{E}\mathbf{Z}^{(kl)}$ and $\operatorname{Var} \mathbf{Z}^{(kl)}$. These dynamics follow from the moment equations (8), as discussed in Appendix C.

Table 2 lists the C-quantities we have to consider to compute mean and variance of the similarity $\mathbf{Z}^{(kl)}$. If the metacommunity consists of P patches, then mean $\mathbb{E}\mathbf{Z}^{(kl)}$ and variance $\operatorname{Var} \mathbf{Z}^{(kl)}$ satisfy a system of linear differential equations of dimension $\mathcal{O}(P^2)$ and $\mathcal{O}(P^4)$, respectively. E.g., for $P = 10$, the dynamical system for $\mathbb{E}\mathbf{Z}^{(kl)}$ has dimension 65, and the dynamical system for $\operatorname{Var} \mathbf{Z}^{(kl)}$ has dimension 2,990. The same number of variables is required to compute mean and variance of the intra- and inter-patch concentration indices $\mathbf{Z}_{\text{intra}}$ and $\mathbf{Z}_{\text{inter}}$.

Table 2 C-quantities determining the dynamics of $\mathbb{E}\mathbf{Z}^{(kl)}$ and Var $\mathbf{Z}^{(kl)}$

	C-quantity	Number of variables without symmetry	Number of variables with full symmetry
$\mathbb{E}\mathbf{Z}^{(kl)}$	$C_0^{(ab)}$	$\frac{P(P+1)}{2}$	2
	$C_1^{(a)}$	P	1
Var $\mathbf{Z}^{(kl)}$	$C_0^{(abc)}$	$\frac{P(P+1)(P+2)}{6}$	3
	$C_1^{(ab)}$	$\frac{P(P+1)}{2}$	2
	$C_2^{(a)}$	P	1
	$C_0^{(abcd)}$	$\frac{P(P+1)(P+2)(P+3)}{24}$	5
	$C_1^{(abc)}$	$\frac{P(P+1)(P+2)}{6}$	3
	$C_2^{(ab)}$	$\frac{P(P+1)}{2}$	2
	$C_3^{(a)}$	P	1
	$C_{0;0}^{(ab;cd)}$	$\frac{P(P+1)(P(P+1)+2)}{8}$	7
	$C_{1;0}^{(a;bc)}$	$\frac{P^2(P+1)}{2}$	4
	$C_{1;1}^{(a;b)}$	$\frac{P(P+1)}{2}$	2

There are two types of C-quantities for $\mathbb{E}\mathbf{Z}^{(kl)}$, and ten types of C-quantities for Var $\mathbf{Z}^{(kl)}$. The third column gives the number of variables for a network of patches without any symmetry. The fourth column gives the number of variables for a network of patches with maximal symmetry. An example of the latter is discussed in Sect. 5.2

5 Examples

We apply the results obtained above to two special cases. In Sect. 5.1, we show that for a metacommunity consisting of a single patch ($P = 1$) our equations lead to previously published results. In Sect. 5.2, we consider a metacommunity in which all pairs of patches have the same coupling ($\phi^{(kl)}$ constant for $k \neq l$). This symmetry allows us to further reduce the model complexity, and derive manageable dynamical equations for mean and variance of the intra- and inter-patch concentration indices $\mathbf{Z}_{\text{intra}}$ and $\mathbf{Z}_{\text{inter}}$.

For the examples we consider, the resulting dynamical equations are given by a set of linear differential equations, which can be represented in matrix from,

$$\frac{\mathrm{d}\vec{x}}{\mathrm{d}t} = A\vec{x} + \vec{b}. \tag{15}$$

The solution of the dynamical system (15) reads

$$\vec{x}(t) = \mathrm{e}^{tA}\left(\vec{x}(0) + A^{-1}\vec{b}\right) - A^{-1}\vec{b}, \tag{16}$$

where e^{tA} denotes the matrix exponential of the square matrix tA. As can be verified for the examples, all eigenvalues of the matrix A have strictly negative real part, so that the dynamical system is exponentially stable. The equilibrium of the deterministic system (15) characterizes the stationary distribution of the stochastic system, and is given by

$$\lim_{t \to \infty} \vec{x}(t) = -A^{-1}\vec{b}. \tag{17}$$

For the different examples, we derive expressions for the vectors $\vec{x}$ and $\vec{b}$ and the matrix A appearing in (15). We can then obtain the dynamical behaviour by evaluating (16), and the stationary behaviour by evaluating (17).

5.1 One patch

We consider a metacommunity that consists of a single patch, i.e., $P = 1$. This setup corresponds to Hubbell's local community model.

In that case, each C-quantity of Table 2 corresponds to a single variable, and we obtain a 12-dimensional system of linear differential equations. This dynamical system can be represented in matrix form (15), with $\vec{x}$ and $\vec{b}$ 12-dimensional vectors,

$$
\vec{x} =
\begin{bmatrix}
C_0^{(1111)} \\
C_{0;0}^{(11;11)} \\
C_0^{(111)} \\
C_1^{(111)} \\
C_{1;0}^{(1;11)} \\
C_0^{(11)} \\
C_1^{(11)} \\
C_2^{(11)} \\
C_{1;1}^{(1;1)} \\
C_1^{(1)} \\
C_2^{(1)} \\
C_3^{(1)}
\end{bmatrix}
\quad \text{and} \quad
\vec{b} =
\begin{bmatrix}
0 \\
0 \\
0 \\
0 \\
0 \\
2\mu(1-m) \\
0 \\
0 \\
0 \\
\mu m C_2^{(\cdot)} \\
\mu m C_3^{(\cdot)} \\
\mu m C_4^{(\cdot)}
\end{bmatrix},
\tag{18a}
$$

and A a 12-dimensional matrix,

$$
A =
\begin{bmatrix}
4a_3 & 0 & 12c_3 & 4b_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 4a_3 & -4c_3 & 0 & 4b_3 & 4(J-2)c_3 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 3a_2 & 0 & 0 & 6c_2 & 3b_2 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 3a_2 & 0 & 0 & 6c_2 & 3b_2 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 3a_2 & C_2^{(\cdot)}b_2 & -2c_2 & -b_2 & 2b_2 & 2(J-1)c_2 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 2a_1 & 0 & 0 & 0 & 2b_1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 2a_1 & 0 & 0 & 2c_1 & 2b_1 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 2a_1 & 0 & 0 & 2c_1 & 2b_1 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2a_1 & 2C_2^{(\cdot)}b_1 & 0 & -2b_1 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & a_0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & a_0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & a_0
\end{bmatrix},
\tag{18b}
$$

with

$$a_\alpha = -\frac{\mu m}{J} - \alpha \frac{\mu(1-m)}{J(J-1)}$$

$$b_\alpha = \mu m \frac{J-\alpha}{J}$$

$$c_\alpha = \mu(1-m)\frac{J-\alpha}{J(J-1)}.$$

The equations are equivalent to those given in Vanpeteghem et al. (2008). But the equations here take into account a number of dependences between the dynamical variables, that were not taken into account by Vanpeteghem et al. (2008). Therefore, the resulting dynamical system is of dimension 12 instead of dimension 21 as the one presented in Vanpeteghem et al. (2008).

The 12-dimensional dynamical system can be simplified further by considering an extremely diverse regional community (see Fig. 2). The species pool is assumed to be infinitely large ($S \to \infty$), and all species in the pool are assumed to have equal abundance ($p_i = \frac{1}{S}$). This type of immigration process can be considered as a simple model for speciation, as used in the Hubbell's regional community model.

The latter assumption eliminates the dynamical variables that depend on the regional community abundances p_i. E.g., for the variable $C_\alpha^{(ab)}$,

$$C_\alpha^{(ab)} = \lim_{S\to\infty} \sum_{i=1}^{S} \left(\frac{1}{S}\right)^\alpha N_{ii}^{(ab)}$$

$$\leq J^{(a)} \lim_{S\to\infty} \left(\frac{1}{S}\right)^\alpha \sum_{i=1}^{S} N_i^{(b)}$$

$$= J^{(a)} J^{(b)} \lim_{S\to\infty} \left(\frac{1}{S}\right)^\alpha = 0, \quad \text{for } \alpha > 0.$$

This result is consistent with the dynamical equations (18b): the solution for the eliminated C-quantities (e.g., $C_\alpha^{(ab)}$ with $\alpha > 0$) is identically zero (the corresponding components in the vector $\vec{b}$ vanish).

The simplified dynamical system can be represented in matrix form (15), with $\vec{x}$ and $\vec{b}$ four-dimensional vectors,

$$\vec{x} = \begin{bmatrix} C_0^{(1111)} \\ C_{0;0}^{(11;11)} \\ C_0^{(111)} \\ C_0^{(11)} \end{bmatrix} \quad \text{and} \quad \vec{b} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 2\mu(1-m) \end{bmatrix}, \tag{19a}$$

and A a four-dimensional matrix,

$$
A = \begin{bmatrix} 4a_3 & 0 & 12c_3 & 0 \\ 0 & 4a_3 & -4c_3 & 4(J-2)c_3 \\ 0 & 0 & 3a_2 & 6c_2 \\ 0 & 0 & 0 & 2a_1 \end{bmatrix}. \tag{19b}
$$

5.2 Symmetric patches

We consider a metacommunity of P patches (P can be arbitrarily large) with the following assumptions:

- We assume that all patches have the same local community size $J^{(k)}$, the same death rate $\mu^{(k)}$ and the same immigration probability $m^{(k)}$.
- We assume that the parent–offspring probabilities $\phi^{(kl)}$ are

$$
\phi^{(kl)} = \begin{cases} \gamma & \text{for } k \neq l, \\ 1-(P-1)\gamma & \text{for } k = l. \end{cases}
$$

  All pairs of patch communities in the metacommunity interact with the same strength. Note that condition (1) is satisfied.
- We assume that the regional species pool is extremely diverse, so that immigration can be interpreted as speciation (see Fig. 2). As shown in the previous example, this eliminates the dynamical variables that depend on the species pool composition.

For the dynamical simulations, we take initial conditions exhibiting patch symmetry, i.e., invariance under patch permutations. Note that even if the initial condition is not patch symmetric, the abundance distribution will tend to the patch-symmetric stationary state (because the stationary state is unique). Clearly, patch symmetry limits drastically the number of dynamical variables. There are 17 variables, independently of the number of patches P (for $P \geq 4$), see Table 3.

Table 3 C-quantities for metacommunity model with symmetric coupling between patches

	C-quantity	Number	Representation
$\mathbb{E}Z^{(kl)}$	$C_0^{(ab)}$	2	$C_0^{(11)}, C_0^{(12)}$
Var $Z^{(kl)}$	$C_0^{(abc)}$	3	$C_0^{(111)}, C_0^{(112)}, C_0^{(123)}$
	$C_0^{(abcd)}$	5	$C_0^{(1111)}, C_0^{(1112)}, C_0^{(1122)}, C_0^{(1123)}, C_0^{(1234)}$
	$C_{0;0}^{(ab;cd)}$	7	$C_{0;0}^{(11;11)}, C_{0;0}^{(11;12)}, C_{0;0}^{(11;22)}, C_{0;0}^{(12;12)},$ $C_{0;0}^{(11;23)}, C_{0;0}^{(12;13)}, C_{0;0}^{(12;34)}$
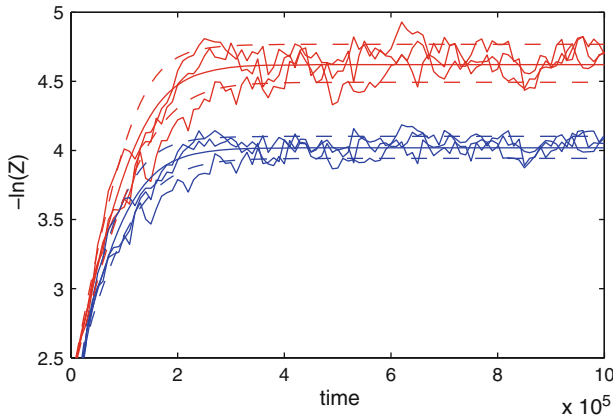
Fig. 3 Comparison between simulations and analytical results for the metacommunity model with symmetric coupling. We simulated three trajectories of the metacommunity, and computed the intra-patch (in *blue*) and inter-patch (in *red*) concentration indices as a function of time. Also, we evaluated (numerically) the analytical solution (16) with (20) to compute mean (in *full line*) and variance (mean $\pm$ standard deviation in *dashed line*) of intra- and inter-patch concentration indices. On the horizontal axis, the time scale corresponds to the mean number of death events in a patch. On the vertical axis, we applied a transformation $x \mapsto -\ln x$ to the concentration indices, to obtain diversity measures. Parameters are $P = 10$, $J^{(k)} = 1,000$ for all k, $\mu^{(k)} = 1$ for all k, $m^{(k)} = 0.01$ for all k, and $\gamma = 0.01$. The initial condition is deterministic, with each patch occupied by only one species, and this species differs from patch to patch

The dynamics of the C-quantities can be represented in matrix form (15), with four interacting subsystems,

$$\vec{x} = \begin{bmatrix} \vec{x}_1 \\ \vec{x}_2 \\ \vec{x}_3 \\ \vec{x}_4 \end{bmatrix} \qquad A = \begin{bmatrix} A_{11} & 0 & A_{13} & A_{14} \\ 0 & A_{22} & A_{23} & 0 \\ 0 & 0 & A_{33} & A_{34} \\ 0 & 0 & 0 & A_{44} \end{bmatrix} \qquad \vec{b} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ \vec{b}_4 \end{bmatrix} \quad (20)$$

The four subsystems correspond to the four lines of Table 3. Explicit expressions for the dynamical variables $\vec{x}_1$, $\vec{x}_2$, $\vec{x}_3$ and $\vec{x}_4$, the matrices A_{11}, A_{13}, A_{14}, A_{22}, A_{23}, A_{33}, A_{34} and A_{44}, and the vector $\vec{b}_4$ are given in Appendix D. After solving the equations for the C-quantities of Table 3, we can compute mean and variance of the intra- and inter-patch concentration indices, see Appendix E. Code to compute these concentration indices, implemented in Matlab (The Mathworks Inc., Natick), is provided as electronic supplementary material.

In Fig. 3, we investigate the dynamical behaviour of our metacommunity model. We have plotted the dynamics of intra- and inter-patch diversities for three simulated trajectories. Also shown are mean and variance of the intra- and inter-patch diversities as computed using (15) with (20). The correspondence is excellent.

The stationary state of the metacommunity model as a function of the migration intensity between patches (parameter γ) is studied in Fig. 4. We note a continuous transition between two extreme cases. When the inter-patch migration intensity γ is small, the patch communities are decoupled. Because the regional species pool
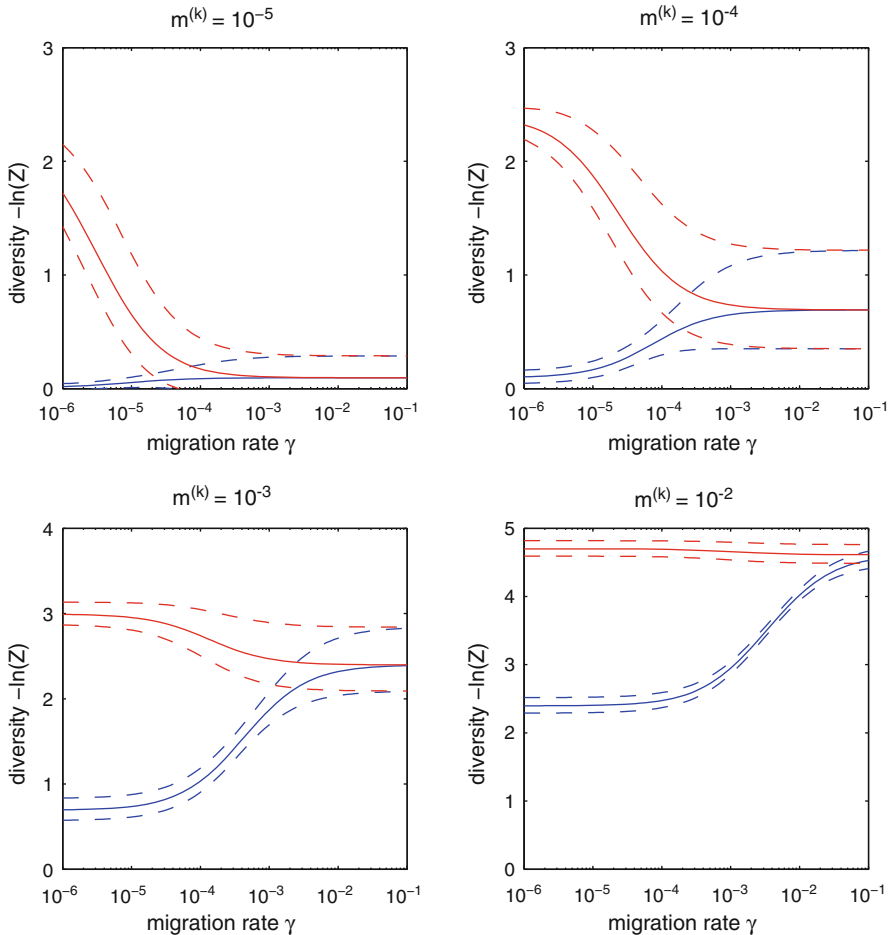
Fig. 4 Stationary intra- and inter-patch diversities as a function of inter-patch migration intensity γ. Concentration indices were computed from the equilibrium solution (17) with (20), and transformed to diversities using the transformation $x \mapsto -\ln x$. In *blue*: intra-patch diversity. In *red*: inter-patch diversity. *Full line*: mean concentration indices. *Dashed line*: mean $\pm$ standard deviation of concentration indices. Panels correspond to different immigration intensity $m^{(k)}$ (the same for all k), which can also be interpreted as a speciation rate (see Fig. 2). The values of the immigration intensity, indicated above the panels, are $m^{(k)} = 10^{-5}, 10^{-4}, 10^{-3}$ and 10^{-2}. Other parameters are $P = 10$ and $J^{(k)} = 1{,}000$ for all k

is very diverse, the patch communities are dissimilar ($Z_{\text{inter}} \approx P Z_{\text{intra}}$). When the inter-patch migration intensity γ tends to $\frac{1}{P}$, migration between two different patches becomes as probable as migration inside a patch. In other words, there is no barrier between patches anymore, and the metacommunity is spatially homogeneous with size $J = \sum_k J^{(k)} = P J^{(k)}$ (because all patches k have the same size $J^{(k)}$).

In Fig. 5, we study the stationary state of the metacommunity model as a function of the immigration intensity from the regional species pool [parameter $m^{(k)}$, which is the same for all patches k]. Again, there is a continuous transition between two
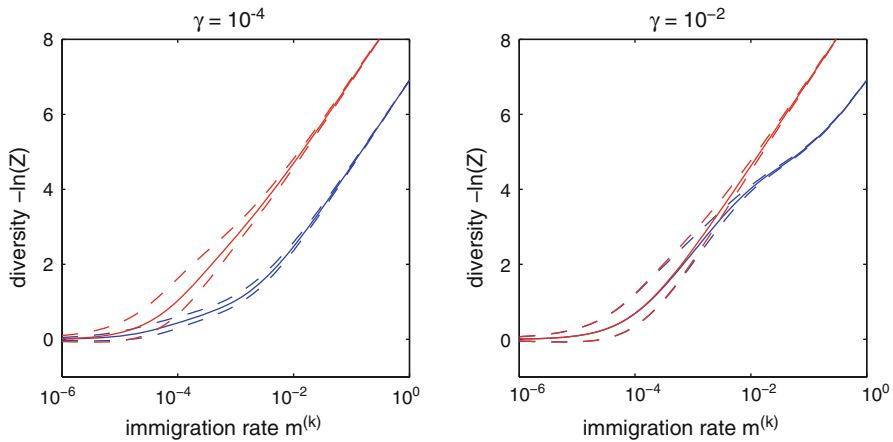
Fig. 5 Stationary intra- and inter-patch diversities as a function of immigration intensity $m^{(k)}$ (the same for all patches k). The same as Fig. 4, except that we interchanged the role of the immigration (or speciation) intensity $\mu^{(k)}$ and the inter-patch migration intensity γ. The values of the migration intensity, indicated above the panels, are $\gamma = 10^{-4}$ and $\gamma = 10^{-2}$

extreme cases. When the immigration intensity $m^{(k)}$ is small, the metacommunity gets isolated from the regional species pool, is dominated by one or a few species, and has low diversity. When the immigration intensity $m^{(k)}$ tends to 1, there are no longer migration events inside the metacommunity. Because the regional species pool is very diverse, the patch communities are dissimilar ($Z_{\text{inter}} \approx P Z_{\text{intra}}$).

6 Concluding remarks

We have derived the dynamical equations necessary for the quantitative description of a neutral community living on a network of interconnected patches. The community diversity has been quantified using two variables: the intra- and inter-patch concentration indices. These are analytically tractable and also have a simple interpretation in terms of sampling experiments. We have devoted considerable attention to the determination of the variance of these quantities. The equations have been solved for two special cases: a single patch community and a symmetrically connected community.

Our model can be used to investigate the effect of immigration from the regional species pool (or, as a special case, speciation) and migration between patches on the spatial repartition of diversity. Also the effect of subdividing the metacommunity in more patches (i.e., varying the parameter P), or taking larger communities in the patches (i.e., varying the paramaters $J^{(k)}$) can be easily investigated. It should be noted again that our results hinge on the species neutrality assumption. Introducing species differences (for example, certain species having a larger affinity for certain patches) might lead to quite different results.

We have used Simpson concentration indices (and related similarity indices) to describe community dynamics. As we have noticed previously (Vanpeteghem et al. 2008), such an approach might be most useful for microbial communities.

Indeed, plant or animal communities are typically studied by collecting data of individual plants or animals. Hence, the link between data and theory is most easily established via (sampled) species abundance distributions. Microbial communities, on the other hand, are too diverse to be studied accurately by a sampling approach. Instead, experimental techniques (such as molecular fingerprinting techniques) that measure global, community-level properties (such as Simpson diversity) are commonly used. For this type of data, models written in terms of diversity indices seem appropriate.

We mention two more reasons why our model might be relevant for microbial ecology. First, microbial communities are characterized by a large diversity. Coexistence of many species (hundreds, or even thousands) in apparently homogeneous environments is often observed. This suggests that coexisting microbial species might be described by similar ecological parameters (in a given environment), as pronounced parameter differences would lead to some species excluding others. Hence, species neutrality might be a reasonable assumption for microbial communities.

Second, the spatial structure of our model consists in subdividing the metacommunity in a finite number of patches. This is an abstraction for most natural communities, for which a continuous landscape would be more realistic. However, the interconnected patch model is an accurate description of microbial microplate experiments. In such experiments, microbial communities are grown in small tubes (i.e. patches), and are mixed with each other at regular time intervals. Interestingly, the amount of mixing [i.e. parameters $\phi^{(kl)}$] can be controlled experimentally. The analytical approach we have presented here, and the diversity predictions (with their variance) we have derived, might therefore be most useful to describe such experiments.

Appendix A

The generating function Φ, defined in (5), satisfies a dynamical equation, that we derive in this appendix. The computation relies on the master equation (3):

$$
\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t}\Phi(\vec{z}) &= \sum_{\vec{N}} \frac{\mathrm{d}}{\mathrm{d}t}\mathbb{P}(\vec{N}) \prod_{i,k}\left(z_i^{(k)}\right)^{N_i^{(k)}} \\
&= \sum_{\vec{N}} \sum_{\substack{i,j,k \\ i\neq j}} \left[R_{ij}^{(k)}(N_i^{(k)}+1; p_j, \vec{N}_j - \vec{e}^{(k)}) \, \mathbb{P}(\vec{N} + \vec{e}_i^{(k)} - \vec{e}_j^{(k)}) \right. \\
&\qquad \left. - R_{ij}^{(k)}(N_i^{(k)}; p_j, \vec{N}_j) \, \mathbb{P}(\vec{N}) \right] \prod_{i,k}\left(z_i^{(k)}\right)^{N_i^{(k)}} \\
&= \sum_{\substack{i,j,k \\ i\neq j}} \left[\sum_{\vec{N}} R_{ij}^{(k)}(N_i^{(k)}; p_j, \vec{N}_j)\,\mathbb{P}(\vec{N}) \frac{z_j^{(k)}}{z_i^{(k)}} \right. \\
&\qquad \left. - \sum_{\vec{N}} R_{ij}^{(k)}(N_i^{(k)}; p_j, \vec{N}_j)\,\mathbb{P}(\vec{N}) \right] \prod_{i,k}\left(z_i^{(k)}\right)^{N_i^{(k)}}
\end{aligned}
$$

$$
= \sum_{\substack{i,j,\,k \\ i \neq j}} \sum_{\vec{N}} \left[\mu^{(k)} m^{(k)} p_j \frac{N_i^{(k)}}{J^{(k)}} \frac{z_j^{(k)} - z_i^{(k)}}{z_i^{(k)}} \right.
$$

$$
+ \mu^{(k)} \left(1 - m^{(k)} \right) \sum_l \phi^{(lk)} \frac{N_i^{(k)} (N_j^{(l)} - \delta_{ij}\delta_{kl})}{J^{(k)}(J^{(l)} - \delta_{kl})} \frac{z_j^{(k)} - z_i^{(k)}}{z_i^{(k)}} \right]
$$

$$
\times \mathbb{P}(\vec{N}) \prod_{i,k} \left(z_i^{(k)} \right)^{N_i^{(k)}}
$$

$$
= \sum_{\substack{i,j,\,k \\ i \neq j}} \left[\mu^{(k)} m^{(k)} p_j \frac{(z_j^{(k)} - z_i^{(k)})}{J^{(k)}} \frac{\partial \Phi(\vec{z})}{\partial z_i^{(k)}} \right.
$$

$$
+ \mu^{(k)} \left(1 - m^{(k)} \right) \sum_l \phi^{(lk)} \frac{z_j^{(l)}(z_j^{(k)} - z_i^{(k)})}{J^{(k)}(J^{(l)} - \delta_{kl})} \frac{\partial^2 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)}} \right],
$$

which proves the dynamical equation (6).

Appendix B

In this appendix, we obtain the dynamical equations (8) for the moments of the abundances $N_i^{(k)}$ from the dynamical equation (6) for the generating function Φ.

B.1 First-order moments

The first moment $\mathbb{E} N_u^{(a)}$ is obtained by differentiating the generating function Φ with respect to $z_u^{(a)}$:

$$
\frac{\mathrm{d}}{\mathrm{d}t} \frac{\partial \Phi(\vec{z})}{\partial z_u^{(a)}} = \sum_{\substack{i,j,\,k \\ i \neq j}} \frac{\mu^{(k)}}{J^{(k)}} \left[m^{(k)} p_j \, \delta_{ka} (\delta_{ju} - \delta_{iu}) \frac{\partial \Phi(\vec{z})}{\partial z_i^{(k)}} \right.
$$

$$
+ m^{(k)} p_j \, (z_j^{(k)} - z_i^{(k)}) \frac{\partial^2 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_u^{(a)}}
$$

$$
+ \left(1 - m^{(k)} \right) \sum_l \phi^{(lk)} \frac{\delta_{al}\delta_{ju}(z_j^{(k)} - z_i^{(k)})}{J^{(l)} - \delta_{kl}} \frac{\partial^2 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)}}
$$

$$
+ \left(1 - m^{(k)} \right) \sum_l \phi^{(lk)} \frac{z_j^{(l)} \delta_{ka}(\delta_{ju} - \delta_{iu})}{J^{(l)} - \delta_{kl}} \frac{\partial^2 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)}}
$$

$$
+ \left. \left(1 - m^{(k)} \right) \sum_l \phi^{(lk)} \frac{z_j^{(l)}(z_j^{(k)} - z_i^{(k)})}{J^{(l)} - \delta_{kl}} \frac{\partial^3 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)} \partial z_u^{(a)}} \right]. \quad (21)
$$

We have to evaluate this expression in E, i.e., we have to put $z_i^{(k)} = 1$ for all i and k. Doing so, the second, third and last term drop, leaving us with

$$\frac{d}{dt}\mathbb{E}N_u^{(a)} = \sum_{i,j,k} \frac{\mu^{(k)}}{J^{(k)}} \left[m^{(k)} p_j \, \delta_{ka}(\delta_{ju} - \delta_{iu})\mathbb{E}N_i^{(k)} \right.$$
$$\left. + \left(1 - m^{(k)}\right) \sum_l \phi^{(lk)} \frac{\delta_{ka}(\delta_{ju} - \delta_{iu})}{J^{(l)} - \delta_{kl}} \mathbb{E}N_{ij}^{(kl)} \right].$$

Note that the requirement $i \neq j$ can be dropped, for the terms with $i = j$ all vanish. Henceforth this requirement will be systematically dropped in the formulas when possible. And so, our previous equation simplifies to

$$\frac{d}{dt}\mathbb{E}N_u^{(a)} = \frac{\mu^{(a)}}{J^{(a)}} \left[m^{(a)} \left(p_u J^{(a)} - \mathbb{E}N_u^{(a)} \right) \right.$$
$$\left. + (1 - m^{(a)}) \sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}} \left(J^{(a)}\mathbb{E}N_u^{(l)} - J^{(l)}\mathbb{E}N_u^{(a)} \right) \right],$$

which is exactly (8a).

B.2 Second-order moments

By differentiating (21) a second time, we get

$$\frac{d}{dt} \frac{\partial^2 \Phi(\vec{z})}{\partial z_u^{(a)} \partial z_v^{(b)}} = \sum_{\substack{i, j, k \\ i \neq j}} \frac{\mu^{(k)}}{J^{(k)}}$$

$$\times \left[m^{(k)} p_j \, \delta_{ka}(\delta_{ju} - \delta_{iu}) \frac{\partial^2 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_v^{(b)}} + \mathcal{P} \right.$$

$$+ m^{(k)} p_j \, (z_j^{(k)} - z_i^{(k)}) \frac{\partial^3 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_u^{(a)} \partial z_v^{(b)}}$$

$$+ \left(1 - m^{(k)}\right) \sum_l \phi^{(lk)} \frac{\delta_{la}\delta_{ju}\delta_{kb}(\delta_{jv} - \delta_{iv})}{J^{(l)} - \delta_{kl}} \frac{\partial^2 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)}} + \mathcal{P}$$

$$+ \left(1 - m^{(k)}\right) \sum_l \phi^{(lk)} \frac{\delta_{la}\delta_{ju}(z_j^{(k)} - z_i^{(k)})}{J^{(l)} - \delta_{kl}} \frac{\partial^3 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)} \partial z_v^{(b)}} + \mathcal{P}$$

$$+ \left(1 - m^{(k)}\right) \sum_l \phi^{(lk)} \frac{z_j^{(l)} \delta_{ka}(\delta_{ju} - \delta_{iu})}{J^{(l)} - \delta_{kl}} \frac{\partial^3 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)} \partial z_v^{(b)}} + \mathcal{P}$$

$$\left. + \left(1 - m^{(k)}\right) \frac{z_j^{(l)} (z_j^{(k)} - z_i^{(k)})}{J^{(l)} - \delta_{kl}} \frac{\partial^4 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)} \partial z_u^{(a)} \partial z_v^{(b)}} \right]. \qquad (22)$$

By adding $\mathcal{P}$, we mean that there is an extra term equal to the preceding one but with the labels permuted: if the term written down is denoted by $X_{uv}^{(ab)}$, the permuted term equals $X_{vu}^{(ba)}$. Evaluating in E, the second, fourth and last term drop. We get

$$
\frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}N_{uv}^{(ab)} = \sum_{i,j,k} \frac{\mu^{(k)}}{J^{(k)}} \left[m^{(k)} p_j\, \delta_{ka}(\delta_{ju} - \delta_{iu})\mathbb{E}N_{iv}^{(kb)} \right.
$$
$$
+ \left(1 - m^{(k)}\right) \sum_l \phi^{(lk)} \frac{\delta_{la}\delta_{ju}\delta_{kb}(\delta_{jv} - \delta_{iv})}{J^{(l)} - \delta_{kl}} \mathbb{E}N_{ij}^{(kl)}
$$
$$
\left. + \left(1 - m^{(k)}\right) \sum_l \phi^{(lk)} \frac{\delta_{ka}(\delta_{ju} - \delta_{iu})}{J^{(l)} - \delta_{kl}} \mathbb{E}N_{ivj}^{(kbl)} \right] + \mathcal{P}.
$$

Replacing the second term with the corresponding permuted term in $\mathcal{P}$, we can work out the sum over k,

$$
\frac{\mathrm{d}}{\mathrm{d}t}N_{uv}^{(ab)} = \sum_{ij} \frac{\mu^{(a)}}{J^{(a)}} \left[m^{(a)} p_j\, (\delta_{ju} - \delta_{iu})\mathbb{E}N_{iv}^{(ab)} \right.
$$
$$
+ \left(1 - m^{(a)}\right) \phi^{(ba)} \frac{\delta_{jv}(\delta_{ju} - \delta_{iu})}{J^{(b)} - \delta_{ab}} \mathbb{E}N_{ij}^{(ab)}
$$
$$
\left. + \left(1 - m^{(a)}\right) \sum_l \phi^{(la)} \frac{\delta_{ju} - \delta_{iu}}{J^{(l)} - \delta_{al}} \mathbb{E}N_{ivj}^{(abl)} \right] + \mathcal{P}.
$$

To do the summations over i and j, we use the identities

$$
\sum_i \mathbb{E}N_{ui}^{(ab)} = (J^{(b)} - \delta_{ab})\mathbb{E}N_u^{(a)}
$$
$$
\sum_i \mathbb{E}N_{uvi}^{(abc)} = (J^{(c)} - \delta_{ac} - \delta_{bc})\mathbb{E}N_{uv}^{(ab)}.
$$

Hence,

$$
\frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}N_{uv}^{(ab)} = \frac{\mu^{(a)}}{J^{(a)}} \left[m^{(a)} p_u\, (J^{(a)} - \delta_{ab})\,\mathbb{E}N_v^{(b)} - m^{(a)}\mathbb{E}N_{uv}^{(ab)} \right.
$$
$$
+ \left(1 - m^{(a)}\right) \frac{\phi^{(ba)}}{J^{(b)} - \delta_{ab}} \delta_{uv}(J^{(a)} - \delta_{ab})\mathbb{E}N_v^{(b)}
$$
$$
- \left(1 - m^{(a)}\right) \frac{\phi^{(ba)}}{J^{(b)} - \delta_{ab}} \mathbb{E}N_{uv}^{(ab)}
$$
$$
+ \left(1 - m^{(a)}\right) \sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}} (J^{(a)} - \delta_{ab} - \delta_{al})\mathbb{E}N_{uv}^{(lb)}
$$
$$
\left. - \left(1 - m^{(a)}\right) \sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}} (J^{(l)} - \delta_{al} - \delta_{bl})\mathbb{E}N_{uv}^{(ab)} \right] + \mathcal{P}.
$$

Twice two terms cancel out against each other, leading to

$$
\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t} \mathbb{E} N_{uv}^{(ab)} = \frac{\mu^{(a)}}{J^{(a)}} \Bigg[& m^{(a)} p_u \left(J^{(a)} - \delta_{ab} \right) \mathbb{E} N_v^{(b)} - m^{(a)} \mathbb{E} N_{uv}^{(ab)} \\
& + \left(1 - m^{(a)} \right) \frac{\phi^{(ba)}}{J^{(b)} - \delta_{ab}} \delta_{uv} (J^{(a)} - \delta_{ab}) \mathbb{E} N_v^{(b)} \\
& + \left(1 - m^{(a)} \right) \sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}} (J^{(a)} - \delta_{ab}) \mathbb{E} N_{uv}^{(lb)} \\
& - \left(1 - m^{(a)} \right) \sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}} J^{(l)} \mathbb{E} N_{uv}^{(ab)} \Bigg] + \mathcal{P},
\end{aligned}
$$

which is identical to (8b).

B.3 Third-order moments

Differentiating (22) once more,

$$
\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t} & \frac{\partial^3 \Phi(\vec{z})}{\partial z_u^{(a)} \partial z_v^{(b)} \partial z_w^{(c)}} \\
= & \sum_{\substack{i,j,k \\ i \neq j}} \frac{\mu^{(k)}}{J^{(k)}} \Bigg[m^{(k)} p_j \, \delta_{ka} (\delta_{ju} - \delta_{iu}) \frac{\partial^3 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_v^{(b)} \partial z_w^{(c)}} + \mathcal{P}_1 \\
& + m^{(k)} p_j \, (z_j^{(k)} - z_i^{(k)}) \frac{\partial^4 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_u^{(a)} \partial z_v^{(b)} \partial z_w^{(c)}} \\
& + \left(1 - m^{(k)} \right) \sum_l \phi^{(lk)} \frac{\delta_{la} \delta_{ju} \delta_{kb} (\delta_{jv} - \delta_{iv})}{J^{(l)} - \delta_{kl}} \frac{\partial^3 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)} \partial z_w^{(c)}} + \mathcal{P}_2 \\
& + \left(1 - m^{(k)} \right) \sum_l \phi^{(lk)} \frac{\delta_{la} \delta_{ju} (z_j^{(k)} - z_i^{(k)})}{J^{(l)} - \delta_{kl}} \frac{\partial^4 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)} \partial z_v^{(b)} \partial z_w^{(c)}} + \mathcal{P}_1 \\
& + \left(1 - m^{(k)} \right) \sum_l \phi^{(lk)} \frac{z_j^{(l)} \delta_{ka} (\delta_{ju} - \delta_{iu})}{J^{(l)} - \delta_{kl}} \frac{\partial^4 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)} \partial z_v^{(b)} \partial z_w^{(c)}} + \mathcal{P}_1 \\
& + \left(1 - m^{(k)} \right) \sum_l \phi^{(lk)} \frac{z_j^{(l)} (z_j^{(k)} - z_i^{(k)})}{J^{(l)} - \delta_{kl}} \frac{\partial^5 \Phi(\vec{z})}{\partial z_i^{(k)} \partial z_j^{(l)} \partial z_u^{(a)} \partial z_v^{(b)} \partial z_w^{(c)}} \Bigg].
\end{aligned}
$$

The lines with $\mathcal{P}_1$ have two extra terms (three in total). For a term $X_{uvw}^{(abc)}$, the permuted terms are $X_{vuw}^{(bac)}$ and $X_{wuv}^{(cab)}$. Note that for such terms,

$$
X_{uvw}^{(abc)} = X_{uwv}^{(acb)}, \quad X_{vuw}^{(bac)} = X_{vwu}^{(bca)}, \quad X_{wuv}^{(cab)} = X_{wvu}^{(cba)}.
$$

The line with $\mathcal{P}_2$ has five extra terms (six in total). They are:

$$X^{(acb)}_{uwv}, \quad X^{(bac)}_{vuw}, \quad X^{(bca)}_{vwu}, \quad X^{(cab)}_{wuv}, \quad X^{(cba)}_{wvu}.$$

By eliminating the terms that cancel after evaluation in E, we get

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}N^{(abc)}_{uvw} = \sum_{i,j,k} \frac{\mu^{(k)}}{J^{(k)}} \left[m^{(k)} p_j \, \delta_{ka}(\delta_{ju} - \delta_{iu})\mathbb{E}N^{(kbc)}_{ivw} + \mathcal{P}_1 \right.$$

$$+ \left(1 - m^{(k)}\right) \sum_l \phi^{(lk)} \frac{\delta_{la}\delta_{ju}\delta_{kb}(\delta_{jv} - \delta_{iv})}{J^{(l)} - \delta_{kl}} \mathbb{E}N^{(klc)}_{ijw} + \mathcal{P}_2$$

$$\left. + \left(1 - m^{(k)}\right) \sum_l \phi^{(lk)} \frac{\delta_{ka}(\delta_{ju} - \delta_{iu})}{J^{(l)} - \delta_{kl}} \mathbb{E}N^{(klbc)}_{ijvw} + \mathcal{P}_1 \right].$$

In the second line, we use the following identity:

$$X^{(abc)}_{uvw} + \mathcal{P}_2 = \left(X^{(bac)}_{vuw} + X^{(cab)}_{wuv} \right) + \mathcal{P}_1.$$

Doing the summation over k, we get

$$\frac{\mathrm{d}}{\mathrm{d}t}N^{(abc)}_{uvw} = \sum_{ij} \frac{\mu^{(a)}}{J^{(a)}} \left[m^{(a)} p_j \, (\delta_{ju} - \delta_{iu})\mathbb{E}N^{(abc)}_{ivw} \right.$$

$$+ \left(1 - m^{(a)}\right) \phi^{(ba)} \frac{\delta_{jv}(\delta_{ju} - \delta_{iu})}{J^{(b)} - \delta_{ab}} \mathbb{E}N^{(abc)}_{ijw}$$

$$+ \left(1 - m^{(a)}\right) \phi^{(ca)} \frac{\delta_{jw}(\delta_{ju} - \delta_{iu})}{J^{(c)} - \delta_{ac}} \mathbb{E}N^{(abc)}_{ivj}$$

$$\left. + \left(1 - m^{(a)}\right) \sum_l \phi^{(la)} \frac{(\delta_{ju} - \delta_{iu})}{J^{(l)} - \delta_{al}} \mathbb{E}N^{(abcl)}_{ivwj} \right] + \mathcal{P}_1.$$

We use the identities

$$\sum_i \mathbb{E}N^{(abc)}_{uvi} = (J^{(c)} - \delta_{ac} - \delta_{bc})\mathbb{E}N^{(ab)}_{uv}$$

$$\sum_i \mathbb{E}N^{(abcd)}_{uvwi} = (J^{(d)} - \delta_{ad} - \delta_{bd} - \delta_{cd})\mathbb{E}N^{(abc)}_{uvw}.$$

to do the summations over i and j,

$$
\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t} \mathbb{E} N_{uvw}^{(abc)} = \frac{\mu^{(a)}}{J^{(a)}} \Bigg[& m^{(a)} p_u \, (J^{(a)} - \delta_{ab} - \delta_{ac}) \, \mathbb{E} N_{vw}^{(bc)} - m^{(a)} \mathbb{E} N_{uvw}^{(abc)} \\
& + \left(1 - m^{(a)} \right) \frac{\phi^{(ba)}}{J^{(b)} - \delta_{ab}} \delta_{uv} (J^{(a)} - \delta_{ab} - \delta_{ac}) \mathbb{E} N_{vw}^{(bc)} \\
& - \left(1 - m^{(a)} \right) \frac{\phi^{(ba)}}{J^{(b)} - \delta_{ab}} \mathbb{E} N_{uvw}^{(abc)} \\
& + \left(1 - m^{(a)} \right) \frac{\phi^{(ca)}}{J^{(c)} - \delta_{ac}} \delta_{uw} (J^{(a)} - \delta_{ab} - \delta_{ac}) \mathbb{E} N_{vw}^{(bc)} \\
& - \left(1 - m^{(a)} \right) \frac{\phi^{(ca)}}{J^{(c)} - \delta_{ac}} \mathbb{E} N_{uvw}^{(abc)} \\
& + \left(1 - m^{(a)} \right) \sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}} (J^{(a)} - \delta_{ab} - \delta_{ac} - \delta_{al}) \mathbb{E} N_{uvw}^{(lbc)} \\
& - \left(1 - m^{(a)} \right) \sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}} (J^{(l)} - \delta_{al} - \delta_{bl} - \delta_{cl}) \mathbb{E} N_{uvw}^{(abc)} \Bigg] + \mathcal{P}_1 .
\end{aligned}
$$

Three times two terms cancel out against each other, leading to

$$
\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t} \mathbb{E} N_{uvw}^{(abc)} = \frac{\mu^{(a)}}{J^{(a)}} \Bigg[& m^{(a)} p_u \, (J^{(a)} - \delta_{ab} - \delta_{ac}) \, \mathbb{E} N_{vw}^{(bc)} - m^{(a)} \mathbb{E} N_{uvw}^{(abc)} \\
& + \left(1 - m^{(a)} \right) \frac{\phi^{(ba)}}{J^{(b)} - \delta_{ab}} \delta_{uv} (J^{(a)} - \delta_{ab} - \delta_{ac}) \mathbb{E} N_{vw}^{(bc)} \\
& + \left(1 - m^{(a)} \right) \frac{\phi^{(ca)}}{J^{(c)} - \delta_{ac}} \delta_{uw} (J^{(a)} - \delta_{ab} - \delta_{ac}) \mathbb{E} N_{vw}^{(bc)} \\
& + \left(1 - m^{(a)} \right) \sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}} (J^{(a)} - \delta_{ab} - \delta_{ac}) \mathbb{E} N_{uvw}^{(lbc)} \\
& - \left(1 - m^{(a)} \right) \sum_l \frac{\phi^{(la)}}{J^{(l)} - \delta_{al}} J^{(l)} \mathbb{E} N_{uvw}^{(abc)} \Bigg] + \mathcal{P}_1 .
\end{aligned}
$$

which is identical to (8c).

B.4 Fourth-order and higher order moments

The dynamical equation (8d) for the fourth-order moments and higher can be derived analogously as the equation for the third-order moments.

Appendix C

In this appendix, we discuss the dynamical equations for the C-quantities needed to compute mean and variance of the similarity index $Z^{(kl)}$. They follow directly from the moment equations (8).

For example, the dynamics of $C_{0;0}^{(ab;cd)}$ are obtained from the dynamics of $N_{iijj}^{(abcd)}$,

$$
\begin{aligned}
\frac{d}{dt} C_{0;0}^{(ab;cd)} =\ & -\left(\frac{\mu^{(a)}}{J^{(a)}} + \frac{\mu^{(b)}}{J^{(b)}} + \frac{\mu^{(c)}}{J^{(c)}} + \frac{\mu^{(d)}}{J^{(d)}} \right) C_{0;0}^{(ab;cd)} \\
& + \frac{\mu^{(a)}}{J^{(a)}} m^{(a)} (J^{(a)} - \delta_{ab} - \delta_{ac} - \delta_{ad}) C_{1;0}^{(b;cd)} \\
& + \frac{\mu^{(b)}}{J^{(b)}} m^{(b)} (J^{(b)} - \delta_{ab} - \delta_{bc} - \delta_{bd}) C_{1;0}^{(a;cd)} \\
& + \frac{\mu^{(c)}}{J^{(c)}} m^{(c)} (J^{(a)} - \delta_{ac} - \delta_{bc} - \delta_{cd}) C_{1;0}^{(d;ab)} \\
& + \frac{\mu^{(d)}}{J^{(d)}} m^{(d)} (J^{(a)} - \delta_{ad} - \delta_{bd} - \delta_{cd}) C_{1;0}^{(c;ab)} \\
& - \sum_l \left(\frac{\mu^{(a)}}{J^{(a)}} \left(1 - m^{(a)}\right) \phi^{(la)} \frac{J^l}{J^l - \delta_{al}} + \frac{\mu^{(b)}}{J^{(b)}} \left(1 - m^{(b)}\right) \right. \\
& \qquad \left. \times \phi^{(lb)} \frac{J^l}{J^l - \delta_{bl}} + \frac{\mu^{(c)}}{J^{(c)}} \left(1 - m^{(c)}\right) \phi^{(lc)} \frac{J^l}{J^l - \delta_{cl}} \right. \\
& \qquad \left. + \frac{\mu^{(d)}}{J^{(d)}} \left(1 - m^{(d)}\right) \phi^{(ld)} \frac{J^l}{J^l - \delta_{dl}} \right) C_{0;0}^{(ab;cd)} \\
& + \frac{\mu^{(a)}}{J^{(a)}} \left(1 - m^{(a)}\right) \sum_l \phi^{(la)} \frac{J^{(a)} - \delta_{ab} - \delta_{ac} - \delta_{ad}}{J^{(l)} - \delta_{al}} \\
& \quad \times \left(C_{0;0}^{(lb;cd)} - \delta_{bl} \left((J^{(b)} - \delta_{bc} - \delta_{bd}) C_0^{(cd)} - C_0^{(bcd)} \right) \right) \\
& + \frac{\mu^{(b)}}{J^{(b)}} \left(1 - m^{(b)}\right) \sum_l \phi^{(lb)} \frac{J^{(b)} - \delta_{ab} - \delta_{bc} - \delta_{bd}}{J^{(l)} - \delta_{bl}} \\
& \quad \times \left(C_{0;0}^{(al;cd)} - \delta_{al} \left((J^{(a)} - \delta_{ac} - \delta_{ad}) C_0^{(cd)} - C_0^{(acd)} \right) \right) \\
& + \frac{\mu^{(c)}}{J^{(c)}} \left(1 - m^{(c)}\right) \sum_l \phi^{(lc)} \frac{J^{(c)} - \delta_{ac} - \delta_{bc} - \delta_{cd}}{J^{(l)} - \delta_{cl}} \\
& \quad \times \left(C_{0;0}^{(ab;ld)} - \delta_{dl} \left((J^{(d)} - \delta_{ad} - \delta_{bd}) C_0^{(ab)} - C_0^{(abd)} \right) \right) \\
& + \frac{\mu^{(d)}}{J^{(d)}} \left(1 - m^{(d)}\right) \sum_l \phi^{(ld)} \frac{J^{(d)} - \delta_{ad} - \delta_{bd} - \delta_{cd}}{J^{(l)} - \delta_{dl}} \\
& \quad \times \left(C_{0;0}^{(ab;cl)} - \delta_{cl} \left((J^{(c)} - \delta_{ac} - \delta_{bc}) C_0^{(ab)} - C_0^{(abc)} \right) \right).
\end{aligned}
$$

Table 4 Dynamical dependencies of C-quantities

	C-quantity	Dependencies
$\mathbb{E} \mathbf{Z}^{(kl)}$	$C_0^{(ab)}$	$C_0^{(ab)}, C_1^{(a)}$
	$C_1^{(a)}$	$C_1^{(a)}$
Var $\mathbf{Z}^{(kl)}$	$C_0^{(abc)}$	$C_0^{(abc)}, C_1^{(ab)}, C_0^{(ab)}$
	$C_1^{(ab)}$	$C_1^{(ab)}, C_2^{(a)}, C_1^{(a)}$
	$C_2^{(a)}$	$C_2^{(a)}$
	$C_0^{(abcd)}$	$C_0^{(abcd)}, C_1^{(abc)}, C_0^{(abc)}$
	$C_1^{(abc)}$	$C_1^{(abc)}, C_2^{(ab)}, C_1^{(ab)}$
	$C_2^{(ab)}$	$C_2^{(ab)}, C_3^{(a)}, C_2^{(a)}$
	$C_3^{(a)}$	$C_3^{(a)}$
	$C_{0;0}^{(ab;cd)}$	$C_{0;0}^{(ab;cd)}, C_{1;0}^{(a;bc)}, C_0^{(abc)}, C_0^{(ab)}$
	$C_{1;0}^{(a;bc)}$	$C_{1;0}^{(a;bc)}, C_{1;1}^{(a;b)}, C_2^{(ab)}, C_1^{(ab)}, C_0^{(ab)}, C_1^{(a)}$
	$C_{1;1}^{(a;b)}$	$C_{1;1}^{(a;b)}, C_3^{(a)}, C_1^{(a)}$

The dynamics of $C_{0;0}^{(ab;cd)}$ do not only depend on C-quantities of the type $C_{0;0}^{(ab;cd)}$, but also on C-quantities of the type $C_{1;0}^{(a;bc)}$, $C_0^{(ab)}$ and $C_0^{(abc)}$.

The dependencies of all C-quantities necessary to compute the dynamics of mean and variance of $\mathbf{Z}^{(kl)}$ are listed in Table 4. The full dynamics decouple in a number of subsystems. For example, lines 1–2 of Table 4 can be solved first, then lines 3–5, followed by lines 6–9, and finally lines 10–12.

Appendix D

In this appendix, we give explicit expressions for the matrix A and the vector $\vec{b}$ in (20). We introduce the constants

$$
a = \frac{\mu m}{J}
$$
$$
b = \frac{\mu(1-m)}{J} \frac{1-(P-1)\gamma}{J-1}
$$
$$
c = \frac{\mu(1-m)}{J} \gamma.
$$

The fourth subsystem (with system matrix A_{44}) corresponds to the two C-quantities with two patch indices,

$$
\vec{x}_4 = \begin{bmatrix} C_0^{(11)} \\ C_0^{(12)} \end{bmatrix}.
$$

The corresponding matrices are given by

$$A_{44} = \begin{bmatrix} -2a-2b-2(P-1)c & 2(P-1)\frac{J-1}{J}c \\ 2c & -2a-2c \end{bmatrix}, \quad \vec{b}_4 = \begin{bmatrix} 2J(J-1)b \\ 2Jc \end{bmatrix}.$$

The third subsystem (with system matrix A_{33}) corresponds to the three C-quantities with three patch indices,

$$\vec{x}_3 = \begin{bmatrix} C_0^{(111)} \\ C_0^{(112)} \\ C_0^{(123)} \end{bmatrix}.$$

The corresponding matrices are given by

$$A_{33} = \begin{bmatrix} -3a-6b-3(P-1)c & 3(P-1)\frac{J-2}{J}c & 0 \\ c & -3a-2b-(2P+\frac{2}{J}-3)c & 2(P-2)\frac{J-1}{J}c \\ 0 & 6c & -3a-6c \end{bmatrix},$$

$$A_{34} = \begin{bmatrix} 6(J-2)b & 0 \\ 2c & 2(J-1)b+2\frac{J-1}{J}c \\ 0 & 6c \end{bmatrix}.$$

The second subsystem (with system matrix A_{22}) corresponds to the five C-quantities with four patch indices and one species index,

$$\vec{x}_2 = \begin{bmatrix} C_0^{(1111)} \\ C_0^{(1112)} \\ C_0^{(1122)} \\ C_0^{(1123)} \\ C_0^{(1234)} \end{bmatrix}.$$

The corresponding matrices are given by

$$A_{22} = \begin{bmatrix} -4a-12b-4(P-1)c & 4(P-1)\frac{J-3}{J}c & 0 & 0 & 0 \\ c & -4a-6b-(3P-2)c & 3\frac{J-2}{J}c & 3(P-2)\frac{J-2}{J}c & 0 \\ 0 & 4\frac{J-1}{J}c & -4a-4b-4(P-1)c & 4(P-2)\frac{J-1}{J}c & 0 \\ 0 & 2c & 2c & -4a-2b-(2P+\frac{4}{J}-2)c & 2(P-3)\frac{J-1}{J}c \\ 0 & 0 & 0 & 12c & -4a-12c \end{bmatrix},$$

$$A_{23} = \begin{bmatrix} 12(J-3)b & 0 & 0 \\ 3c & 6(J-2)b+3\frac{J-2}{J}c & 0 \\ 0 & 4(J-1)b+8\frac{J-1}{J}c & 0 \\ 0 & 6c & 2(J-1)b+4\frac{J-1}{J}c \\ 0 & 0 & 12c \end{bmatrix}.$$

The first subsystem (with system matrix A_{11}) corresponds to the seven C-quantities with four patch indices and two species indices,

$$
\vec{x}_1 =
\begin{bmatrix}
C_{0;0}^{(11;11)} \\
C_{0;0}^{(11;12)} \\
C_{0;0}^{(11;22)} \\
C_{0;0}^{(12;12)} \\
C_{0;0}^{(11;23)} \\
C_{0;0}^{(12;13)} \\
C_{0;0}^{(12;34)}
\end{bmatrix}.
$$

The corresponding matrices are given by

$$A_{11} = \begin{bmatrix} -4a-12b-4(P-1)c & 4(P-1)\frac{J-3}{J}c & 0 & 0 & 0 & 0 & 0 \\ c & -4a-6b-(3P-2)c & \frac{J-2}{J}c & 2\frac{J-2}{J}c & (P-2)\frac{J-2}{J}c & 2(P-2)\frac{J-2}{J}c & 0 \\ 0 & 4\frac{J-1}{J}c & -4a-4b-4(P-1)c & 0 & 4(P-2)\frac{J-1}{J}c & 0 & 0 \\ 0 & 4\frac{J-1}{J}c & 0 & -4a-4b-4(P-1)c & 0 & 4(P-2)\frac{J-1}{J}c & 0 \\ 0 & 2c & 2c & 0 & -4a-2b-(2P+2)c & 4\frac{J-1}{J}c & 2(P-3)\frac{J-1}{J}c \\ 0 & 2c & 0 & 2c & 2\frac{J-1}{J}c & -4a-2b-(2P+\frac{2}{J})c & 2(P-3)\frac{J-1}{J}c \\ 0 & 0 & 0 & 0 & 4c & 8c & -4a-12c \end{bmatrix},$$

$$A_{13} = \begin{bmatrix} -4(J-3)b & 0 & 0 \\ -c & -2(J-2)b-\frac{J-2}{J}c & 0 \\ 0 & -4(J-1)b & 0 \\ 0 & -4\frac{J-1}{J}c & 0 \\ 0 & -2c & -2(J-1)b \\ 0 & -2c & -2\frac{J-1}{J}c \\ 0 & 0 & -4c \end{bmatrix}, \qquad A_{14} = \begin{bmatrix} 4(J-2)(J-3)b & 0 \\ 2(J-2)c & 2(J-1)(J-2)b \\ 4J(J-1)b & 0 \\ 0 & 4\frac{(J-1)^2}{J}c \\ 2Jc & 2J(J-1)b \\ 0 & 4(J-1)c \\ 0 & 4Jc \end{bmatrix}.$$

Appendix E

For the metacommunity model with symmetric coupling between patches, we express the mean and variance of the intra- and inter-patch concentration indices in terms of the dynamical variables as given in Table 3.

For the intra-patch concentration index $\mathbf{Z}_{\text{intra}}$, we have

$$\mathbb{E}\mathbf{Z}_{\text{intra}} = \frac{1}{J^2}\left(C_0^{(11)} + J\right)$$

$$\mathbb{E}\left[(\mathbf{Z}_{\text{intra}})^2\right] = \frac{1}{P^2 J^4}\left(P\left(C_0^{(1111)} + 6C_0^{(111)} + 7C_0^{(11)} + J\right)\right.$$
$$+ P(P-1)\left(C_0^{(1122)} + 2C_0^{(112)} + C_0^{(12)}\right)$$
$$+ P\left(C_{0;0}^{(11;11)} - 2C_0^{(111)} + (2J-5)C_0^{(11)} + J(J-1)\right)$$
$$\left. + P(P-1)\left(C_{0;0}^{(11;22)} - 2C_0^{(112)} + 2JC_0^{(11)} - C_0^{(12)} + J^2\right)\right)$$

$$\text{Var}\,\mathbf{Z}_{\text{intra}} = \mathbb{E}\left[(\mathbf{Z}_{\text{intra}})^2\right] - (\mathbb{E}\mathbf{Z}_{\text{intra}})^2.$$

For the inter-patch concentration index $\mathbf{Z}_{\text{inter}}$, we have

$$\mathbb{E}\mathbf{Z}_{\text{inter}} = \frac{1}{P^2 J^2}\left(P\left(C_0^{(11)} + J\right) + P(P-1)C_0^{(12)}\right)$$

$$\mathbb{E}\left[(\mathbf{Z}_{\text{inter}})^2\right] = \frac{1}{P^4 J^4}\left(P\left(C_0^{(1111)} + 6C_0^{(111)} + 7C_0^{(11)} + J\right)\right.$$
$$+ 4P(P-1)\left(C_0^{(1112)} + 3C_0^{(112)} + C_0^{(12)}\right)$$
$$+ 3P(P-1)\left(C_0^{(1122)} + 2C_0^{(112)} + C_0^{(12)}\right)$$
$$+ 6P(P-1)(P-2)\left(C_0^{(1123)} + C_0^{(123)}\right)$$
$$+ P(P-1)(P-2)(P-3)\left(C_0^{(1234)}\right)$$
$$+ P\left(C_{0;0}^{(11;11)} - 2C_0^{(111)} + (2J-5)C_0^{(11)} + J(J-1)\right)$$
$$+ 4P(P-1)\left(C_{0;0}^{(11;12)} - C_0^{(112)} + (J-1)C_0^{(12)}\right)$$
$$+ P(P-1)\left(C_{0;0}^{(11;22)} - 2C_0^{(112)} + 2JC_0^{(11)} - C_0^{(12)} + J^2\right)$$
$$+ 2P(P-1)\left(C_{0;0}^{(12;12)}\right)$$
$$+ 2P(P-1)(P-2)\left(C_{0;0}^{(11;23)} - C_0^{(123)} + JC_0^{(12)}\right)$$
$$+ 4P(P-1)(P-2)\left(C_{0;0}^{(12;13)}\right)$$
$$\left. + P(P-1)(P-2)(P-3)\left(C_{0;0}^{(12;34)}\right)\right)$$

$$\text{Var}\,\mathbf{Z}_{\text{inter}} = \mathbb{E}\left[(\mathbf{Z}_{\text{inter}})^2\right] - (\mathbb{E}\mathbf{Z}_{\text{inter}})^2.$$

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