

Continuous probabilistic approach to species dynamics in Hubbell's zero-sum local community

Petro Babak*

Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, Alberta, Canada, T6G 2H1

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In this paper a continuous probabilistic approach formulated using Kolmogorov-Fokker-Planck forward and backward models is applied to Hubbell's zero-sum neutral theory for species dynamics in local community. Using this technique the probability density of species abundance, distribution of the first passage time to extinction or fixation and probability of extinction are defined. The resulting values for the distribution of the first passage time to extinction are verified by the simulation study of Hubbell's zero-sum neutral model for the local community. Based on the sensitivity analysis for the continuous probabilistic models, the realistic classification of local communities subject to their diversity and species dynamics is proposed with respect to the immigration probability, the species metacommunity relative abundance, and the size of local community.

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The main goals of biodiversity study are to explain and quantify the distribution, abundance, and dynamics of living organisms in ecological communities. These questions are also of central theoretical and practical importance in conservation biology and ecosystem management [1,2], since understanding the mechanisms of species abundance dynamics is of high concern in viability analysis.

Species abundance relationships have long been studied by ecologists, who defined them as species commonness and rarity in ecological communities [1,3,4]. These relationships are usually described by species abundance distributions which show the number of species as the functions of their observed abundances.

Early studies on species abundance relationships were focused on finding distributions that could fit well empirical data. Among the proposed distributions were the log-series [5] and the log-normal [6]. Later the preference was given to modeling species abundance relationships using one or another ecological theory of community organization. Using this approach the broken-stick model was proposed by MacArthur [7,8]; the log-normal patterns of species abundances were explained using the niche preemption model [9–11], and using the dynamic population model with Gompertz density dependence [12]. The gamma type of abundance distribution, including Fisher's log-series, the extended gamma distribution, and MacArthur's broken-stick model, was elucidated using the dynamic approach with logistic density dependence [13].

In this paper another theory of the species abundance relationships is discussed. This theory is based on the assumption of neutrality, which, on the contrary to the niche theory, does not assume differences between individuals of different species and trophic hierarchy of community [14–16]. Although the concept of neutral community appeared a long time ago [17], it has not attracted much attention until Hubbell published his monograph [16], where he proposed a neutral theory that unifies theories of biodiversity and biogeography. The reference ecosystem of Hubbell's neutral theory

is a group of trophically similar, sympatric species that complete for the same or similar resources [15,16]. Hubbell's theory was constructed on the basis of the assumption about the zero-sum dynamics, which states that the sum of all changes in species abundances is always zero, that is, the total number of individuals in the community is a conserved quantity [16]. Based on this assumption, the neutral theory predicts the existence of new statistical distribution of relative species abundance, called the zero-sum multinomial [16]. This distribution is close to a log-series for large immigration probabilities, and is more "humped" for small immigration probabilities [14,18]. The analytical formalization for zero-sum multinomials and other distributions generated under assumption of neutrality was obtained in Refs. [19–23]. The performance of the zero-sum multinomial has been intensively compared only with the log-normal distribution [16,18,23–27]. Hubbell showed that the zero-sum multinomial distribution fits tropical forest tree and coral reefs datasets better than the log-normal [16,28]. However, according to recent analysis, even if the log-normal theories do not lead to biologically realistic species abundance distributions [27], one cannot always distinguish between these two distributions from empirical data [18].

Since the time when Hubbell's neutral theory was established, the neutral theories in ecology has been developed in many published works, they have been enriched with a large amount of theoretical results [16,19–23,27,29–34], intensive discussion [15,24,26,27,35–38] and testing [14,16,18,23–25,27].

In the framework of Hubbell's neutral theory the populations are studied in two scales: local community and regional metacommunity [16,21]. The dynamics of species abundances on the local scale depends on species representation in the metacommunity—a large reservoir of all trophically similar individuals and species with constant fractional species abundances, on the intensity of immigration from the metacommunity and, of course, on the size of local community. Based on the principle of neutrality and zero-sum assumption Hubbell defined the model for the abundance N_i of species i ($i=1, \dots, S$) in a local community of size J , $J = \sum_{j=1}^S N_j$, using the following transition probabilities [16]:

*FAX: 780-492-4323. Email address: petro@ualberta.ca

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

where ω_i is the fractional metacommunity relative species abundance of the i th species, m is the probability that a death in the local community will be replaced by an immigrant, and S is the total number of species.

Hubbell's model is neutral, so it does not involve any effect of mating system. Each individual has equal opportunity to migrate and reproduce independently of species abundance and size of local community. The dynamics of species abundance in neutral local community is described, basically, in the same way as the dynamics of haploid genes in population genetics [38].

For Hubbell's model governed by Eq. (1), the species abundance distribution and the first passage time of the species to extinction or fixation in a local community were investigated using the Markov chain approach [16]. Hubbell noticed that the species abundance distribution can take on different shapes with respect to the immigration probability, metacommunity relative abundance, and community size. In the case of an isolated community it was shown that the mean time to fixation (extinction or complete dominance) varies as a function of community size and initial species abundance, and this time is maximal when the initial abundance of the species is half of the community size. For non-isolated local communities the mean and variance of the first passage time of the species to extinction were also investigated and, moreover, it was proposed that the time to local extinction in the ergodic community is approximately gamma distributed [16].

The same results for the species abundance distribution were obtained using Birth-Death Master equation approach [21–23], by which the probability that the i th species contains N individuals at time t is governed by the following system of ordinary differential equations:

$$\begin{aligned}
 \frac{dp_{N,i}}{dt} &= W_i(N|N+1)p_{N+1,i} + W_i(N|N-1)p_{N-1,i} \\
 &\quad - [W_i(N+1|N) + W_i(N-1|N)]p_{N,i}, \quad (2)
 \end{aligned}$$

where $N=0, \dots, J$ and $W_i(0|-1) = W_i(J|J+1) = 0$.

Based on the Birth-Death Master equation approach Volkov *et al.* [23] obtained the average number of species with specified abundance in a local community. The number of species $\phi_N(t)$ containing N individuals at time t was defined as

$$\phi_N(t) = \sum_{j=1}^S I_j(N, t), \quad (3)$$

where the indicator $I_j(N, t)$ is a random variable, which takes the value 1 with probability $p_{N,j}(t)$ and 0 with probability

$1 - p_{N,j}(t)$, and the average number of species containing N individuals was calculated as

$$\langle \phi_N(t) \rangle = \sum_{j=1}^S p_{N,j}(t). \quad (4)$$

For S demographically identical species in a community the average number of species was obtained as

$$\langle \phi_N(t) \rangle = S p_N(t), \quad (5)$$

where $p_N(t)$'s satisfy system of Eq. (2) with $\omega = \omega_i = 1/S$.

Up to this time, for analysis of Hubbell's zero-sum neutral local community only discrete methods were applied. Such methods are used when the main focus of research is on the investigation of small living systems; for large systems these methods are inextricable due to a large number of variables and equations. In contrast to discrete methods, continuous methods not only allow us to analyze arbitrary large communities, but also investigate such important quantities for community ecology and conservation biology as persistence probability, risk, or probability of extinction, the distribution of the first passage time of the species to extinction, see Refs. [39,40].

In this paper a continuous probabilistic technique will be applied for the investigation of Hubbell's zero-sum neutral community theory. It will give as a possibility not only to derive the species abundance distribution and the moments of the first passage time to extinction or fixation, but also to define the distribution of the first passage time to extinction and make a classification of the species dynamics in local communities with respect to the immigration, species abundance in the metacommunity, and size of local community. Note that the distribution of the first time to extinction and the quantitative classification of Hubbell's zero-sum local communities have not been obtained before.

The paper is organized as follows. In Sec. I, the continuous model for the probability density of species abundance is derived using the Kolmogorov-Fokker-Planck forward equation. Based on the probability density of species abundance in the local community the distribution of the number of species with the specified abundance is obtained. In Sec. II, the continuous approach is applied to the study of the time development of species abundance distribution in the local community. Using the Kolmogorov-Fokker-Planck backward equation technique the distribution and moments of the first passage time to extinction, and the probability of the species extinction from the local community are obtained. In Sec. III, the sensitivity analysis is performed for the equilibrium species abundance distribution, extinction, and fixation times. According to this analysis four realistic scenarios for the species dynamics are distinguished with respect to the immigration probability, species metacommunity relative abundance, and the size of the local community. And, finally, a comparison of the simulation study results with the results of the continuous analysis is presented.

I. SPECIES ABUNDANCE DISTRIBUTION

A. Modified model

In order to derive the continuous model for the species abundance distribution in a zero-sum local community of size J , we define the transition probabilities for the change ΔN_i of the number of individuals N_i of the i th species per time step Δt as

$$\Pr(\Delta N_i = -1 | N_i = N) = \mu \Delta t W_i(N-1 | N),$$

$$\Pr(\Delta N_i = 1 | N_i = N) = \mu \Delta t W_i(N+1 | N),$$

$$\Pr(\Delta N_i = 0 | N_i = N) = 1 - \mu \Delta t [W_i(N-1 | N) + W_i(N+1 | N)], \quad (6)$$

where $J = \sum_{j=1}^S N_j$, S is the number of all species, $\Delta N_i = N_i(t + \Delta t) - N_i(t)$, ω_i is the fractional metacommunity relative species abundance of the i th species, $i = 1, \dots, S$, m is the probability that a death in the local community will be replaced by an emigrant, and μ is the number of death events per unit time interval. Note that the system of transition probabilities (6) is derived from Hubbell's zero-sum model (1).

For the random variable ΔN_i , which takes the values -1 , 0 , and 1 with probabilities specified in (6), the first and second moments per the infinitely small time interval Δt can be easily calculated as

$$V_i(N) = \lim_{\Delta t \rightarrow 0} \frac{E(\Delta N_i | N_i = N)}{\Delta t} = \mu m \left(\omega_i - \frac{N}{J} \right),$$

$$\begin{aligned} D_i(N) &= \lim_{\Delta t \rightarrow 0} \frac{E[(\Delta N_i)^2 | N_i = N]}{\Delta t} \\ &= \mu \left[2(1-m) \frac{N(J-N)}{J(J-1)} + m(1-\omega_i) \frac{N}{J} + m\omega_i \left(1 - \frac{N}{J} \right) \right]. \end{aligned} \quad (7)$$

B. Dynamics of species abundance distribution.

Kolmogorov-Fokker-Planck forward equation

To introduce a continuous model for the distribution of the species abundance, we define the abundance n of the i th species as a continuous variable allowing any real values from the interval $[0, J]$. Then the conditional probability density, $p_i(n, t)$, that the i th species has abundance n at time t satisfies the Kolmogorov-Fokker-Planck forward equation

$$\frac{\partial p_i}{\partial t} = \frac{1}{2} \frac{\partial^2}{\partial n^2} [D_i(n) p_i] - \frac{\partial}{\partial n} [V_i(n) p_i], \quad (8)$$

where $n \in (0, J)$, $t > \tau$, and $V_i(n)$ and $D_i(n)$ are the first moment and the variance of the change in the abundance per time step Δt as $\Delta t \rightarrow 0$ defined in (7).

Equation (8) is supplemented with the initial condition defining the probability density of species abundance $p_i^0(n)$ at the initial time moment $t = \tau$

$$p_i(n, \tau) = p_i^0(n), \quad n \in [0, J]. \quad (9)$$

Equation (8) is considered subject to the following natural boundary conditions:

$$\frac{1}{2} \frac{\partial}{\partial n} [D_i(n) p_i] - [V_i(n) p_i] = 0, \quad (10)$$

at $n=0$ and $n=J$. The boundary conditions (10) are sufficient for the conservation of probability density

$$\int_0^J p_i(n, t) dn = \int_0^J p_i^0(n) dn = 1, \quad \text{for all } t > \tau. \quad (11)$$

C. Equilibrium species abundance distribution

The equilibrium (the steady state) solution P_i of Eqs. (8)–(11) fulfills the following ordinary differential equation of the second order:

$$0 = \frac{1}{2} \frac{d^2}{dn^2} [D_i(n) P_i] - \frac{d}{dn} [V_i(n) P_i], \quad n \in (0, J), \quad (12)$$

and boundary conditions (10), where the total probability over the interval $[0, J]$ equals 1.

Equation (12) can be easily transformed to the ordinary differential equation of the first order

$$0 = \frac{1}{2} \frac{d}{dn} [D_i(n) P_i] - [V_i(n) P_i], \quad n \in (0, J), \quad (13)$$

with the integral condition,

$$\int_0^J P_i(n) dn = 1, \quad (14)$$

representing the total probability instead of boundary conditions.

Eqs. (13) and (14) can be explicitly solved. The steady state solution is

$$\begin{aligned} P_i(n) &= \exp \left(\int_0^n \frac{2V_i(y) - D_i'(y)}{D_i(y)} dy \right) \\ &\times \left[\int_0^J \exp \left(\int_0^x \frac{2V_i(y) - D_i'(y)}{D_i(y)} dy \right) dx \right]^{-1}. \end{aligned} \quad (15)$$

For known coefficients V_i and D_i from (7), expression (15) can be transformed to

$$P_i(n) = C_i \left(\frac{n_- - n}{n_-} \right)^{\alpha_-} \left(\frac{n_+ - n}{n_+} \right)^{-\alpha_+},$$

$$C_i = \left[\int_0^J \left(\frac{n_- - y}{n_-} \right)^{\alpha_-} \left(\frac{n_+ - y}{n_+} \right)^{-\alpha_+} dy \right]^{-1}, \quad (16)$$

where $n_{\pm} = -(d_1 \pm \sqrt{d_1^2 - 4d_0 d_2} / 2d_2)$, $\alpha_{\pm} = -[2n_{\pm}(v_1 - d_2) + 2v_0 - d_1] / d_2(n_+ - n_-)$, $d_0 = v_0 = m\omega_i$, $v_1 = -m/J$, $d_1 = 2(1-m)/J - 1 + m(1-2\omega_i)/J$, and $d_2 = -1 - m/J(J-1)$.

It follows from Eqs. (15) and (16) that the steady state distribution of the species abundance is independent of the

parameter μ which corresponds to the time scale.

We would like to emphasize on the symmetry property of the probability density of species abundance in a local community of size J stated as

$$P_i(n)|_{\omega_i=\omega} = P_i(J-n)|_{\omega_i=1-\omega}. \quad (17)$$

This property can be easily explained for the distribution of two species with the metacommunity relative abundances ω and $1-\omega$, respectively. In view of (17), the probabilities that the first species abundance is n and the second species abundance is $J-n$ are equal.

D. Number of species with specified abundances

By an analogy with Eqs. (3)–(5), see Refs. [23,32], the number of species containing from n_1 to n_2 individuals at time t can be defined as

$$\phi(n_1, n_2, t) = \sum_{j=1}^S I_j(n_1, n_2, t), \quad (18)$$

where S is the total number of species and indicator $I_j(n_1, n_2, t)$ is a random variable which takes the value 1 with probability $\int_{n_1}^{n_2} p_j(n, t) dn$ and 0 with probability $1 - \int_{n_1}^{n_2} p_j(n, t) dn$; p_j satisfies Eqs. (8), (9), and (11) for the evolution of the probability of species abundance or Eqs. (13) and (14) for the probability of species abundance in an equilibrium community. Thus, the average number of species containing from n_1 to n_2 individuals at time t is given by

$$\langle \phi(n_1, n_2, t) \rangle = \sum_{j=1}^S \int_{n_1}^{n_2} p_j(n, t) dn. \quad (19)$$

When a community consists of S demographically identical species, the previous expression can be rewritten as

$$\langle \phi(n_1, n_2, t) \rangle = S \int_{n_1}^{n_2} p(n, t) dn, \quad (20)$$

where $p = p_j$ satisfies Eqs. (8)–(11) for dynamic community or Eqs. (13) and (14) for the equilibrium community with $\omega_j = \omega = 1/S$.

II. PERSISTENCE AND EXTINCTION

A. Distribution of the first passage time to extinction.

Kolmogorov-Fokker-Planck backward equation

The aim of this section is to study the probability of species extinction within the specified time interval. Note that this probability is often accepted as a measure of extinction risk in conservation management [1,2,41].

Let the initial abundance of the i th species at time $t=0$ be n . Then the probability that the i th species has not gone extinct by time t in a zero-sum neutral community of size J is defined as

$$G_i(t, n) = \Pr(T \geq t) = \int_0^J p_i(y, t | n, 0) dy. \quad (21)$$

This probability fulfills the Kolmogorov-Fokker-Planck backward equation [39,1]

$$\frac{\partial G_i}{\partial t} = \frac{1}{2} D_i(n) \frac{\partial^2 G_i}{\partial n^2} + V_i(n) \frac{\partial G_i}{\partial n}, \quad n \in (0, J), \quad t > 0, \quad (22)$$

with the initial condition

$$G_i(n, 0) = 1, \quad n \in [0, J], \quad (23)$$

where the coefficients V_i and D_i are defined by (7).

Then the distribution function for the persistence time or the first passage time to extinction of the i th species with the initial abundance n from the interval of abundances $(0, J]$ is

$$F_i(n, t) = 1 - G_i(n, t). \quad (24)$$

And, furthermore, the probability density for the first persistence time is equal to

$$f_i(n, t) = -\partial G_i(n, t) / \partial t. \quad (25)$$

Note that the distribution of the persistence time and the first extinction time are extremely important in the Eqs. of conservation biology. Since, from the known distribution of the persistence time, one can find, for example, the probability that the species is present in the community within given fixed time interval.

In order to completely define the problem for the probability of remaining in the interval of species abundances $(0, J]$, the boundary conditions for the probability at the species abundances $n=N_-=0$ and $n=N_+=J$ have to be specified. Since we are interested in the first passage time to the zero species abundance, we specify the absorbing boundary condition at the boundary species abundance $n=N_-=0$

$$G_i(0, t) = 0, \quad t \geq 0. \quad (26)$$

Another type of boundary condition, called reflecting boundary condition, is stated at the boundary abundance $n=N_+=J$

$$\partial G_i(n, t) / \partial n |_{n=J} = 0, \quad t \geq 0. \quad (27)$$

This type of boundary condition is specified when it is known that the species abundance cannot jump over some abundance level.

B. Moments of the first passage time to extinction

For the known distribution function [Eqs. (22), (23), (26), and (27)], the mean first passage time to the zero species abundance

$$T_i^1(n) = \int_0^\infty t \frac{F_i(n, t)}{\partial t} dt = \int_0^\infty G_i(n, t) dt, \quad (28)$$

can be obtained from the ordinary differential equation

$$\frac{1}{2} D_i(n) \frac{d^2 T_i^1}{dn^2} + V_i(n) \frac{dT_i^1}{dn} = -1, \quad n \in (0, J) \quad (29)$$

supplemented with the absorbing boundary condition at the boundary $n=0$ and the reflecting boundary condition at the boundary $n=J$,

$$T_i^1(0) = 0, \quad dT_i^1(n) / dn |_{n=J} = 0. \quad (30)$$

Similarly, the k th moment of the first passage time,

$$T_i^k(n) = \int_0^\infty t^k d_i F_i(n, t) = -k \int_0^\infty t^{k-1} G_i(n, t) dt, \quad (31)$$

can be computed from the differential equation

$$\frac{1}{2} D_i(n) \frac{d^2 T_i^k}{dn^2} + V_i(n) \frac{dT_i^k}{dn} = -T_i^{k-1}, \quad n \in (0, J), \quad (32)$$

subject to boundary conditions (30) for T_i^k .

Note that the k th moment of the first passage time to extinction of the i th species satisfies the following property

$$T_i^k(n)|_{\mu=\bar{\mu}} = \frac{1}{\bar{\mu}^k} T_i^k(n)|_{\mu=1}. \quad (33)$$

It follows from (33) that the k th moment of the first extinction time is inversely proportional to the k th power of μ . Thus, we can say that the parameter μ , the number of death events per the unit time interval, plays a role of the time scale for the time evolution of the species abundance in local community. The importance of the time scale and the problems with it defining in neutral theory of biodiversity was noticed and discussed by Nee [36], Lande *et al.* [1], and Leigh [42].

Note also that the problem for the mean first extinction time can be solved explicitly [39] as

$$T_i^1(n) = 2 \int_0^n \frac{dy}{D_i(y) P_i(y)} \int_y^J P_i(z) dz, \quad (34)$$

where P_i is the equilibrium probability density of the i th species abundance. Furthermore, it can be shown that $T_i^1(n)$ is an increasing function of the initial abundance n , and, moreover, $dT_i^1(n)/dn > 0$ for $n \in [0, J]$.

C. Moments of the first passage time to fixation

The problem of the first passage time to species fixation (extinction or monodominance) can be also addressed using the backward Kolmogorov-Fokker-Planck technique. In this case we replace the reflecting boundary conditions at $n=N_+ = J$ by the absorbing boundary conditions in Eqs. (27) and (30).

Note also that as the equilibrium density of species abundance, the first fixation time satisfies the symmetry property, that is, the mean first passage times to fixation are equal for two species with the metacommunity relative abundances equal to $\omega_i = \omega$ and $\omega_j = 1 - \omega$, if their initial abundances are n

and $J - n$, respectively, where J is the size of the local community

$$T_{\text{fix},i}^1(n)|_{\omega_i=\omega} = T_{\text{fix},i}^1(J-n)|_{\omega_j=1-\omega}. \quad (35)$$

D. Probability of the species extinction

The probability of the species extinction is another characteristic of species behavior in local community. Using this probability we can estimate the chance of the species to go extinct in comparison with the chance of it to monodominate. The probability of extinction for the i th species $\pi_i^0(n)$ can be calculated from the following ordinary differential equation [39]:

$$\frac{1}{2} D_i(n) \frac{d^2 \pi_i^0}{dn^2} + V_i(n) \frac{d\pi_i^0}{dn} = 0, \quad n \in (0, J) \quad (36)$$

with the boundary conditions

$$\pi_i^0(0) = 1, \quad \pi_i^0(J) = 0. \quad (37)$$

The probability of complete dominance for the i th species in the local community, $\pi_i^J(n)$, can be obtained from the equation

$$\pi_i^0(n) + \pi_i^J(n) = 1,$$

or from Eq. (36) supplemented with the reverse boundary conditions to (37).

E. Quasiextinction

Quasiextinction is another concept related to the extinction process. By this concept a species is considered extinct once it reaches or falls below some small level (quasiextinction level) of abundance [1,41]. Assuming that $C > 0$ is a level of quasiextinction (a lower absorbing boundary of species abundance), the problems for the first passage time to a quasiextinction of the i th species and for the probability of the species quasiextinction can be formulated by replacing the lower bound for critical species abundance $N_- = 0$ by $N_- = C$ in the respective problems for the first passage time to extinction and the probability of extinction. Note that the mean first passage time to quasiextinction can also be calculated from the following expression:

$$T_i^1(n) = T_i^1(n, C) + T_i^1(C, 0), \quad n > C,$$

where $T_i^1(n, k)$ is the mean first passage time for the i th species from the initial abundance $n > C$ to the abundance k , $n > k$.

III. SENSITIVITY ANALYSIS FOR SPECIES DYNAMICS IN LOCAL COMMUNITY

A. Analysis of species abundance distributions

In this section, the properties of species abundance distribution with respect to different values of the immigration probability m , the species metacommunity relative abundance ω_i , and the community size J will be investigated.

Let us first consider mixed boundary conditions (10). At both ends $n=0$ and $n=J$ of the abundance interval, these boundary conditions can be rewritten as

$$D_i(n) \frac{\partial p_i}{\partial n} + [D_i'(n) - 2V_i(n)]p_i = 0. \quad (38)$$

At the abundance level $n=0$ condition (38) degenerates to the zero flux boundary condition, also known as the Neumann boundary condition, in the form $\partial p_i / \partial n|_{n=0} = 0$ when $D_i'(0) - 2V_i(0) = 0$. At the abundance $n=J$, condition (38) also transforms to the Neumann boundary condition $\partial p_i / \partial n|_{n=J} = 0$ when $D_i'(J) - 2V_i(J) = 0$. The zero flux boundary conditions imply zero gradient of the probability of species abundances at $n=0$ and $n=J$, that is they state that the changes in the species abundance at the boundaries are negligible. The values of the immigration probability, m , for which the above conditions are fulfilled can be calculated at each boundary. Specifically at the abundance level $n=0$

$$m_0 = \frac{1}{(J-1)(\omega_i + \omega_i/J + 1/J - 1 - 1/2J)},$$

and at $n=J$

$$m_J = \frac{1}{(J-1)(1 - \omega_i - \omega_i/J + 1/J - 1 + 1/2J)}.$$

For large local community sizes these values are equal to the drift with respect to the specific species i in the local community and to the drift with respect to all species other than the species i , that is, $m_0 \approx 1/(\omega_i J)$ and $m_J \approx 1/[(1-\omega_i)J]$, respectively. Note that for the species with small metacommunity relative abundance, the drift with respect to all species other than the species i in the local community is approximately equal to the drift in the local community, $1/J$.

Let us restrict our analysis of the probability density to the species with the metacommunity relative abundance smaller than $\frac{1}{2}$, i.e., $\omega_i < \frac{1}{2}$. The results for $\omega_i \geq \frac{1}{2}$ can be obtained in an analogous manner and will be only commented.

We shall examine the structure of the species abundance distribution separately for the three intervals of the immigration probability $(0, m_J)$, (m_J, m_0) , and $(m_0, 1)$. For the first interval of the immigration probability $(0, m_J)$, we observe the probability that the species will go extinct or monodominant in the local community is very high, see Fig. 1 for $0 < m \leq 0.005 = 1/J \approx m_J$. In this case the probability density of the species abundance has a *U* shape, see also Ref. [16], the immigration events are so rare that the species most of the time are either at the abundance level 0, or J . Since the new immigrants are rare and fundamentally change the structure of the local community, this type of immigration can be considered rather as catastrophic than regular. Note also that because the immigration probability is smaller than the drift with respect to the specific species in the local community and to the drift with respect to all species other than the specific species, the immigration effect is too small for species turnover in the local community, and diversity of such community is very low.

When the immigration probability belongs to the second interval from m_J to m_0 , new individuals immigrate to the

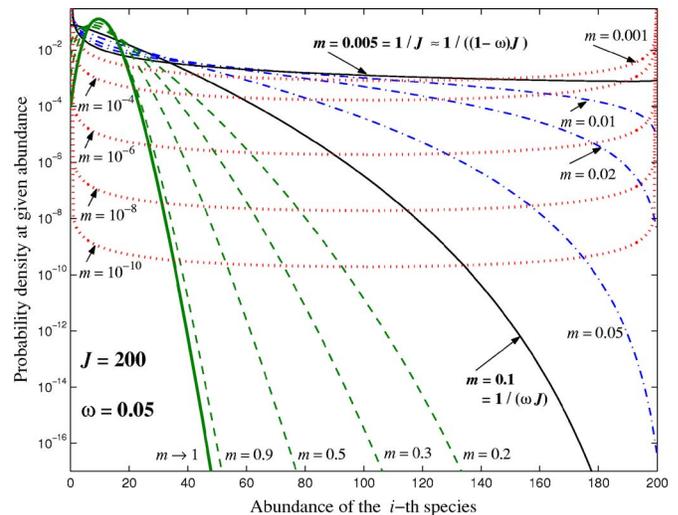


FIG. 1. (Color online) The effect of varying the probability of immigration m on the equilibrium probability density function for the abundance of the i th species in Hubbell’s zero-sum local community. Numerical results for a local community of $J=200$ individuals and the species metacommunity relative abundance $\omega_i = 0.05$ are obtained from the exact solution (16) of Eqs. (13) and (14).

local community much more often than in the first case. This type of immigration essentially increases the diversity of the community, and decreases the chance of the species monodominance. Nevertheless, the intensity of immigration is still too low to essentially decrease the probability of extinction of the specific species. In this case the equilibrium probability density for the species abundance has an “S” shape with the maximal value at zero abundance, see Fig. 1 for $m_J \approx 1/J = 0.005 < m < 0.1 = 1/[(1-\omega)J] \approx m_0$.

Finally, for the third interval of the immigration probability from m_0 to 1, the species in the local community becomes much more stable around nonzero species abundance than in the first two cases, see Fig. 1 for $m > 1/[(1-\omega)J] = 0.1$. And the level of stabilization increases with an increase of the immigration probability. The mode of the probability density for the species abundance is near ωJ , and the probability density has a reverse *U* shape. Moreover, the species turnover is very intensive for the immigration probabilities higher than the drift with respect to the specific species in the local community.

The immigration probability has a different effect on the common species with $\omega_i > \frac{1}{2}$. In this case the first interval for the immigration probability from 0 to m_0 can be classified as the interval with a high chance of species fixation. As in the case with $\omega < \frac{1}{2}$ the species will occupy all local community or go extinct most of the time. The second interval, where the immigration probability is between m_0 and m_J , is characterized by high probability of the species monodominance, that is, most of the time the species will occupy all local community. And, finally, for the immigration probabilities larger than m_J , the mode of the probability density of the species abundance is located between 0 and J . Note also that if the metacommunity relative abundance $\omega_i = \frac{1}{2}$, the intermediate interval of the probability of immigration is degenerated, see Fig. 2(a).

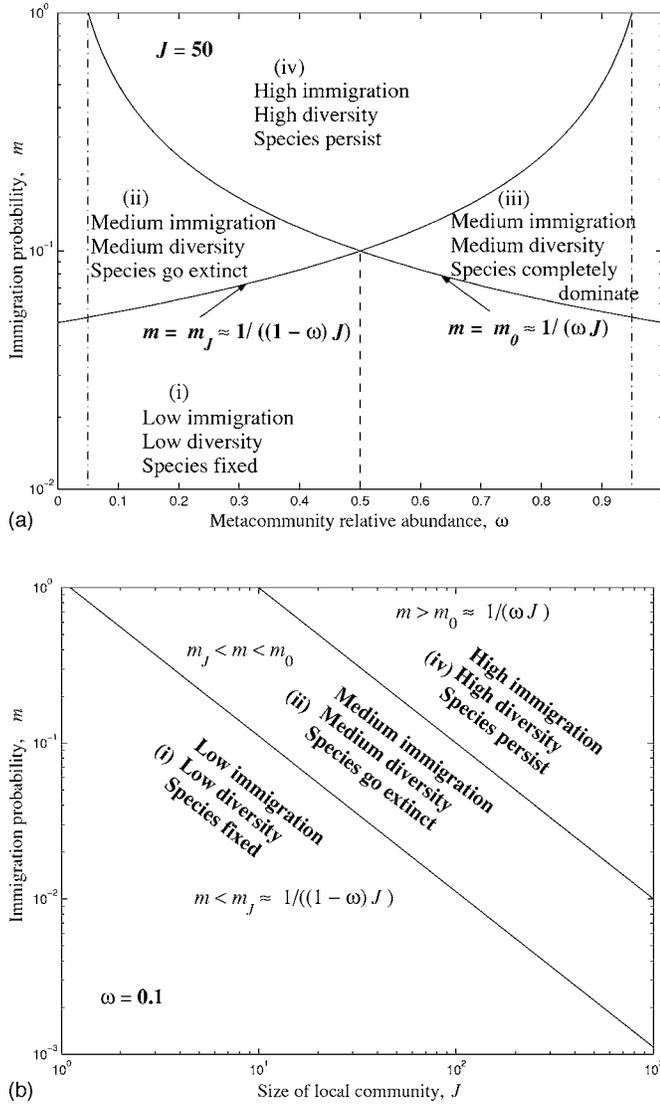


FIG. 2. Classification for the local community species dynamics with respect to (a) different values of the immigration probability and the metacommunity species relative abundance; (b) different values of the immigration probability and the size of local community.

The results for species dynamics in the local community obtained from the above analysis are summarized in Figs. 2(a) and 2(b). Figure 2(a) shows four possible scenarios for the species dynamics in the local community: (i) low immigration intensity: the species most of the time is either not present or monodominant in the local community, see also Ref. [16]; (ii) medium immigration intensity with small metacommunity relative abundance: the species most of the time is absent from the local community; (iii) medium immigration intensity with high metacommunity relative abundance: the species most of the time is monodominant; and (iv) high immigration intensity: the species in the local community persists with high probability, and its relative abundance in the local community is more similar to those in the metacommunity, see also Ref. [16].

With an increase in the immigration probability, scenario (i) changes first into either scenario (ii) or (iii), and then into

scenario (iv). Also it is worth noting that when the metacommunity relative abundances is either very small or very high, the species dynamics can follow only two scenarios, see Fig. 2(a). In the first case because the immigration probability is never high enough for the species abundance to be stabilized around a nonzero mode in the local community, the probability for this species to go extinct is very high. In the second case, when the metacommunity relative abundance is very high, the probability that the species will occupy all community is also very high.

Figure 2(b) shows results of the sensitivity analysis for species dynamics with respect to different local community sizes. Specifically, it shows that for larger local communities, a smaller immigration probability is required for species persistence.

B. Effect of immigration probability

In the previous section we defined four possible scenarios for species dynamics in the local community with respect to the immigration probability, metacommunity relative abundance, and size of the local community. Here we look at the first passage time of the species to either extinction or fixation (extinction or monodominance) in the local community with respect to the immigration probability and initial species abundance. We shall consider the effect of the immigration probability separately for each possible scenario for low metacommunity species abundance. The case with high metacommunity species abundance will not be considered in detail, since the behavior of the first passage time dynamics is essentially the same.

We start from scenario (i) for which the immigration probability is very small. In this case the species becomes fixed in a much shorter time interval than the time to the next immigration event, thus the distribution and dynamics of the species abundance are very similar to the case without immigration. Since the species most of the time stays at the abundance level equal to the local community size or zero, each immigration event can be viewed as a catastrophic perturbation into the stabilized system at the constant species abundance.

In general, the first extinction time problem for scenario (i) is not very informative, since the species can have abundance close to the local community size most of the time (Fig. 1) and the probability that the species abundance will change to a smaller level is very low [Fig. 3(f)]. This persuades to very high uncertainty in the result for the first extinction time [Fig. 3(e)]. More intensive immigration to the local community leads to an increase in the probability of change in the species abundance from very large initial abundance to the abundance close to zero. Thus, as a result, the mean and variance of the first passage time to extinction decreases [Figs. 3(b) and 3(e)].

Since the uncertainty in the first passage time to fixation for species with low immigration intensity is of smaller order than the uncertainty in the first passage time to extinction, the first fixation time can be considered as a more effective measure of species viability in this case. Note also that the first fixation time, on the contrary to the first extinction time,

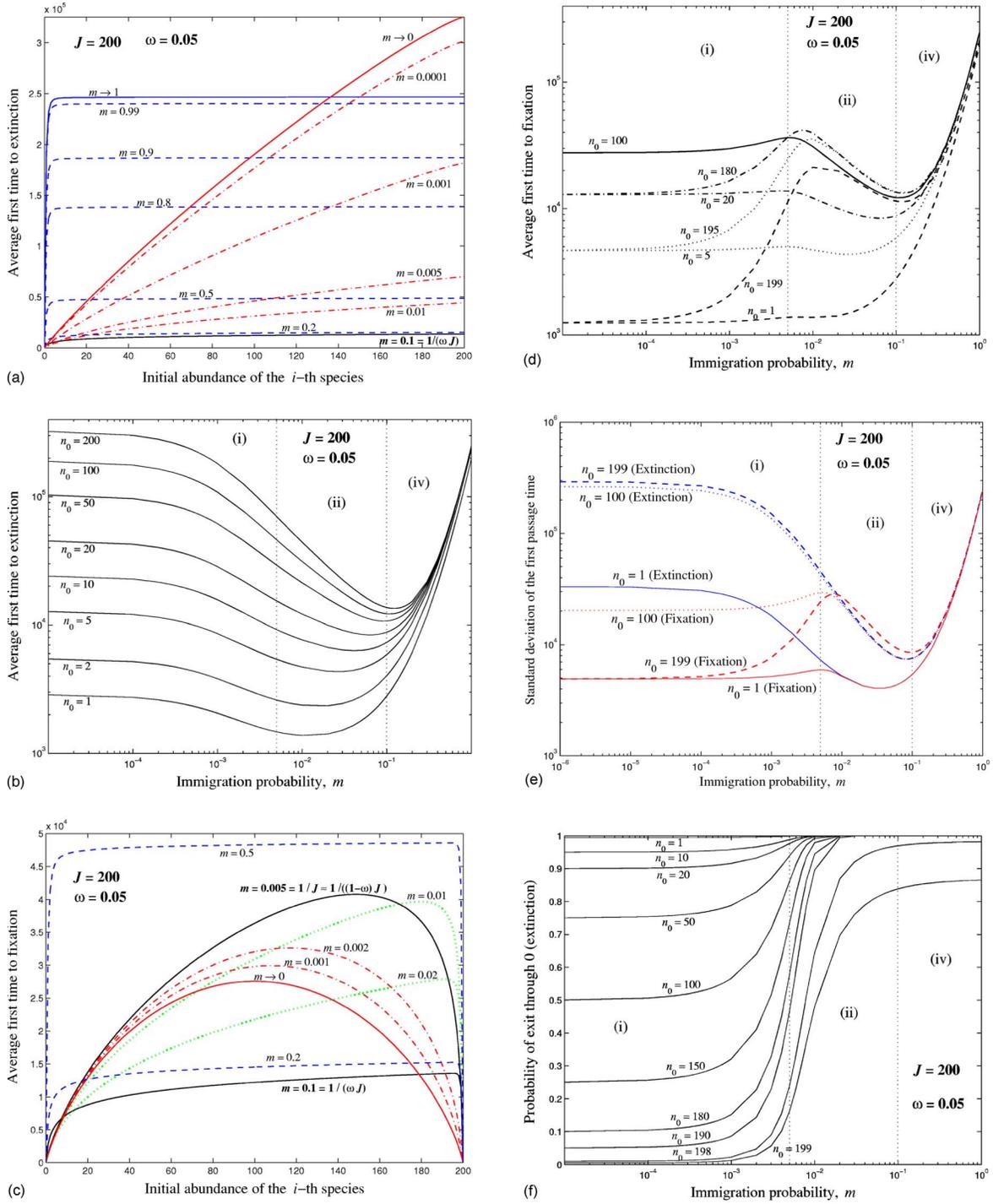


FIG. 3. (Color online) The effect of varying the probability of immigration m on the first passage times to extinction and fixation and on the probability of extinction for the i th species in Hubbell's zero-sum local community of $J=200$ individuals and the species metacommunity relative abundance $\omega=0.05$: (a) the mean first passage time to extinction as a function of the initial species abundance for different values of m [Eqs. (29) and (30)]; (b) the mean first passage time to extinction as a function of the immigration probability for different values of the initial species abundance [Eqs. (29) and (30)]; (c) the mean first passage time to fixation as a function of the initial species abundance for different values of m [Eq. (29) with absorbing boundary conditions at $n=N_-=0$ and $n=N_+=J$ (see Sec. II C)]; (d) the mean first passage time to fixation as a function of the immigration probability for different values of the initial species abundance [Eq. (29) with absorbing boundary conditions (see Sec. II C)]; (e) the standard deviations of the first extinction and fixation times [Eqs. (29) and (32) with boundary conditions (30) for extinction time and absorbing boundary conditions for fixation time (see Sec. II C)]; (f) the probability of species extinction [Eqs. (36) and (37)]. All results are obtained using numerical approximations.

increases with an increase in the immigration probability, see Figs. 3(b) and 3(d) for small m .

Another interesting question for investigation concerns comparison of the first passage time to fixation or extinction in communities with small immigration probability to the communities without immigration, $m=0$. For $m=0$ there are two absorbing states for the species abundance of 0 and J , and the extinction event never occurs if the species totally occupies the local community. However, even for very small immigration intensity, the probability of extinction is always non-negative. Figure 3(a) illustrates the asymptotic convergence of the first passage time to extinction as $m \rightarrow 0$. The asymptotic analysis shows that the mean first passage time to extinction $T_{ext}^1(n)$ converges to

$$-J(J-1) \left(\frac{J-n}{J} \ln \frac{J-n}{J} + \frac{n}{J} \ln \frac{n}{J} \right) + C_0 \frac{n}{J} \quad (39)$$

as $m \rightarrow 0$, where C_0 is the positive constant, while the mean first passage time to fixation can be approximated by

$$T_{fix}^1(n) \rightarrow -J(J-1) \left(\frac{J-n}{J} \ln \frac{J-n}{J} + \frac{n}{J} \ln \frac{n}{J} \right) \quad (40)$$

as $m \rightarrow 0$. Hubbell [16] in his analysis of the isolated local community ($m=0$) based on discrete Markov chain approach, obtained the following explicit formula for the mean first passage time to fixation:

$$T(N) = (J-1) \left[(J-N) \sum_{k=1}^N (J-k)^{-1} + N \sum_{k=N+1}^{J-1} k^{-1} \right].$$

It is easy to note that the above expression is in agreement with our result, that is, $T_{fix}^1(N)$ converges to $T(N)$ as $m \rightarrow 0$, see also Fig. 3(c).

Note also that approximations (39) and (40) state that in communities with very small immigration probabilities, the species metacommunity relative abundance plays almost no role in community species dynamics.

A further increase of the immigration probability [scenario (ii)] makes the local community richer on newcomers, the community becomes more diverse, and the turnover rate increases. As a result the species abundance distribution curve becomes S shaped with the mode at the zero abundance. Naturally, the dynamics of extinction and fixation processes go through many changes during this transition scenario. From Fig. 3(b) we can observe that the switching between the decrease and increase of the mean first passage time to extinction with respect to the immigration probability takes place around the immigration probabilities from scenario (ii). For this scenario the mean and variance of the first fixation time becomes closer to the mean and variance of the first extinction time. This is due to the fact that for small species metacommunity relative abundance only the extinction is highly probable, the probability of monodominance is very small, see Figs. 3(b), 3(d), and 3(e).

Finally, we shall consider the interval of large immigration probabilities [scenario (iv)]. For this interval, the maximal probability of the species abundance is achieved for an abundance close to the mode $\omega_i J$ and this probability in-

creases with an increase in the immigration probability. The species abundance is more stable around the mode $\omega_i J$ for higher immigration intensity, see Fig. 1. As a consequence the mean and variance of the first passage times to extinction and fixation for these species increase with the increase in the immigration probability, see Figs. 3(b) and 3(d).

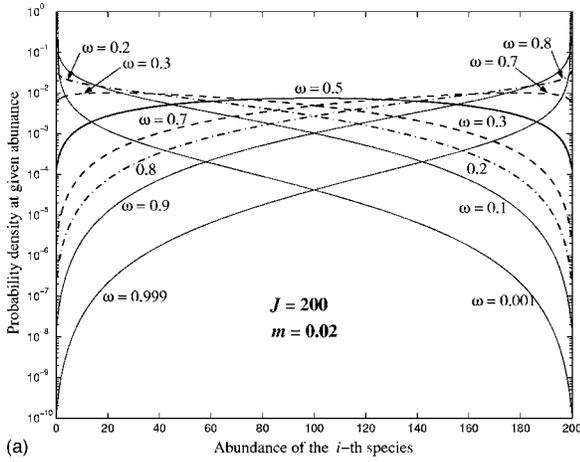
Now let us summarize the relationship between the mean first passage times to extinction and fixation and the initial species abundance. It was already mentioned above that for very small values of the immigration probability the mean first extinction and fixation times are independent of the species metacommunity relative abundance. For small immigration probabilities, the mean first extinction time is almost proportional to the initial species abundance; the mean first fixation time increases on the interval $(0, J/2)$, and decreases symmetrically on $(J/2, J)$, see Figs. 3(a) and 3(c). As the immigration probability increases the mean first fixation and extinction times become closer to each other for all initial abundances distinct from the abundances close to J . Note also that for communities with large immigration intensities the first extinction and fixation times are almost constant for the initial species abundances inside of the interval $(0, J)$. At the initial abundances close to zero the mean first extinction and fixation times increase sharply from the zero level to some positive constant level. Similarly, the mean first fixation time decreases to zero sharply in the small vicinity of the initial abundance J , see Figs. 3(a) and 3(c).

C. Effect of species metacommunity relative abundance

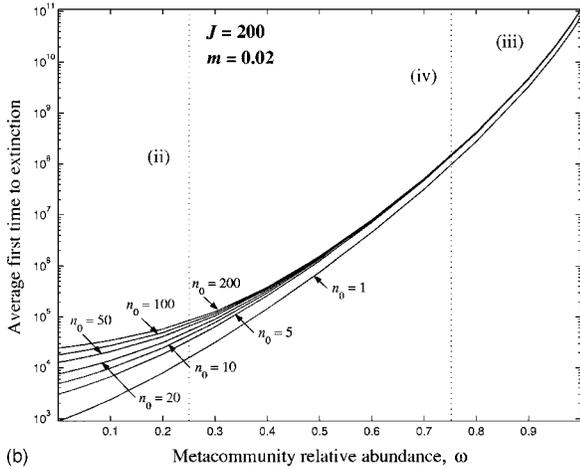
Figure 4(a) illustrates the effect of varying species metacommunity relative abundance, ω_i , on the equilibrium species abundance probability density for the immigration probability $m=0.02 > 0.01 = 2/J$. For small metacommunity relative abundance $\omega_i \leq 0.2$, it can be seen from Fig. 4(a) that the species dynamics follows scenario (ii); for large metacommunity relative abundance $\omega_i \geq 0.8$, the species dynamics follows scenario (iii), and for $0.2 < \omega_i < 0.8$, the species dynamics follows scenario (iv).

Analogous analysis can be carried out for small values of the immigration probability m . Specifically, it can be shown that for $m < 0.005 = 1/J$ the species dynamics follows scenario (i) for all possible values of the metacommunity relative abundance, while for the immigration probabilities from the interval $(1/J, 2/J)$, the species dynamics first follows scenario (ii) for small ω_i , then switches to scenario (i) and, finally, for large ω_i to scenario (iii).

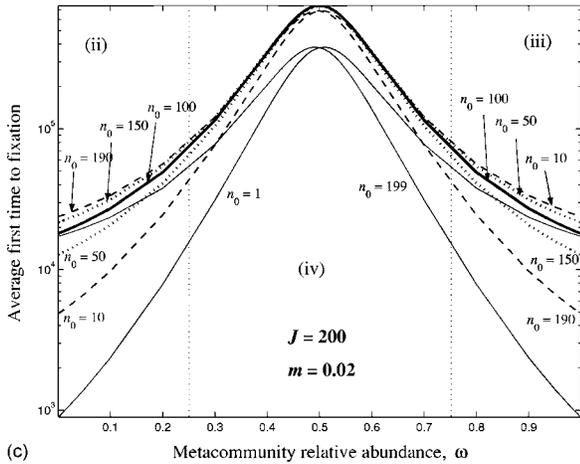
Figures 4(b) and 4(c) show the behavior of the mean first passage time to extinction and fixation. From Fig. 4(b) one can easily see that the mean first passage time to extinction is an increasing function of the metacommunity relative abundance, and the initial species abundance. This behavior of the extinction time is related to the species persistence in the local community: the persistence time is longer for the species with larger abundance and for the species with a larger number of members in the metacommunity. From Fig. 4(c) one can infer that the mean first passage time to fixation satisfies the symmetry property given by Eq. (35). Note that this property is essentially straightforward for an understand-



(a)

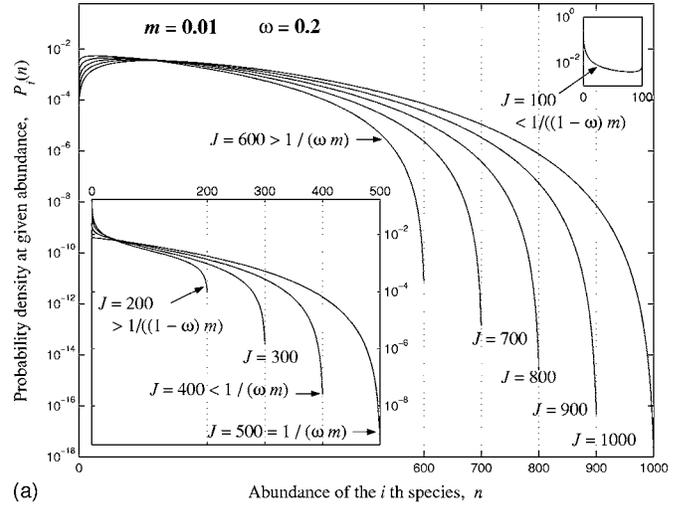


(b)

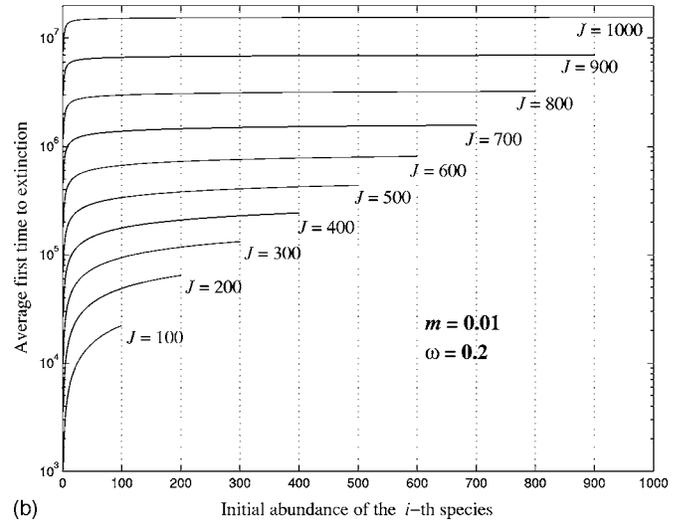


(c)

FIG. 4. The effect of varying the metacommunity relative abundance ω_i of the i th species on (a) the equilibrium probability density function of the species abundance obtained from the exact solution (16) of Eqs. (13) and (14); (b) the mean first passage time to extinction of the i th species obtained from the numerical approximations of Eqs. (29) and (30); (c) the mean first passage time to fixation of the i th species obtained from the numerical approximations of Eq. (29) with absorbing boundary conditions at $n=N_-=0$ and $n=N_+=J$ (see Sec. II C). Example for a local community of $J=200$ individuals and the immigration probability $m=0.02$.



(a)



(b)

FIG. 5. The effect of varying the local community size J on (a) the equilibrium (steady state) probability density function of the i th species abundance obtained from the exact solution (16) of Eqs. (13) and (14); (b) the mean first passage time to extinction of the i th species in Hubbell's zero-sum local community obtained from the numerical approximations of Eqs. (29) and (30). Example for the species metacommunity relative abundance $\omega_i=0.2$, and the immigration probability $m=0.01$.

ing in the case of two species in the zero-sum local community, since extinction of one species means monodominance of another species in the community.

D. Effect of community size

The effect of varying local community size, J , on the steady state (equilibrium) probability density function is shown in Fig. 5(a). For the present analysis, the immigration probability was fixed at the level of 0.01, and the metacommunity relative abundance was chosen to be 0.2. It can be seen from Fig. 5(a) that the patterns of equilibrium species abundance are changing when the size of the local community increases. For small local communities, i.e., $J=100$, the immigration intensity is too low for species persistence,

$m=0.01 < \min\{m_0, m_J\}$, and the species dynamics follows scenario (i) with a very high chance of species fixation. For the local communities of size $J=200, 300, 400,$ and 500 , the species dynamics follows scenario (ii) with a very high chance of extinction ($m_J < m \leq m_0$). And, finally, for the local communities of size $J > 500$, the species follow scenario (iv) with a high probability of persistence and high diversity ($m > \max\{m_0, m_J\}$). The dynamics of the first passage time to extinction also differs with respect to the size of the local community, see Fig. 5(b). If the size of the local community is small, then the species follows scenarios (i) or (ii) with a high probability of extinction and, moreover, the first passage time to species extinction is a strictly increasing function of the initial species abundance. Since, for larger communities, smaller immigration intensity is required for species persistence, see Fig. 2(b), the species abundance is inside of the interval $(0, J)$ most of the time, and thus, the mean first passage time to species extinction is almost independent of the initial species abundance.

E. Probability density of the first passage time to extinction

To complete our analysis of the species dynamics, let's consider the distribution function $F_i(n, t)$ of the first passage time to extinction of the i th species. Note that the distribution function of the first extinction time $F_i(n, t)$ in the local community defines the risk or probability of extinction of the i th species with the initial abundance n before time t . It is directly related to another fundamental quantity for conservation biology, the probability of species persistence, $G_i(n, t)$, by the following expression $G_i(n, t) = 1 - F_i(n, t)$.

Figures 6(a) and 6(b) present the effects of varying initial abundance n_0 of the i th species on the probability distribution and density of the first extinction time t in a local community of $J=200$ individuals undergoing zero-sum ecological drift ($\omega_i=0.05, m=0.05$). Note that numeric approximations for the probability distribution function shown in Fig. 6(a) were obtained from Eqs. (22), (23), (26), and (27). The probability density functions shown in Fig. 6(b) were calculated as $\partial F_i(n, t) / \partial t$ using the distribution functions of the first extinction time $F_i(n, t)$. Alternatively, they could also be obtained from Eq. (22) or as $\frac{1}{2}D_i(n)\partial^2 F_i / \partial n^2 + V_i(n)\partial F_i / \partial n$.

Unfortunately, there is no explicit formula for the distribution of the first passage time to extinction. So, we will compare our numerical results for the distribution of the first passage time to gamma distribution. It was presumed by Hubbell [16] that gamma distribution is giving a good fit for the distribution of the first passage time to extinction. To verify this observation of Hubbell, the theoretical probability densities of the first passage time to extinction obtained from Eqs. (25) for the species with small and large initial abundances were compared to the relative frequencies of the first passage time to extinction calculated based on the simulations of Hubbell's model (1), and to the shifted gamma distributions fitted to simulated values of the first extinction times, see Fig. 7. From Fig. 7 one can note that for the initial abundance of the species $n_0=50$ in a local community of size $J=200$, a shifted gamma distribution gives a good fit to the

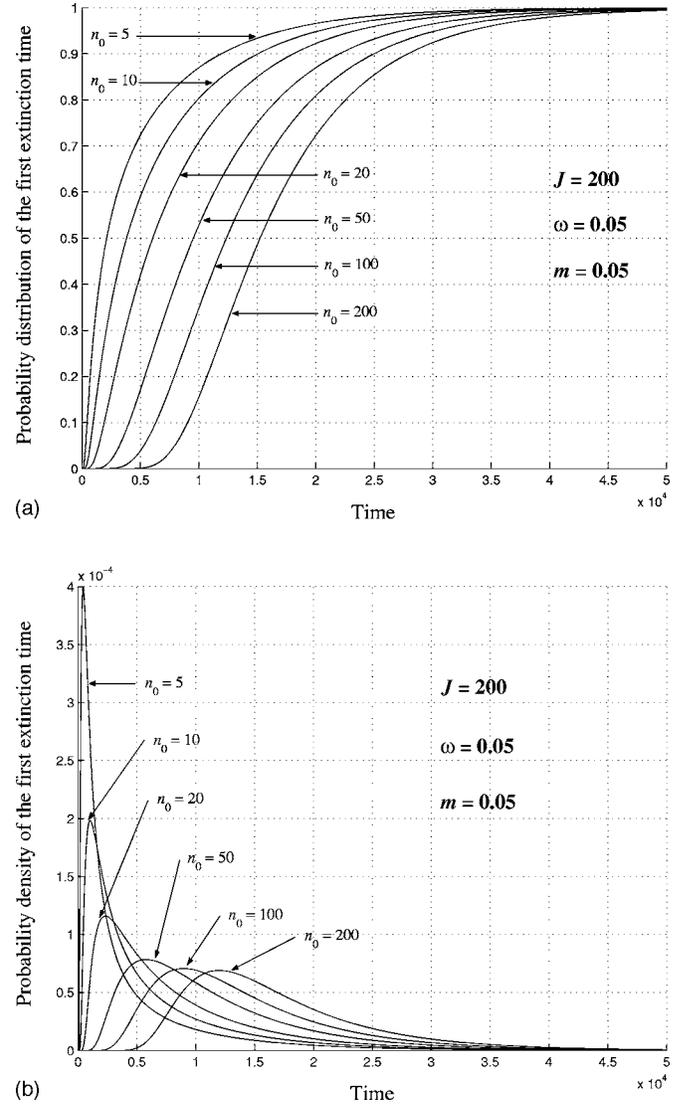


FIG. 6. The effect of varying the initial abundance n_0 of the i th species on (a) the probability distribution function, and (b) the probability density function for the first passage time to extinction. Results are obtained from numerical approximations of Eqs. (22), (23), (26), and (27) and (a) Eq. (24), (b) Eq. (25). Example for a local community of $J=200$ individuals, the species metacommunity relative abundance $\omega_i=0.05$, the immigration probability $m=0.05$, and the number of death events per unit time $\mu=1$.

simulated frequencies of the first extinction time and is close to the probability density of the first passage time to extinction calculated from Eq. (22); however, for smaller initial species abundance, i.e., $n_0=5$, a shifted gamma distribution does not give a good fit to the distribution of the first passage time to extinction. Thus, we can conclude that gamma distribution produces a good fit to the probability density of the first passage time to extinction only for large initial species abundances, but for small initial species abundances such fit is unsatisfactory.

IV. DISCUSSION AND CONCLUSIONS

The unified neutral theory of biodiversity and biogeography proposed by Hubbell [19] aims to explain the species

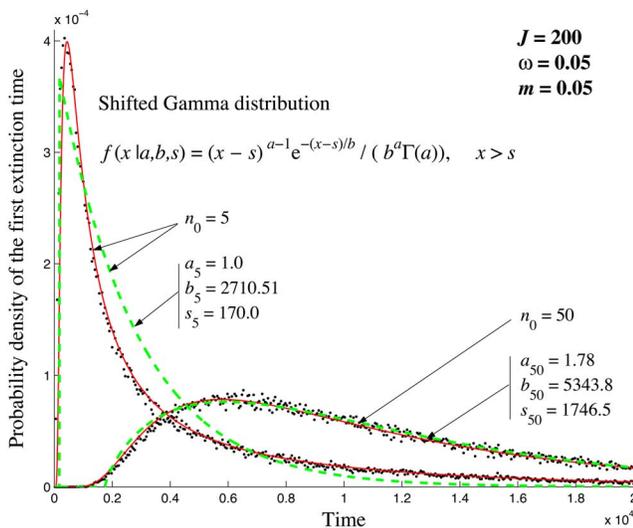


FIG. 7. (Color online) Comparison of the probability density of the first passage time to extinction (solid lines) obtained from numerical approximations for continuous probabilistic model [Eqs. (22), (23), (26), and (27)], and Eq. (25) to the relative frequencies of the first extinction time (dots) calculated from simulations of Hubbell model (1), and to the probability density functions of shifted gamma distributions fitted to the simulated first extinction times (dashed lines). Example for the initial species abundances $n_0=5$ and $n_0=50$ in a local community of size $J=200$, the species metacommunity relative abundance $\omega_i=0.05$, the immigration probability $m=0.05$, and the number of death events per unit time $\mu=1$.

diversity and relative species abundance in ecological communities relying on the principles of zero-sum game and neutrality. Up to this time the zero-sum neutral model of Hubbell was analyzed using only discrete techniques such as Markov chain analysis [19] and analysis of master birth-death ordinary differential equations for the species abundance probability distribution [21–23]. In this work, Hubbell’s model was considered from a different perspective. A continuous technique based on the Kolmogorov-Fokker-Planck forward and backward equations was applied for the investigation of the processes in the local communities. This technique gave us a possibility not only to work with communities of any size, but also derive such important measures in conservation biology as the probability distributions of the persistence time and the first passage time to extinction and fixation. Note that the model for the distribution of the first passage time of the species to extinction in zero-sum local community has not been obtained before. The presented model was evaluated and verified through the simulation study of Hubbell’s neutral zero-sum model, see Fig. 7. Figure 7 shows that for the species with large initial abundances, the distribution of the first passage time to extinction is very close to gamma distribution, as it was presumed by Hubbell [19], but for the species with small initial abundance, gamma distribution does not give a good fit to the first passage time to extinction.

Moreover, the main significance of this work lies in proposing a realistic classification for the species dynamics in the local community, see Figs. 2(a) and 2(b). The species dynamics classification was obtained from the sensitivity analysis of the species abundance distribution and was formulated with respect to the immigration intensity, species metacommunity relative abundance, and, of course, the size of the local community. According to this classification, the four possible scenarios for the species abundance dynamics in the local community are the following.

(i) Low immigration intensity ($m < \min\{m_0, m_J\}$): the species most of the time is either monodominant or not present in the local community; the local community is characterized by low diversity (only one monodominant species); the species abundance distribution is U shaped; immigration has catastrophic character.

(ii) Medium immigration intensity ($m_J < m < m_0$) with small metacommunity relative abundance ($\omega < \frac{1}{2}$): the species goes extinct with high probability; the local community is characterized by medium diversity; the species abundance distribution is S shaped.

(iii) Medium immigration intensity ($m_0 < m < m_J$) with high metacommunity relative abundance ($\omega < \frac{1}{2}$): the species becomes monodominant with high probability; the local community is characterized by medium diversity; the species abundance distribution has reverse S shape.

(iv) High immigration intensity ($m > \min\{m_0, m_J\}$): the species in the local community has approximately stable abundance ωJ ; the turnover of species is high; the local community is characterized by high diversity; the species abundance distribution has reverse U shape.

Note that such quantitative characterization of the species abundance distributions has not been obtained before.

Also in this paper, the time scale parameter was investigated. It is known that this parameter plays an important role in the species dynamics of living communities [36], since it defines how fast the community structure changes with time. A scale parameter for the time evolution of the species abundance distribution in our model is the parameter μ , which denotes the number of death events per unit time. We have shown that the k th moment of the first passage time to extinction and the k th power of μ are inversely related, but the equilibrium distribution of species abundance is independent of the time scale parameter μ .

Finally, in this paper a complicated behavior of the mean first passage time to extinction with respect to the immigration intensity was studied. It was noticed [16] that for small immigration probabilities, the first extinction time decreases with an increase in the immigration intensities, see Fig. 3(b). As our analysis shows, this behavior is typical for the local communities with small immigration probabilities [scenario (i)]. The species in such communities not only have a high chance to go extinct, but also have a high chance to monodominate. Moreover, more intensive immigration in such a community leads to an increase in the probability of the species to leave the monodominant state and, therefore, will lead to an increase in the probability of the species extinction. As a result, the mean of the first extinction time will decrease.

For large immigration intensities [scenario (iv)], the mean first passage time to extinction increases with the increase in the immigration probability. This is connected to the fact that the rate of species turnover in such local community increases and the species abundance stabilizes around ωJ . Note that the change in the monotonicity of the mean first time to extinction will occur only for the values of the immigration probabilities from the intermediate scenario (ii) or (iii).

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