



Species abundance distribution and dynamics in two locally coupled communities

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ABSTRACT

This study considered a model for species abundance dynamics in two local community (or islands) connected to a regional metacommunity. The model was analyzed using continuous probabilistic technique that employs Kolmogorov–Fokker–Planck forward equation to derive the probability density of the species abundance in the two local communities. Using this technique, we proposed a classification for the species abundance dynamics in the local communities. This classification was made based on such characteristics as immigration intensity, species representation in the metacommunity and the size of local communities. We further distinguished several different scenarios for species abundance dynamics using different ecological characteristics such as species persistence, extinction and monodominance in one or both local communities. The similarity of the species abundance distributions between the two local communities was studied using the correlation coefficient between species abundances in two local communities. The correlation is a function of migration rates between local communities and between local and metacommunity. Immigration between local communities drives the homogenization of the local communities, while immigration from the metacommunity will differentiate them. This community subdivision model provides useful insights for studying the effect of landscape fragmentation on species diversity.

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1. Introduction

Understanding the mechanisms of species abundance dynamics in ecological communities is of high concern in viability analysis and ecosystem management and restoration (Lande et al., 2003). Studies on the species abundance relationships have focused on finding distributions that could fit empirical data of species abundances in ecological communities (Fisher et al., 1943; Preston, 1948) or model species abundance relationships using theories of community organization (MacArthur, 1957; May, 1975; Caswell, 1976; Engen and Lande, 1996). The latest development on the subject is the neutral theory of biodiversity (Hubbell, 2001). This theory, in contrast to the niche theory, assumes that the species abundance distribution can be purely generated and maintained by ecological drift without the involvement of differences between species (Hubbell, 2001). If a community undergoes a zero-sum dynamics, as Hubbell further assumes, the

neutral theory will predict the existence of a new statistical distribution of relative species abundance, called the zero-sum multinomial.

Hubbell's neutral theory was proposed to model species abundance distribution for two scales: local community and regional metacommunity (McKane et al., 2004). The metacommunity can be considered as a closed evolutionary biogeographic unit in which species can generate, live and go extinct (Hu et al., 2006). The dynamics of species abundances on the local scale depends on species representation in the metacommunity, the intensity of immigration from the metacommunity and the size of local community. To describe the model, Hubbell defined the change in the number of individuals of species i per unit time step using the following transition probabilities (Hubbell, 2001, Chapter 4):

$$\begin{aligned} W_i(N-1|N) &= \frac{N}{J} \left[(1-m) \frac{J-N}{J-1} + m(1-\omega_i) \right], \\ W_i(N+1|N) &= \frac{J-N}{J} \left[(1-m) \frac{N}{J-1} + m\omega_i \right], \\ W_i(N|N) &= 1 - W_i(N-1|N) - W_i(N+1|N), \end{aligned} \quad (1)$$

where $N = N_i$ is the number of individuals of species i in a local community of the size J , ω_i is the relative abundance of species i in

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metacommunity, and m is the probability that a death in the local community will be replaced by an immigrant. Note since the local community follows the zero-sum assumption, the sum of abundances for all S species is always equal to J , i.e., $J = \sum_{i=1}^S N_i$.

Model given by Eq. (1) is spatially implicit because the species dynamics is studied in the local community that does not involve spatial characteristics such as spatial locations of species and geographic positions of communities. In reality, rarely are species homogeneously distributed. Hubbell (2001, Chapter 7) proposed a model for species abundance dynamics in two local communities connected with each other and with the metacommunity through migration. This model considers the spatial structure in the metacommunity by discretizing it into several small but connected local communities. Therefore, the model for two local communities is a step closer to developing spatially explicit models. Hubbell (2001) employed the covariance in abundance of a species in two local communities to analyze species abundance distribution at the equilibrium state in two local communities. He found that the covariance in two local communities is affected not only by immigration from the metacommunity, but also by the immigrants between the two local communities. The covariance is large when the intensity of migrants between the local communities is large relative to the intensity from the metacommunity. However, because of the high computational cost for the discrete Markov chain approach used by Hubbell to obtain the equilibrium species abundance distribution in two local communities, the study of species abundance dynamics in two local communities was restricted only to very small local communities (size = 8 and 16).

Another model for species abundance distribution and population dynamics in two local communities of different sizes was studied by Vallade and Houchmandzadeh (2006). The dynamics of species in these local communities is affected by migration process between communities and by mutations in both communities. The master equation technique was applied to describe the time evolution of the systems of two communities. In their study, the exact expressions for the steady-state species abundance distribution were derived and the dynamical correlations of species in the two communities were discussed.

In this paper we proposed a new model for species abundance dynamics in two zero-sum local communities of the same size. All processes in the local communities are considered much faster than in the metacommunity. We considered the species abundance dynamics in local communities, whereas in the metacommunity all species were assumed to have constant relative abundances. The species abundances in two local communities can also change at different time scales. These time scales are controlled by different frequencies of death events for these local communities. Our model for two local communities is analyzed using the continuous probabilistic technique. This technique allows us not only to derive the species abundance distribution for the local communities of any sizes, but also to make a classification of the species abundance dynamics in the two local communities with respect to the immigration intensities, species abundance in the metacommunity and size of local communities. Such classification makes it possible to distinguish species at high risk of extinction and species persistent in local communities.

2. Discrete model for species abundance dynamics in two local communities

Let us consider two zero-sum local communities of the same size connected through migration with each other and with the metacommunity that has a large reservoir of organisms of different species with unchanged species abundance fractions.

The change in the number of individuals $N_p = N_{p,i}$ of species i per unit time step in the p th local community, $p = 1, 2$, can be defined using the transition probabilities:

$$\begin{aligned}
 W_{p,i}(N_p + 1|N_p, N_q) &= \frac{\overbrace{J - N_p}^{\text{death}}}{J} \left[\frac{\overbrace{N_p}{\text{birth}}}{J - 1} (1 - m) + \overbrace{m^m \omega_i}^{\text{immigration from metacommunity}} + \overbrace{m^l \frac{N_q}{J}}^{\text{immigration between local communities}} \right], \\
 W_{p,i}(N_p - 1|N_p, N_q) &= \frac{N_p}{J} \left[(1 - m) \frac{J - N_p}{J - 1} + m^m (1 - \omega_i) + m^l \frac{J - N_q}{J} \right], \\
 W_{p,i}(N_p|N_p, N_q) &= 1 - W_{p,i}(N_p - 1|N_p, N_q) - W_{p,i}(N_p + 1|N_p, N_q), \tag{2}
 \end{aligned}$$

where J is the size of local communities, ω_i is the fractional abundance of species i in metacommunity, m^m is the probability that a death in a local community will be replaced by an immigrant from the metacommunity, m^l is the probability that a death in a local community will be replaced by an immigrant from the other local community, $m = m^m + m^l$, and $q = 1, 2, q \neq p$.

The transition probabilities given by expressions (2) can be explained as follows. The fractions N_p/J and $(J - N_p)/J$ in the transition probabilities $W_{p,i}(N_p - 1|N_p, N_q)$ and $W_{p,i}(N_p + 1|N_p, N_q)$, respectively, account for death of one individual in species i and one individual in other species. The numbers $(1 - m^m - m^l)[N_p/(J - 1)]$ and $(1 - m^m - m^l)[(J - N_p)/(J - 1)]$ define the probabilities of one birth in local community p in species i and in other species. The probabilities of immigration from the metacommunity into the p th local community of species i and other species are given by $m^m \omega_i$ and $m^m (1 - \omega_i)$, respectively. Finally, the numbers $m^l(N_q/J)$ and $m^l((J - N_q)/J)$ define the probabilities of immigration from local community q into local community p of species i and other species.

We further assume that the processes of birth, death and immigration in two local communities are independent. Therefore, the transition probabilities for the dynamics of species i in both local communities are:

$$\begin{aligned}
 W_i(N_1 + \Delta_1, N_2 + \Delta_2|N_1, N_2) &= W_{1,i}(N_1 + \Delta_1|N_1, N_2) \times W_{2,i}(N_2 + \Delta_2|N_2, N_1), \tag{3}
 \end{aligned}$$

where $p = 1, 2$ and $\Delta_p = -1, 0$ or 1 .

Hubbell (2001) also proposed a model for species abundance dynamics in two discrete habitats or islands. In that model Hubbell used the transition probabilities for dynamics of given species in both local communities, where he assumed that the abundance of this species can change only in one local community per one time step. In contrast, we assume that the abundance of given species can change in both local communities in one time step. This is a more realistic assumption as there is no reason why death cannot occur in another community in the same time.

Another major difference between our discrete model and Hubbell's model lies in the parameterization for immigration probabilities. Hubbell used the parameter m to denote the probability that either local community receives an immigrant from the metacommunity in which they are imbedded. In our model, the immigration probability is denoted by m^m .

To define the probability of immigration from one local community to the other local community, we use the parameter m^l . This probability corresponds to the parameter m' in Hubbell's model, which defines the conditional probability of immigration into a local community from the other local community given that there is no immigration from the metacommunity. m^l and m' are related: $m' = m^l/(1 - m^m)$ or $m^l = m'/(1 - m)$. It is clear that there is one to one correspondence between the immigration probabilities in Hubbell's model and our model. However, the parameterization of the immigration probabilities proposed in model (2) is more

convenient for analyzing and visualizing results because it allows for formulation of the transition probabilities directly using m^m and m^l .

3. Continuous probabilistic approach

To formulate the corresponding continuous model for species abundance dynamics in the two local communities defined by Eqs. (2) and (3), we first denote the change of the species abundance in local community p per time step Δt by $\Delta N_{p,i}$, thus, $\Delta N_{p,i} = N_{p,i}(t + \Delta t) - N_{p,i}(t)$, $p = 1, 2$. And let $N = (N_1, N_2)$, $N_i = N_{1,i}, N_{2,i}$ and $\Delta N_i = (\Delta N_{1,i}, \Delta N_{2,i})$.

We assume that the species abundance in one local community per one time step Δt can change only by one individual or remains the same. Therefore, the transition probabilities for the non-zero change in the number of individuals of species i in the p th community, $p = 1, 2$, per time step Δt can be defined as:

$$\Pr(\Delta N_{p,i} = \pm 1 | N_{p,i} = N_p, N_{q,i} = N_q) = \mu_p \Delta t W_{p,i}(N_p \pm 1 | N_p, N_q), \tag{4}$$

where μ_p is the number of death per unit time in the p th local community. The joint transition probabilities for the change in species abundance in both communities are:

$$\Pr(\Delta N_{1,i} = \Delta_1, \Delta N_{2,i} = \Delta_2 | N_{1,i} = N_1, N_{2,i} = N_2) = \Pr(N_{1,i} = \Delta_1 | N_{1,i} = N_1, N_{2,i} = N_2) \times \Pr(N_{2,i} = \Delta_2 | N_{2,i} = N_2, N_{1,i} = N_1), \tag{5}$$

where $\Delta_p = -1, 0, 1$ and $p = 1, 2$.

On the basis of the transition probabilities Eqs. (4) and (5), we can easily calculate the first and second moments of the change in the abundance of species i per infinitely small time interval Δt as:

$$V(N) = \begin{pmatrix} V_{11}(N) \\ V_{22}(N) \end{pmatrix} = \lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} \begin{pmatrix} E(\Delta N_{1,i} | N_i = N) \\ E(\Delta N_{2,i} | N_i = N) \end{pmatrix},$$

$$D(N) = \begin{pmatrix} D_{11}(N) & D_{12}(N) \\ D_{21}(N) & D_{22}(N) \end{pmatrix} = \lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} \begin{pmatrix} E(\Delta N_{1,i}^2 | N_i = N) & E(\Delta N_{1,i} \Delta N_{2,i} | N_i = N) \\ E(\Delta N_{1,i} \Delta N_{2,i} | N_i = N) & E(\Delta N_{2,i}^2 | N_i = N) \end{pmatrix}, \tag{6}$$

where (see Appendix)

$$V_p(N) = \mu_p m^m \left(\omega_i - \frac{N_p}{J} \right) + \mu_p m^l \left(\frac{N_q}{J} - \frac{N_p}{J} \right),$$

$$D_{pp}(N) = \mu_p \left[2(1-m) \frac{N_p(J-N_p)}{J(J-1)} + m^m (1-\omega_i) \frac{N_p}{J} + m^m \omega_i \frac{J-N_p}{J} + m^l \frac{J-N_q}{J} \frac{N_p}{J} + m^l \frac{N_q J - N_p}{J} \right],$$

$$D_{12}(N) = D_{21}(N) = 0, \quad p = 1, 2, \quad q = \begin{cases} 2 & \text{if } p = 1, \\ 1 & \text{if } p = 2. \end{cases} \tag{7}$$

Let us now define the abundances x_1 and x_2 of species i in the first and second local communities as continuous variables allowing any real values from the abundance interval, $[0, J]$, $x = (x_1, x_2)$. Then the conditional probability density, $p(x, t)$, that species i has abundances x_1 and x_2 in local communities 1 and 2 at time t satisfies the following Kolmogorov–Fokker–Planck forward equation (Kimura, 1994; Gardiner, 1983):

$$\frac{\partial p}{\partial t} = \frac{1}{2} \left(\frac{\partial^2 D_{11}(x)p}{\partial x_1^2} + \frac{\partial^2 D_{22}(x)p}{\partial x_2^2} \right) - \frac{\partial V_1(x)p}{\partial x_1} - \frac{\partial V_2(x)p}{\partial x_2}, \tag{8}$$

where $x = (x_1, x_2) \in \Omega = (0, J) \times (0, J)$, $t > \tau$, and V and D are the first and second moments of the change in the abundance of species i per time step Δt as $\Delta t \rightarrow 0$ defined in Eqs. (6) and (7).

Eq. (8) is constrained with the initial conditions, defining the probability density of abundance for species i in the two local communities at the initial time moment $t = \tau$:

$$p(x, \tau) = p^0(x), \quad x \in \Omega, \tag{9}$$

and the natural boundary conditions are:

$$\left(\frac{1}{2} \frac{\partial D_{11}p}{\partial x_1} - V_1 p \right) n_1 + \left(\frac{1}{2} \frac{\partial D_{22}p}{\partial x_2} - V_2 p \right) n_2 = 0, \quad x \in \Gamma, \quad t \geq \tau, \tag{10}$$

where Γ is the boundary of the abundance domain Ω , and the vector $\vec{n} = (n_1, n_2)$ is the outward normal to the boundary. Note that the boundary conditions (Eq. (10)) are sufficient for the conservation of probability density:

$$\iint_{\Omega} p(x, \tau) dx_1 dx_2 = \iint_{\Omega} p^0(x) dx_1 dx_2 = 1, \quad \text{for all } t \geq \tau. \tag{11}$$

In order to define the natural boundary conditions (Eq. (10)) more precisely, we need to specify the boundary Γ of the abundance domain $\Omega = (0, J) \times (0, J)$ and the outward normal vectors \vec{n} at each boundary abundance of Ω . It is clear that the abundance boundary Γ consists of four parts $\Gamma = \Gamma^{0*} \cup \Gamma^{*1} \cup \Gamma^{1*} \cup \Gamma^{*0}$, where $\Gamma^{0*} = \{0\} \times (0, J)$, $\Gamma^{*1} = (0, J) \times \{J\}$, $\Gamma^{1*} = \{J\} \times (0, J)$ and $\Gamma^{*0} = (0, J) \times \{0\}$. Therefore, the outward normal vectors are given by $\vec{n}^{0*} = (n_1^{0*}, n_2^{0*}) = (-1, 0)$ for Γ^{0*} , $\vec{n}^{*1} = (n_1^{*1}, n_2^{*1}) = (1, 0)$ for Γ^{*1} , $\vec{n}^{1*} = (n_1^{1*}, n_2^{1*}) = (0, -1)$ for Γ^{1*} and $\vec{n}^{*0} = (n_1^{*0}, n_2^{*0}) = (0, 1)$ for Γ^{*0} . Now we can rewrite the boundary conditions (Eq. (10)) for each part of the boundary, separately, as:

$$\frac{1}{2} \frac{\partial D_{11}p}{\partial x_1} - V_1 p = 0, \quad x \in \Gamma^{0*} \cup \Gamma^{*1},$$

$$\frac{1}{2} \frac{\partial D_{22}p}{\partial x_2} - V_2 p = 0, \quad x \in \Gamma^{*0} \cup \Gamma^{1*}. \tag{12}$$

Equilibrium species abundance distribution of local communities can be considered as a steady state of a long time limit or as a stabilized distribution in the absence of external perturbations. It follows from models (8)–(11) that the equilibrium abundance density of species i in two local communities fulfils the following elliptic differential equation:

$$0 = \frac{1}{2} \left(\frac{\partial^2 D_{11}P}{\partial x_1^2} + \frac{\partial^2 D_{22}P}{\partial x_2^2} \right) - \frac{\partial V_1 P}{\partial x_1} - \frac{\partial V_2 P}{\partial x_2}, \quad x \in \Omega, \tag{13}$$

with boundary conditions (10) or (12) and the total probability over domain Ω equal to 1.

Another problem of interest is the additive species abundance distribution in both local communities, that is the distribution of $x_1 + x_2$. This distribution is useful for comparing the abundance distributions in a local community and a larger local community formed by merging two smaller local communities. The additive species abundance distribution in both local communities can be defined as:

$$p^*(z, t) = \int_0^z p(x_1, z - x_1, t) dx_1 = \int_0^z p(z - x_2, x_2, t) dx_2, \quad z \in \hat{\Omega} = (0, 2J), \tag{14}$$

where $p(x_1, x_2, t)$ under the integral sign is set to be 0 outside the domain Ω .

Finally, using the probability density of the species abundance in two local communities, we can calculate the correlation coefficient between species abundances in the two communities. This coefficient can be used to analyze the association between species abundance dynamics in two linked communities for different immigration probabilities between the local communities and between the metacommunity and local communities.

4. Sensitivity analysis and classification of species abundance dynamics

4.1. Sensitivity analysis of critical species abundance distributions

In this section we propose a sensitivity analysis of species abundance distribution at critical states of abundances in two local communities, that is, in the case when the species is extinct or monodominant in one of the local communities. It is clear that the critical values of species abundances form the boundary Γ of the abundance domain Ω . Therefore, we start our analysis of the type of critical species abundance distributions from boundary conditions (12) for Eq. (8) or (13). These mixed boundary conditions can be rewritten in the form:

$$\begin{aligned} \frac{\partial p}{\partial x_1} + \frac{1}{D_{11}} \left(\frac{\partial D_{11}}{\partial x_1} - 2V_1 \right) p &= 0, \quad x \in \Gamma^{0*} \cup \Gamma^{1*}, \\ \frac{\partial p}{\partial x_2} + \frac{1}{D_{22}} \left(\frac{\partial D_{22}}{\partial x_2} - 2V_2 \right) p &= 0, \quad x \in \Gamma^{*0} \cup \Gamma^{*1}. \end{aligned} \tag{15}$$

We investigate the boundary points at which the change in the abundance across the boundary is negligible or zero. At such boundary points, the respective mixed boundary conditions (see Eq. (15)) degenerate to the reflecting boundary condition. Note that the reflecting boundary conditions, also known as Neumann boundary conditions, imply zero gradient of the probability of species abundances at the boundary abundances.

Let us denote by $(0, x_2^0)$, (J, x_1^1) , $(x_1^0, 0)$ and (x_2^1, J) the boundary points at which the respective reflecting boundary condition holds. These critical points can be found by solving the following equations:

$$\frac{\partial D_{pp}}{\partial x_p} - 2V_p \Big|_{x_p=0} = 0 \quad \text{and} \quad \frac{\partial D_{pp}}{\partial x_p} - 2V_p \Big|_{x_p=J} = 0, \quad p = 1, 2. \tag{16}$$

These solutions can be easily calculated as:

$$\begin{aligned} x^0 &= x_1^0 = x_2^0 \\ &= \left[\frac{1 - (m^m + m^l) J^2}{m^l J^2 - 1} + \frac{m^m + m^l J}{2m^l J + 1} \right] - \omega_i \frac{m^m}{m^l} J, \\ x^1 &= x_1^1 = x_2^1 = - \left[\frac{1 - (m^m + m^l) J^2}{m^l J^2 - 1} + \frac{m^m + m^l J}{2m^l J + 1} \right] \\ &\quad + J + (1 - \omega_i) \frac{m^m}{m^l} J. \end{aligned} \tag{17}$$

Since $x_1^0 = x_2^0$ and $x_1^1 = x_2^1$, the behavior of the species abundance distribution in the first local community if the species is absent or monodominant in the second local community is the same as the behavior in the second local community if the species is absent or monodominant in the first local community. In this case we also see that the signs of the derivatives $\partial p / \partial x_1$ and $\partial p / \partial x_2$ are symmetrical at the parts of the boundaries $\Gamma^{0*} \cup \Gamma^{1*}$ and $\Gamma^{*0} \cup \Gamma^{*1}$. Thus, in order to show the behavior of the species abundance distribution at the boundary Γ of the domain Ω , it is enough to study this distribution at only one pair of the parallel sides $\Gamma^{0*} \cup \Gamma^{1*}$ or $\Gamma^{*0} \cup \Gamma^{*1}$ of the boundary Γ , since the structure of this distribution is the same at another pair of the parallel sides of Γ .

The location of the critical points on the boundary of the abundance domain implies the following statements about the direction of the gradients at the boundary points:

- (a) If $x^0 > 0$, then $(\partial p / \partial x_p) |_{x_p=0} < 0$ for $x_q < x^0$, and if $x^0 < J$, then $(\partial p / \partial x_p) |_{x_p=0} > 0$ for $x_q > x^0$;
 - (b) If $x^1 > 0$, then $(\partial p / \partial x_p) |_{x_p=J} < 0$ for $x_q < x^1$, and if $x^1 < J$, then $(\partial p / \partial x_p) |_{x_p=J} > 0$ for $x_q > x^1$;
- where $q = 2$ if $p = 1$ and $q = 1$ if $p = 2$.

On the basis of the statements (a) and (b), it is straightforward to classify the critical species abundance distributions at the boundary abundances $x_p = 0$ and $x_p = J$ with respect to the abundance values x^0 and x^1 , where the mixed boundary conditions (Eq. (15)) degenerate to the reflecting boundary conditions. The possible cases for the critical species abundance distributions at the boundaries can be distinguished with respect to nine different locations of the abundances x^0 and x^1 in the intervals: $(-\infty, 0)$, $[0, J)$ and $[J, +\infty)$. Fig. 1 shows the shapes of two contours of the species abundance distribution on the critical boundary sides $x_p = 0$ (lower curve) and $x_p = J$ (upper curve).

The type of species abundance distribution is different for species with small metacommunity relative abundances ω_i , i.e., $\omega_i < 1/2$, and for species with large metacommunity relative abundances, i.e., $\omega_i \geq 1/2$. It is unlikely that in the real world species in the metacommunities can reach the relative abundance to 1/2 or higher. Here we use 1/2 cut point as an example of mathematical convenience. Later on we will analyze all possible cases of ω_i .

It follows directly from Table 1, that there are only six possible combinations for x^0 and x^1 for $\omega_i < 1/2$. These are cases (i), (ii), (iii), (v), (vi) and (ix) (see Fig. 1). On the other hand, for $\omega_i \geq 1/2$ there are also only six possible combinations for x^0 and x^1 , that correspond to cases (i), (iv), (v), (vii), (viii) and (ix) in Fig. 1. In Table 1, the conditions for different types of species abundance distribution at the boundary abundances $x_p = 0$ and $x_p = J$ are given using linear combinations of the immigration probabilities m^m and m^l . The ranges of the immigration probabilities m^m and m^l for possible types of critical species abundance distribution at $x_p = 0$ and $x_p = J$ are shown in Fig. 2 for different values of the species abundance fraction in the metacommunity ω_i . These ranges are separated by the lines which connect the points $(m_0^m, 0)$, $(m_1^m, 0)$ and $(0, m_0^l)$, $(0, m_1^l)$, and are located inside the triangle which corresponds to the nonnegative immigration probabilities m^m and m^l with the sum at most 1. The last inequality constraint yields oftentimes reduction in the number of possible combinations for the critical species abundance distributions at the boundary abundances $x_p = 0$ and $x_p = J$ (see Fig. 2). For example, in the case when ω_i is very small or very large, i.e., $0 \leq \omega_i \leq \omega^* = 1/[2(J+1)]$ or $1 - \omega^* \leq \omega_i \leq 1$, Fig. 2 shows that combination (i) is not feasible. Therefore, combination (i) is possible only for the species with the metacommunity relative abundances from the interval: $\omega^* < \omega_i < 1 - \omega^*$. It is also possible to define the conditions for the type of the species abundance distribution in terms of the size of local communities J . For example, combination (i) is only possible when the size of the local community is large enough, that is when $J > 1/[2\min\{\omega_i, 1 - \omega_i\}] - 1$.

The two separate cases for the critical species abundance distribution in two local communities are of the particular interest. These cases are for isolated local communities from the metacommunity when $m^m = 0$, and for isolated local communities from each other when $m^l = 0$. In the case when $m^m = 0$, the type of the species abundance distribution in the local communities differs for the values of the immigration probability between local communities m^l that are smaller or larger than $m_1^l \approx 2/(2J - 1)$. Similarly, in the case when $m^l = 0$, the type of the species abundance distribution depends on the values $m_0^m = 2J/[(J+1)(2\omega_i(J-1)+1)]$ and $m_1^m = 2J/[(J+1)(2(1-\omega_i)(J-1)+1)]$ for the immigration probability from the metacommunity m^m (see Fig. 2).

Finally, it is worth noting, that the type of the critical species abundance distribution at the boundary of the abundance domain is independent of the numbers of death events per unit time step in local communities, μ_1 and μ_2 . For unequal parameters μ_1 and μ_2 , the equilibrium species abundance distributions in both local

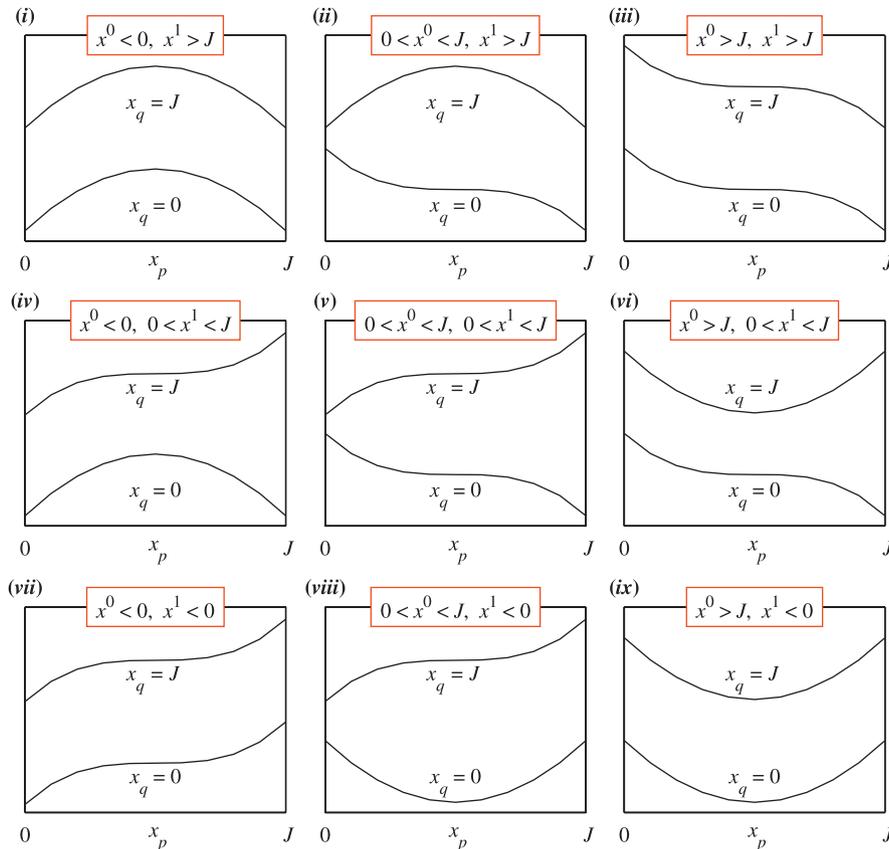


Fig. 1. The shapes of the critical probability density of the species abundance in the p th local community if the species is absent $x_q = 0$ (lower line) and monodominant $x_q = J$ in the q th local community. These shapes are constructed based on the location of x^0 and x^1 with respect to the interval $[0, J]$. Possible combinations for $\omega_i < 1/2$ are in the upper triangle of the figure, i.e., cases (i)–(iii), (v), (vi) and (ix). Possible combinations for $\omega_i \geq 1/2$ are in the lower triangle of the figure, i.e., cases (i), (iv), (v) and (vii)–(ix).

communities will not be identical. These parameters are related rather to the time scale of the species abundance dynamics in the local communities than to the type of species distribution at the equilibrium state.

4.2. Species abundance dynamics

Using the results of Section 4.1, we can extend the analysis of the species abundance distribution to the case when the species is present in both local communities. Moreover, we are able to propose a classification of the species abundance dynamics in local communities with respect to the immigration probabilities, metacommunity relative abundance and the sizes of local communities.

The type of critical species abundance distribution at the boundaries of the abundance domain defines the behavior of the species and the type of species abundance distribution in both local communities. On the basis of the behavior of the species at the critical boundary states, we can conclude whether the species in the system of local communities is persistent, goes extinct or becomes monodominant in one or both local communities. Hereafter, we refer to the different types of joint species abundance distributions as the scenarios of species abundance dynamics in two local communities. The ecological characteristics for all scenarios for species abundance distribution and their respective species abundance dynamics are presented in Table 2.

Fig. 3 shows the possible species abundance dynamics scenarios in two local communities of size $J = 200$. The frequencies of the death events in both local communities are equal,

$\mu_1 = \mu_2$. We assume that species of interest, say species i , has small relative abundance in the metacommunity, $\omega_i = 0.2 < 1/2$. Note that the analysis of the common species ($\omega_i > 1/2$) can be provided in analogous manner.

There are at most six possible scenarios for the species abundance dynamics in the case when the metacommunity relative abundance is smaller than 1/2, these are scenarios (i)–(iii), (v), (vi) and (ix). To illustrate all these scenarios, we have chosen the values for the immigration probabilities from each scenario (Fig. 2 and Table 1). Fig. 3 shows the 3D and contour plots of the abundance density of species i for each possible species abundance dynamics scenario. It also shows the additive species abundance distributions in both local communities. Note that in this experiment, equilibrium species abundance distributions is independent of the equal values of the parameters μ_1 and μ_2 , since these parameters specify the speed of the convergence to equilibrium species abundance distributions and play a role of the time scale in the dynamics of the species abundances in the local communities. Therefore, a constant value of 0.0001 for the parameters μ_1 and μ_2 was used in all experiments.

The types of the species abundance distributions presented in Fig. 3 correspond to the description of the species abundance dynamics scenarios given in Table 2. These species abundance dynamics scenarios can be explained well in terms of the immigration processes between local communities and between local communities and the metacommunity. For example, in Scenario (ix), the local communities are very weakly connected with each other and with the metacommunity. These local communities behave very similarly to the isolated local communities in which the species goes extinct or becomes

Table 1
Conditions for parameters of the model required for each combination of values x^0 and x^1 specified by cases (i)–(ix)

Combination	x^0 and x^1	Conditions
(i)	$x^0 \leq 0$ $J < x^1$	$2J/(J+1) \leq w_{\omega_1}^l(m^m, m^l)$ $2J/(J+1) < w_{1-\omega_1}^l(m^m, m^l)$
(ii)	$0 < x^0 \leq J$ $J < x^1$	$w_{\omega_1}^l(m^m, m^l) < 2J/(J+1) \leq v_{\omega_1}^l(m^m, m^l)$ $2J/(J+1) < w_{1-\omega_1}^l(m^m, m^l)$
(iii)	$J < x^0$ $J < x^1$	$v_{\omega_1}^l(m^m, m^l) < 2J/(J+1)$ $2J_p/(J_p+1) < w_{1-\omega_1}^p(m_p^m, m_p^l)$
(iv)	$x^0 \leq 0$ $0 < x^1 \leq J$	$2J/(J+1) \leq w_{\omega_1}^l(m^m, m^l)$ $w_{1-\omega_1}^l(m^m, m^l) \leq 2J/(J+1) < v_{1-\omega_1}^l(m^m, m^l)$
(v)	$0 < x^0 \leq J$ $0 < x^1 \leq J$	$w_{\omega_1}^l(m^m, m^l) < 2J/(J+1) \leq v_{\omega_1}^l(m^m, m^l)$ $w_{1-\omega_1}^l(m^m, m^l) \leq 2J/(J+1) < v_{1-\omega_1}^l(m^m, m^l)$
(vi)	$J < x^0$ $0 < x^1 \leq J$	$v_{\omega_1}^l(m^m, m^l) < 2J/(J+1)$ $w_{1-\omega_1}^l(m^m, m^l) \leq 2J/(J+1) < v_{1-\omega_1}^l(m^m, m^l)$
(vii)	$x^0 \leq 0$ $x^1 \leq 0$	$2J/(J+1) \leq w_{\omega_1}^l(m^m, m^l)$ $v_{1-\omega_1}^l(m^m, m^l) \leq 2J/(J+1)$
(viii)	$0 < x^0 \leq J$ $x^1 \leq 0$	$w_{\omega_1}^l(m^m, m^l) < 2J/(J+1) \leq v_{\omega_1}^l(m^m, m^l)$ $v_{1-\omega_1}^l(m^m, m^l) \leq 2J/(J+1)$
(ix)	$J < x^0$ $x^1 \leq 0$	$v_{\omega_1}^l(m^m, m^l) < 2J/(J+1)$ $v_{1-\omega_1}^l(m^m, m^l) \leq 2J/(J+1)$

$$w_{\omega_1}^l(m^m, m^l) = m^m(2\omega(J-1) + 1) + m^l \quad \text{and} \quad v_{\omega_1}^l(m^m, m^l) = m^m(2\omega(J-1) + 1) + m^l(2J-1).$$

monodominant (Hubbell, 2001). Therefore, in Scenario (ix), the species abundance combinations (0, 0), (J, 0), (0, J) and (J, J) have maximal probabilities. For closely connected local communities species behavior becomes more similar. In this case, a species has very high chance of simultaneous extinction or simultaneous monodominance in both local communities (Fig. 3(v) and (vi)). For close connection between local communities and the metacommunity, species in the metacommunity have strong effect on the species abundance behavior in the local communities. As a result, the chance of species extinction is very high from both local communities (Fig. 3(ii) and (iii)); or the species becomes highly persistent in the local communities (Fig. 3(i)).

Finally, in the case when the frequencies of death events in both local communities are different, i.e., $\mu_1 \neq \mu_2$, we can perform the same analysis of the species abundance dynamics as in the case $\mu_1 = \mu_2$. Since the frequencies of the death events in local communities can be eliminated from boundary conditions (12), we can conclude that the type of species abundance distribution at the boundary of the domain Ω , and, therefore, the species abundance dynamics scenario are independent of death frequencies, μ_1 and μ_2 .

5. Correlation between species abundances in two local communities

Correlation between species abundances in two local communities can be considered as a measure of similarity of local communities. It can be easily calculated using the probability

density of the species abundances in two local communities. Fig. 4 shows the plot of correlation between species abundances in two local communities as a function of immigration probabilities m^m and m^l . This correlation can be well-quantified by an empirical relationship that was numerically obtained from simulated correlation coefficients based on Eqs. (12) and (13):

$$r \approx \frac{m^l}{m^m + m^l}. \tag{18}$$

It is clear that for very small immigration probability from the metacommunity m^m , the correlation between species abundance in two local communities is close to 1. For very small immigration probability between local communities m^l , the correlation is close to 0.

Let us consider all of these cases more closely. When the two local communities are isolated from the metacommunity, i.e., $m^m = 0$, the abundance dynamics for a given species possesses two absorbing states corresponding to extinction and monodominance of the species in both local communities. Note that the same was observed for the species abundance dynamics in one local community (Hubbell, 2001; Babak, 2006). When species abundances in both local communities become equal to (0, 0) or (J, J), the correlation coefficient between species abundances in the two deterministic local communities becomes 1, i.e., we observe perfect linear correlation between the local communities. When the immigration probability m^m is very small, the species abundances in two local communities are most of the time at the levels (0, 0) or (J, J). This is because new immigrants seldom perturb the species abundance compositions of the local communities. As a result, correlation between species abundances in two local communities is close to 1.

On the other hand, when the local communities are isolated one from the other, i.e., $m^l = 0$, the species abundances in mutually isolated local communities are changing independent of each other, and, therefore, the correlation between species abundances is zero. If the connection between local communities is very weak, the species abundance dynamics in one local community is almost independent of the other local community, thus, the correlation coefficient in this case is very small.

From Fig. 4, we can also note that when the probability of immigration from the metacommunity is fixed, the correlation increases with increase in immigration between local communities. This is because the similarity of species abundance dynamics in two local communities increases with the intensity of the immigration between local communities. On the other hand, when the probability of immigration between local communities is fixed, the correlation between the two local communities reduces with the increase in the probability of immigration from the metacommunity. In this case, the balance between local and global immigration is shifted towards the prevalence of the immigration from the metacommunity. Thus, less similarity in the species abundance composition for both local communities is observed. Note that Hubbell (2001, Chapter 7) qualitatively obtained the same conclusions for the covariance between species abundances in two local communities. Our empirical Eq. (18) is a useful extension of this finding.

6. Discussion

In this paper species abundance dynamics in two local communities of equal size was studied. We analyzed a model that describes species dynamics in similar patches or islands connected to a large metacommunity. The model for species abundance dynamics in two local communities of equal size was developed in line with the framework of Hubbell's zero-sum local

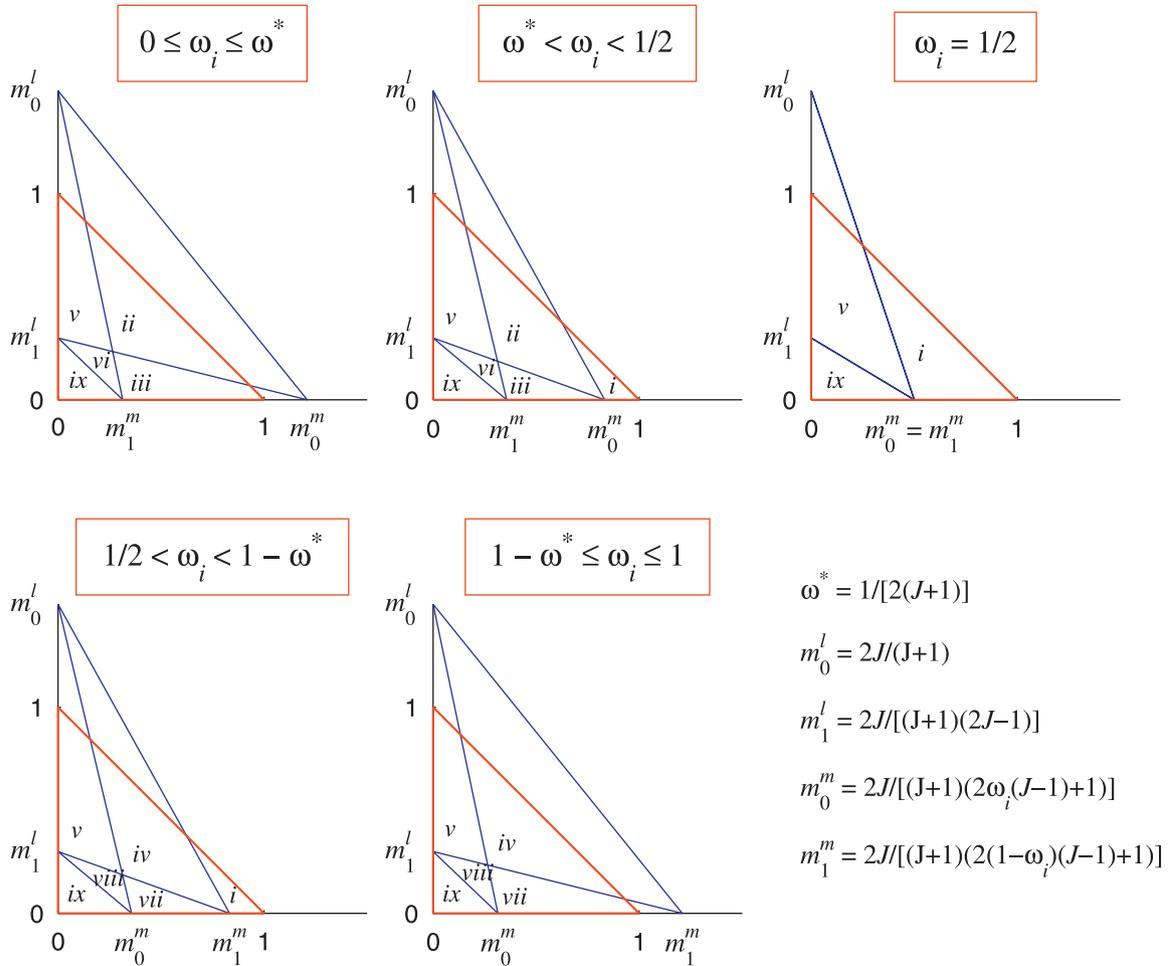


Fig. 2. Illustration of different cases for species abundance distribution with respect to the values of immigration probabilities m^m and m^l subject to the conditions $m^m + m^l \leq 1$, and $m^m \geq 0$, $m^l \geq 0$. There are only three possible scenarios for $\omega_i = 1/2$, six possible scenarios if $\omega^* < \omega_i < 1/2$ or $1/2 < \omega_i < 1 - \omega^*$, and five possible combinations if $0 \leq \omega_i < \omega^*$ or $1 - \omega^* < \omega_i \leq 1$. The scenarios (i), (ii), etc. are defined in Table 1.

Table 2
Description of species abundance scenarios in terms of species extinction (E), monodominance (M) and persistence (P) in one or both local communities

Scenario	Behavior of a species		
	In both communities	In one community given that the species in the other community is	
		Extinct	Monodominant
(i)	SP	P	P
(ii)	SE	E	P
(iii)	SE	E	E
(iv)	SM	P	M
(v)	SE or SM	E	M
(vi)	SE or SM	E	E or M
(vii)	SM	M	M
(viii)	SE or SM	E or M	M
(ix)	E or M	E or M	E or M

The abbreviations SP, SE and SM correspond to simultaneous persistence, simultaneous extinction and simultaneous monodominance of the species in both local communities, respectively.

community. To analyze the model for species abundance dynamics, a continuous probabilistic approach was applied. Specifically, Kolmogorov–Fokker–Planck forward equation for

the distribution of species abundance in two local communities was derived and analyzed.

We did a detailed analysis of species abundance distributions for two local communities at the equilibrium state. We obtained a classification of species abundance dynamics in two local communities with respect to different species characteristics such as immigration intensity, species representation in the metacommunity and the size of local communities. On the basis of different ecological features such as species persistence, extinction and monodominance in one or both local communities, several different scenarios for species abundance dynamics were distinguished.

The similarities of the species abundance dynamics in two local communities are useful for understanding the distribution of species assemblages on landscapes. It was found that for a fixed probability of immigration from the metacommunity, the correlation increases with an increase in the immigration between local communities. On contrary, for a fixed probability of immigration between local communities, the correlation decreases with an increase in the immigration from the metacommunity. Therefore, immigration between local communities has a homogenization effect, while immigration from the metacommunity has a differentiation effect. Moreover, approximation (Eq. (18)) provides a method for inferring the correlation between species abundance in local communities.

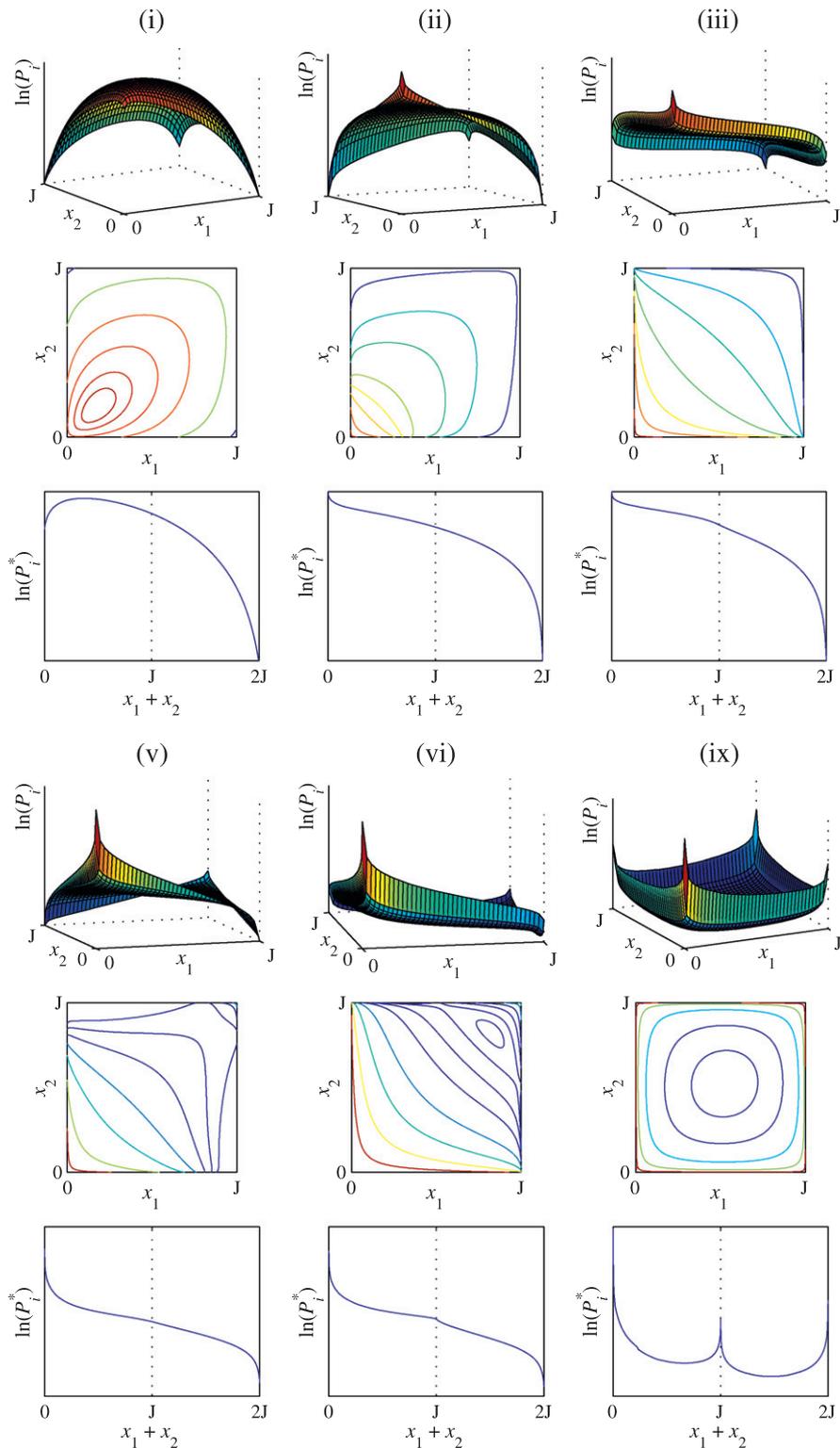


Fig. 3. Illustration of possible scenarios for species abundance probability density in two equal local communities of size $J = 200$, and $\mu_1 = \mu_2$ with respect to different values of immigration probabilities. The metacommunity species relative abundance is assumed to be $\omega_i = 0.2 < 1/2$. Panels on the top row are 3D log-plots and the middle row are the contour plots for the equilibrium species abundance probability densities obtained using numerical approximations for problem Eqs. (11)–(13). Panels on the bottom row show the additive equilibrium species abundance probability functions calculated using Eq. (14). The values of immigration probabilities for each scenario are chosen to be: (i) $m^m = 0.1$, $m^l = 0.1$; (ii) $m^m = 0.01$, $m^l = 0.01$; (iii) $m^m = 0.01$, $m^l = 0.001$; (v) $m^m = 0.005$, $m^l = 0.005$; (vi) $m^m = 0.005$, $m^l = 0.002$; (ix) $m^m = 0.001$, $m^l = 0.001$.

The model for species abundance dynamics in two local communities proposed in this study allows us to better understand the processes in the subdivision of landscapes. Although our model,

like Hubbell's model, is also spatially implicit, the discrete consideration of local communities provides useful insights for studying the effect of landscape fragmentation on species diversity.

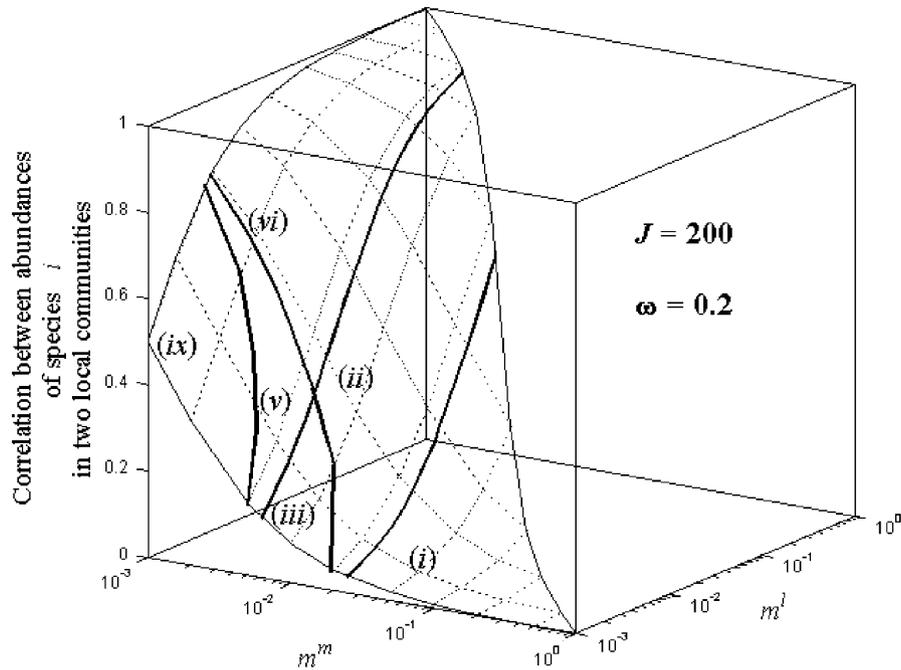


Fig. 4. Correlation between abundance of species i in two local communities as a function of probability of immigration from the metacommunity m^m and from another local community m^l , $m^m + m^l \leq 1$. The size of local community $J = 200$, and the metacommunity species relative abundance $\omega_i = 0.2$. The surface is divided into the areas of the immigration probabilities from different types of species abundance dynamics represented by scenarios (i), (ii), (iii), (v), (vi) and (ix).

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Appendix

Using Eqs. (4) and (5), we get for the first local community

$$\begin{aligned} & \frac{1}{\Delta t} E(\Delta N_{1,i} | N_i = N) \\ &= \frac{1}{\Delta t} \left[1 \times \sum_{z=-1,0,1} Pr(\Delta N_{1,i} = 1, \Delta N_{2,i} = z | N_{1,i} = N_1, N_{2,i} = N_2) \right. \\ & \quad \left. + (-1) \times \sum_{z=-1,0,1} Pr(\Delta N_{1,i} = -1, \Delta N_{2,i} = z | N_{1,i} = N_1, N_{2,i} = N_2) \right] \\ &= \frac{1}{\Delta t} [Pr(\Delta N_{1,i} = 1 | N_{1,i} = N_1, N_{2,i} = N_2) \\ & \quad - Pr(\Delta N_{1,i} = -1 | N_{1,i} = N_1, N_{2,i} = N_2)] \\ &= \mu_1 W_{1,i}(N_1 + 1 | N_1, N_2) - \mu_1 W_{1,i}(N_1 - 1 | N_1, N_2), \end{aligned}$$

analogously, for the second local community

$$\begin{aligned} & \frac{1}{\Delta t} E(\Delta N_{2,i} | N_i = N) \\ &= \mu_2 W_{2,i}(N_2 + 1 | N_2, N_1) - \mu_2 W_{2,i}(N_2 - 1 | N_2, N_1). \end{aligned}$$

Using Eq. (2), we obtain the identities for $V_1(N)$ and $V_2(N)$ in Eq. (7). Similarly, we can compute

$$\begin{aligned} & \frac{1}{\Delta t} E(\Delta N_{1,i}^2 | N_i = N) \\ &= \frac{1}{\Delta t} \left[1^2 \times \sum_{z=-1,0,1} Pr(\Delta N_{1,i} = 1, \Delta N_{2,i} = z | N_{1,i} = N_1, N_{2,i} = N_2) \right. \\ & \quad \left. + (-1)^2 \times \sum_{z=-1,0,1} Pr(\Delta N_{1,i} = -1, \Delta N_{2,i} = z | N_{1,i} = N_1, N_{2,i} = N_2) \right] \end{aligned}$$

$$\begin{aligned} &= \frac{1}{\Delta t} [Pr(\Delta N_{1,i} = 1 | N_{1,i} = N_1, N_{2,i} = N_2) \\ & \quad + Pr(\Delta N_{1,i} = -1 | N_{1,i} = N_1, N_{2,i} = N_2)] \\ &= \mu_1 W_{1,i}(N_1 + 1 | N_1, N_2) + \mu_1 W_{1,i}(N_1 - 1 | N_1, N_2) \end{aligned}$$

and

$$\begin{aligned} & \frac{1}{\Delta t} E(\Delta N_{2,i}^2 | N_i = N) \\ &= \mu_2 W_{2,i}(N_2 + 1 | N_2, N_1) + \mu_2 W_{2,i}(N_2 - 1 | N_2, N_1). \end{aligned}$$

Therefore, in view of Eq. (2), the identities for $D_{11}(N)$ and $D_{22}(N)$ in Eq. (7) hold.

Finally,

$$\begin{aligned} & \frac{1}{\Delta t} E(\Delta N_{1,i} \Delta N_{2,i} | N_i = N) \\ &= \frac{1}{\Delta t} [1 \times 1 \times Pr(\Delta N_{1,i} = 1, \Delta N_{2,i} = 1 | N_{1,i} = N_1, N_{2,i} = N_2) \\ & \quad + (-1) \times 1 \times Pr(\Delta N_{1,i} = -1, \Delta N_{2,i} = 1 | N_{1,i} = N_1, N_{2,i} = N_2) \\ & \quad + 1 \times (-1) \times Pr(\Delta N_{1,i} = 1, \Delta N_{2,i} = -1 | N_{1,i} = N_1, N_{2,i} = N_2) \\ & \quad + (-1) \times (-1) \times Pr(\Delta N_{1,i} = -1, \Delta N_{2,i} = -1 | N_{1,i} = N_1, N_{2,i} = N_2)] \\ &= \Delta t \mu_1 \mu_2 [W_{1,i}(N_1 + 1 | N_1, N_2) W_{2,i}(N_2 + 1 | N_2, N_1) \\ & \quad - W_{1,i}(N_1 - 1 | N_1, N_2) W_{2,i}(N_2 + 1 | N_2, N_1) \\ & \quad - W_{1,i}(N_1 + 1 | N_1, N_2) W_{2,i}(N_2 - 1 | N_2, N_1) \\ & \quad + W_{1,i}(N_1 - 1 | N_1, N_2) W_{2,i}(N_2 - 1 | N_2, N_1)] \sim \Delta t. \end{aligned}$$

Hence,

$$\begin{aligned} D_{12}(N) &= D_{21}(N) \\ &= \lim_{\Delta t \rightarrow 0} (1/\Delta t) E(\Delta N_{1,i} \Delta N_{2,i} | N_i = N) = 0. \end{aligned}$$

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