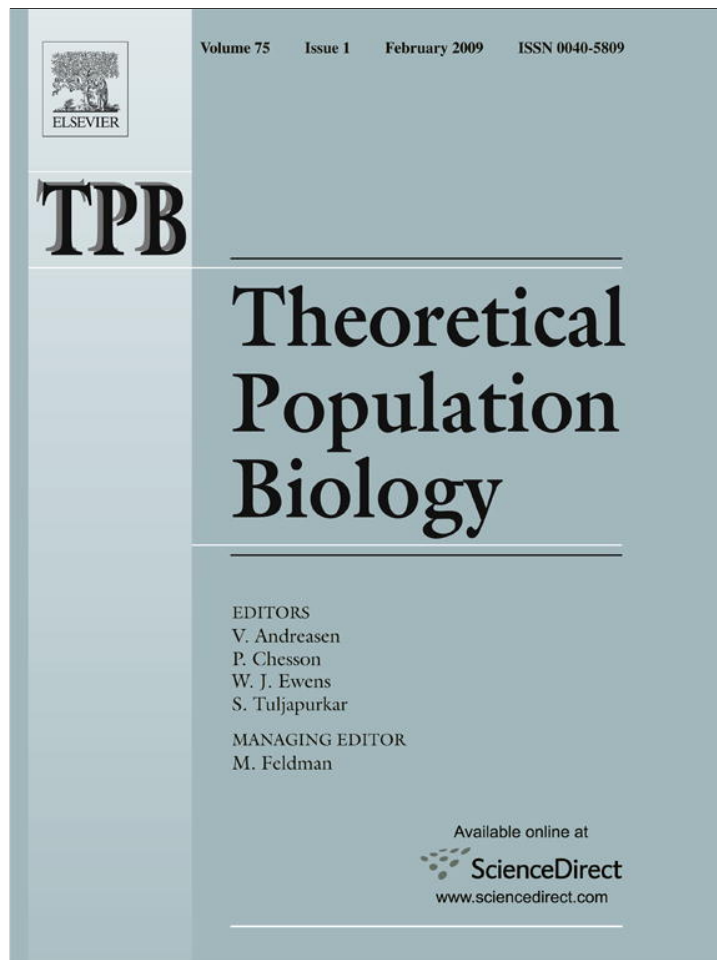


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

Theoretical Population Biology

journal homepage: www.elsevier.com/locate/tpb

A neutral model of edge effects

Petro Babak^{a,*}, Fangliang He^b^a Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton T6G 2G1, Canada^b Department of Renewable Resources, University of Alberta, Edmonton T6G 2H1, Canada

ARTICLE INFO

Article history:

Received 30 October 2007

Available online 9 December 2008

Keywords:

Neutral theory

Edge effect

Ecotone

Species abundance dynamics

Species extinction

Biodiversity indices

Kolmogorov–Fokker–Planck equation

ABSTRACT

In this paper a spatially implicit neutral model for explaining the edge effects between habitats is proposed. To analyze this model we use two different approaches: a discrete approach that is based on the Master equation for a one step jump process and a continuous approach based on the approximation of the discrete jump process with the Kolmogorov–Fokker–Planck forward and backward equations. The discrete and continuous approaches are applied to analyze the species abundance distributions and the time to species extinction. Moreover, with the aid of the continuous approach a realistic classification of the behavior of species in local communities is developed. The species abundance dynamics at the edge between two distinct habitats is compared with those located in the homogeneous interior habitats using species abundance distributions and the first time to species extinction. We show that the structure of the links between local community and the metacommunity plays an important role on species persistence. Specifically, species at the edge between two distinct metacommunities have higher extinction rate than those in the interior habitats connected only to one metacommunity. Moreover, the same species might be persistent in the homogeneous interior habitat, but its probability of extinction from the edge local community could be very high.

© 2008 Elsevier Inc. All rights reserved.

1. Introduction

It is widely observed that the structure and function of the community at the boundaries between different habitats are significantly different from that in the homogeneous interior habitats (Strayer et al., 2003; Ries et al., 2004). This phenomenon is referred to as edge effect and the boundary community is called ecotone. Ecotones (e.g., riparian zone) are of special interest in biological conservation because of the unique habitat conditions and high species diversity, yet they are vulnerable to disturbances. The study of the structure and functioning of ecotones has been a major undertaking in ecology (Ries et al., 2004). The importance lies both in theory and application. Ecotones not only play a fundamental role for the functioning of many biological processes such as dispersal, competition, species invasibility and speciation (Fagan et al., 1999; Schilthuizen, 2000; Schultz and Crone, 2001; Ries et al., 2004), but also are important for understanding landscape characterization and quality for the purpose of management (Strayer et al., 2003; Forman and Godron, 1986). Despite their high value for conservation, our current knowledge about edge effects and ecotones is mostly gained from empirical studies (Matlack, 1994; Peters et al., 2006; Walker

et al., 2003) or computer simulations (Shugart, 1987; Kupfer and Runkle, 2003). Theoretical analysis is still rather limited, of which diffusion models (Fagan et al., 1999; Ovaskainen, 2004) and matrix transition models (Schooley and Wiens, 2005) are the primary tools for modeling edge effects. All these theoretical analyses are restricted to studying the dynamics of individual populations. A similar theoretical account for edge effects on biodiversity patterns is still lacking.

Hubbell (2001) develops the unified neutral theory of biodiversity and biogeography that describes population dynamics on two spatial scales: local community and regional metacommunity. The local community is considered to be open, that is, new individuals could be either generated inside this community or immigrated from the region. Ecotone is a local, open community that receives immigrants from surrounding habitats. As such, species abundance dynamics at ecotone is subject to two processes: birth and death within the ecotone and immigration from the region.

In this paper the effect of edges on the species abundance distribution and dynamics is investigated using the neutral theory by which individuals of all species are assumed to be ecologically equivalent on the basis of per capita vital rates (Hubbell, 2001; Bell, 2001). Although the assumption of ecological equivalence of trophically similar species may not strictly held in reality, the neutral theory is an ideal starting point for testing for community assembly rules and for analyzing diversity in ecotones.

The main objective of this paper is to model and explain diversity patterns on the edges of distinct habitats. Specifically,

* Corresponding author.

E-mail addresses: petro@ualberta.ca (P. Babak), fhe@ualberta.ca (F. He).

we are interested in (1) describing the species abundance dynamics in ecotones, (2) modeling species extinction time, and (3) comparing the difference in diversity between ecotone and interior communities. In order to attain our objectives we will compare the ecotone and the community that is of the same size as the ecotone but locates within the homogeneous interior region.

2. Model formulation

To formulate a model for the species abundance dynamics in a zero-sum community located at the edge between two distinct regions, we first consider Hubbell's local community connected to a region (a metacommunity). This model assumes that a non-isolated local community can obtain new individuals through immigration from the regional metacommunity. The transition probabilities for abundance $N = N_i$ of the i th species in the local community nested within the regional community are (Hubbell, 2001):

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

where ω_i is the relative abundance of the i th species in the regional metacommunity, m is the probability that a death in the local community is replaced by an immigrant from the metacommunity, and $J = \sum_{i=1}^S N_i$ is the total abundance of the local community and S is its total number of species.

In the case of ecotone edged between two distinct communities, individuals from both regions could immigrate into the ecotone. To describe the dynamics of abundance for species i in the local community of size J , we assume that the fractions of species i in these two regions are constant and equal to ω_i^1 and ω_i^2 , respectively, and the proportion of new immigrants from the k th regions into the local community is θ^k , $k = 1, 2$, where $\theta^1 + \theta^2 = 1$. Then the transition probabilities for the abundance of species i in the ecotone are given by

$$\begin{aligned} W_i^E(N-1|N) &= \frac{N}{J} \left((1-m) \frac{J-N}{J-1} + m\theta^1(1-\omega_i^1) + m\theta^2(1-\omega_i^2) \right), \\ W_i^E(N+1|N) &= \frac{J-N}{J} \left((1-m) \frac{N}{J-1} + m\theta^1\omega_i^1 + m\theta^2\omega_i^2 \right), \\ W_i^E(N|N) &= 1 - W_i^E(N-1|N) - W_i^E(N+1|N). \end{aligned} \quad (2)$$

In this paper we, respectively, consider a local community connected to one region and to two regions. The local community defined by Eq. (1) is nested within the regional metacommunity and describes the abundance dynamics of species i in the interior community, while Eq. (2) defines a local community located on the edge between two distinct regions. It is a neutral model of ecotone. By comparing these two models, we can gain insights about edge effects on species dynamics.

It is worth noting that the model for the species abundance dynamics in the ecotone contains two new parameters θ^k 's that are not in the Hubbell's model. Because these parameters describe the proportion of immigrants into the ecotone from either metacommunity, it is reasonable to assume that θ^k 's are proportional to the length of the common boundaries of the ecotone with these metacommunities. This measure can also be used to generalize the ecotone model for local communities merged to more than two metacommunities.

3. Master equation approach

3.1. Species abundance distribution and dynamics

To analyze the species abundance dynamics in the ecotone, we will use a master equation approach. Let $p_{i,N}^E(t)$ be the probability of species i having abundance N at time t in the ecotone. Then the evolution of $p_{i,N}^E(t)$ is governed by the master equation (Gardiner, 1983)

$$\begin{aligned} \frac{\partial p_{i,N}^E}{\partial t} &= W_i^E(N|N+1)p_{i,N+1}^E + W_i^E(N|N-1)p_{i,N-1}^E \\ &\quad - (W_i^E(N+1|N) + W_i^E(N-1|N))p_{i,N}^E, \end{aligned} \quad (3)$$

where $N = 0, \dots, J$, W_i^E 's are specified by Eq. (2), and $W_i^E(-1|0) = W_i^E(0|-1) = 0$,

$$W_i^E(N+1|N) = W_i^E(N|N+1) = 0.$$

The steady-state solution $P_{i,N}^E$, calculated from the master equation, gives the equilibrium abundance probability density of species i in the ecotone (Volkov et al., 2003; McKane et al., 2004)

$$P_{i,N}^E = \frac{J!}{N!(J-N)!} \frac{\Gamma(N+\lambda_i)}{\Gamma(\lambda_i)} \frac{\Gamma(\vartheta_i-N)}{\Gamma(\vartheta_i-J)} \frac{\Gamma(\lambda_i+\vartheta_i-J)}{\Gamma(\lambda_i+\vartheta_i)}, \quad (4)$$

where

$$\begin{aligned} \lambda_i^E &= \frac{m}{1-m}(J-1)\tilde{\omega}_i, & \vartheta_i^E &= J + \frac{m}{1-m}(J-1)(1-\tilde{\omega}_i), \\ \tilde{\omega}_i &= \tilde{\omega}_i^E = \theta^1\omega_i^1 + \theta^2\omega_i^2. \end{aligned}$$

Note that the equilibrium abundance probability density of species i in the local community nested within the regional community $P_{i,N}^l$ can be obtained from (4) by choosing $\tilde{\omega}_i = \tilde{\omega}_i^l = \omega_i$ (Volkov et al., 2003).

3.2. Biodiversity indices

Using the abundance probability density of species i in the local community given by Eq. (3) or (4), several biodiversity indices can be defined using the generalized diversity index D_α of Hill (1973)

$$D_\alpha = \exp(H_\alpha), \quad (5)$$

where H_α is the Rényi entropy (Renyi, 1970)

$$H_\alpha = \frac{1}{1-\alpha} \ln \sum_{i=1}^S \sum_{N=0}^J \left(\frac{N}{J} \right)^\alpha p_N(\omega_i) \quad (6)$$

with the abundance probability density $p_N(\omega_i)$ of species i defined either by $p_N(\omega_i) = p_{i,N}^E(t)$ from the evolution equation (3) or by $p_N(\omega_i) = P_{i,N}^E$ from the steady-state solution (4).

For different α , the index D_α differs only in its sensitivity to the presence of rare species. Different exponent α describes different aspects of species abundance composition in the community. For example, D_0 is the total number of species S , D_2 the Simpson index D ,

$$D = D_2 = \left[\sum_{i=1}^S \sum_{N=0}^J \left(\frac{N}{J} \right)^2 p_N(\omega_i) \right]^{-1}, \quad (7)$$

while H_α converges to the Shannon entropy as $\alpha \rightarrow 1$, i.e.,

$$H_\alpha \rightarrow H = - \sum_{i=1}^S \sum_{N=0}^J \left(\frac{N}{J} \right) \ln \left(\frac{N}{J} \right) p_N(\omega_i), \quad (8)$$

and $D_\alpha \rightarrow \exp H$.

In addition, to calculate the species richness in a local community of size J , we can define the average number of species containing individuals between n_1 and n_2 as (Volkov et al., 2003)

$$\langle \phi(n_1, n_2) \rangle = \sum_{i=1}^S \sum_{N=n_1}^{n_2} p_N(\omega_i). \quad (9)$$

Then the species richness in the local community of size J is $\langle \phi(1, J) \rangle$.

3.3. Mean time to species extinction

Assume that the i th species has abundance $N > 0$, then the mean time to species extinction $T_{i,N}^E$ can be calculated as the mean first passage time to zero species abundance. In that case $T_{i,N}^E$ fulfills the following equation (Gardiner, 1983)

$$W_i^E(N+1|N)(T_{i,N+1}^E - T_{i,N}^E) + W_i^E(N-1|N)(T_{i,N-1}^E - T_{i,N}^E) = -1, \quad (10)$$

with the absorbing–reflecting boundary conditions in the form

$$T_{i,0}^E = 0, \quad T_{i,N}^E = T_{i,N+1}^E. \quad (11)$$

The solution to Eqs. (10) and (11) can be explicitly calculated as

$$T_{i,N}^E = \sum_{K=1}^N \phi(K) \sum_{L=K}^J \frac{1}{\phi(L)W_i^E(L+1|L)}, \quad (12)$$

where

$$\phi(N) = \prod_{K=1}^N \frac{W_i^E(K-1|K)}{W_i^E(K+1|K)}.$$

4. Continuous approach

Another effective tool in analysis of species abundance distribution and dynamics is a continuous approach based on the diffusion approximation of the one step species abundance dynamics process governed by Eq. (2). To do that, we define the transition probabilities for the change $\Delta N_i(t) = N_i(t + \Delta t) - N_i(t)$ in the abundance N_i of species i per time step Δt as

$$\Pr(\Delta N_i = \Delta | N_i = N) = \mu \Delta t W_i^E(N + \Delta | N), \quad (13)$$

where $\Delta = 1$ or -1 , and μ is the number of deaths per unit time interval.

Using the transition probabilities specified in (13), the first and second moments of the random variable ΔN_i can be easily calculated as follows. The superscript E denotes ecotone community.

$$\begin{aligned} V_i^E(N) &= \lim_{\Delta t \rightarrow 0} \frac{E(\Delta N_i | N_i = N)}{\Delta t} = \mu m \left(\tilde{\omega}_i - \frac{N}{J} \right) \\ D_i^E(N) &= \lim_{\Delta t \rightarrow 0} \frac{E((\Delta N_i)^2 | N_i = N)}{\Delta t} \\ &= \mu \left(2(1-m) \frac{N(J-N)}{J(J-1)} + m(1-\tilde{\omega}_i) \frac{N}{J} + m\tilde{\omega}_i \frac{J-N}{J} \right), \end{aligned} \quad (14)$$

where $\tilde{\omega}_i = \theta^1 \omega_i^1 + \theta^2 \omega_i^2$. Note that $\tilde{\omega}_i = \omega_i$ in Hubbell's zero-sum model (1) (Babak, 2006).

4.1. Species abundance distribution and dynamics

Further assuming that the abundance n of species i is a continuous variable falling within the interval $[0, J]$, we proceed to the Kolmogorov–Fokker–Planck forward equation as (Gardiner, 1983)

$$\frac{\partial p_i^E}{\partial t} = \frac{1}{2} \frac{\partial^2 D_i^E(n) p_i^E}{\partial n^2} - \frac{\partial V_i^E(n) p_i^E}{\partial n}, \quad (15)$$

where $p_i^E = p_i^E(n, t)$ is the probability of species i having abundance n at time t . It has to be subject to the initial condition

$$p_i^E(n, 0) = p_i^{E,0}(n), \quad n \in [0, J], \quad (16)$$

and to the natural boundary conditions at $n = 0$ and $n = J$

$$\frac{1}{2} \frac{\partial D_i^E(n) p_i^E}{\partial n} - V_i^E(n) p_i^E \Big|_{n=0, J} = 0, \quad t \geq 0. \quad (17)$$

Eqs. (15)–(17) together define the evolution of species abundance probability $p_i^E(n, t)$ in the ecotone given the probability density of the species abundance $p_i^{E,0}(n)$ at the initial time $t = 0$. The boundary conditions (17) make p_i^E in Eq. (15) be a probability density function of the species abundance n through the constraint:

$$\int_0^J p_i^E(n, t) dn = \int_0^J p_i^{E,0}(n) dn = 1, \quad \text{for all } t \geq 0. \quad (18)$$

The steady-state solution $P_i^E(n)$ of the forward problem, Eqs. (15)–(18), gives the equilibrium abundance probability density of species i . This density describes the long time behavior of species abundance in the ecotone. It can be easily verified that the equilibrium probability density $P_i^E(n)$ satisfies the ordinary differential equation of the first order

$$\frac{1}{2} \frac{dD_i^E(n) P_i^E}{dn} - V_i^E(n) P_i^E = 0, \quad n \in (0, J), \quad (19)$$

conditional on $\int_0^J P_i^E(n) dn = 1$. This condition guarantees the existence of unique solution of (19).

It worth noting that the approximations of the species abundance probability evolution and equilibrium species abundance distribution in a local community obtained using the Kolmogorov–Fokker–Planck forward equation gives a good practical and reliable approximations to the discrete master equation approach (Aalto, 1989). However, the theoretical validity of this approximation is true for the case of large local communities with the immigration probability m of order $1/J^\xi$, $\xi \geq 1$ (Van Kampen, 2007). The number ξ corresponds to the dispersal limitation parameter measuring the effect of immigration decline due to dilution from increasing size of the local community J (Hubbell, 2001).

4.2. Biodiversity indices

By analogy to the discrete case described in Section 3.2, we can introduce the generalized diversity index D_α using Eq. (5) with the Rényi continuous entropy (Vinga and Almeida, 2004) H_α defined as

$$H_\alpha = \frac{1}{1-\alpha} \ln \sum_{i=1}^S \int_0^J \left(\frac{n}{J} \right)^\alpha p(n, \omega_i) dn \quad (20)$$

where the abundance probability density $p(n, \omega_i)$ of species i is defined either by $p(n, \omega_i) = p_i^E(n, t)$ from the evolution Eqs. (15)–(17) or by $p(n, \omega_i) = P_i^E(n)$ from the steady-state equation (19). Similarly to the discrete case, D_0 is equal to the total number of species S , D_2 is the Simpson index D , and H_α converges to the Shannon entropy as $\alpha \rightarrow 1$. In addition, the average number of

species containing between n_1 and n_2 individuals can be defined as (Babak, 2006)

$$\langle \phi(n_1, n_2) \rangle = \sum_{i=1}^S \int_{n_1}^{n_2} p(n, \omega_i) dn, \quad (21)$$

and the species richness in the local community of size J is $\langle \phi(1, J) \rangle$.

4.3. Species extinction

The Kolmogorov–Fokker–Planck backward equation is given as (Gardiner, 1983)

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

where $n \in (0, J)$ and $t > 0$. This backward equation governs the probability $G_i^E(n, t)$ that species i has not gone extinct from the ecotone by time t given the initial species abundance n at the initial time $t = 0$. It has to meet the following three conditions: the initial condition

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

the absorbing boundary condition at $n = 0$

$$G_i^E(0, t) = 0, \quad t > 0, \quad (24)$$

and the reflecting boundary condition at $n = J$

$$\frac{\partial G_i^E}{\partial n}(J, t) = 0, \quad t > 0. \quad (25)$$

Because $G_i^E(n, t)$ is the probability that species i does not go extinct, the probability distribution function for the first passage time to the extinction of the species with initial abundance n is

$$F_i^E(n, t) = 1 - G_i^E(n, t). \quad (26)$$

Therefore, the probability density function for the first passage time to extinction is equal to

$$f_i^E(n, t) = -\partial G_i^E(n, t) / \partial t. \quad (27)$$

From Eq. (26) or (27), the k th moment of the first passage time to extinction of species i from the ecotone, $T_i^{E,k} = T_i^{E,k}(n)$, is easy to derive:

$$\frac{1}{2} D_i^E(n) \frac{d^2 T_i^{E,k}}{dn^2} + V_i^E(n) \frac{dT_i^{E,k}}{dn} = -k T_i^{E,k-1}, \quad n \in (0, J), \quad (28)$$

with subjection to the absorbing–reflecting boundary conditions in the form

$$T_i^{E,k}(0) = 0, \quad \frac{dT_i^{E,k}}{dn}(J) = 0, \quad (29)$$

here $T_i^{E,0} = 1$.

5. Analysis of abundance distribution and dynamics

Species abundance dynamics in the ecotone can be investigated by analyzing boundary conditions (17) for Kolmogorov–Fokker–Planck forward equation (15). These boundary conditions can be rewritten in the form

$$\frac{\partial p_i^E}{\partial n} + \frac{1}{D_i^E(n)} \left(\frac{dD_i^E(n)}{dn} - 2V_i^E(n) \right) p_i^E \Big|_{n=0,J} = 0, \quad t \geq 0. \quad (30)$$

At the abundance level $n = 0$, boundary condition (17) degenerates to the Neumann boundary condition when

$$m_0^E = \frac{1}{(J-1)(\tilde{\omega}_i + \tilde{\omega}_i/J + 1/(J-1) - 1/(2J))} \approx \frac{1}{\tilde{\omega}_i \cdot J}, \quad (31)$$

and at the abundance level $n = J$, boundary condition (17) degenerates to the Neumann boundary condition when

$$m_J^E = \frac{1}{(J-1)(1 - \tilde{\omega}_i - \tilde{\omega}_i/J + 1/(J-1) + 1/(2J))} \approx \frac{1}{(1 - \tilde{\omega}_i) \cdot J}, \quad (32)$$

where $\tilde{\omega}_i = \tilde{\omega}_i^E = \theta^1 \omega_i^1 + \theta^2 \omega_i^2$. Note that in Hubbell's zero-sum model (1): $\tilde{\omega}_i = \tilde{\omega}_i^I = \omega_i$. It is worth mentioning that the Neumann boundary condition implies zero gradient in the probability of species abundances at a boundary abundance. Ecologically, the Neumann boundary condition at the zero species abundance means that the rare species have a similar extinct behavior, i.e., the rare species has approximately the same chance to go extinct or to recover in the community. The Neumann boundary condition at the monodominant abundance level means the species has approximately the same chance to become monodominant or to decrease from the abundance level close to the monodominant state.

It is straightforward that at the abundance $n = 0$ the gradient of the species abundance probability density is positive when $m > m_0^E$ and negative when $m < m_0^E$. Thus, for $m > m_0^E$ the probability that the species abundance is close to zero is small, and for $m < m_0^E$ this probability is large. In contrast, at the abundance $n = J$ the gradient of the species abundance probability density is positive when $m < m_J^E$ and negative when $m > m_J^E$. Therefore, only when $m < m_J^E$ the species of interest occupies the entire local community, i.e., becomes a monodominant with high probability. Based on this analysis we can predict the fate of the species in ecotone for given values of immigration rate, the species relative abundances in the two distinct regional communities and the size of ecotone community.

For simplicity, we assume that immigration from each meta-community into the ecotone is equiprobable, i.e., $\theta^1 = \theta^2 = 1/2$, and let species i present only in the first metacommunity, that is, $\omega_i^1 = \omega > 0$ and $\omega_i^2 = 0$. This scenario characterizes the situation where the ecotone has equal boundary with both communities. In this case there are three different types of abundance distributions for species i at the equilibrium state: there are the U-shaped distribution for $m < m_J^E$ (Fig. 1G and H), reverse S-shaped distribution for $m_J^E < m < m_0^E$ (Fig. 1B, C, E and F), and hump shaped distribution for $m > m_0^E$ (Fig. 1A and D). Fig. 2 shows the parameter space of ω (the relative abundance of the species in the metacommunity) and m (immigration probability). Different subspaces produce different species abundance distributions.

The differences between the abundance distributions of the species in ecotone and in the interior local community of the same size are evident from Figs. 1 and 2. For example, region A in Fig. 2 defines a subspace of ω and m in which the species is persistent in both ecotone and the interior local community, while in region B the species is still persistent in the ecotone community, but it has a very high chance of extinction from the interior community. In region E the species has a high chance to dominate the ecotone but goes extinct from the interior community. In region H, the species has a high probability to either dominate or go extinct, depending on its initial abundance. Only in the regions of A, C and H (see Fig. 1) do the ecotone and the internal local community share similar shapes of species abundance distributions.

From the comparison between the ecotone and the interior local community, we can see that the differences between species abundance dynamics in these two types of communities are caused by the structure of the community network. Specifically, because the ecotone is connected to two distinct regions with species i present in only one of them, species i has a smaller

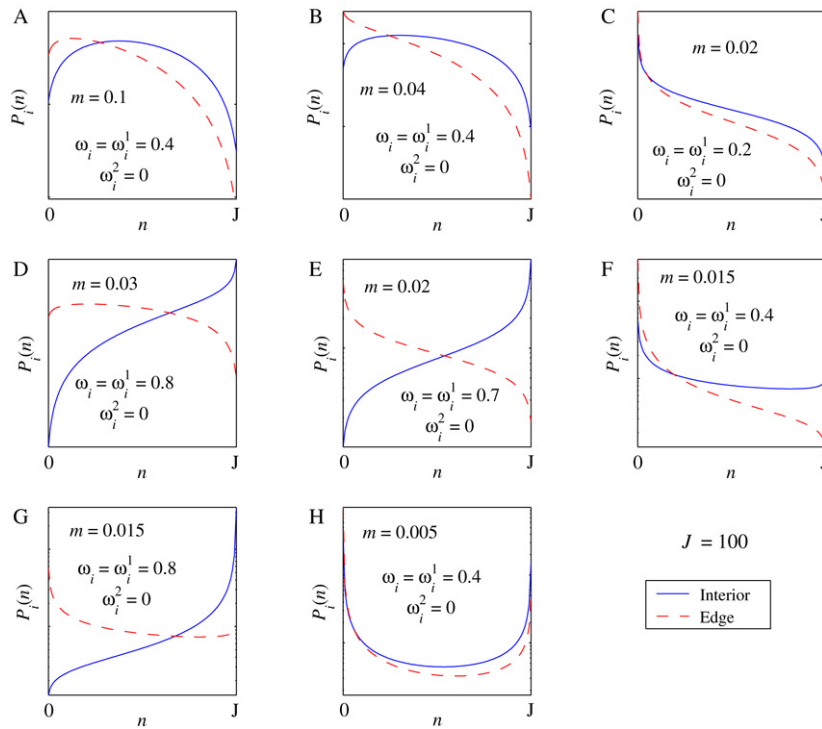


Fig. 1. Comparison of the equilibrium probability densities of the abundance of a species in the local community located within the homogeneous metacommunity (dashed line) and the ecotone on the edges of two communities (solid line).

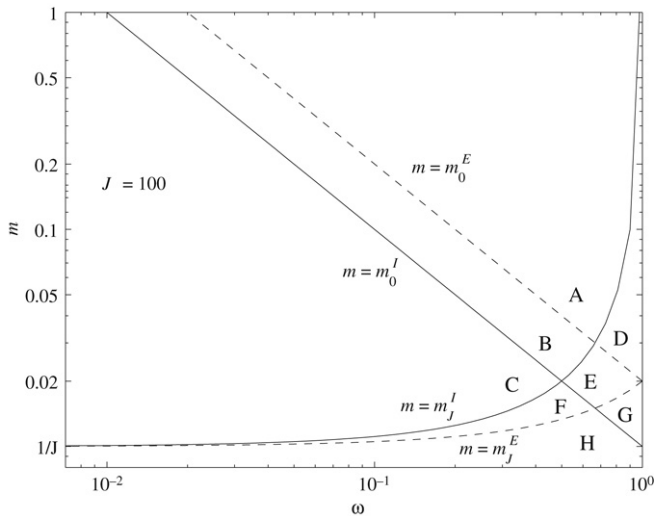


Fig. 2. The parameter space of ω and m that generate different species abundance distribution for the internal local community and the ecotone. The letters indicate the parameter space at which the corresponding species abundance distributions shown in Fig. 1 are produced.

chance of immigration into the ecotone than into the interior local community of the same size. If the species of interest is present in both regions with the same abundance frequency, the difference between the ecotone and the interior community will diminish.

Finally, it is worth noting that the values of the immigration probabilities m_0^E and m_J^E are very close to the values of the immigration probabilities

$$\tilde{m}_0^E = \frac{J}{\tilde{\omega}_i J^2 + 1 - \tilde{\omega}_i} \approx \frac{1}{\tilde{\omega}_i \cdot J}, \quad (33)$$

$$\tilde{m}_J^E = \frac{1}{(1 - \tilde{\omega}_i)(J + 1)} \approx \frac{1}{(1 - \tilde{\omega}_i) \cdot J}.$$

Here, the immigration probabilities \tilde{m}_0^E and \tilde{m}_J^E are defined from the explicit solution of the equilibrium species abundance distribution given by discrete analysis in Eq. (4). The value \tilde{m}_0^E defines the case where the species has equal probabilities of abundances 0 and 1, and the value \tilde{m}_J^E defines the case where the species has equal probabilities of abundances J and $J - 1$.

6. Numerical results

6.1. Time to species extinction

The average first time to the extinction of species i in the ecotone community can be calculated either from the Master equation, Eq. (12), or from the Kolmogorov–Fokker–Planck backward equation, Eqs. (28) and (29) for $k = 1$, while the average first time to extinction of the species for the interior local community [Eq. (1)] is given by Hubbell (2001) and Babak (2006). The ratio of these two extinction times is shown in Fig. 3. It is clear that time to extinction in the ecotone is always shorter than that in the interior community, i.e., the species in the interior local community persists longer than the species on the edge. Thus, the chance of species extinction is always higher on the edge than in the interior.

Fig. 3 shows that the ratio of extinction times decreases with initial species abundance, n . When the abundance of a species is small, the species in the ecotone goes extinct much faster than in the interior community of the same size. Thus, rare species have a higher chance of extinction from the edge community than from the interior community due to the difference in immigration flux from the regions. The difference in the extinction times between the two communities is amplified by immigration rate. Although the persistence of the species in both communities increases with the immigration rate m , the positive effect of immigration on persistence is stronger in the interior community than in the ecotone (Fig. 4). This phenomenon is related to the available pool of species which can immigrate into the community and their relative

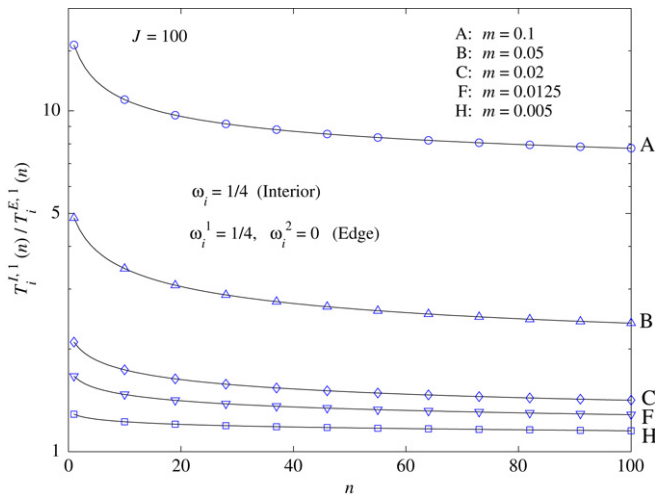


Fig. 3. Ratio between the average first times to extinction in the interior community, $T_i^I(n)$, and in the ecotone adjacent to two different communities, $T_i^E(n)$. The ecotone and its counterpart interior community are the functions of immigration rate (m) and of the initial population size (n) of the species in respective communities.

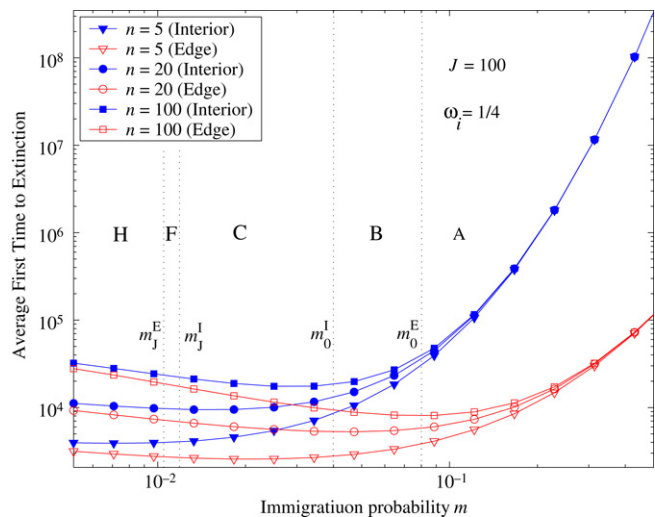


Fig. 4. Effect of varying immigration probability m on the average time to species extinction from the local community located in the interior of one metacommunity ($\omega_i = \omega$) and from the local community at the edge between two different communities ($\omega_i^1 = \omega, \omega_i^2 = 0$). The average first times to species extinction are shown for different initial species abundances in local communities n .

abundance in it. The number of possible species which can arrive into the ecotone is in general larger than that into the interior local community. Consequently, the ecotone becomes more crowded than the interior community. Results in Fig. 4 show that the effect of the initial species abundance on persistence diminishes with the increase in immigration rate. It should also be pointed out that species persistence in both communities first slightly decreases with the increase in m and then increases significantly with m . This phenomenon appears as an interplay between the probability of immigration and probability of leaving the monodominant species abundance. In the case of isolated local communities the species which have attained the monodominant state cannot leave it, and, therefore, the time to its extinction is indefinite. With the increase in the probability of immigration the chance that the species would leave the monodominant state and reach the extinction state increases, leading to the decrease of the time to species extinction. However, if the immigration probability becomes large enough, we can observe the stabilization of species in the local communities. As

a result, the species becomes more persistent or the time to species extinction increases with respect to the immigration probability.

The species extinction times shown in Figs. 3 and 4 correspond well to the type of species abundance dynamics described in Figs. 1 and 2 for the edge and interior communities. For example, in region A when the species in both communities has a high chance to persist at intermediate abundance (i.e., small chance to go extinct or to monodominate), the species also takes longer times to go extinct in both communities as shown in Figs. 3 and 4, and is thus of higher persistence. In contrast, in region H the immigration rate is small (Figs. 1 and 2), the average first times to extinction from both communities could also be long. In this case, the long extinction time describes a high chance of monodominance of the species in the community (Fig. 1H). This is the scenario where one species excludes all other species, leading to a diversity-poor community.

6.2. Species diversity

In the previous two sections we discussed the dynamics and distribution of individual species in ecotone and the interior local community. In this section we compare the diversity of the ecotone and the interior local community. Particularly, we consider the case where the species abundances in all metacommunities satisfy the Fisher log series distribution with the same $x = b/d$ (b and d are per-capita birth and death rates, respectively; see Volkov et al. (2003)). To simulate the species abundances in the metacommunities that satisfy the Fisher log series distribution we used the Fisher log series cumulative distribution function

$$F(n) = 1 + \frac{B_x(n+1, 0)}{\ln(1-x)} \quad (34)$$

where $B_x(n+1, 0)$ is the incomplete beta function. First, for a given x we simulated S numbers α_i from the uniform distribution in the interval $(0, 1)$. Then, we defined the corresponding integer numbers β_i according to $F(\beta_i - 1) \leq \alpha_i < F(\beta_i)$, assuming that $F(0) = 0$. Finally, we defined the species abundance fractions ω_i that correspond to the simulated Fisher log series species abundances as $\beta_i / \sum \beta_i$.

Moreover, for our comparison analysis the species in the two metacommunities connected to the ecotone are assumed to be distinct. Of course, the assumption that the two metacommunities are completely non-overlapping is an artificial and idealized assumption. Although this can be easily relaxed to allow overlapping of the metacommunities, the overlapped communities will not change the results of our analysis for the reason that if a species present in both metacommunities, its effect on the ecotone is simply a weighted sum of the two communities (weighted by θ^1 and θ^2 , Eq. (2)).

Fig. 5 illustrates the three diversity indices (Species richness, Simpson and Shannon Entropy Indices) calculated for the ecotone and interior local communities. These indices were evaluated for varying immigration probability and the species richness in the metacommunities. The species richness and the Simpson index were calculated using the approximations of the equilibrium species abundance distributions obtained from the Kolmogorov–Fokker–Planck forward equation (19) and Eq. (21) with $n_1 = 1$ and $n_2 = J$ for the species richness and Eq. (20) with $\alpha = 2$ for the Simpson index. The Shannon entropy index was calculated using Eq. (8) for exact equilibrium species abundance distribution obtained in Eq. (4).

Fig. 5 shows that the three diversity indices of the ecotone are always higher than the diversity of the corresponding interior community connected to only one of the metacommunities. These figures also show that the diversity in the local communities increases with the species richness in the metacommunities and the immigration probability m . Despite of these general

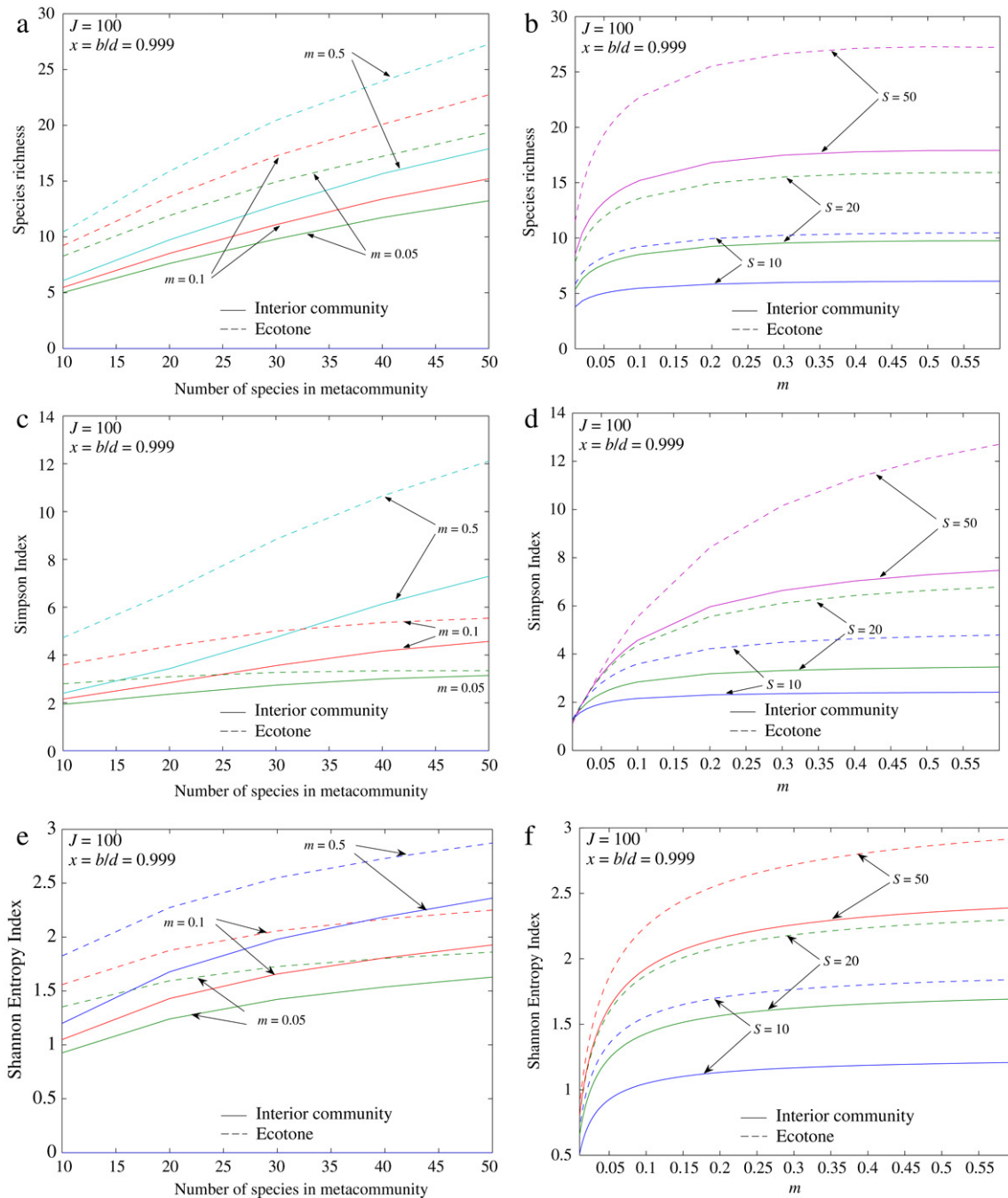


Fig. 5. Species richness, Simpson and Shannon entropy indices for the ecotone located between two metacommunities and in the interior local community of the same size but connected only to one metacommunity. The species abundance distributions in the metacommunities were simulated from the Fisher log series distribution. The comparison is presented for different richness of the metacommunities and for different immigration probabilities.

patterns, the diversity indices behave differently with respect to the metacommunity richness and the immigration probability. Specifically, for the weakly connected local communities, i.e., for local communities with immigration probability smaller than 0.05 (Fig. 5d), the Simpson index is almost equal at the edge and in the interior communities. In contrast, the Shannon index and the species richness in this range of immigration rate show noticeable difference (Fig. 5b, f). This is because the Simpson index is less sensitive to rare species than the Shannon index and the species richness. As a consequence, we can suggest that when the local communities are weakly connected to the metacommunities, the large component in the diversity of local communities is more affected by rare species. Therefore, the major difference between

the ecotone and the interior local community is that the ecotone contains much more rare species than the interior community of the same size. On the other hand, if the immigration rate is high (e.g., larger than 0.05, Fig. 5b, d and f), there is a large difference in the values of the three diversity indices between the edge and the interior local communities.

Finally, since the size of a relatively small local community is a limiting factor for its diversity, with the increase of the metacommunity species richness we observe much smaller increase in diversities of the local communities. Therefore, the diversities of the edge and interior local communities of the same size will eventually become very similar to each other when the species richness in the metacommunities are very high.

7. Discussion

In practice it is not very easy to define the local community at the edge of different habitats because there is lack of a clear-cut boundary from one community (e.g., forest) to the other (e.g., grassland). Spatially explicit models of population dynamics are useful for analyzing edge effects between two different habitats (Fagan et al., 1999; Potapov and Lewis, 2004). Because of the difficulty involving in the development of spatially explicit models, spatially implicit models are often used to provide important ecological insights. Using spatially implicit models for species abundance dynamics could not only simplify technical disadvantages of spatially explicit models, but also provide easily testable null hypotheses about edge effects. In this work we analyzed the edge effects using the neutral model of biodiversity. This model incorporates the spatial structure of the links between habitats implied by the neutral theory.

To explain the edge effects we first performed a comparison study of the abundance dynamics for single species in the ecotone located between two different homogeneous metacommunities and in the interior community of the same size embedded in a homogeneous metacommunity. Clearly, if a species is present only in one metacommunity, the chance of immigration for this species to disperse into the ecotone is lower than into the interior local community. Using the zero-sum game model of Hubbell (2001), we defined the transition probabilities for the change of the species abundance in the ecotone. In our model for the ecotone we proposed that the immigration intensity of each species is proportional to the relative species abundance in each metacommunity and to the length of the common border between the local community and the metacommunity.

The comparison analysis shows the differences between the species abundance dynamics in the edge and interior communities. Specifically, it was observed that each species is more persistent in the interior community than in the edge local community of the same size. For example, Figs. 1 and 2 illustrate that the species can persist in the interior for long time while it is extinct from the edge most of the time (Cases B, E, G). The analysis of the time to species extinction from both types of local communities also shows that the species goes extinct from the ecotone faster than from the interior community, therefore, each species is more persistent at the interior of the homogeneous habitat than at the edge between two distinct habitats. In contrast, ecotones would be more diverse than the interior local communities, although the life span of each species in the edge community is shorter than in the interior community of the same size. This result suggests that the temporal turnover of species is faster in ecotones.

Our analysis of the species abundance behavior in the ecotone and interior local community was completed by considering the biodiversity in those two types of communities. This analysis was performed using the diversity indices including the species richness, the Simpson index and the Shannon index. For the ecotone we assumed that the metacommunities connected to it are distinct, that is, each species can live only in one of these metacommunities. Furthermore, the species abundance composition in the metacommunities is assumed to follow the log series distributions. The results show that diversity in the ecotone is higher than in the interior community of the same size. Moreover, the types of species abundance distributions in the ecotone and the interior are also different. For example, for the weakly connected local communities to the metacommunities, the

species abundance distribution in the ecotone prescribes higher weight of rare species than in the interior local community of the same size.

In conclusion, in this paper we attempted to explain the edge effects by comparing the differences between edge and interior communities from the perspective of neutral theory of biodiversity. Our spatially structured model for species abundance dynamics in ecotone was constructed in accordance to the principle of Hubbell's zero-sum neutral model (Hubbell, 2001). Our model has shown that immigration is a critical process in maintaining species diversity in ecotones. As a result, species turnover rates and species diversity are higher in ecotones than in interior communities.

Acknowledgments

This work is supported by the Alberta Ingenuity Fund and the Natural Science and Engineering Research Council of Canada.

References

- Aalto, E., 1989. The Moran model and validity of the diffusion approximation in population genetics. *Journal of Theoretical Biology* 140, 317–326.
- Babak, P., 2006. Continuous probabilistic approach to species dynamics in Hubbell's zero-sum local community. *Physical Review E* 74, 021902.
- Bell, G., 2001. Neutral macroecology. *Science* 293, 2413–2417.
- Fagan, W.F., Cantrell, R.S., Cosner, C., 1999. How habitat edges change species interactions. *American Naturalist* 153, 165–182.
- Forman, R.T.T., Godron, M., 1986. *Landscape Ecology*. John Wiley and Sons, New York.
- Gardiner, C.W., 1983. *Handbook of Stochastic Methods for Physics, Chemistry and the Natural Sciences*. Springer-Verlag, Berlin, Heidelberg.
- Hill, M.O., 1973. Diversity and evenness - unifying notation and its consequences. *Ecology* 54, 427–432.
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Kupfer, J.A., Runkle, J.R., 2003. Edge-mediated effects on stand dynamic processes in forest interiors: A coupled field and simulation approach. *Ecology* 101, 135–146.
- Matlack, G.R., 1994. Vegetation dynamics of the forest edge - trends in space and successional time. *Journal of Ecology* 82, 113–123.
- McKane, Alonso, A.D., Sole, R.V., 2004. Analytic solution of Hubbell's model of local community dynamics. *Theoretical Population Biology* 65, 67–73.
- Ovaskainen, O., 2004. Habitat-specific movement parameters estimated using mark-recapture data and a diffusion model. *Ecology* 85, 242–257.
- Peters, D.P.C., Gosz, J.R., Pockman, W.T., Small, E.E., Parmenter, R.R., Collins, S.L., Muldavin, E., 2006. Integrating patch and boundary dynamics to understand and predict biotic transitions at multiple scales. *Landscape Ecology* 21, 19–33.
- Potapov, A., Lewis, M., 2004. Climate and competition: The effect of moving range boundaries on habitat invasibility. *Bulletin of Mathematical Biology* 66, 975–1008.
- Renyi, A., 1970. *Probability Theory*. North Holland Publishing Company, Amsterdam.
- Ries, L., Fletcher Jr, R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35, 491–522.
- Schilthuisen, M., 2000. Ecotone: Speciation-prone. *Trends in Ecology and Evolution* 15, 130–131.
- Schooley, R.L., Wiens, J.A., 2005. Spatial ecology of cactus bugs: Area constraints and patch connectivity. *Ecology* 86, 1627–1639.
- Schultz, C.B., Crone, E.E., 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82, 1879–1892.
- Strayer, D.L., Power, M.E., Fagan, W.F., Pickett, S.T.A., Belnap, J., 2003. A Classification of ecological boundaries. *BioScience* 53, 723–729.
- Shugart, C.B., 1987. Dynamic ecosystem consequences of tree birth and death patterns. *BioScience* 37.
- Van Kampen, N.G., 2007. *Stochastic Processes in Physics and Chemistry*, third ed. Elsevier.
- Vinga, S., Almeida, J.S., 2004. Renyi continuous entropy of DNA sequences. *Journal of Theoretical Biology* 231, 377–388.
- Volkov, I., Banavar, J.R., Hubbell, S.P., Maritan, A., 2003. Neutral theory and relative species abundance in ecology. *Nature* 424, 1035–1037.
- Walker, S., Wilson, J.B., Steel, J.B., Rapson, G.L., Smith, B., King, W.McG., Cottam, Y.H., 2003. Properties of ecotones: Evidence from five ecotones objectively determined from a coastal vegetation gradient. *Journal of Vegetation Science* 14, 579–590.