**University of Alberta**

# Continuous Probabilistic Analysis of Neutral Macroecological Models for Species Abundance Dynamics

by

Petro Babak ©

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*to my wife Olena and son Stephan*

# Abstract

Neutral macroecological models explain the assembly of natural communities based on the simplified assumption that all species in a community are ecologically equivalent. In this dissertation I proposed a general continuous probabilistic approach to analyze the species abundance dynamics and extinction processes in neutral local communities governed by the principle of zero-sum game. This principle asserts that every death in a local community is rapidly compensated by the birth of an individual belonging to the same or to a different species.

Firstly, I considered the species abundance dynamics in a local community governed by the principles of Hubbell's zero-sum neutral theory. Using a continuous probabilistic approach I calculated the persistence probability, the probability of extinction and the distribution of the extinction time. Moreover, I proposed a classification of the species abundance dynamics based on different types of species abundance distributions and species extinction dynamics in local communities. This classification allows one to distinguish which species are at high risk of extinction.

I developed three new models for the species abundance dynamics in spatially structured ecological communities. The first model was designed to understand diversity in local communities located at the edge of two different habitats. Using this model I explained higher species richness and higher extinction risk in local communities located at the edge between two different habitats than in local communities located in a homogeneous habitat. The second model was formulated for two local communities connected with each other and with the metacommunity through immigration, and the third model was formulated for two connected local communities in such way that the immigration from the metacommunity is possible only to one of them. From these models I showed that (1) higher similarity of the species abundance dynamics in two local communities is observed for larger values of the immigration probability between local communities, (2) the average first time to species extinction from local community is larger if the local community is more closely connected to the metacommunity and/or to the other local community, and (3) the time to species extinction is larger for local communities with more complex spatial structure.

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# List of Abbreviations

| | |
|---|---|
| $N$, $n$, $x$, $x^0$, $x^J$ | species abundances |
| $x_k$ | species abundance in the $k$-th local community |
| $N_i$ | abundance of species $i$ in local community |
| $N_{k,i}$ | abundance of species $i$ in the $k$-th local community |
| $J$ | size of local community, i.e., the sum of abundances of all species in local community |
| $\Omega$ | abundance domain for two local communities, $\Omega = (0,J)\times(0,J)$ |
| $\Gamma$ | abundance boundary for two local communities |
| $S$ | total number of species |
| $M$ | immigration probability |
| $m^m$ | immigration probability from the metacommunity |
| $m^l$ | immigration probability from the other local community |
| $m^l_J$, $m^m_{J,\omega}(m^l)$ | critical values of immigration probabilities |
| $\omega_i$ | fractional metacommunity relative species abundance of species $i$ |
| $\omega_i^k$ | fractional relative species abundance of species $i$ in the $k$-th metacommunity |
| $W_i$, $W_i^e$, $W_{k,i}$ | transition probabilities |
| $\mu$ | number of death events per unit time interval |
| $\mu_k$ | number of death events per unit time interval in the $k$-th local community |
| $\theta^k$ | probability of immigration from the $k$-th metacommunity |
| $t$, $\tau$ | time |
| $\Delta t$ | time step |
| $V$, $V_i$ | first moment of the change in the abundance per time step $\Delta t$ as $\Delta t \to 0$ |
| $D$, $D_i$ | variance of the change in the abundance per time step $\Delta t$ as $\Delta t \to 0$ |
| $p_i(n,t)$ | probability density of abundance $n$ for species $i$ at time $t$ |
| $P_i(n)$ | equilibrium (steady-state) probability density of abundance $n$ for species $i$ |
| $p_i^0$ | initial probability density of abundance for species $i$ at time $t = \tau$ or $t = 0$ |
| $p_{i,N}$ | probability that the $i$th species contains $N$ individuals |
| $p_i{*}(z,t)$ | additive probability density of abundance $z$ for species $i$ at time $t$ for two local communities |
| $p_k(x_k,t)$ | marginal probability density of abundance $x_k$ for species $i$ in the $k$-th local community at time $t$ |
| $\phi_N$ | number of species containing $N$ individuals |
| $<\phi_N>$ | average number of species containing $N$ individuals |
| $\phi(n_1,n_2)$ | number of species containing from $n_1$ to $n_2$ individuals |
| $<\phi(n_1,n_2)>$ | average number of species containing from $n_1$ to $n_2$ individuals |
| $G_i(t,n)$ | probability that species $i$ with initial abundance $n$ has not gone extinct by time $t$ |

| | |
|---|---|
| $F_i(t,n)$ | probability distribution of the first time to extinction of species $i$ with initial abundance $n$, i.e., probability that species $i$ with initial abundance $n$ has not gone extinct by time $t$ |
| $f_i(t,n)$ | probability density of the first time to extinction of species $i$ with initial abundance $n$ |
| $G_i^k(x,t)$ | probability that species $i$ with initial abundance $x = (x_1,x_2)$ in two local communities has not gone extinct by time $t$ from the $k$-th local community |
| $G_i^{1\text{v}2}(x,t)$ | probability that species $i$ with initial abundance $x = (x_1,x_2)$ in two local communities has not gone extinct by time $t$ from the first and second local communities |
| $T_i^1(n)$ | mean first time to extinction of species $i$ with initial abundance $n$ |
| $T_i^k(n)$ | $k$-th moment of the first time to extinction of species $i$ with initial abundance $n$ |
| $T_{\text{fix},i}^1(n)$ | mean first time to fixation (extinction or complete dominance) of species $i$ with initial abundance $n$ |
| $\pi_i^0(n)$ | probability of extinction of species $i$ with initial abundance $n$ before its complete dominance |
| $\pi_i^J(n)$ | probability of complete dominance of species $i$ with initial abundance $n$ before its extinction |
| $Q_i^1$ | probability of extinction of species $i$ from the first local community before its extinction from the second local community |
| $Q_i^2$ | probability of extinction of species $i$ from the second local community before its extinction from the first local community |
| $H_\alpha$ | Rényi continuous entropy |
| $D_\alpha$ | generalized diversity index |
| $D$ | Simpson index |
| $H$ | Shannon index (Shannon entropy) |
| $E$ | mean |
| $Var$ | Variance |
| $Cov$ | covariance |
| $r_{12}$ | correlation coefficient between species abundances in two local communities |

# List of Definitions

**Diversity index:** an index which is intended to measure the biodiversity of an ecosystem. E.g.: species richness, Simpson index, Shannon index, Simpson evenness index.
**Extinction:** "the disappearance of a species or taxon from a given habitat or biota, not precluding later recolonization from elsewhere" (Linkoln et al. 1998).
**Extinction risk:** the probability of extinction of a species or taxon within a given time interval.
**Extinction time:** the time to the disappearance of a species or taxon from a given habitat or biota (Linkoln et al. 1998).
**Neutral theory:** the theory that "treats organisms in the community as essentially indentical in their per capita probabilities of giving birth, dying, migrating, and speciating" (Hubbell 2001).
**Neutrality assumption:** "the assumption of per capita ecological equivalence of all individuals of all species in a trophically defined community" (Hubbell 2001).
**Niche theory:** the theory constructed based on the assumption that "communities are groups of interacting species whose presence or absence and even their relative abundance can be deduced from "assembly rules" that are based on the ecological niches or functional roles of each species" (Hubbell 2001).
**Persistence:** the survival of the ecosystem or some part of the system (Linkoln et al. 1998).
**Spatially implicit model:** the model that incorporates spatial location of studied plots and spatially contagious or neighborhood processes that connect studied plots (Peters 2004).
**Spatially explicit model:** the model that does not incorporate spatial location of studied plots and spatially contagious or neighborhood processes that connect studied plots (Peters 2004).
**Species abundance distribution:** (1) a measure describing how abundances are distributed over species in a community, when referred to all species (Alonso et al. 2006); (2) a measure describing the distribution of given species in a community as a random variable, when referred to one species.
**Zero-sum assumption:** the sum of all changes in abundance is always zero, that is, the increase in abundance of one species must company the same amount decrease in abundance of other species (Hubbell 2001).

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# Chapter 1
# Introduction

## 1.1 Species abundance models and extinction dynamics

One of the main goals of ecology is to explain the distribution, abundance and persistence of living organisms in ecological communities (Anderwartha 1961, Pielou 1975, Krebs 2001). These questions are also of central theoretical and practical importance in conservation biology (Soulé 1986, Primack 2002), since understanding the mechanisms of species abundance dynamics is of great concern in viability analysis.

### 1.1.1 Species abundance relationships and models

The species-abundance relationship is described by a species abundance distribution which represents the number of species as a function of their observed abundance. These relationships are often shown using Preston's (1948) grouping method based on abundance intervals of log base 2 containing 1, 2, 3-4, 5-8, 9-16,… individuals, or Williams (1964) method based on abundance intervals of log base 3 containing 1, 2-4, 5-13, 14-40,… individuals. A rank abundance plot is another way of portraying the same information as the species abundance distribution does. This type of plot shows the species abundance against the upper cumulative species abundance (May 1975).

To describe the species abundance relationship, inductive approaches were initially employed. By these approaches, observed distributions are fit to statistical distributions with little knowledge about the underlying biological mechanisms. The first such study is the classic work of Fisher, Corbet and Williams (1943) who fitted the logseries model to 620 species of butterflies collected from Malay Peninsula. Recently, Magurran (2005) reconsidered Fisher's log-series model and discovered its potential for describing large scale patterns of species abundance. Preston (1948) argued that the species abundance distributions were more often bell-shaped and the logseries distribution did not describe this shape well. To fit the data that Preston had on bird species abundances, he log transformed the species abundances and discovered that the relative species abundance curve could then be normalized. To display the lognormal distribution he introduced doubling categories of species abundance, "octaves", and proposed a simple discrete formula for approximating the continuous lognormal distribution. Grundy (1951) proposed a precise mathematical definition of the truncated lognormal distribution for species abundances, but a proper estimation method was not published until Bulmer (1974) derived the maximum likelihood estimators assuming Poisson sampling. A combination of log-series and log-normal distributions was proposed by Magurran and Henderson (2003) for description of two components of ecological communities: log-normal distributed core species which are persistent and abundant; and log-series distributed occasional species which occur infrequently in the long term record. These distributions were overlaid and produced a negative skew, which is typical for real data.

Later the preference was given to the theories of species abundance based on one or another ecological theory of community organization. MacArthur (1957) reasoned that the groups of trophically similar species in ecological communities randomly divide up a common pool of limiting resources. Therefore, he suggested that the species' relative abundances are proportional to the fraction of total resource each utilizes. By idealizing the resource pool as a stick of unit length, he proposed the broken-stick hypothesis (MacArthur 1957) and the broken-stick hypothesis with niche overlap (MacArthur 1960, 1967). But the relative species abundances based on the broken–stick hypothesis do not fit well the empirical data. Note also that the theories based on the broken-stick hypotheses explain neither logseries, nor lognormal species abundance patterns. In 1975, a theoretical explanation for the logseries distribution was suggested by May (1975). He noticed that a steep geometric distribution for the relative abundances of species obtained from the niche-preemption model (Motomura 1932, Whittaker 1965) produces a straight line on a dominance-diversity plot, typical of the logseries of Fisher et al. (1943). A few years later, by making an analogy to the sequential breakage by the action of a rock-crushing machine Sugihara (1980) modified the broken-stick model and explained the canonical lognormal distribution (Preston 1962) of relative species abundances.

It is worthy to mention that the "broken-stick" models are based on niche theory, which assumes species abundances are proportional to the resource each exploits. And while the niche theory is conceptually appealing, it is not clear how such theory could help us understand the relationship between abundances and fundamental birth-death demographic processes in population dynamics, which we know are key to controlling population sizes (Hubbell, 2001).

Stochastic modeling of species abundance dynamics in living communities has a long tradition in ecology (e.g., Bartlett 1960, Engen 1974, Lande et al. 2003). It is also possible to explain several species abundance relationships using stochastic population models (Lande et al. 2003). For example, Engen and Lande (1996a, b) developed stochastic models that allow species abundances to change due to specific environmental stochasticity in density-independent growth rate and deterministic density dependence within species. The underlying assumption of their model is that taxonomically related species in the same trophic guild compete for the same or similar limited resources. Following their assumption, Engen and Lande showed that different forms of intraspecific density dependence produce different shapes of species abundance distributions (Lande et al. 2003). For example, logistic density dependence within species produces a Gamma distribution of species abundances; Gompertz density dependence (linear on the log scale) produces a lognormal species abundance distribution. By applying a diffusion approximation for each species' dynamics with density regulation of the θ-logistic type, Dieserud and Engen (2000) proposed a general species abundance model that embraces the lognormal and gamma distributions, allowing intermediate and more extreme fits than these two restricted distributions of the model.

It is interesting to note that recently, analyzing the properties the lognormal distribution, Williamson and Gaston (2005) concluded that the lognormal is not an appropriate null model for any distributions of species abundances.

### 1.1.2 Extinction dynamics

The extinction of animal and plant populations is affected by diverse processes, including environmental variability and catastrophes (Mangel and Tier 1993, Lande 1993, Engen et al. 2005), habitat size reduction and habitat fragmentation (Sole et al. 2004, Keymer et al. 2000, MacArthur and Wilson 1967), dispersal (Poethke et al. 2003), harvesting (Lande et al. 1994, 1995), life history traits (Reynolds et al. 2005), loss of genetic variability (Gaggiotti 2003), inbreeding depression (Frankham 2005), accumulation of deleterious mutations (Lande et al. 1994, Gaggiotti 2003, Abu-Raddad and Ferguson 2004), sexual selection (Kokko and Brooks 2003, Moller 2003) and mating system (Bessa-Gomes et al. 2003, Saether et al. 2004), see also (Benton 2003).

A central problem in extinction processes is estimation and analysis of quantities associated with time to extinction, probability of extinction, and extinction thresholds. A substantial amount of work has been done on the analysis of extinction processes using various analytic, numerical and statistic methods, including parametric and non-parametric estimation (Solow and Roberts 2003, Bascompte 2003, Solow 2005), maximum likelihood methods (Ludwig 1996a, Solow and Smith 2000, Hakoyama and Iwasa 2000), Bayesian analysis (Solow 1993, Ludwig 1996b), Fourier series analysis (Sole et al. 1997, Newman and Eble 1999), time series analysis (Ludwig 1999, Hakoyama and Iwasa 2000), diffusion approximations (Gardiner 1983, Lande et al. 1995, 2003, Ludwig 1996a, Grasman 1996, Nasell 1999, van Herwaarden and van der Wal 2002, Engen et al. 2005), and simulation studies (Mangel and Ludwig 1977, Grasman 1996, Akcakaya et al. 1997, Grimm and Wissel 2004).

The extinction dynamics of populations was investigated for several population models. For example, Keymer et al. (2000), Jablonski (2000), Alonso and McKane (2002), Engen et al. (2002), Ovaskainen and Hanski (2003) studied spatial models and extinction, Ludwig (1996a) investigated the extinction time and probability for Gompertz population model, Grasman (1996), Hakoyama and Iwasa (2000), Newman et al. (2004) investigated logistic models.

The effect of various factors on extinction dynamics have been investigated in detail by many researchers. These include the effect of demographic stochasticity (Lande 1988, 1993, 1994, Mangel and Tier 1993, Ludwig 1996b, Hakoyama and Iwasa 2000, Moller 2003, Bessa-Gomes et al. 2003, Abu-Raddad and Ferguson 2004, Saether et al. 2004, Engen et.al. 2004, 2005), the impact of random environmental fluctuations and catastrophes (Lande and Orzack 1988, Lande 1993, 1994, Newman 1997, Lande et al. 1995, 2003, Mangel and Tier 1993, Abrams 2002, Poethke et al. 2003, Ovaskainen and Hanski 2003, Engen et.al. 2002, 2004, 2005), the effect of density dependence (Lande and Orzack 1988; Hakoyama and Iwasa 2000; Engen et al. 2002; Bascompte 2003), and the effect of migration processes (Mangel and Tier 1993; Lande et al. 1998, 2003; Engen et al. 2002; Alonso and McKane 2002; Gaggiotti 2003). In addition to extinction processes, Ginzburg et al. (1982), Ludwig (1999) and Engen et.al. (2002) studied quasi-extinction processes, which describe the decrease in population size to some given low level of density.

The statistical analysis of field datasets on species abundances over long time intervals allows comparison of different theories on extinction dynamics with field observations. When the observations of certain rare animal species are given only in the form of occasional chance sightings, then it is possible to infer extinction from the time of most recent sighting (Solow 1993a, 1993b, 2005, Solow and Roberts 2003). Detecting a terminal mass extinction event has been studied using fossil records (Harvey et al. 1994, Jablonski 2000, 2002, Newman 1997, Newman and Eble 1999a, 1999b, Newman and Sibani 1999, Sole et al. 1997, Solow and Smith 2000, Solow et al. 2006). The risk of extinction and extinction time were computed for various datasets from short-term survival of several different populations. For example, Pimm et al. (1988) presented an analysis of the extinction risk using an abundance dataset of 355 populations of British land birds observed during 10's of years. Aebischer (1986) analyzed the die-off of snags (*Phalacrocorax*) on the Isle of May in southeast Scotland. Ricklefs (2006), using data for passerine birds (*Passeriformes*), tested the prediction that the time to extinction of a population of size N is approximately 2N generations. Hakoyama and Iwasa (2000) illustrated the time series method using data for a freshwater fish, Japanese crucian carp (*Carassius auratus*) in Lake Biwa. Ovaskainen and Hanski (2003) analyzed extinction threshold in metapopulation models using the Glanville fritillary butterfly (*Melitaea cinxia*) metapopulation in the Aland Island in southwest Finland.

## 1.2 Neutral theories in ecology

Although the neutral community concept appeared three decades ago (Watterson 1974, Caswell 1976, Leigh et al. 1993), the theory attracted little attention until Hubbell published the provocative monograph (Hubbell 2001), where he proposed a general theoretical framework that unifies theories of biodiversity and biogeography and combined the processes of birth, death, immigration and speciation. Hubbell's theory was in large part developed by borrowing ideas from the neutral theory of molecular evolution by Kimura (1968, 1983). Similar to the neutral theory in genetics, Hubbell's theory construction is based on the assumption that the distribution of species abundance in a community is predominately due to the neutral drift of species abundances (He and Hu 2005). The connection between evolutionary and ecological aspects of biodiversity aids understanding and interpretation of the neutral theory in ecology (Hubbell 2001, Nee and Stone 2003, Etienne and Olff 2004, Turner 2004, He and Hu 2005, Nee 2005, Hu et al. 2006). Similar to the neutrality-natural selection debate in evolution, the neutral theory resulted in the great neutrality-competition debate in ecology (Turner 2004).

Traditionally, ecologists assume that species differ in many aspects and that tradeoffs in life-history traits allow them to coexist in the same habitat (Hutchinson 1959). Neutral theory makes diametral assumptions to niche theory about the necessity and importance of species traits in determining species abundance and diversity patterns (Hubbell 2001, Harpole and Tilman 2006). The key assumption of models constructed on the basis of neutral theory of biodiversity is that all individuals of a trophic level are assumed to be functionally equivalent (Hubbell 2001, Bell 2001). Therefore, the neutral theory concerns a group of trophically similar species typically occurring in sympatry and potentially competing for similar resources (Gaston and Chown, 2005; Chave, 2004).

It noteworthy that the assumption of neutrality should only be referred to biological mechanisms of species dynamics, but not to the species patterns in ecological communities or to the species dynamics itself. For example, the neutrality assumption can concern the mechanisms of birth, death, immigration and emigration. However, such concepts as species abundance patterns, diversity indices, species extinction dynamics are rather deductions of one or another biological model of species dynamics. It is possible that similar species abundance patterns, diversity indices, species extinction dynamics can be obtained from either neutral models, or niche based models, however, these models are dissimilar because of different biological hypotheses.

The idea of neutrality has challenged the classic niche theory and has been controversial since the publication of Hubbell's book in 2001. There have been many attempts to criticize the neutrality assumptions and to reject the neutral model on the basis of different statistical tests in favor of niche-based models (Tokeshi and Schmid 2002, Clark and McLachlan 2003, Maurer and McGill 2004, Tilman 2004, Adler 2004, Ulrich and Ollik 2004, Turnbull et al. 2005, Gilbert and Lechowicz 2004, Wootton 2005, Dornelas et al.2006, McGill et al. 2006). However, the assumption that trophically similar species in communities might be ecologically equivalent is an ideal starting point for analysis and testing for community assembly rules due to its simplicity. The neutral theory provides a first approximation in describing real ecological communities (Hubbell 2005, 2006, Alonso et al. 2006, Bell et al. 2006). In the case of insignificant differences between predictions of neutral and niche-based models, according to the Occam's razor principle, the preference should be given to the simpler neutral model (Chase 2005). If a simple neutral model and a complex niche model both make accurate predictions about some features of community structure, it is not possible to give the preference to the niche model, because the niche hypothesis is known on independent grounds to be true. In this case the differences between models are not the same as differences between hypotheses. It is possible to construct several different models based on niche or neutral hypothesis. However, statistical tests for model comparison do not compare niche and neutral hypotheses. Such tests concern the model mechanisms and parameters, and do not incorporate explicitly the information about niche or neutral nature of models.

The future development of the theories of community organization should rely on the results obtained from neutral theories, and introduction of non-neutral mechanisms in neutral models might be considered as the next steps in analysis of species composition and dynamics in ecological communities (Chave 2004, Nee and Stone 2003, Chase 2005, Leibold and McPeek 2006). The first attempts to model species abundance dynamics in this theoretical niche-neutral framework have been proposed for variable mortality (Yu et al. 1998, Antonovics et al. 2006) and for variable deleterious and beneficial mutations (Fuentes 2004). Sole et al. (2000) introduced an ecosystem model of many interacting species in which the species are connected through a random matrix with a given connectivity. Etienne and Olff (2004a) developed a simple model that unites a neutral community model with niche-based theory by considering different guilds of species, assuming that within the same guild, all individuals are equivalent in their competition for resources, and have the same speciation rate and dispersal capacities. Pueyo (2006) illustrated that both neutral and non-neutral mechanisms coexist in nature, and have different weights in different groups of organisms.

Hubbell's unified neutral theory of biodiversity and biogeography concerns population dynamics on two scales: local communities and regional metacommunities (McKane et al. 2004). To formulate the models for species abundance dynamics in ecological communities Hubbell assumed that the dynamics of ecological communities obey a zero-sum game, i.e., the sum of all changes in abundance is always zero – the increase in abundance of one species must company the same amount decrease in abundance of other species. Based on this assumption, the neutral theory predicts the existence of a new statistical distribution of relative species abundance, called the zero-sum multinomial. This distribution equals a log-series for large immigration probabilities, and is more ''humped'' for small immigration probabilities, like a lognormal (Pueyo, 2006). Hubbell (2001) showed that the zero-sum multinomial distribution fits tropical forest tree data better than the lognormal. Based on the fossil record, Olszewski and Erwin (2004) showed that branchiopod abundance distributions from four temporally distinct ecological landscapes can be better described using zero-sum multinomial distribution than using the log-normal distributions. However, according to recent analyses (McGill 2003, Volkov et al. 2003, Etienne and Olff 2004, Pueyo, 2006, McGill et al. 2006), one cannot always distinguish between these two distributions by using empirical data. Based on a set of best practices for testing the fit of the zero-sum multinomial vs. a lognormal null hypothesis developed by McGill et al. (2006), it was concluded that the lognormal outperforms the neutral theory on robust tests. It was also shown that neutral models are not robust to relaxation of the assumption of ecological equivalence (Zhang and Lin 1997, Yu et al. 1998, Fuentes 2004). Also, the fits of the zero-sum ecological drift model to frequent and to occasional species can be worse than the respective fits of the occasional-frequent species model (Magurran and Henderson 2003) and the self-similarity model (Moulliot et al. 2000, Sole and Alonso 1998), see analysis of species abundance datasets from a large community of forest Hymenoptera conducted by Ulrich and Ollik (2004). Latimer et al. (2005), using neutral ecological theory, showed that the relative species abundance distributions of South Africa's Mediterranean-climate fynbos shrubland can be explained by migration rates that are two orders of magnitude lower than they are in tropical rain forests, and speciation rates are estimated to be higher than in any previously examined plant system.

Up to this date, successful development of the neutral theory of biodiversity was achieved in several directions and on different spatial scales. There has been considerable interest in both spatially implicit and spatially explicit neutral models for species abundance dynamics on different spatial scales.

McKane et al. (2000) used "mean-field approximation", in which one of the species interacts with the combination of all of the other species in the community, to analyze dynamic models for species abundance. He (2005) developed a neutral spatially implicit model for species-abundance relationships. This model incorporates four fundamental processes of population dynamics: birth, death, immigration and emigration. Volkov et al. (2003) presented an analytical solution for the distribution of relative species abundances both in the metacommunity (Fisher's log series) and in the local community. Volkov et al. (2005) proposed a model with symmetric density dependence to explain the rare species advantage in species abundance distributions. They also showed that both dispersal and density-dependence mechanisms offer sufficient and independent explanations for relative species abundances. Vallade and Houchmandzadeh (2003) derived an analytical solution for the distributions of species abundances in the metacommunity and in a local community as a function of speciation, migration rates and the size of the community. Zhou and Zhang (2006) showed that incorporation of the Allee effect in a neutral community results in a considerable decrease in species richness and radically different dominance-diversity curves. Dominance-diversity curves, which incorporate the Allee effect, show an excess of both very abundant and very rare species but a shortage of intermediate species.

Sole et al. (2000) introduced an ecosystem model of many interacting species in which the species are connected through a random matrix with a given connectivity. Using this model, a natural link between log-normal and power-law distributions of species abundances was suggested. Sole et al. (2004) explored both spatially-implicit and spatially-explicit metapopulation models for a competitive community, where the colonization-extinction dynamics takes place through neutral interactions, and species are not hierarchical at all but are somehow ecologically equivalent and just compete for space and resources through recruitment limitation. It was proven that there exists a common destruction threshold for all species. That is, it was shown that whenever habitat loss reaches a certain value a sudden biodiversity collapse takes place. Houchmandzadeh and Vallade (2003) showed by exact analytical methods for a spatially explicit model of species abundances that under assumption of neutrality, organisms tend to aggregate and form clusters. Chave and Leigh (2002) proposed a neutral model where seeds disperse a limited distance from their parents, and speciation is in equilibrium with random extinction. To describe beta diversity the similarity function was calculated as the probability that two trees separated by some distance belong to the same species. Bell (2000) presented a spatially explicit neutral model assuming constant a immigration probability and non-exponential density regulation. Zillio et al. (2005) proposed an analytically tractable variant of a spatially explicit voter neutral model that provided a quantitatively accurate description of beta diversity in two tropical forests and formed links between relative species abundance and the species area relationship.

The neutral theory of biodiversity is designed to apply to samples from a community, not only to the community as a whole. Therefore, special attention was devoted to development of sampling techniques and estimates. Alonso and McKane (2004) developed a sampling theory of Hubbell's neutral spatially implicit theory and derived simple abundance distributions for a random sample both from a local community and a metacommunity. Their result was given in terms of the average number of species with a given abundance in any randomly extracted sample. Etienne and Alonso (2005) presented sampling distributions that contain binomial or hypergeometric sampling on the one hand, and dispersal limitation on the other hand. They concluded that metacommunity size does not independently affect the outcome of neutral models. Etienne (2005) presented a simplified expression for the expected number of species of a particular abundance in a local community with dispersal limitation that can be regarded as an enhanced version of the Ewens (1972) sampling formula. This expression can be used in maximum likelihood methods for quick estimation of the model parameters. Moreover, Etienne (2005) showed how to rapidly generate examples of species-abundance distributions for a given set of model parameters and how to calculate Simpson's diversity index. Etienne and Olff (2005) compared three classical distributions: the zero-sum multinomial distribution, based on Hubbell's neutral model, the multivariate Poisson lognormal distribution, based on niche arguments, and the discrete broken stick distribution, based on MacArthur's broken stick model. They gave explicit formulas for the probability of observing a particular species-abundance data set in each model using a Bayesian analysis of species-abundance data. Condit et al. (2002) presented quantitative estimates of beta-diversity for tropical trees by comparing species composition plots. They found that beta diversity is higher in Panama than in western Amazonia and that patterns in both areas are inconsistent with the neutral model in which habitat is uniform and only dispersal and speciation influence species turnover. Gilbert and Lechowicz (2004) proposed a sampling design that decoupled distance and environment in the understory plant communities of an old-growth, temperate forest. Gray et al. (2006) investigated the effect of binning methods on the differences of species abundance distributions and studied statistical fits to the zero-sum multinomial and log-normal models. The discussions of neutral theory in ecology were not only restricted to biological mechanisms (Chave et al. 2002) and comparisons with classical niche-based theories (Leibold and McPeek 2006, Harpole and Tilman 2006). Attention also has been devoted to tests of neutral theory (Holoyak and Loreau 2006, McGill et al. 2006) and spatial scale (Ostling 2005).

Using neutral models (Caswell 1976, Bell 2000, 2001, Hubbell 1997, 2001, Fuentes 2004) and stochastic population models (Lande et al. 2003, Tilman 2004) predictions can be made not only about species abundance relationships, patterns of species richness, species-area relationships, turnover in species composition with distance, but also about time to extinction or fixation, risk of extinction, etc. Leigh (1981) determined that the average time to extinction under neutrality when a population cannot exceed size $K$ is equal to $2N(1+\ln[K/N])$ ($> 2N$). This result agrees with Fisher's (1930) calculation that the number of descendants of a single neutral mutant will not exceed a small multiple of the number of generations elapsed since the mutant occurred. Ricklefs (2003) suggested that drift is too slow to account for the observed turnover of species within a regional flora and other forces must act. This result was confirmed experimentally by observing rapid increases in populations of introduced species, and relatively rapid declines in species richness in communities. Ricklefs (2006) also tested the prediction from ecological drift that the time to extinction of a population of size N is approximately $2N$ generations (Leigh 1981). Based on data for passerine birds (*Passeriformes*), Ricklefs found that the waiting times to extinction are much less than twice the product of average population size and generation length.

Nee (2005) discussed the time scale for extinction of common species in a neutral community. Hubbell in his book (2001) introduced the probability that a species will suffer the death of given number of individuals, and showed that the time to fixation (local extinction or complete dominance) is inversely proportional to the death rate in the isolated local communities. He also established that the times to fixation and local extinction are approximately Gamma distributed, calculated the average number of deaths in a community until extinction of the given species using a discrete Markov chain approach, studied the extinction time of newly arisen species, and reviewed the extinction dynamics in neutral models in phylogeny. Rosenzweig (1995) proposed a neutral model for the evolution of continental diversity and showed that increased diversity per se will cause increased extinction rates per species. Raup et al. (1973) and Nee et al. (1995) investigated the extinction dynamics for neutral models in phylogeny. Abu-Raddad and Ferguson (2004) examined how ecosystem properties change as a function of the number of pathogen strains, and presented the analysis of how the interactions between diversification processes (i.e. mutation), inter-strain competition (via cross-immunity) and demographic stochasticity determine the equilibrium diversity of a pathogen in a finite-sized host population. Gilbert et al. (2006) used Hubbell's neutral theory to predict the impact of habitat fragmentation on Amazonian tree communities. It was shown that the neutral theory in this case correctly predicts the rate of species extinction as a function of the diversity and mortality rate. However, they showed that the rate of change in species composition in a real communities is much faster than predicted in fragments from neutral theory, indicating that different tree species respond differently to environmental changes.

Finally, to understand the mechanisms of neutral models for local communities proposed in my thesis, I would like to detail the assumption of functional equivalence of individuals in more precise way. I consider different type of models for opened ecological communities at small scale connected through immigration to metacommunities, closed ecological communities at large scale. I assume that individuals of two different species are functionally equivalent if the following conditions are fulfilled:

a) if two different species have the same abundances in a local community, then in this local community the abundances of these species have equal probabilities of decrease in the same time interval due to death process, and equal probabilities of increase in the same time interval due to birth process;

b) if two different species have the same abundances in the metacommunity, then the abundances of these species in the local community have equal probabilities of increase in the same time interval due to immigration process.

This more precise definition of neutrality allows formulation of the models for species abundance dynamics in local communities in more formal way.

## 1.3 Thesis outline

Although much progress has been made with the neutral theory, there is still a great need for a more thorough understanding about the distribution and extinction dynamics of species. Questions such as distribution of extinction times for species in local communities, probability of species extinction within a fixed time interval, species coexistence, and qualitative classification of species dynamics with respect to parameter values have not yet been studied for many types of ecological communities in the framework of the neutral theory of biodiversity. These problems determine the main directions of my research. Moreover, in my study I also covered such important problems as the species distribution and extinction in spatially structured communities including local communities on the edge of different ecosystems, and local communities involving immigration from different sources of ecological network of living habitats.

My thesis on the analysis of neutral models of community organization is organized as follows.

### Chapter 2. Continuous Probabilistic Approach to Species Dynamics in Hubbell's Zero-Sum Local Community

In this chapter I analyzed species abundance distribution and extinction dynamics for Hubbell's zero-sum neutral model for species abundance dynamics in a local community connected through immigration to the metacommunity (see Figure 1.1(a) for the case when a local community is embedded into the metacommunity, and Figure 1.1(b) for the case when a local community represents an island and the metacommunity represents mainland). Using a continuous probabilistic technique I studied the probability density of species abundance, distribution of the first passage time to species extinction or fixation and probability of species extinction. Based on the sensitivity analysis for the continuous probabilistic models, I proposed a realistic classification of local communities subject to their diversity and species dynamics based on such ecological characteristics as the probability of species persistence, extinction and complete dominance. I also investigated the effect of immigration probability, the species metacommunity relative abundance and the size of the local community on the species abundance distribution and the time to species extinction and monodominance. Finally, by the simulation study of Hubbell's zero-sum neutral model for the local community I verified the derived theoretical distribution of the first passage time to extinction. Based on the simulation study I concluded that for species with large initial abundances, the distribution of the first passage time to extinction is very close to the Gamma distribution, as it was presumed by Hubbell (2001), but for the species with small initial abundance, the Gamma distribution does not produce a good fit to the first passage time to extinction.

## Chapter 3. A Neutral Macroecological Model of Edge Effects

Edge effects are one of the most extensively studied ecological phenomena, because understanding the processes that occur at the edges between different living habitats can significantly improve our knowledge of species abundance dynamics and composition of heterogenous communities. In this chapter a new spatially implicit neutral model for explaining the edge effects between habitats with different species abundance structures was proposed (see Figure 1.2(a) for the case when a local community is located between two metacommunities, and Figure 1.2(b) for the case when a local community represents an island and the two metacommunities represent two parts of disconnected mainland). Using this model, I investigated the diversity and evenness in local communities at the edge between two different metacomminities. Using a continuous probabilistic approach based on the Kolmogorov-Fokker-Planck forward equation, I also developed a realistic classification of local communities with respect to immigration probability, species relative abundances of metacommunity and size of local community. The structure and dynamics of local communities at the edge between two distinct habitats were compared to those located in the interior of homogeneous habitat based on diversity measures such as species richness, Simpson and Shannon diversity indices, and evenness index. It was found that the proposed model of edge effects can explain higher species diversity in local communities located at the edge between two distinct metacommunities than in interior local communities; however, the species persistence is higher in interior local communities than in local communities at the edge.

## Chapter 4. Analysis of species abundance distribution in two connected equal local communities

In this chapter I investigated the species abundance dynamics and distribution in similar patches or islands connected to a large source of organisms – the metacommunity (see Figure 1.3(a) for the case when local communities are embedded into the metacommunity, and Figure 1.3(b) for the case when local communities represent two islands and the metacommunity represents mainland). I developed a new model for species abundance dynamics in two equal local communities connected with each other and with the metacommunity through immigration. Using continuous probabilistic technique based on Kolmogorov-Fokker-Planck forward equation, I investigated the effect of the immigration probabilities, species representation in the metacommunity and the size of local communities on the type of species abundance dynamics in local communities. Based on the sensitivity analysis, I proposed a realistic classification of the species abundance dynamics in local communities with respect to such species characteristics as extinction, monodominance and persistence in one or both local communities. I also studied the similarity or dissimilarity of the species abundance distributions between two local communities using the correlation coefficient between species abundances in the two local communities. It was found that higher similarity of the species abundance dynamics in two local communities was observed for larger values of the immigration probability between local communities. Specifically, for fixed probability of immigration from the metacommunity, the correlation between species abundances in two local communities increases with an increase in the immigration between local communities, and, vice versa, for fixed probability of immigration between local communities, the correlation decreases with an increase in the immigration from the metacommunity.

## Chapter 5. Species extinction time and probability in two connected equal local communities

This chapter investigates the extinction time and extinction probability of a species in the neutral model for species abundance dynamics in two equal local communities connected with each other and with the metacommunity formulated in Chapter 4. Using Kolmogorov-Fokker-Planck backward equation, I derived models for the species persistence probability in two local communities, and the average first time to species extinction. I considered two scenarios for species extinction: species extinction from one given local community, and species extinction from either the first or second local community. In addition, I calculated the probability of species extinction from one local community before the other local community for different species abundances in two local communities. Using this probability I can define from each local community the species would most likely go extinct first. Finally, I made a comparison analysis of species extinction dynamics in two local communities and in one local community. This analysis gives us an example of comparison between species abundance dynamics in spatially structured ecological communities (ecological communities involving interaction between many different neighboring habitat patches) and unstructured ecological communities (ecological communities with no spatial factors). It was found that the structure of the ecological system has an important effect on the species persistence in local habitats. Specifically, if the local community is located in a homogeneous landscape, the species extinction time is shorter than in the case when the habitat is non-homogeneous and spatially structured.

## Chapter 6. Analysis of species abundance distribution in two semi-isolated local communities

In this chapter a new spatially implicit model for species abundance dynamics in two semi-isolated local communities was developed. The two local communities connected with each other are positioned in the global ecological network of communities in such a way that only one of them can obtain immigrants directly from the rest of the metacommunity (Figure 1.4). Figure 1.4(a) shows the case when one (semi-isolated) local community is located at the boundary and the other (non-isolated) local community is located between the main part of the metacommunity and the semi-isolated local community. Figure 1.4(b) shows two local communities are connected but only one of them is connected to the mainland. The diversity models for two semi-isolated local communities were analyzed using continuous probabilistic technique. Using this technique, I developed the realistic classification of the species abundance dynamics in two semi-isolated local communities based on species characteristics such as immigration probability, species representation in the metacommunity and the size of local communities. Based on different ecological characteristics such as species persistence, extinction and monodominance in one or both local communities, several different scenarios for species abundance dynamics were distinguished. The similarity or dissimilarity of the species abundance distributions between the two local communities was studied using the correlation coefficient between species abundances in two local communities. I found higher similarity of the species abundance dynamics in two semi-isolated local communities with larger values of the immigration probability between local communities, whereas the immigration probability from the metacommunity has a negative effect on the similarity between species abundance dynamics in two semi-isolated local communities.

## Chapter 7. Species extinction time and probability in two semi-isolated local communities

In this chapter the relationships between the extinction processes and immigration-demographic processes were investigated for structured neutral local communities, using the neutral model for the species abundance dynamics in two semi-isolated local communities developed in Chapter 6. The extinction time and probability of a species in two semi-isolated local communities were studied by means of a continuous probabilistic approach. Using Kolmogorov-Fokker-Planck backward equation, I derived models for the species persistence probability in two local communities, and the average first time to species extinction. I considered two scenarios for species extinction: species extinction from one given local community (from only non-isolated or only semi-isolated local community), and species extinction from either the non-isolated or semi-isolated local community. In addition, I calculated the probability of species extinction from one local community before the other local community for different species abundances in two local communities. Using this probability it was possible to define from each local community the species would most likely go extinct first. It was found that if the species abundance is equal in two local communities, the species has more chances to go extinct from the semi-isolated local community than from the non-isolated local community. Finally, I compared analysis of species extinction dynamics in two local communities and in one local community. This analysis compares species abundance dynamics in spatially structured ecological communities (ecological communities involving interaction between many different neighboring habitat patches) and unstructured ecological communities (ecological communities with no spatial factors). It was found that the species has higher risk of extinction in local community connected only to the homogeneous metacommunity, than in spatially structured ecological communities.

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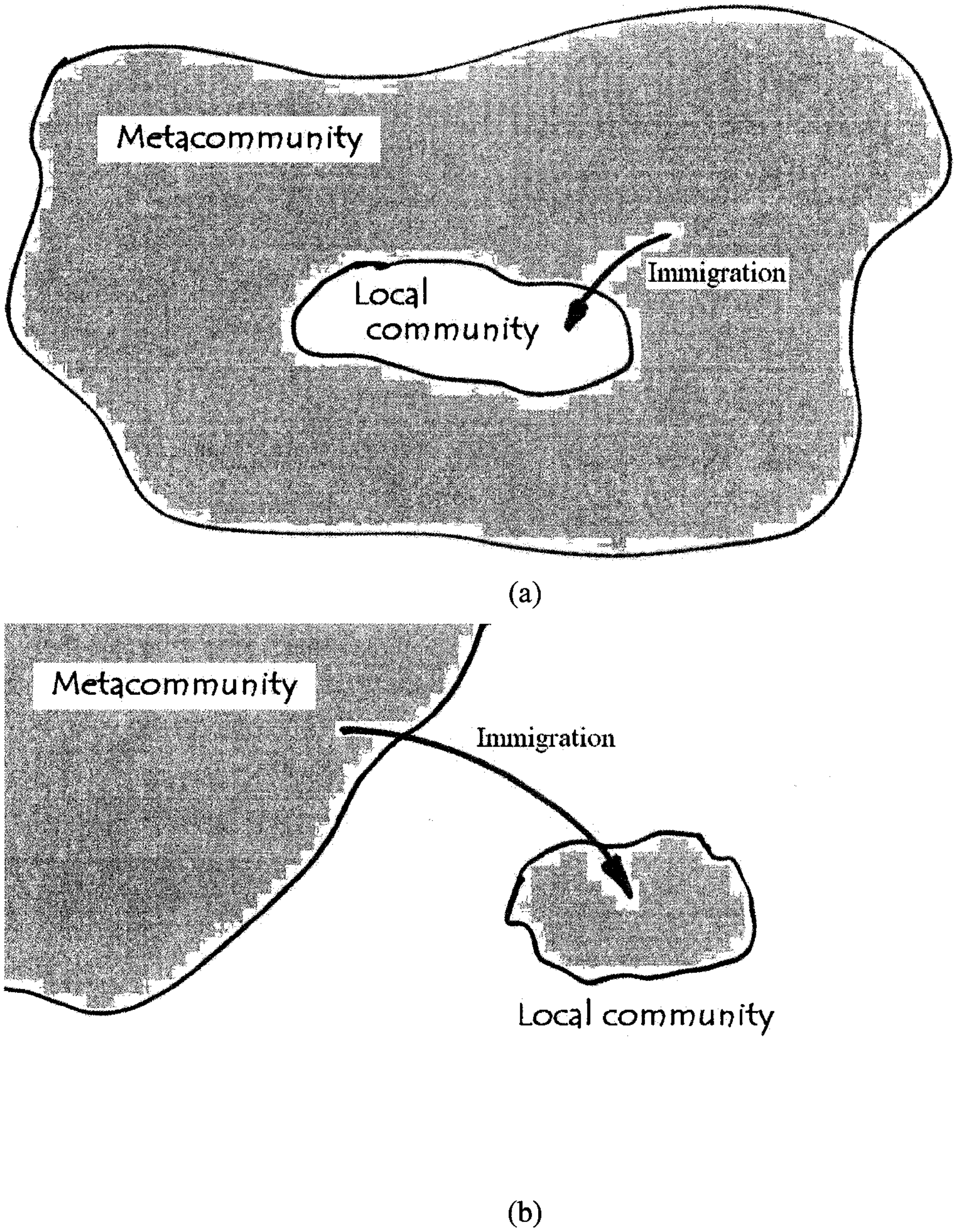
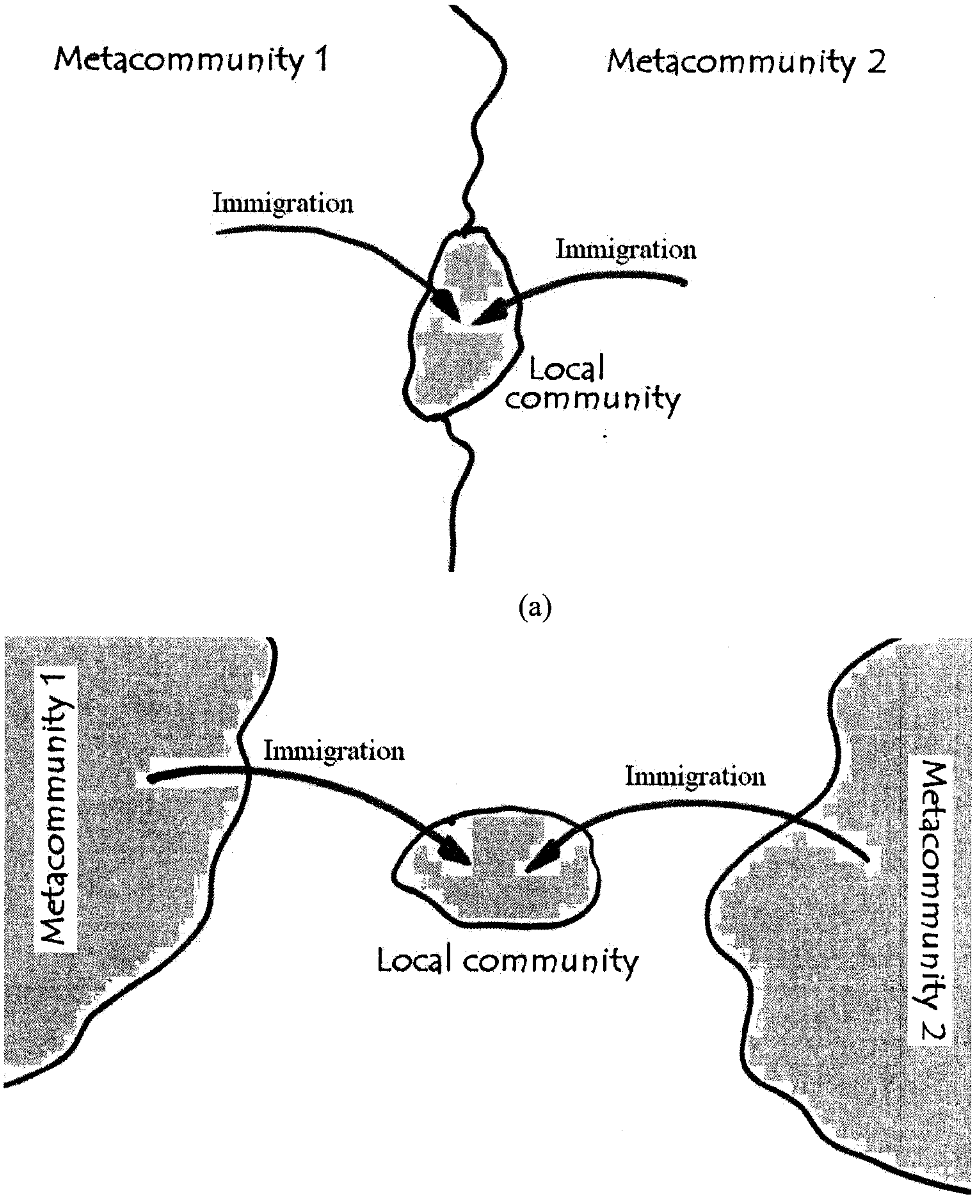


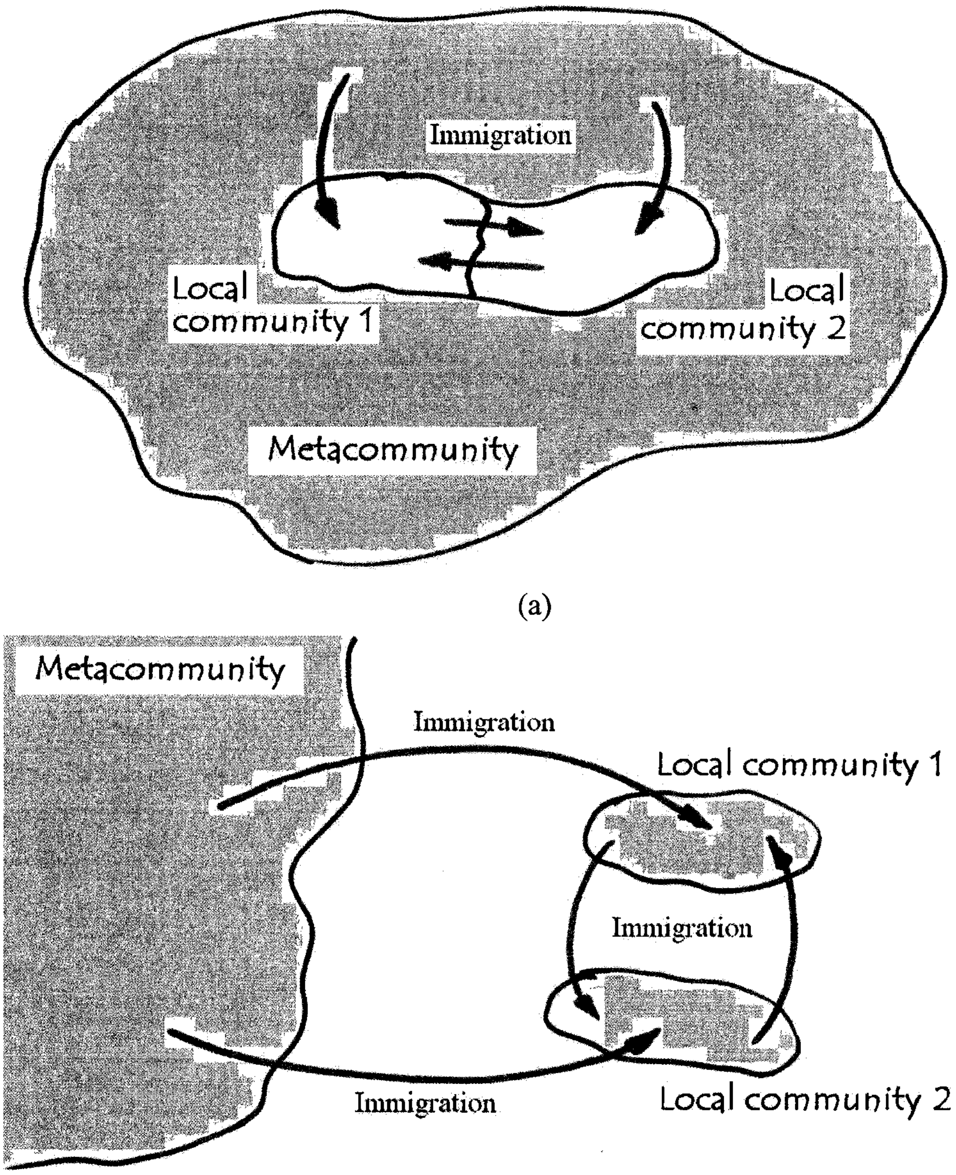
Figure 1.1: Graphical illustration of the model for species abundance dynamics in one local community connected through immigration to the metacommunity [Hubbell's zero-sum model] (Chapter 2). Figure (a) represents the case when the local community is embedded into the metacommunity, figure (b) represents the case when the local community is an island not directly connected to the mainland (the metacommunity).



(a)

(b)

Figure 1.2: Graphical illustration of the model for species abundance dynamics in one local community at the edge between two metacommunities (Chapter 3). Figure (a) represents the case when the local community is directly connected to both metacommunities, figure (b) represents the case when the local community is an island not directly connected to either of two distinct the mainlands (two metacommunities).



(a)

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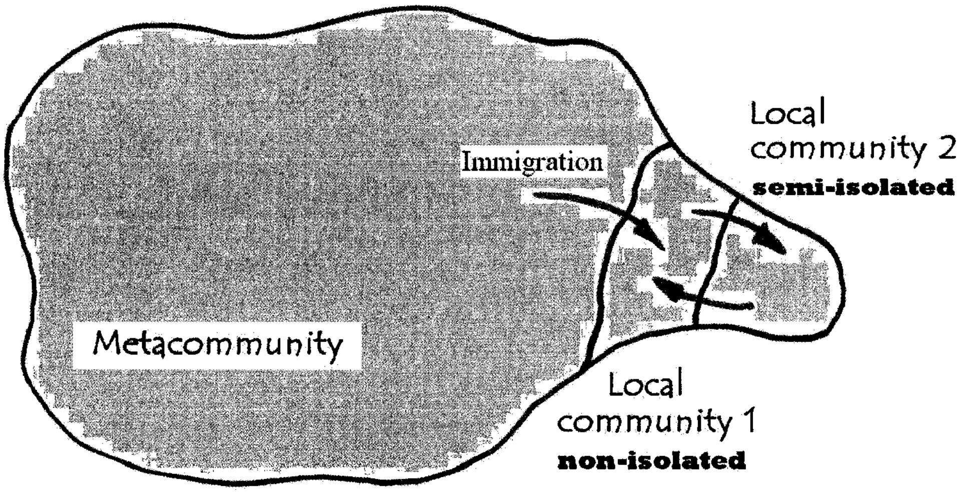
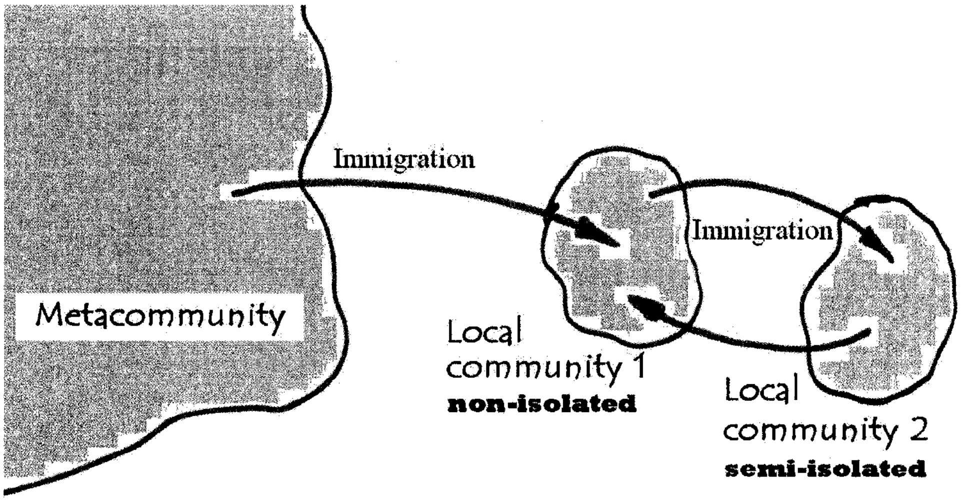
Figure 1.3: Graphical illustration of the model for species abundance dynamics in two equal local communities connected with each other and with the metacommunity through immigration (Chapters 4 and 5). Figure (a) represents the case when the local communities are embedded into the metacommunity, figure (b) represents the case when the local communities are islands not directly connected to the mainland.



(a)



(b)

Figure 1.4: Graphical illustration of the model for species abundance dynamics in two connected local communities to each other, but only one of them is connected to the metacommunity through immigration (Chapters 6 and 7). Figure (a) represents the case when local communities are located close to the boundary of the metacommunity (the second local community may represent a peninsula), figure (b) represents the case when local communities are islands not directly connected to the mainland.

# Chapter 2

# Continuous Probabilistic Approach to Species Dynamics in Hubbell's Zero-Sum Local Community

Babak, P. 2006. Continuous probabilistic approach to species dynamics in Hubbell's zero-sum local community. Physical Review E **74**, 021902.

## 2.1 Introduction

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 (Lande et al., 2003; Primack, 2002), since understanding the mechanisms of species abundance dynamics is of great concern in viability analysis.

Species abundance relationships have long been studied by ecologists, who defined them as species commonness and rarity in ecological communities (Engen, 1978; Lande et al., 2003; Magurran, 2004). These relationships are usually described by species abundance distributions that 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 with empirical data. Among the proposed distributions were the log-series (Fisher et al., 1943) and the log-normal (Preston, 1948). Later the preference was given to modelling species abundance relationships using one or another ecological theory of community organization. Using this approach the broken-stick model was proposed by MacArthur (1957, 1960); the log-normal patterns of species abundances were explained using the niche preemption model (Bulmer, 1974; May, 1975; Sugihara, 1980), and using the dynamic population model with Gompertz density dependence (Engen and Lande, 1996). 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 (Engen and Lande, 1996).

In this chapter I discuss the theory of the species abundance relationships. 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 (Gaston, and Chown, 2005; Hubbell, 2001; Bell, 2001). Although the concept of neutral community appeared long time ago (Caswell, 1976), it did not attract much attention until Hubbell published his monograph (Hubbell, 2001), where he proposed a neutral theory that unified theories of biodiversity and biogeography. The reference ecosystem of Hubbell's neutral theory is a group of throphically similar, sympatric species that complete for the same or similar resources (Hubbell, 2001; Gaston, and Chown, 2005). 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 (Hubbell, 2001). Based on this assumption, the neutral theory predicts the existence of new statistical distribution of relative species abundance, called the zero-sum multinomial (Hubbell, 2001). This distribution is close to a log-series for large immigration probabilities, and is more "humped" for small immigration probabilities (Pueyo, 2006; Bell, 2001). The analytical formalization for zero-sum multinomial and other distributions generated under assumption of neutrality was obtained in (Volkov et al., 2003; Vallade, and Houchmandzadeh, 2003; McKane et al., 2004; Alonso, and McKane, 2004; Etienne, and Alonso, 2005). The performance of the zero-sum multinomuial has been intensively compared only with the log-normal distribution (Hubbell, 2001; Williamson, and Gaston, 2005; Pueyo, 2006; McGill, 2003; Nee and Stone, 2003; Maurer, and McGill, 2004; Volkov et al., 2003). Hubbell showed that the zero-sum multinomial distribution fits tropical forest tree and coral reefs datasets better than the log-normal (Hubbell, 1997, 2001). However, according to recent analysis, even if the log-normal theories do not lead to biologically realistic species abundance distributions (Williamson, and Gaston, 2005), one cannot always distinguish between these two distributions from empirical data (Pueyo, 2006).

Since the time when Hubbell's neutral theory was popularized, the neutral theories in ecology has been developed in many published works, they have been enriched with a large amount of theoretical results (Alonso, and McKane, 2004; Etienne, and Alonso, 2005; Etienne and Olff, 2004; He, and Hu, 2005; Houchmandzadeh, and Vallade, 2003; Hubbell, 2001; McKane et al., 2000, 2004; Sole et al., 2004; Vallade, and Houchmandzadeh, 2003; Volkov et al., 2003, 2005; Williamson, and Gaston, 2005), intensive discussion (Chave, 2004; Gaston, and Chown, 2005; Maurer, and McGill, 2004; Hu, He, and Hubbell, 2006; Nee and

Stone, 2003; Nee, 2005; Ricklefs, 2003; Williamson, and Gaston, 2005) and testing (Bell, 2001; Hubbell, 2001; Maurer, and McGill, 2004; McGill, 2003; Pueyo, 2006; Volkov et al., 2003; Williamson, and Gaston, 2005).

In the framework of Hubbell's neutral theory the populations are studied in two scales: local community and regional metacommunity (Hubbell, 2001; McKane et al., 2004). 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 (Hubbell, 2001)

$$\begin{aligned} W_i(N-1|N) &= \frac{N}{J}\Big((1-m)\frac{J-N}{J-1} + m(1-\omega_i)\Big), \\ W_i(N+1|N) &= \frac{J-N}{J}\Big((1-m)\frac{N}{J-1} + m\omega_i\Big), \\ W_i(N|N) &= 1 - W_i(N-1|N) - W_i(N+1|N), \end{aligned} \tag{2.1}$$

where $\omega_i$ 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 (Hu, He, and Hubbell, 2006).

For Hubbell's model governed by Eq. (2.1), the species abundance distribution and the first passage time of the species to extinction or fixation in a local community were investigated using Markov chain approach (Hubbell, 2001). 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 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 a 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 (Hubbell, 2001).

The same results for the species abundance distribution were obtained using Birth-Death Master equation approach (Volkov et al., 2003; Vallade, and Houchmandzadeh, 2003; McKane et al., 2004), 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

$$\begin{aligned}\frac{dp_{N,i}}{dt} &= W_i(N|N+1)p_{N+1,i} + W_i(N|N-1)p_{N-1,i} \\ &-(W_i(N+1|N) + W_i(N-1|N))p_{N,i},\end{aligned} \tag{2.2}$$

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. (2003) 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

$$\phi_N(t) = \sum_{j=1}^{S} I_j(N,t), \tag{2.3}$$

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

$$\langle \phi_N(t) \rangle = \sum_{j=1}^{S} p_{N,j}(t). \tag{2.4}$$

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

$$\langle \phi_N(t) \rangle = S p_N(t), \tag{2.5}$$

where $p_N(t)$'s satisfy system of equations (2.2) with $\omega = \omega_i = 1/S$.

Note that this approach to the problem of species abundance relationships can be accepted only for the communities with very large number of species. Because the species do not behave independently in Hubbell's zero-sum local communities due to zero-sum assumption (Etienne and Olff, 2004, 2005).

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 large number of variables and equations. In contrast to discrete methods, continuous methods not only allow 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 (Lande, 1993; Gardiner, 1983).

In this chapter 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 chapter is organized as follows. In Section 2.2, the continuous model for the probability density of species abundance is derived using Kolmogorov-Fokker-Planck forward equation. Based on the probability density of species abundance in the local community the distribution of number of species with the specified abundance is obtained. In Section 2.3, the continuous approach is applied to study of the time development of species abundance distribution in the local community. Using 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 Section 2.4, 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 local community. And, finally, a comparison of the simulation study results with the results of the continuous analysis is presented.

## 2.2 Species abundance distribution

### 2.2.1 Modified model

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

$$\begin{aligned}
&\Pr(\Delta N_i = -1 | N_i = N) = \mu \Delta t W_i(N-1|N),\\
&\Pr(\Delta N_i = 1 | N_i = N) = \mu \Delta t W_i(N+1|N),\\
&\Pr(\Delta N_i = 0 | N_i = N) = 1 -\\
&\qquad - \mu\Delta t(W_i(N-1|N) + W_i(N+1|N)),
\end{aligned} \tag{2.6}$$

where $J = \sum_{j=1}^{S} N_j$, $S$ is the number of all species, $\Delta N_i = N_i(t+\Delta t) - N_i(t)$, $\omega_i$ is the fractional metacommunity relative species abundance of the $i$th species, $i = 1, \ldots, S$, $m$ is the probability that a death in the local community will be replaced by an emigrant, and $\mu$ is the number of death events per unit time interval. Note that the system of transition probabilities (2.6) is derived from Hubbell's zero-sum model (2.1).

For the random variable $\Delta N_i$, which takes the values -1, 0 and 1 with probabilities specified in (2.6), the first and second moments per infinitely small time interval $\Delta t$ can be easily calculated as

$$\begin{aligned} V_i(N) &= \lim_{\Delta t \to 0} \frac{E(\Delta N_i | N_i = N)}{\Delta t} = \mu m \Big(\omega_i - \frac{N}{J}\Big), \\ D_i(N) &= \lim_{\Delta t \to 0} \frac{E((\Delta N_i)^2 | N_i = N)}{\Delta t} = \\ &\mu \left(2(1-m)\frac{N(J-N)}{J(J-1)} + m(1-\omega_i)\frac{N}{J} + m\omega_i\Big(1 - \frac{N}{J}\Big)\right). \end{aligned} \tag{2.7}$$

## 2.2.2 Dynamics of species abundance distribution. Kolmogorov-Fokker-Planck forward equation

To introduce a continuous model for the distribution of the species abundance, I 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 Kolmogorov-Fokker-Planck forward equation

$$\frac{\partial p_i}{\partial t} = \frac{1}{2}\frac{\partial^2}{\partial n^2}(D_i(n)p_i) - \frac{\partial}{\partial n}(V_i(n)p_i), \tag{2.8}$$

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 $\Delta t$ as $\Delta t \to 0$ defined in (2.7).

Equation (2.8) is supplemented with the initial condition defining the probability density of species abundance $p_i^0(n)$ at the initial time moment $t = \tau$

$$p_i(n,\tau) = p_i^0(n), \quad n \in [0, J]. \tag{2.9}$$

Equation (2.8) is considered subject to the following natural boundary conditions

$$\frac{1}{2}\frac{\partial}{\partial n}(D_i(n)p_i) - (V_i(n)p_i) = 0, \tag{2.10}$$

at $n = 0$ and $n = J$. The boundary conditions (2.10) are sufficient for the conservation of probability density

$$\int_0^J p_i(n,t)dn = \int_0^J p_i^0(n)dn = 1, \quad \text{for all } t > \tau. \tag{2.11}$$

## 2.2.3 Equilibrium species abundance distribution

The equilibrium (the steady state) solution $P_i$ of problem (2.8)-(2.11) fulfils the following ordinary differential equation of the second order

$$0 = \frac{1}{2}\frac{d^2}{dn^2}(D_i(n)P_i) - \frac{d}{dn}(V_i(n)P_i), \quad n \in (0, J), \tag{2.12}$$

and boundary conditions (2.10), where the total probability over the interval $[0, J]$ equals 1.

Equation (2.12) can be easily transformed to the ordinary differential equation of the first order

$$0 = \frac{1}{2}\frac{d}{dn}(D_i(n)P_i) - (V_i(n)P_i), \quad n \in (0, J), \tag{2.13}$$

with the integral condition,

$$\int_0^J P_i(n)dn = 1, \tag{2.14}$$

representing the total probability instead of boundary conditions.

Problem (2.13), (2.14) can be explicitly solved. The steady state solution is

$$\begin{aligned} P_i(n) = &\exp\Big(\int_0^n \frac{2V_i(y) - D_i'(y)}{D_i(y)}dy\Big)\times \\ &\Big(\int_0^J \exp\Big(\int_0^x \frac{2V_i(y) - D_i'(y)}{D_i(y)}dy\Big)dx\Big)^{-1}. \end{aligned} \tag{2.15}$$

For known coefficients $V_i$ and $D_i$ from (2.7), expression (2.15) can be transformed to

$$\begin{aligned} P_i(n) &= C_i\Big(\frac{n_- - n}{n_-}\Big)^{\alpha_-}\Big(\frac{n_+ - n}{n_+}\Big)^{-\alpha_+}, \\ C_i &= \Big(\int_0^J \Big(\frac{n_- - y}{n_-}\Big)^{\alpha_-}\Big(\frac{n_+ - y}{n_+}\Big)^{-\alpha_+}dy\Big)^{-1}, \end{aligned} \tag{2.16}$$

where $n_\pm = -\frac{d_1 \pm \sqrt{d_1^2 - 4d_0d_2}}{2d_2}$, $\alpha_\pm = -\frac{2n_\pm(v_1-d_2)+2v_0-d_1}{d_2(n_+-n_-)}$, $d_0 = v_0 = m\omega_i$, $v_1 = -\frac{m}{J}$, $d_1 = \frac{2(1-m)}{J-1} + \frac{m(1-2\omega_i)}{J}$ and $d_2 = -\frac{1-m}{J(J-1)}$.

It follows from Eqs. (2.15) and (2.16) that the steady state distribution of the species abundance is independent of the parameter $\mu$ which corresponds to the time scale.

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

$$P_i(n)|_{\omega_i=\omega} = P_i(J-n)|_{\omega_i=1-\omega}. \tag{2.17}$$

This property can be easily explained for the distribution of two species with the metacommunity relative abundances $\omega$ and $1-\omega$, respectively. In view of (2.17), the probabilities that the first species abundance is $n$ and the second species abundance is $J-n$ are equal.

### 2.2.4 Number of species with specified abundances

By an analogy with Eqs. (2.3)-(2.5), see (McKane et al., 2000; Volkov et al., 2003), the number of species containing from $n_1$ to $n_2$ individuals at time $t$ can be defined as

$$\phi(n_1, n_2, t) = \sum_{j=1}^{S} I_j(n_1, n_2, t), \tag{2.18}$$

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 problem (2.8)-(2.11) for the evolution of the probability of species abundance or problem (2.13)-(2.14) 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

$$\langle \phi(n_1, n_2, t) \rangle = \sum_{j=1}^{S} \int_{n_1}^{n_2} p_j(n,t)dn. \tag{2.19}$$

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

$$\langle \phi(n_1, n_2, t) \rangle = S \int_{n_1}^{n_2} p(n,t)dn, \tag{2.20}$$

where $p = p_j$ satisfies problem (2.8)-(2.11) for dynamic community or problem (2.13)-(2.14) for the equilibrium community with $\omega_j = \omega = 1/S$.

However, this approach to the problem of species abundance relationships can be validated only for very large local communities and for large number of species. In local communities governed by zero-sum assumption all species are not really independent, see (Etienne and Olff, 2004, 2005).

## 2.3 Persistence and extinction

### 2.3.1 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 (Ginzburg et al., 1982; Primack, 2002; Lande et al., 2003).

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

$$G_i(t,n) = \Pr(T \geq t) = \int_0^J p_i(y,t|n,0)dy. \tag{2.21}$$

This probability fulfills the Kolmogorov-Fokker-Planck backward equation (Gardiner, 1983; Lande et al., 2003)

$$\frac{\partial G_i}{\partial t} = \frac{1}{2} D_i(n) \frac{\partial^2 G_i}{\partial n^2} + V_i(n) \frac{\partial G_i}{\partial n}, \quad n \in (0, J), \ t > 0, \tag{2.22}$$

with the initial condition

$$G_i(n,0) = 1, \quad n \in [0, J], \tag{2.23}$$

where the coefficients $V_i$ and $D_i$ are defined by (2.7).

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

$$F_i(n,t) = 1 - G_i(n,t). \tag{2.24}$$

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

$$f_i(n,t) = -\partial G_i(n,t)/\partial t. \tag{2.25}$$

Note that the distribution of the persistence time and the first extinction time are extremely important in the problems 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.

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 $n = N_- = 0$

$$G_i(0,t) = 0, \quad t \geq 0. \tag{2.26}$$

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

$$\partial G_i(n,t)/\partial n|_{n=J} = 0, \quad t \geq 0. \tag{2.27}$$

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

### 2.3.2 Moments of the first passage time to extinction

For the known distribution function (problem (2.22),(2.23),(2.26),(2.27)), the mean first passage time to the zero species abundance

$$T_i^1(n) = \int_0^\infty t\frac{F_i(n,t)}{\partial t}dt = \int_0^\infty G_i(n,t)dt, \tag{2.28}$$

can be obtained from the ordinary differential equation

$$\frac{1}{2}D_i(n)\frac{d^2T_i^1}{dn^2} + V_i(n)\frac{dT_i^1}{dn} = -1, \quad n \in (0,J) \tag{2.29}$$

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

$$T_i^1(0) = 0, \qquad dT_i^1(n)/dn|_{n=J} = 0. \tag{2.30}$$

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

$$T_i^k(n) = \int_0^\infty t^k d_t F_i(n,t) = -k \int_0^\infty t^{k-1} G_i(n,t)dt, \tag{2.31}$$

can be computed from the differential equation

$$\frac{1}{2}D_i(n)\frac{d^2T_i^k}{dn^2} + V_i(n)\frac{dT_i^k}{dn} = -T_i^{k-1}, \quad n \in (0,J), \tag{2.32}$$

subject to boundary conditions (2.30) 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

$$T_i^k(n)|_{\mu=\bar{\mu}} = \frac{1}{\bar{\mu}^k} T_i^k(n)|_{\mu=1}. \tag{2.33}$$

It follows from (2.33) that the $k$th moment of the first extinction time is inversely proportional to the $k$th power of $\mu$. Thus, we can say that the parameter $\mu$, the number of death events per 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 (2005), Lande et al. (2003), Leigh (1999).

Note also that the problem for the mean first extinction time can be solved explicitly (Gardiner, 1983) as

$$T_i^1(n) = 2\int_0^n \frac{dy}{D_i(y)P_i(y)} \int_y^J P_i(z)dz, \tag{2.34}$$

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 $n \in [0,J)$.

### 2.3.3 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 equations (2.27) and (2.30).

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

$$T^1_{\mathrm{fix},i}(n)|_{\omega_i=\omega} = T^1_{\mathrm{fix},i}(J-n)|_{\omega_j=1-\omega}. \tag{2.35}$$

### 2.3.4 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 (Gardiner, 1983)

$$\frac{1}{2}D_i(n)\frac{d^2\pi_i^0}{dn^2} + V_i(n)\frac{d\pi_i^0}{dn} = 0, \quad n \in (0, J) \tag{2.36}$$

with the boundary conditions

$$\pi_i^0(0) = 1, \qquad \pi_i^0(J) = 0. \tag{2.37}$$

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. (2.36) supplemented with the reverse boundary conditions to (2.37).

### 2.3.5 Quasi-extinction

Quasi-extinction 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 (quasi-extinction level) of abundance (Ginzburg et al., 1982; Lande et al., 2003). Assuming that $C > 0$ is a level of quasi-extinction (a lower absorbing boundary of species abundance), the problems for the first passage time to quasi-extinction of the $i$th species and for the probability of the species quasi-extinction 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 quasi-extinction can be also 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 $k$, $n > k$.

## 2.4 Sensitivity analysis for species dynamics in local community

### 2.4.1 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 $\omega_i$ and the community size $J$ will be investigated.

Let us first consider mixed boundary conditions (2.10). At both ends $n = 0$ and $n = J$ of the abundance interval, these boundary conditions can be rewritten as

$$D_i(n)\frac{\partial p_i}{\partial n} + (D_i'(n) - 2V_i(n))p_i = 0. \tag{2.38}$$

At the abundance level $n = 0$ condition (2.38) degenerates to the zero flux boundary condition, also known as 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 (2.38) 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 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 $n = 0$

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

and at $n = J$

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

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 then 1/2, i.e., $\omega_i < 1/2$. The results for $\omega_i \geq 1/2$ can be obtained in 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 that the probability that the species will go extinct or monodominate in the local community is very high, see Figure 2.1 for $0 < m \leq 0.005 = 1/J \approx m_J$. In this case the probability density of the species abundance has "U" shape, see also (Hubbell, 2001), the immigration events are so rare that the species most of 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 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 "S" shape with the maximal value at zero abundance, see Figure 2.1 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 Figure 2.1 for $m > 1/((1-\omega)J) = 0.1$. And the level of stabilization increases with increase of the immigration probability. The mode of the probability density for the species abundance is near $\omega J$, and the probability density has 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 different effect on the common species with $\omega_i > 1/2$. In this case the first interval for the immigration probability from 0 to $m_0$ can be classified as the interval with high chance of species fixation. As in the case with $\omega < 1/2$ 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 $\omega_i = 1/2$, the intermediate interval of the probability of immigration is degenerated, see Figure 2.2(a).

The results for species dynamics in the local community obtained from the above analysis are summarized in Figures 2.2(a,b). Figure 2.2(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 (Hubbell, 2001); (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 (Hubbell, 2001).

With increase in the immigration probability, scenario (i) changes first into either scenario (ii) or (iii), and then into scenario (iv). Also it worth to notice that when the metacommunity relative abundances is either very small or very high, the species dynamics can follow only two scenarios, see Figure 2.2(a). In the first case because the immigration probability is never high enough for the species abundance to be stabilized around 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 local community is also very high.

Figure 2.2(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, smaller immigration probability is required for species persistence.

### 2.4.2 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 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 (Figure 2.1) and the probability that the species abundance will change to smaller level is very low (Figure 2.3(f)). This persuades to very high uncertainty in the result for the first extinction time (Figure 2.3(e)). More intensive immigration to the local community leads to 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 (Figures 2.3(b,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 more effective measure of species viability in this case. Note also that the first fixation time, on the contrary to the first extinction time, increases with increase in the immigration probability, see Figures 2.3(b,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 nonnegative. Figure 2.3(a) illustrates the asymptotic convergence of the first passage time to extinction as $m \to 0$. The asymptotic analysis shows that the mean first passage time to extinction $T^1_{ext}(n)$ converges to

$$-J(J-1)\Big(\frac{J-n}{J}\ln\frac{J-n}{J}+\frac{n}{J}\ln\frac{n}{J}\Big)+C_0\frac{n}{J} \tag{2.39}$$

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

$$T^1_{fix}(n) \to -J(J-1)\Big(\frac{J-n}{J}\ln\frac{J-n}{J}+\frac{n}{J}\ln\frac{n}{J}\Big) \tag{2.40}$$

as $m \to 0$. Hubbell (2001) 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

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

It is easy to note that the above expression is in agreement with our result, that is, $T^1_{fix}(N)$ converges to $T(N)$ as $m \to 0$, see also Figure 2.3(c).

Note also that approximations (2.39) and (2.40) state that in communities with very small immigration probabilities, the species metacommunity relative abundance plays almost no role in community species dynamics.

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 Figure 2.3(b) we can observe that the switching between 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 Figures 2.3(b,d,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 increases with increase in the immigration probability. The species abundance is more stable around the mode $\omega_i J$ for higher immigration intensity, see Figure 2.1. 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 Figures 2.3(b,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 Figures 2.3(a,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 Figures 2.3(a,c).

### 2.4.3 Effect of species metacommunity relative abundance

Figure 2.4(a) illustrates the effect of varying species metacomunity relative abundance, $\omega_i$, 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 Figure 2.4(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 $\omega_i$, then switches to scenario (i) and, finally, for large $\omega_i$ to scenario (iii).

Figures 2.4(b,c) show the behavior of the mean first passage time to extinction and fixation. From Figure 2.4(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 larger number of members in the metacommunity. From Figure 2.4(c) one can infer that the mean first passage time to fixation satisfies the symmetry property given by Eq. (2.35). Note that this property is essentially straightforward for understanding 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.

### 2.4.4 Effect of community size

The effect of varying local community size, $J$, on the steady state (equilibrium) probability density function is shown in Figure 2.5(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 Figure 2.5(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 very high chance of species fixation. For the local communities of size $J =$200, 300, 400 and 500, the species dynamics follows scenario (ii) with very high chance of extinction ($m_J < m \leq m_0$). And, finally, for the local communities of size $J > 500$, the species follow scenario (iv) with 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 Figure 2.5(b). If the size of the local community is small, then the species follows scenarios (i) or (ii) with 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 Figure 2.2(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.

### 2.4.5 Probability density of the first passage timeto extinction

To complete our analysis of the species dynamics, let 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 2.6(a,b) present the effect 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 Figure 2.6(a) were obtained from Eqs. (2.22),(2.23),(2.26) and (2.27). The probability density functions shown in Figure 2.6(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. (2.22) 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 extinction time to Gamma distribution. It was presumed by Hubbell (2001) 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. (2.25) 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 (2.1), and to the shifted Gamma distributions fitted to simulated values of the first extinction times, see Figure 2.7. From Figure 2.7 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 simulated frequencies of the first extinction time and is close to the probability density of the first passage time to extinction calculated from Eq. (2.22); 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.

## 2.5 Discussion and conclusions

The unified neutral theory of biodiversity and biogeography proposed by Hubbell (2001) aims to explain the species 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 (Hubbell, 2001) and analysis of master birth-death ordinary differential equations for the species abundance probability distribution (Volkov et al., 2003; Vallade, and Houchmandzadeh, 2003; McKane et al., 2004). In this work, Hubbell's model was considered from a different prospective. 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 Figure 2.7. Figure 2.7 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 (2001), 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 Figures 2.2 (a,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 ($\omega < 1/2$): 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 ($\omega < 1/2$): 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 $\omega J$; 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 characterizations of the species abundance distributions have not been obtained before.

Also in this chapter, the time scale parameter was investigated. It is known that this parameter plays an important role in the species dynamics of living communities (Nee, 2005), 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 $\mu$, 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 $\mu$ are inversely related, but the equilibrium distribution of species abundance is independent of the time scale parameter $\mu$.

Finally, in this chapter a complicated behavior of the mean first passage time to extinction with respect to the immigration intensity was studied. It was noticed (Hubbell, 2001) that for small immigration probabilities, the first extinction time decreases with increase in the immigration intensities, see Figure 2.3(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 community leads to increase in the probability of the species to leave the monodominant state and, therefore, will lead to 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 $\omega J$. 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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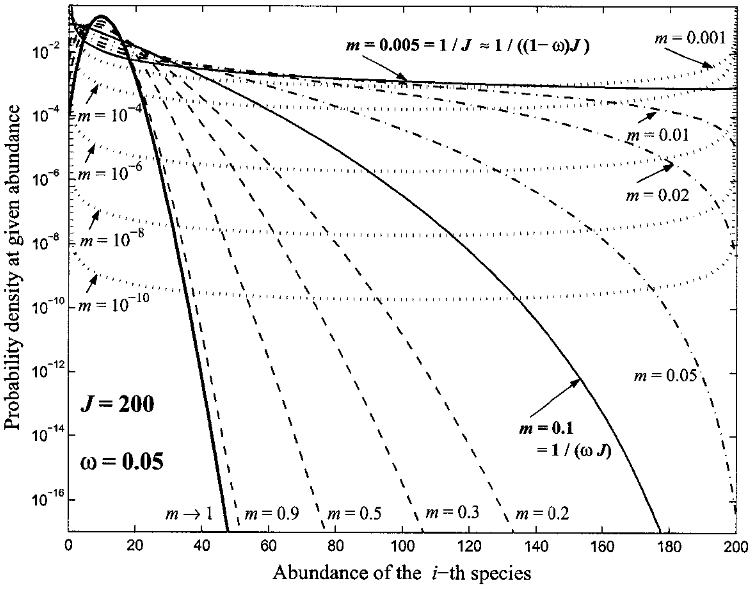


Figure 2.1: The effect of varying the probability of immigration $m$ on the equilibrium probability density function for the abundance of the $i$th species in Hubbell's zero-sum local community. Numerical results for a local community of $J = 200$ individuals and the species metacommunity relative abundance $\omega_i = 0.05$ are obtained from the exact solution (2.16) of Problem (2.13),(2.14).

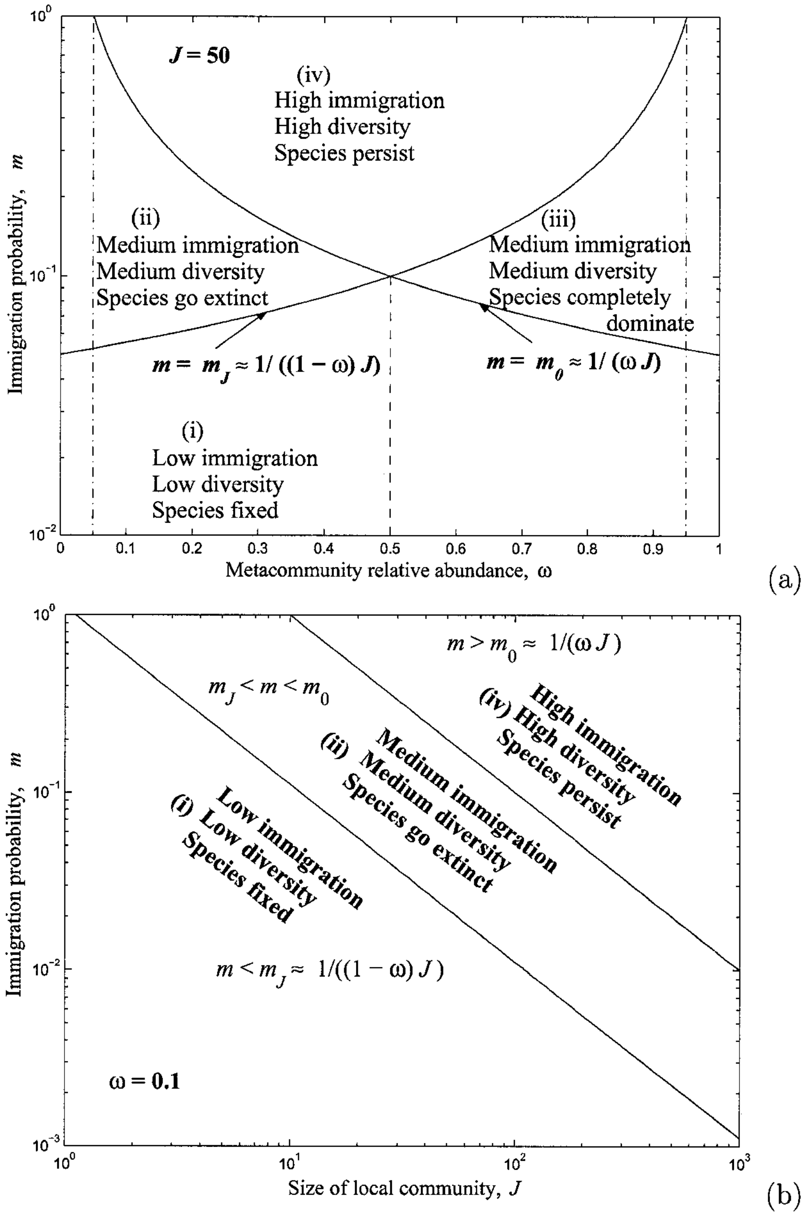


Figure 2.2: Classification for the local community species dynamics with respect to (a) different values of the immigration probability and the metacommunity species relative abundance; (b) different values of the immigration probability and the size of local community.

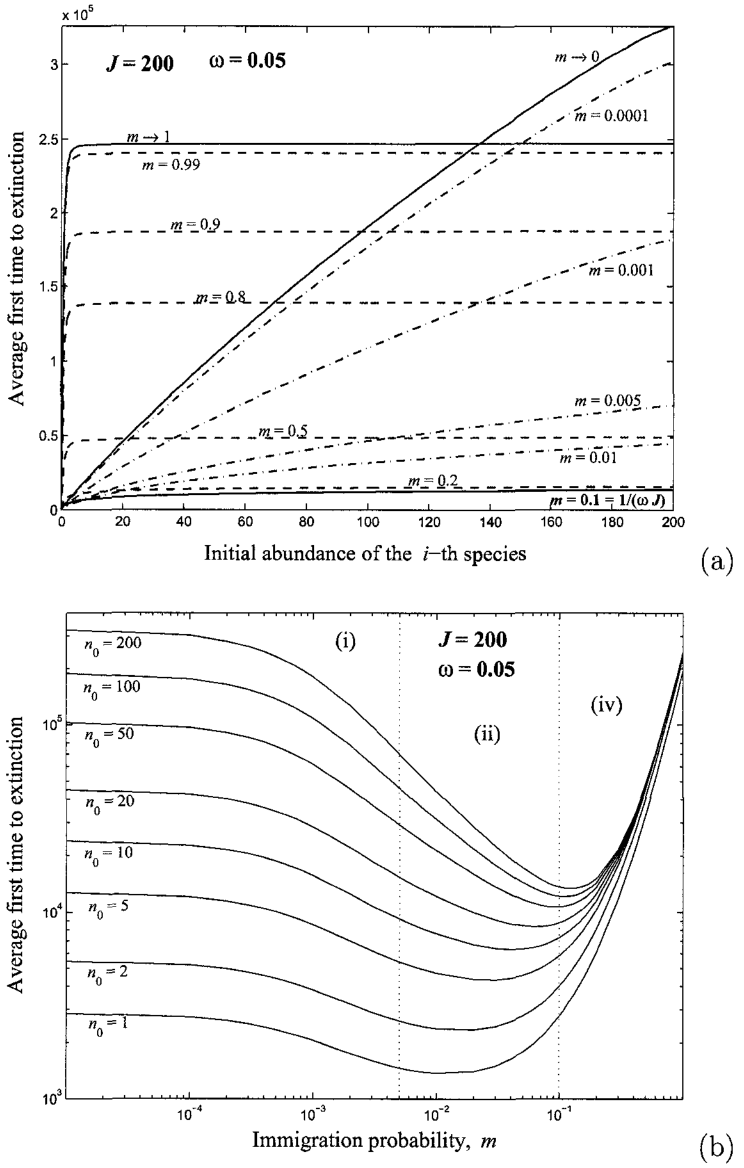


Figure 2.3: The effect of varying the probability of immigration $m$ on the first passage times to extinction and fixation and on the probability of extinction for the $i$th species in Hubbell's zero-sum local community of $J = 200$ individuals and the species metacommunity relative abundance $\omega = 0.05$: (a) the mean first passage time to extinction as a function of the initial species abundance for different values of $m$ [Eqs. (2.29),(2.30)]; (b) the mean first passage time to extinction as a function of the immigration probability for different values of the initial species abundance [Eqs. (2.29),(2.30)];

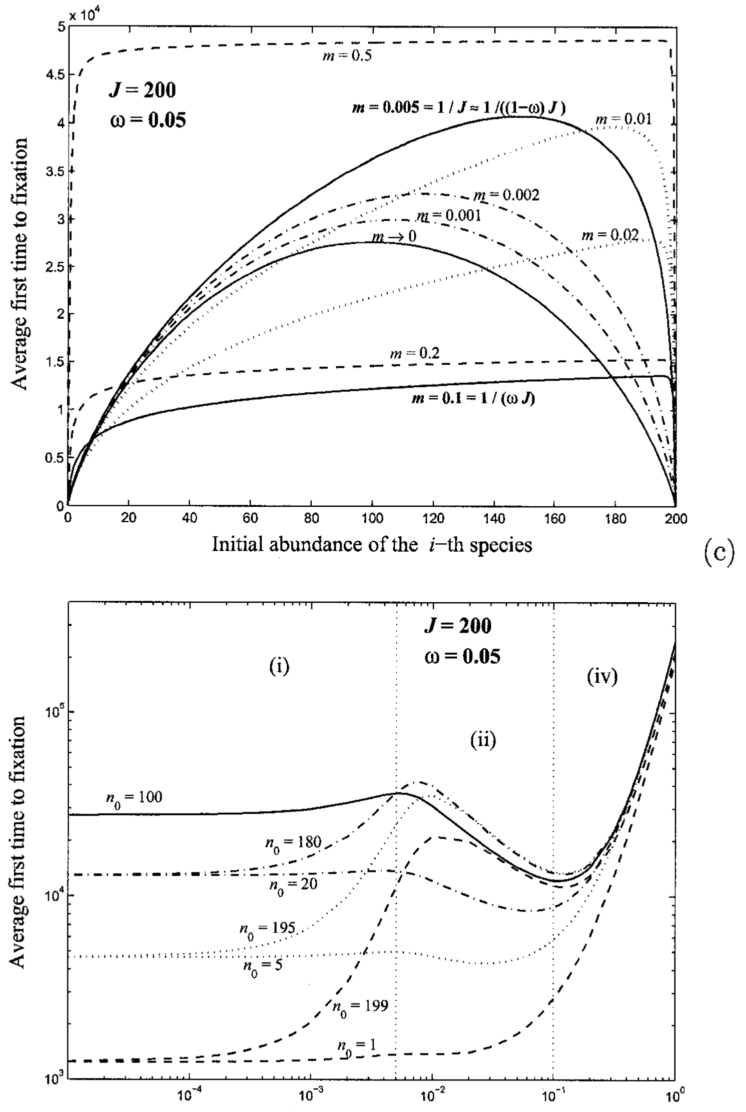


Figure 2.3: Cont. (c) the mean first passage time to fixation as a function of the initial species abundance for different values of $m$ [Eq. (2.29) with absorbing boundary conditions at $n = N_{-} = 0$ and $n = N_{+} = J$ (see Sec. 2.3.3)]; (d) the mean first passage time to fixation as a function of the immigration probability for different values of the initial species abundance [Eq. (2.29) with absorbing boundary conditions (see Sec. 2.3.3)];

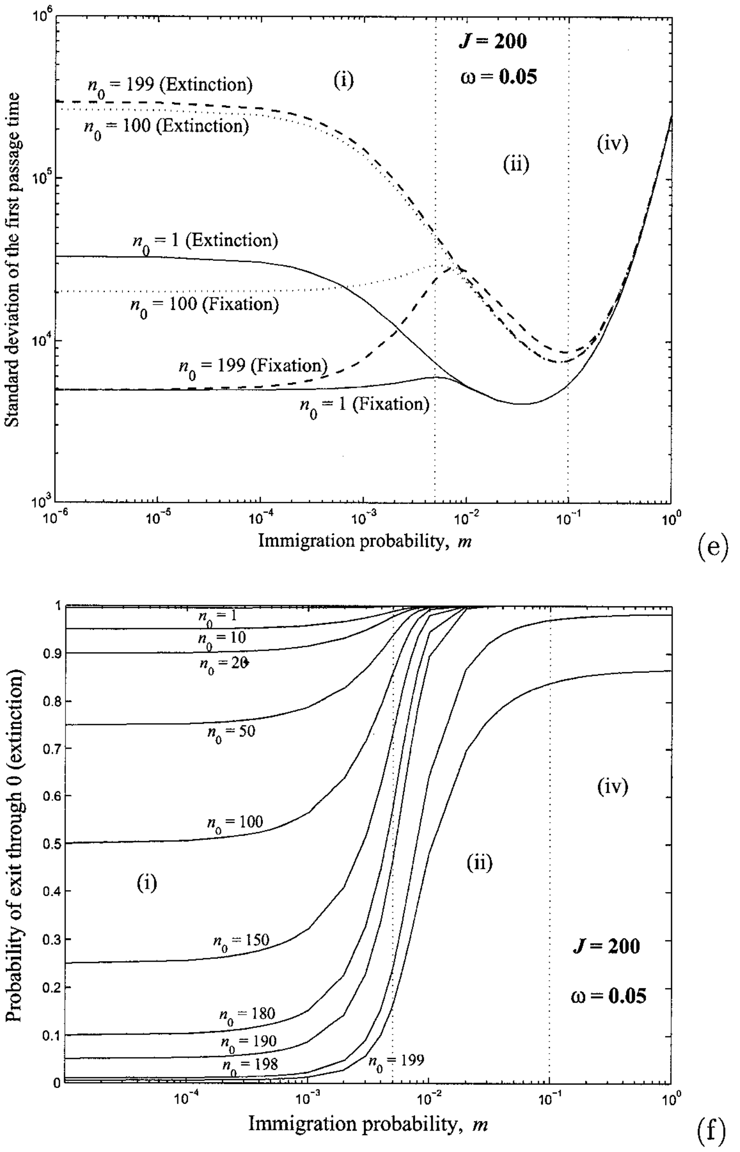


Figure 2.3: Cont. (e) the standard deviations of the first extinction and fixation times [Eqs. (2.29),(2.32) with boundary conditions (2.30) for extinction time and absorbing boundary conditions for fixation time (see Sec. 2.3.3)]; (f) the probability of species extinction [Eqs. (2.36),(2.37)]. All results are obtained using numerical approximations.

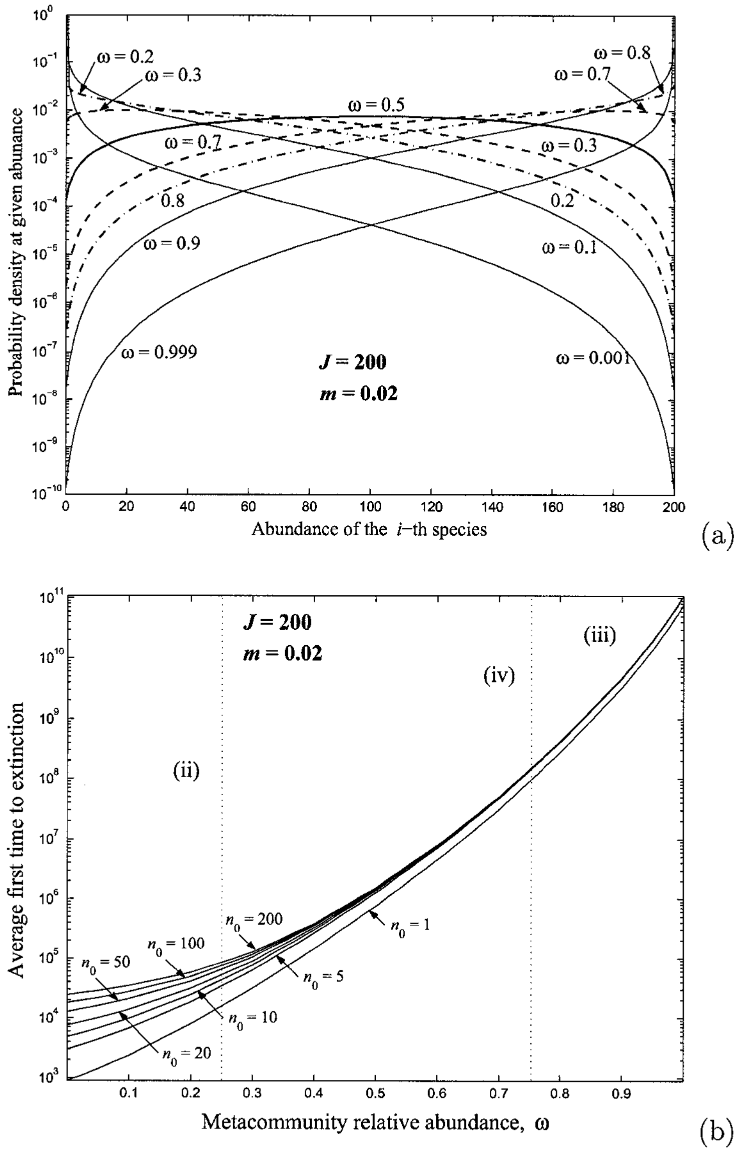
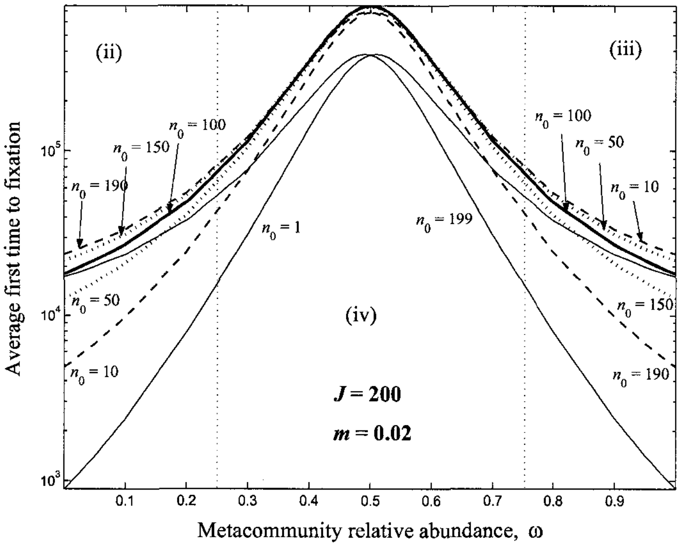


Figure 2.4: The effect of varying the metacommunity relative abundance $\omega_i$ of the $i$th species on (a) the equilibrium probability density function of the species abundance obtained from the exact solution (2.16) of Problem (2.13),(2.14); (b) the mean first passage time to extinction of the $i$th species obtained from the numerical approximations of Problem (2.29),(2.30);



(c)

Figure 2.4: Cont. (c) the mean first passage time to fixation of the $i$th species obtained from the numerical approximations of Eq. (2.29) with absorbing boundary conditions at $n = N_- = 0$ and $n = N_+ = J$ (see Sec. 2.3.3). Example for a local community of $J = 200$ individuals and the immigration probability $m = 0.02$.

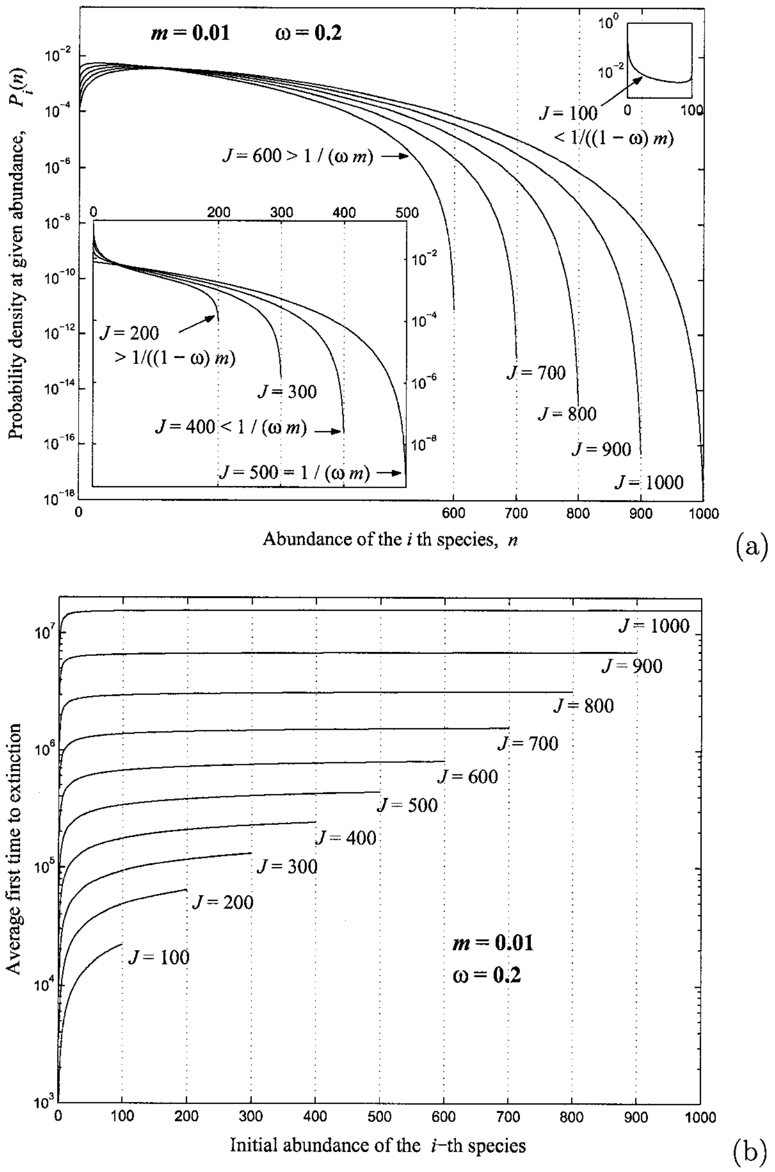


Figure 2.5: The effect of varying the local community size $J$ on (a) the equilibrium (steady state) probability density function of the $i$th species abundance obtained from the exact solution (2.16) of Problem (2.13),(2.14); (b) the mean first passage time to extinction of the $i$th species in Hubbell's zero-sum local community obtained from the numerical approximations of Problem (2.29),(2.30). Example for the species metacommunity relative abundance $\omega_i = 0.2$, and the immigration probability $m = 0.01$.

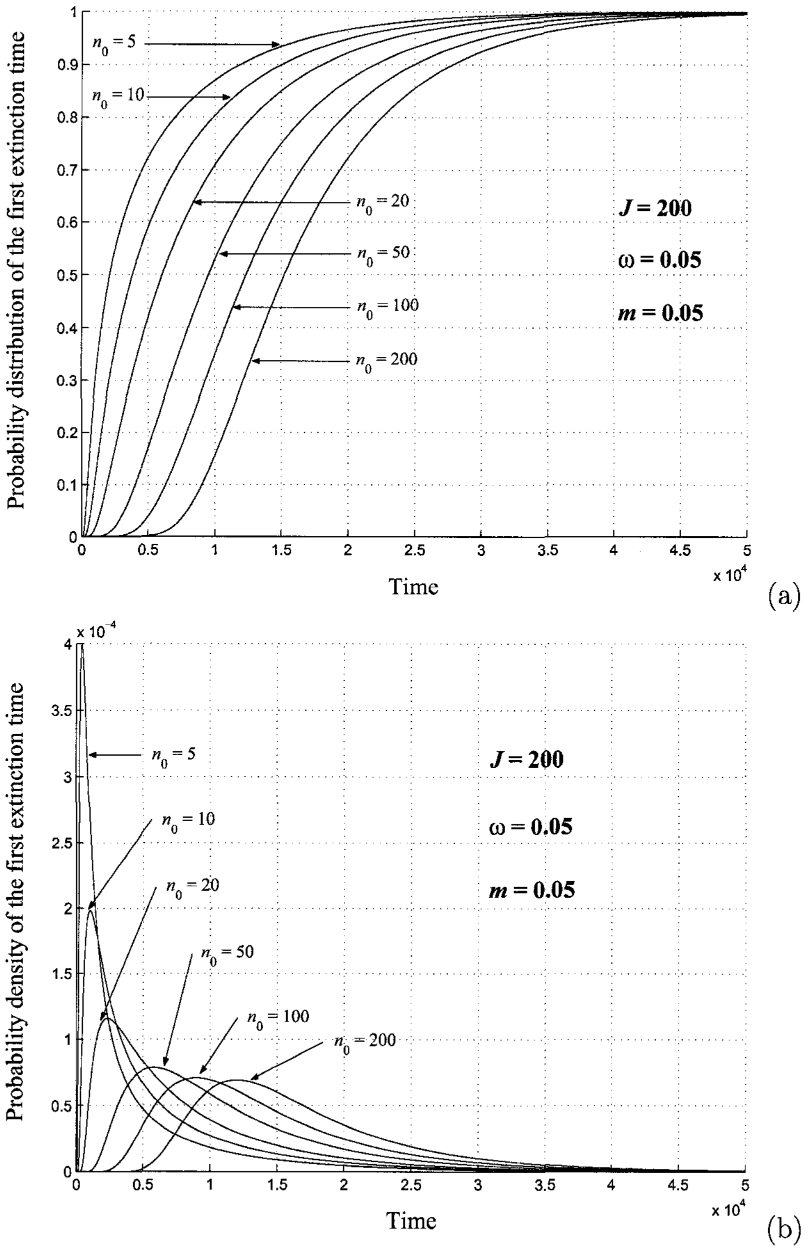


Figure 2.6: The effect of varying the initial abundance $n_0$ of the $i$th species on (a) the probability distribution function, and (b) the probability density function for the first passage time to extinction. Results are obtained from numerical approximations of Problem (2.22),(2.23),(2.26),(2.27) and (a) Eq. (2.24), (b) Eq. (2.25). 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 $\mu = 1$.

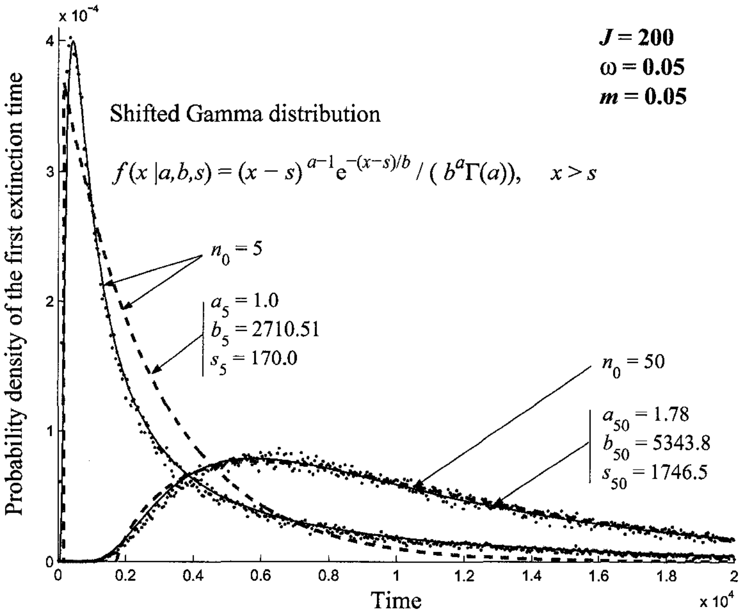


Figure 2.7: Comparison of the probability density of the first passage time to extinction (solid lines) obtained from numerical approximations for continuous probabilistic model (2.22),(2.23),(2.26),(2.27) and Eq. (2.25) to the relative frequencies of the first extinction time (dots) calculated from simulations of Hubbell model (2.1), 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 $\mu = 1$.

# Chapter 3

# A Neutral Macroecological Model of Edge Effects

## 3.1 Introduction

It is frequently observed in ecology that the structure of living communities and species abundance dynamics at boundaries between different habitats is significantly different from that in the interior of homogeneous habitat (Ries et al., 2004; Strayer et al., 2003). This is referred to as an edge effect. The most severe impacts of the edge effect are related to changes in dispersal, microclimate, ecological functions, decreasing regeneration, and facilitating invasion of other species (Ries et al., 2004). Analysis of the edge effect including identification and measurement of edges (Strayer et al., 2003; Ovaskainen, 2004), impact of edges on migration, competition, growth and speciation (Fagan et al., 1999; Ovaskainen, 2004; Schilthuizen, 2000) movement and development of edges (Potapov, 2004) have been conducted using several different spatially implicit and explicit models, i.e., diffusion models (Fagan et al., 1999; Ovaskainen, 2004), cellular automata model (Kupfer, 2003), random walk models (Schultz, 2001), matrix transition models (Schooley, 2005), etc.

In this chapter the impact of edge effects on the species abundance distribution and dynamics is investigated using the neutral macroecological theory by which individuals of all species are assumed to be per capita ecological equivalent, and communities do not have trophic hierarchy (Hubbell, 2001). For the purpose of analysis, a new model is constructed for the change in the species abundance in a local community at the edge between two different metacommunities, large reservoirs of all trophically similar individuals and species with constant fractional species abundances. The proposed model is developed under the zero-sum assumption which states that the total number of individuals in the community is a conserved quantity (Hubbell, 2001).

## 3.2 Model formulation

The model for the dynamics of species abundance in a local community at the edge introduced in this chapter will be compared to the Hubbell's zero-sum neutral model in a local community connected to only one metacommunity (Hubbell, 2001). Recall that Hubbell's model for the change in the abundance $N_i = N$ of species $i$ in an internal local community of size $J$ connected to the metacommunity with the total number of species $S$ is formulated using the following transition probabilities

$$\begin{aligned} W_i(N-1|N) &= \frac{N}{J}\Big((1-m)\frac{J-N}{J-1} + m(1-\omega_i)\Big), \\ W_i(N+1|N) &= \frac{J-N}{J}\Big((1-m)\frac{N}{J-1} + m\omega_i\Big), \\ W_i(N|N) &= 1 - W_i(N-1|N) - W_i(N+1|N), \end{aligned} \tag{3.1}$$

where $\omega_i$ 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 $J = \sum_{j=1}^{S} N_j$.

Our model for the dynamics of species abundance in a local community at the edge is formulated as follows. Let us assume that a local community of size $J$ is located at the edge between two metacommunities with unchanged relative abundances $\omega_i^1$ and $\omega_i^2$ of the $i$th species. Let us also assume that the probability of a new immigrant in the local community appeared from the $k$th metacommunity is $\theta^k$, $k = 1, 2$, where $\theta^1 + \theta^2 = 1$. Then for the local community at the edge we can define the change in the number of individuals $N_i = N$ of species $i$ per unit time step using the following transition probabilities

$$\begin{aligned} W_i^e(N-1|N) &= \frac{N}{J}\Big((1-m)\frac{J-N}{J-1} + m\theta^1(1-\omega_i^1) + m\theta^2(1-\omega_i^2)\Big), \\ W_i^e(N+1|N) &= \frac{J-N}{J}\Big((1-m)\frac{N}{J-1} + m\theta^1\omega_i^1 + m\theta^2\omega_i^2\Big), \\ W_i^e(N|N) &= 1 - W_i^e(N-1|N) - W_i^e(N+1|N). \end{aligned} \tag{3.2}$$

## 3.3 Continuous probabilistic approach

To analyze the discrete model (3.2) for species abundance dynamics in a zero-sum local community at the edge between two metacommunities using continuous probabilistic technique, this model has to be adapted for any continuous time steps and species abundances. Further, let assume that the species abundance can attain any value from the interval $[0, J]$. Then the transition probabilities for the non-zero change $\Delta N_i = N_i(t + \Delta t) - N_i(t)$ in the number of individuals $N_i$ of species $i$ per time step $\Delta t$ can be evaluated as follows

$$\Pr(\Delta N_i = \Delta | N_i = N) = \mu \Delta t W_i^e(N + \Delta|N), \tag{3.3}$$

for $\Delta = 1$ or $-1$, where $\mu$ is the number of death events per unit time interval.

Using the transition probabilities specified in (3.3), the first and second moments of the random variable $\Delta N_i$ can be easily calculated as

$$\begin{aligned} V_i(N) &= \lim_{\Delta t \to 0} \frac{E(\Delta N_i | N_i = N)}{\Delta t} = \mu m\Big(\omega - \frac{N}{J}\Big), \\ D_i(N) &= \lim_{\Delta t \to 0} \frac{E((\Delta N_i)^2 | N_i = N)}{\Delta t} = \\ &\mu\Big(2(1-m)\frac{N(J-N)}{J(J-1)} + m(1-\omega)\frac{N}{J} + m\omega\frac{J-N}{J}\Big), \end{aligned} \tag{3.4}$$

where $\omega = \theta^1\omega_i^1 + \theta^2\omega_i^2$; note also that in the Hubbell's zero-sum model (3.1): $\omega = \omega_i$ (Babak, 2006).

Assuming that the abundance $n$ of species $i$ is a continuous variable from the abundance interval $[0, J]$, we proceed to Kolmogorov-Fokker-Planck forward and backward equations in the form

$$\frac{\partial p_i}{\partial t} = \frac{1}{2}\frac{\partial^2 D_i(n) p_i}{\partial n^2} - \frac{\partial V_i(n) p_i}{\partial n}, \tag{3.5}$$

where $n \in \Omega = (0, J)$ and $t > 0$.

Forward equation (3.5) supplemented with the initial condition

$$p_i(n, 0) = p_i^0(n), \quad n \in [0, J], \tag{3.6}$$

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

$$\frac{1}{2}\frac{\partial D_i(n) p_i}{\partial n} - V_i(n) p_i \Big|_{n=0,J} = 0, \quad t \geq 0, \tag{3.7}$$

defines the evolution of species abundance probability $p_i = p_i(n, t)$ given the probability density of the species abundance $p_i^0(n)$ at the initial time moment $t = 0$.

Note that the boundary conditions (3.7) are sufficient for conservation of probability density

$$\int_0^J p_i(n, t) dn = \int_0^J p_i^0(n) dn = 1, \quad \text{for all } t > 0. \tag{3.8}$$

The steady-state solution $P_i$ of the forward problem [Eqs. (3.5) and (3.6)-(3.8)] gives the equilibrium abundance probability density of species $i$. This density describes the long time behavior of species abundance in the local community. It can be easily verified that in our case the equilibrium probability density $P_i$ satisfies the ordinary differential equation of the first order

$$\frac{1}{2}\frac{dD_i(n) P_i}{dn} - V_i(n) P_i = 0, \quad n \in (0, J), \tag{3.9}$$

supplemented with the integral condition

$$\int_0^J P_i(n)\, dn = 1, \tag{3.10}$$

representing the total probability instead of boundary conditions, see also (Babak, 2006).

## 3.4 Biodiversity indices

Using the abundance probability density of species $i$ in the local community given by Eqs. (3.5) and (3.6)-(3.8) or Eqs. (3.9) and (3.10), several diversity indices can be defined, that is, Simpson and Shannon indices, evenness indices, species richness, etc.

The Simpson and Shannon diversity indices can be introduced by first considering Rényi continuous entropy (Renyi, 1970; Vinga, 2004)

$$H_\alpha = \frac{1}{1-\alpha} \ln \sum_{i=1}^{S} \int_0^J \left(\frac{n}{J}\right)^\alpha p_i(n)\, dn, \tag{3.11}$$

where the abundance probability density $p_i(n)$ of species $i$ is defined either by $p_i(n) = p_i(n,t)$ from the evolution equations (3.5)–(3.8), or by $p_i(n) = P_i(n)$ from the steady-state equations (3.9) and (3.10). Then the generalized diversity index $D_\alpha$ as a continuum of possible diversity measures can be defined as follows (Hill, 1973)

$$D_\alpha = \exp H_\alpha. \tag{3.12}$$

For different $\alpha$, the index $D_\alpha$ differs only in its sensitivity to the presence of rare species. Turning the exponent $\alpha$ we can focus on different aspects of species abundance composition in the community, for example, for $\alpha = 0$, $D_0$ is equal to the total number of species $S$; for $\alpha = 2$, $D_2$ defines the Simpson index $D = 1 - \sum_{i=1}^{S} \int_0^J \left(\frac{n}{J}\right)^2 p_i(n)\, dn = 1 - 1/D_2$, and if $\alpha \to 1$, $H_\alpha$ converges to Shannon entropy $H = -\sum_{i=1}^{S} \int_0^J \frac{n}{J} \ln\left(\frac{n}{J}\right) p_i(n)\, dn$, and $D_\alpha \to \exp H$.

To calculate the species richness in a local community of size $J$, we define the average number of species containing from $n_1$ to $n_2$ individuals as (Babak, 2006)

$$\langle \phi(n_1, n_2) \rangle = \sum_{i=1}^{S} \int_{n_1}^{n_2} p_i(n)\, dn \tag{3.13}$$

with $p_i(n) = p_i(n,t)$ or $p_i(n) = P_i(n)$. Then the species richness in the local community is given by $\langle \phi(1, J) \rangle$.

## 3.5 Comparison study

To explain the diversity at the edge between two metacommunities, let us consider two metacommunities with the same number of evenly distributed distinct species, i.e., $S_1 = S_2 = S$, $\omega_i^1 = \omega_i^2 = 1/S$, $i = 1, \ldots, S$; and with the same probabilities of immigration into the local community at the edge, $\theta^1 = \theta^2 = 1/2$. Note that the model for the local community at the edge can be easily converted to the model for the internal local community by choosing $\omega_i = 1/(2S)$ for each species. In subsequent analysis we will compare the species abundance dynamics in a local community at the edge and in an internal local community of the same size with evenly distributed $S$ species, $\omega_i = 1/S$, $i = 1, \ldots, S$.

Let us first compare the dynamics of a given species in the local community at the edge with that in the internal local community of the same size. For the species abundance dynamics in the internal local community four different scenarios were distinguished in (Babak, 2006) with respect to the size of local community $J$, the relative species abundance in the metacommunity $\omega$ and the probability of immigration $m$. According to this classification, the species is persistent in the internal local community if $m > m_0 \approx J^{-1} \cdot S$ (Scenario (iv)), it has a high probability of extinction if $m_J < m < m_0$ (Scenario (ii)) with $m_J \approx J^{-1} \cdot S/(S-1)$, and it has very high chance of either extinction or monodominance if $m < m_J$ (Scenario (i)). Alternatively, for the local community at the edge between the two metacommunities, the species is persistent for $m > m_0^e \approx J^{-1} \cdot 2S$ (Scenario (iv)), it has high chance of extinction if $m_J^e < m < m_0^e$ (Scenario (ii)) with $m_J^e \approx J^{-1} \cdot 2S/(2S-1)$, and it has very high probability of either extinction or monodominance if $m < m_J^e$ (Scenario (i)). Using these results we can easily compare the species abundance dynamics in the internal local community to that in the local community of the same size at the edge between two metacommunities. Figure 3.1 shows an example of such comparison study for $J = 100$. Specifically, this figure reveals two regions for the immigration probability with different types of species abundance dynamics in the internal local community and in the local community at the edge between two metacommunities. For the first region with relatively large immigration probabilities, that is, for probabilities between $J^{-1} \cdot S$ and $J^{-1} \cdot 2S$, the species is persistent in the internal local community, and its abundance dynamics is typical for Scenario (iv); however, in the local community at the edge between two metacommunities the species has very high chance to go extinct and its abundance dynamics is typical for Scenario (ii). For the second region with relatively small immigration probabilities, that is, probabilities between $J^{-1} \cdot 2S/(2S-1)$ and $J^{-1} \cdot S/(S-1)$, the species has very high chance of extinction and monodominance in the internal local community (Scenario (i)); on the other hand for the local community at the edge the probability of this species to go extinct is also very high and the probability of its monodominance is very small (Scenario (ii)).

Let us now compare the species richness in the internal local community to that in the local community at the edge between two metacommunities, see Figure 3.2. This figure shows that for large immigration probability $m$ and small total number of species in one metacommunity $S$ (Scenario (iv)), the total number of species in the local community at the edge between two metacommunities is almost twice larger than in the internal local community. With decrease in the immigration probability and/or increase in the total number of species $S$, the difference between the average number of species in these local communities becomes relatively smaller; and, eventually, for very small immigration probabilities (Scenario (i)), the average number of species is almost identical in the local communities at the edge and in the interior. This is because in each local community most of the time only one species is monodominant.

Simpson diversity index ($D$) defines the probability that two randomly selected individuals belong to two different species. Figure 3.3(a) shows that for large immigration probability $m$ and for small total number of species $S$ (Scenario (iv)), the Simpson index is much larger for the local community at the edge between two metacommunities than in the interior of one metacommunity, thus the probability that two randomly selected individuals from the local community belong to two different species and, therefore, the diversity is much higher at the edge than in the interior. However, for large total number of species (Scenarios (i) and (ii)), the values of the Simpson index are almost identical for the local communities of both types; moreover, with decrease in the immigration probability $m$ and increase in the total number of species $S$ these values become smaller. Note also from Figure 3.3(a) that the Simpson index increases with respect to the immigration probability for both types of communities.

To measure the order of species abundances in a local community Shannon entropy index $H$ was used, see Figure 3.3(b). This diversity index is applied to determine how well each species abundance category is represented in the local community. Figure 3.3(b) clearly displays that the Shannon index of diversity is always larger for the local community at the edge between two metacommunities than for the internal local community. Therefore we can conclude that different species abundance categories are worse represented in the local community at the edge between two metacommunities than in the interior. Because Shannon index for each local community increases with increase in the total number of species $S$, each abundance category becomes worse represented in the local communities for larger $S$.

Finally, let us consider how similar the abundances of different species are in community at the edge between two metacommunities and in the interior of the metacommunity. To measure similarity several evenness indices are used. Figure 3.3(c) shows the Simpson evenness index of diversity $D/D_{\max}$ for both local communities. Note from Figure 3.3(c) that the Simpson evenness index is always larger for the internal local community, thus the species are more evenly distributed in the internal local community than in the local community at the edge between two metacommunities. Also note that the Simpson evenness index increases with respect to the immigration probability and decreases with respect to the total number of species, moreover, this index is very close to zero when the immigration probability is very small and the total number of species is large. The above evenness characterization can be explained in terms of the species abundance scenarios. Specifically, for small immigration probabilities (Scenario (i)) only one species is present in the local community most of the time and the evenness index is close to zero. In contrast, for large immigration probability $m$ and small total number of species $S$ (Scenario (iv)), all species persist in the local community most of the time and, therefore, the evenness index is very high.

## 3.6 Discussion

In this chapter I proposed the neutral macroecological model for species abundance dynamics at the edge of two different metacommunities. The model describes the species dynamics in well defined local communities located between differen habitats. In reality it is not very easy to define the local community at the edge of different habitats, since there is a continuous gradation from one metacommunity (e.g., forest) to the other (e.g., grassland). Therefore, spatially explicit models of population dynamics are often used to analyze edge effects.

The model I propose is, however, spatially implicit. It does not incorporate any spatial factors explicitly, and it is not very clear how to define local communities at the edge of two homogeneous habitats. In this case I propose to consider the gradient of species abundances as a determining factor for the edge local community. To define the local community at the edge of two distinct metacommunities for the implicit model proposed in this chapter, we can consider how significant is non-zero gradation of the species abundance composition of some site located close to both metacommunities in comparison to the gradation of the species abundance composition in the homogeneous metacommunities. Thus, if the gradients of the (most) species abundances from both metacommunities in some small area are significantly different from zero, then this area can be considered as a part of local community at the edge of two metacommunities, otherwise, this area belongs to the interior of one homogeneous metacommunity. In this case, the size of the local community at the edge of two different metacommunities should be relatively much smaller than the size of metacommunities. Once the strict borders of relatively small (narrow) local community at the edge of two distinct homogeneous large (wide) habitats are defined, it is not necessary to use spatially explicit models to describe the species abundance dynamics. Using spatially implicit models for species abundance dynamics in this case could not only simplify technical disadvantages of spatially explicit models, but also provide easy testable null hypotheses and good explanations of edge effects.

In conclusion, I considered the two distinct metacommunities with the same number of species and the same probabilities of immigration from these metacommunities into the local community between them in this chapter . However, the analysis of species abundance dynamics and diversity in the local communities at the edge between two metacommunities can be easily extended to the case with different number of species in two metacommunities and/or different immigration probabilities from the metacommunities, and to the case when the same species is present in two metacommunities. In these more general cases the diversity will be always higher in the local community connected to two metacommunities by immigration than in the internal local community connected to only one of these metacommunities, moreover, the persistence of species will be higher in the internal local community than in the local community at the edge between two metacommunities.

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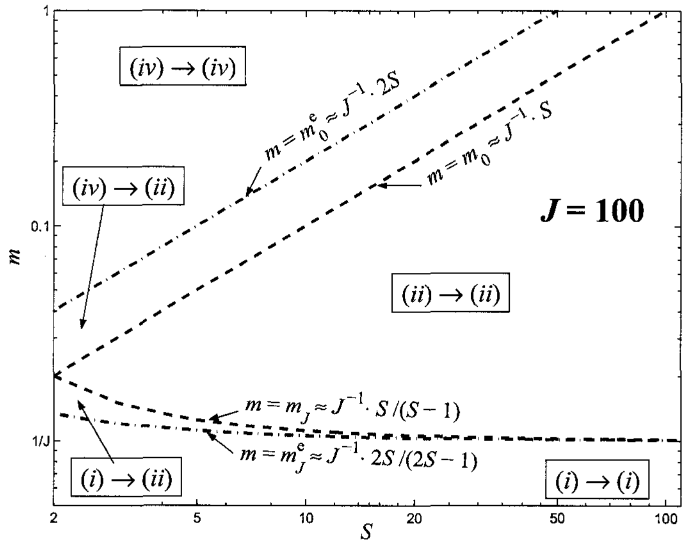


Figure 3.1: Effect of varying total number of species $S$ and the immigration probability $m$ on the species abundance dynamics scenario in the internal local community (first roman number) and the species abundance dynamics scenario in the local community at the edge between two metacommunities (second roman number).

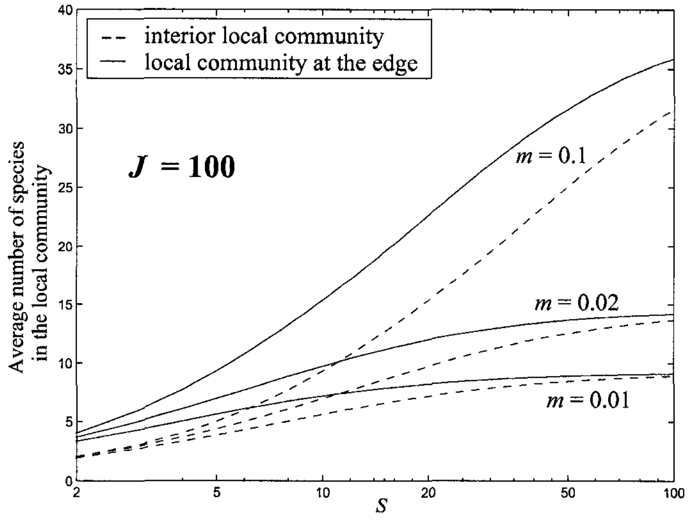


Figure 3.2: Effect of varying total number of species $S$ and the immigration probability $m$ on the average number of species in the local community at the edge (solid line) and in the interior of the metacommunity (dashed line).

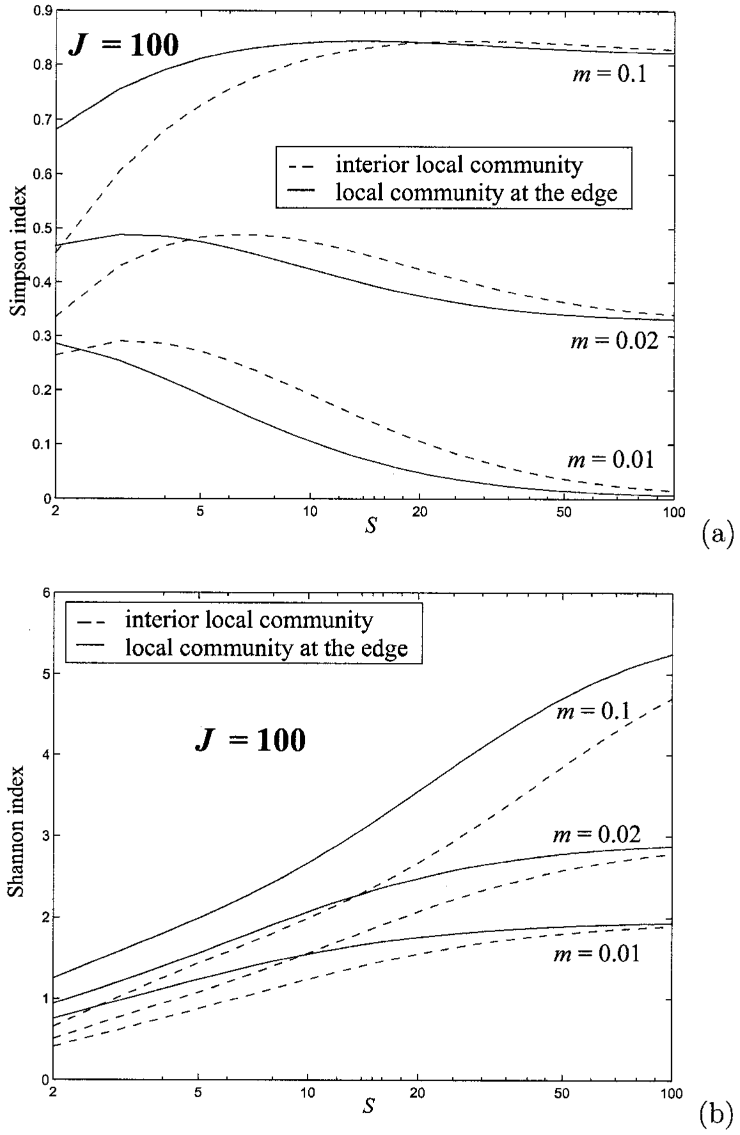
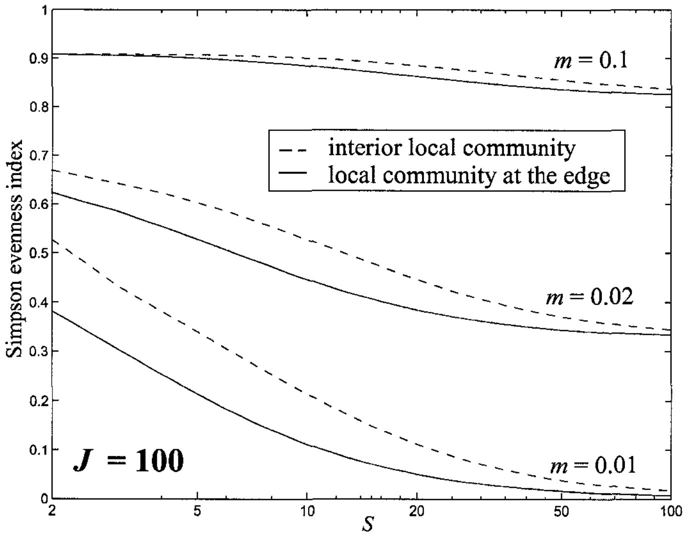


Figure 3.3: Effect of varying total number of species $S$ and immigration probability $m$ on (a) Simpson index, (b) Shannon index.



(c)

Figure 3.3: Cont. Effect of varying total number of species $S$ and immigration probability $m$ on (c) Simpson evenness index in the local community at the edge (solid line) and in the internal local community (dashed line).

# Chapter 4

# Analysis of species abundance distribution in two connected equal local communities

## 4.1 Introduction

Understanding the mechanisms of species abundance dynamics in ecological communities is of high concern in viability analysis and ecosystem management and restoration (Lande et al. 2003; MacArthur and Wilson 1967). Early studies on the species abundance relationships were focused on finding distributions that could fit empirical data of species abundances in ecological communities (Fisher et al. 1943; Preston 1948). Later the preference was given to modeling species abundance relationships using one or another ecological theory of community organization (MacArthur 1957; 1960; Bulmer 1974; May 1975; Caswell 1976; Sugihara 1980; Engen & Lande 1996). Currently, ecologists are involved in a strong discussion about the principles of the unified neutral theory of biodiversity and biogeography (Hubbell 2001). This theory is based on the assumption of neutrality, which, in contrast to the niche theory, does not assume differences between individuals of different species and trophic hierarchy of community (Hubbell 2001; Gaston & Chown 2005). Another assumption of Hubbell's theory - the zero-sum dynamics - states that the sum of all changes in abundances is always zero, that is, the total number of individuals in the community is a conserved quantity (Hubbell 2001). Based on this assumption, the neutral theory predicts the existence of a new statistical distribution of relative species abundance, called the zero-sum multinomial, which explains species area relationships.

The analytical formalization of Hubbell's neutral theory was proposed in two scales: local community and regional metacommunity (McKane et al. 2004). The metacommunity can be considered as a closed evolutionary biogeographic unit in which species can generate, live and go extinct (Hu et al. 2006). The metacommunity can be subdivided into several opened local communities linked by dispersal of species. The dynamics of species abundances on the local scale depends on species representation in the metacommunity, on the intensity of immigration from the metacommunity and, of course, on the size of local community. To describe the model, Hubbell defined the change in the number of individuals of species $i$ per unit time step using the transition probabilities for the species abundances. If we denote the number of individuals of the $i$th species in a local community by $N_i$ and the size of local community by $J$. Then, the respective transition probabilities for abundance of species $i$ per unit time step are (Hubbell 1997, 2001)

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

where $\omega_i$ is the fractional metacommunity relative species abundance of the $i$th species, and $m$ is the probability that a death in the local community will be replaced by an immigrant (Hubbell, 1997; 2001). $J = \sum_{i=1}^{S} N_i$ where $S$ is the total number species.

Hubbell's model is spatially implicit, since the species dynamics is studied in the local community which does not involve any spatial structure. Because the living organisms are not distributed in homogeneous surroundings in nature, the incorporation of the spatial structure is very important. Therefore, Hubbell (2001) modified his model for one local community to propose a model for species abundance dynamics in two local communities connected with each other and with the metacommunity through immigration. This model forms a link between spatially implicit and spatially explicit models for distribution of organisms in the metacommunity, because introduction of the spatial structure requires spatial discretization of the metacommunity landscape into small connected local communities. To analyze the model for species abundance distribution at the equilibrium state in two local communities Hubbell (2001) employs the covariance in abundance of a species in two local communities. He found that the covariance in abundance of a species in two local communities is affected not only by immigration from the metacommunity, but also via exchange of immigrants, and it is maximal when the intensity of immigrants between local community is large relative to the intensity from the metacommunity. However, in the view of high computation difficulty of the discrete Markov chain approach used by Hubbell to obtain the equilibrium species abundance distribution in two local communities, the study of the model for species abundance dynamics in two local communities is restricted only to very small local communities.

In this chapter we propose a new model for species abundance dynamics in two zero-sum local communities of the same size. This model for two local communities, in contrast to Hubbell's discrete analysis, is formulated using the continuous probabilistic technique. This technique allows us not only to derive the species abundance distribution for the local communities of any sizes, but also to make a classification of the species abundance dynamics in the two local communities with respect to the immigration intensities, species abundance in the metacommunity and size of local communities. It noteworthy that in our analysis we consider the local communities at different time scales, that is, we consider communities with different frequencies of death events. As to our knowledge, such analysis has not been done before. The local communities are considered at small spatial scale, and all processes in the local communities are much faster than in the metacommunity. Therefore, in the model for two local communities we concentrate on the species abundance dynamics in local communities, whereas in the metacommunity all species are considered with constant relative abundances.

The chapter is organized as follows. In Section 2, we will propose a discrete model for species abundance dynamics in two local communities. In Section 3, we modify this discrete model to formulate a continuous model for probability density of species abundance in two local communities using Kolmogorov-Fokker-Planck forward equation. Moreover, in this section we also derive the models for species abundance density function in equilibrium local communities and additive species abundance density function in both local communities. In Section 4, we analyze the model for equilibrium species abundance distribution in two local communities, and make a classification of species abundance dynamics in two local communities. According to this classification we distinguish nine realistic scenarios for the species abundance dynamics in two local communities with respect to the immigration probability, species metacommunity relative abundance and the size of local community. And, finally, in Sections 5 and 6, we present several examples for possible scenarios of species abundance dynamics in two local communities. The ecological motives underlying each of the scenarios are discussed.

## 4.2 Discrete model for species abundance dynamics in two local communities

Let us consider two zero-sum local communities of the same size connected through immigration with each other and with the metacommunity, a large reservoir of organisms of different species with unchanged species abundance fractions. The discrete model for species abundance dynamics in this case can be formulated as follows.

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

$$W_{p,i}\left(N_p-1 \mid N_p,N_q\right)=\frac{N_p}{J}\left((1-m^m-m^l)\frac{J-N_p}{J-1}+m^m(1-\omega_i)+m^l\frac{J-N_q}{J}\right),$$

$$W_{p,i}\left(N_p+1 \mid N_p,N_q\right)=\frac{J-N_p}{J}\left((1-m^m-m^l)\frac{N_p}{J-1}+m^m\omega_i+m^l\frac{N_q}{J}\right), \qquad (2)$$

$$W_{p,i}(N_p \mid N_p, N_q) = 1 - W_{p,i}(N_p - 1 \mid N_p, N_q) - W_{p,i}(N_p + 1 \mid N_p, N_q)$$

where $J$ is the size of local communities, $q = \begin{cases} 1: & p = 2, \\ 2: & p = 1; \end{cases}$ $N_r = N_{r,i}$, $r = 1,2$; $\omega_i$ is a fractional metacommunity relative species abundance of species $i$, $m^m$ is the probability that a death in a local community will be replaced by an immigrant from the metacommunity and $m^l$ is the probability that a death in a local community will be replaced by an immigrant from the other local community, $m = m^m + m^l$.

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

Further, we assume that the species abundance dynamics in one local community is independent of the species abundance dynamics in another local community. Then, the transition probabilities for the dynamics of species $i$ in both local communities can be defined as

$$W_i(N_1 + \Delta_1, N_2 + \Delta_2 \mid N_1, N_2) = W_{1,i}(N_1 + \Delta_1 \mid N_1, N_2) \times W_{2,i}(N_2 + \Delta_2 \mid N_2, N_1) \quad (3)$$

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

Recall that Hubbell (2001) also proposed a model for species abundance dynamics in two discrete habitat patches or islands (local communities). In his model Hubbell used the transition probabilities for dynamics of given species in both local communities, where he assumed that the abundance of this species can be changed only in one local community per one time step. On the contrary to Hubbell, we assume that the abundance of given species can be changed in both local communities in one time step. Because the local communities are located separately in the space and the death in one local community may occur at the same time as in another local community, the assumption underlying our model is more realistic than that of Hubbell.

Another major difference between our discrete model for species abundance dynamics in two local communities and Hubbell's model lies in parameterization for the immigration probabilities. Hubbell used the variable $m$ to denote the probability that either local community receives an immigrant from the metacommunity in which they are imbedded. In our model this immigration probability is denoted by $m^m$, see equations (2). To define the probability that two local communities exchange migrants per birth, Hubbell used the variable $m'$, that is related to the respective immigration probability from our model as $m' = m^l/(1-m^m)$, or $m^l = m'(1-m)$. Recall that $m^l$ in our discrete model for species abundance dynamics in two local communities denotes the probability that a death in a local community is replaced by an immigrant from another local community. It is clear from the above analysis that there is one to one correspondence between the immigration probabilities in Hubbell model and our model for the species abundance dynamics in two local communities. However, on the contrary to Hubbell's (2001) parameterization, the parameterization for the immigration probabilities proposed is this chapter is much more convenient for analysis and visualization of the species abundance results due to the fact that it allows formulation of the transition probabilities for the change in species abundance using simple linear relationships of $m^m$ and $m^l$.

# 4.3 Continuous probabilistic approach

## 4.3.1 Model for species abundance dynamics in two local communities

The continuous model for the species abundance distribution in two zero-sum local communities is derived as follows. Let define the transition probabilities for the change $\Delta N_{p,i}$ in the number of individuals $N_{p,i}$ of the $i$th species in local community $p$, $p=1,2$ per time step $\Delta t$ as

$$\begin{aligned}
&\Pr(\Delta N_{p,i} = \pm 1 \mid N_{p,i} = N_p, N_{q,i} = N_q) = \mu_p \Delta t W_{p,i}(N_p \pm 1 \mid N_p, N_q),\\
&\Pr(\Delta N_{p,i} = 0 \mid N_{p,i} = N_p, N_{q,i} = N_q) = 1 - \Pr(\Delta N_{p,i} = 1 \mid N_{p,i} = N_p, N_{q,i} = N_q)\\
&\qquad\qquad - \Pr(\Delta N_{p,i} = -1 \mid N_{p,i} = N_p, N_{q,i} = N_q),
\end{aligned} \tag{4}$$

where $\mu_p$ is the number of death events per unit time interval in local community $p$.

Then the joint transition probabilities for the change in the species abundance in both local communities are given by

$$\begin{aligned}
&\Pr(\Delta N_{1,i} = \Delta_1, \Delta N_{2,i} = \Delta_2 \mid N_{1,i} = N_1, N_{2,i} = N_2)\\
&= \Pr(N_{1,i} = \Delta_1 \mid N_{1,i} = N_1, N_{2,i} = N_2) \times \Pr(N_{2,i} = \Delta_2 \mid N_{2,i} = N_2, N_{1,i} = N_1)
\end{aligned} \tag{5}$$

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

### 4.3.2 Dynamics of species abundance distribution. Kolmogorov-Fokker-Planck forward equation

Let define the change in the abundance of the $i$th species in both local communities per time step $\Delta t$ as a vector $\Delta N_i = (\Delta N_{1,i}, \Delta N_{2,i})$, where $\Delta N_{p,i} = N_{p,i}(t+\Delta t) - N_{p,i}(t)$, $p = 1,2$; and let $N_i = (N_{1,i}, N_{2,i})$ and $x = (x_1, x_2)$.

Because the species abundance in one local community per one time step $\Delta t$ can change only by one individual or remain the same, the variables $\Delta N_{p,i}$ attain only values -1,0 and 1. And therefore the mean and the second moment of the change in the abundance of the $i$th species per infinitely small time interval $\Delta t$ can be calculated as

$$V(x) = \begin{pmatrix} V_1(x) \\ V_2(x) \end{pmatrix} = \lim_{\Delta t \to 0} \frac{1}{\Delta t} \begin{pmatrix} E(\Delta N_{1,i} \mid N_i = x) \\ E(\Delta N_{2,i} \mid N_i = x) \end{pmatrix},$$

$$V_1(x) = \mu_1 m^m \left( \omega_i - \frac{x_1}{J} \right) + \mu_1 m^l \left( \frac{x_2}{J} - \frac{x_1}{J} \right), \quad V_2(x) = \mu_2 m^m \left( \omega_i - \frac{x_2}{J} \right) + \mu_2 m^l \left( \frac{x_1}{J} - \frac{x_2}{J} \right); \tag{6}$$

$$D(x) = \begin{pmatrix} D_{11}(x) & D_{12}(x) \\ D_{21}(x) & D_{22}(x) \end{pmatrix} = \lim_{\Delta t \to 0} \frac{1}{\Delta t} \begin{pmatrix} E(\Delta N_{1,i}{}^2 \mid N_i = x) & E(\Delta N_{1,i} \Delta N_{2,i} \mid N_i = x) \\ E(\Delta N_{1,i} \Delta N_{2,i} \mid N_i = x) & E(\Delta N_{2,i}{}^2 \mid N_i = x) \end{pmatrix},$$

$$D_{11}(x) =$$

$$\mu_1 \left( 2(1 - m^m - m^l) \frac{x_1 (J - x_1)}{J(J-1)} + m^m (1 - \omega_i) \frac{x_1}{J} + m^m \omega_i \frac{J - x_1}{J} + m^l \frac{J - x_2}{J} \frac{x_1}{J} + m^l \frac{x_2}{J} \frac{J - x_1}{J} \right),$$

$$D_{22}(x) =$$

$$\mu_2 \left( 2(1 - m^m - m^l) \frac{x_2 (J - x_2)}{J(J-1)} + m^m (1 - \omega_i) \frac{x_2}{J} + m^m \omega_i \frac{J - x_2}{J} + m^l \frac{J - x_1}{J} \frac{x_2}{J} + m^l \frac{x_1}{J} \frac{J - x_2}{J} \right),$$

$$D_{12}(x) = D_{21}(x) = 0. \tag{7}$$

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

$$\frac{\partial p}{\partial t} = \frac{1}{2} \left( \frac{\partial^2 D_{11} p}{\partial x_1{}^2} + \frac{\partial^2 D_{22} p}{\partial x_2{}^2} \right) - \frac{\partial V_1 p}{\partial x_1} - \frac{\partial V_2 p}{\partial x_2}, \quad x = (x_1, x_2) \in \Omega = (0,J) \times (0,J), \quad t > \tau, \tag{8}$$

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

Equation (8) is supplemented with the initial condition defining $p^0(x)$, the probability density of the $i$th species abundances $x_1$ and $x_2$ in the two local communities at the initial time moment $t=\tau$

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

and the natural boundary conditions

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

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

$$\iint_{\Omega} p(x,\tau)\,\mathrm{d}x_1\mathrm{d}x_2 = \iint_{\Omega} p^0(x)\,\mathrm{d}x_1\mathrm{d}x_2 = 1, \quad \text{for all } t\geq\tau. \tag{11}$$

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

Now let us rewrite the boundary conditions (10) for each part of the boundary separately as

$$\frac{1}{2}\frac{\partial D_{11}p}{\partial x_1}-V_1 p=0, \quad x\in\Gamma^{0*}\cup\Gamma^{1*}, \qquad \frac{1}{2}\frac{\partial D_{22}p}{\partial x_2}-V_2 p=0, \quad x\in\Gamma^{*0}\cup\Gamma^{*1}. \tag{12}$$

### 4.3.3 Equilibrium species abundance distribution in two local communities

Equilibrium species abundance distribution can be considered as a long time limit of species abundance distribution in local communities or as a stabilized species abundance distribution in absence of external perturbations.

It follows from model (8)-(11), that the equilibrium (steady state) abundance density of species $i$ in two local communities fulfils the following elliptic differential equation

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

and boundary conditions (10) or (12) with the total probability over domain $\Omega$ equal to 1 (see also Eq.(11)).

### 4.3.4 Additive species abundance distribution in both local communities

Another problem of interest for community ecologists is the additive species abundance distribution in both local communities, that is the distribution of $x_1 + x_2$. This distribution is useful for comparison study of the abundance distributions in two local communities and in one large local community formed by merging both of them.

The species abundance distribution in both local communities can be defined as

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

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

### 4.3.5 Correlation between species abundances in two local communities

One of the important characteristics of the relationship between species abundance distributions in two local communities is the magnitude of their correlation. In order to define it, we derive first the formulae for the covariance and variances of the species abundance in local communities

$$Cov(N_{1,i}, N_{2,i}) = \iint_\Omega (x_1 - E(N_{p,i}))(x_2 - E(N_{p,i}))p(x_1, x_2, t)dx_1dx_2\,, \qquad (15)$$

$$Var(N_{p,i}) = \iint_\Omega (x_p - E(N_{p,i}))(x_p - E(N_{p,i}))p(x_1, x_2, t)dx_1dx_2\,,\ p = 1,2;$$

where

$$E(N_{p,i}) = \iint_\Omega x_p p(x_1, x_2, t)dx_1dx_2\,,\ p = 1,2;$$

Then, the correlation coefficient can be found as

$$r_{12} = \frac{Cov(N_{1,i}, N_{2,i})}{\sqrt{Var(N_{1,i})Var(N_{2,i})}}. \qquad (16)$$

## 4.4 Analysis of the model

### 4.4.1 Analysis of the boundary conditions for the species abundance density function

A change in species abundance distribution with respect to different values of the immigration probabilities, the species metacommunity relative abundance, the community sizes and the number of death events per unit time interval can be investigated by analyzing boundary conditions (12) on equation (8) or (13).

Let us consider the type of boundary conditions (12). These mixed boundary conditions can be rewritten as

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

$$\frac{1}{2}D_{22}\frac{\partial p}{\partial x_2}+\left(\frac{1}{2}\frac{\partial D_{22}}{\partial x_2}-V_2\right)p=0,\quad x\in\Gamma^{*0}\cup\Gamma^{*1} \tag{17}$$

The critical boundary abundances at which the mixed boundary conditions degenerate to the zero flux boundary conditions can be found by solving the following equations

$$\left.\frac{1}{2}\frac{\partial D_{pp}}{\partial x_p}-V_p\right|_{x_p=0}=0,\qquad \left.\frac{1}{2}\frac{\partial D_{pp}}{\partial x_p}-V_p\right|_{x_p=J}=0,\qquad p=1,2, \tag{18}$$

where

$$\frac{1}{2}\frac{\partial D_{pp}p}{\partial x_p}-V_p p=$$
$$\mu_p\left(\frac{(m^m+m^l)(J+1)-2}{J(J-1)}x_p-m^l\frac{J+1}{J^2}x_q+\frac{1}{J-1}-\left(\frac{(m^m+m^l)}{2(J-1)}+m^m\omega_i\right)\frac{J+1}{J}\right), \tag{19}$$

is non-increasing function with respect to $x_q$, $q=1$ if $p=2$ and $q=2$ if $p=1$.

Note that the zero flux boundary conditions, also known as Neumann Boundary conditions, imply zero gradient of the probability of species abundances at the boundary abundances.

After substitution of Eq. (19) into Eq. (18), we obtain the following formulae for calculation of the boundary abundances $(0,x_2^0)$, $(J,x_2^1)$, $(x_1^0,0)$ and $(x_1^1,J)$ where boundary conditions (17) degenerate to the zero-flux boundary conditions

$$x^0=x_1^0=x_2^0=\left(\frac{1-(m^m+m^l)}{m^l}\frac{J^2}{(J-1)(J+1)}+\frac{m^m+m^l}{2m^l}\frac{J}{J+1}\right)-\omega_i\frac{m^m}{m^l}J,$$

$$x^1 = x_1^1 = x_2^1 = -\left(\frac{1-(m^m+m^l)}{m^l}\frac{J^2}{(J-1)(J+1)} + \frac{m^m+m^l}{2m^l}\frac{J}{J+1}\right) + J + (1-\omega_i)\frac{m^m}{m^l}J. \quad (20)$$

For large local communities, the above formulae can be simplified to the subsequent

$$x^0 = \left(\frac{1-(m^m+m^l)}{m^l} + \frac{m^m+m^l}{2m^l}\right) - \omega_i\frac{m^m}{m^l}J,$$

$$x^1 = -\left(\frac{1-(m^m+m^l)}{m^l} + \frac{m^m+m^l}{2m^l}\right) + J + (1-\omega_i)\frac{m^m}{m^l}J.$$

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

## 4.4.2 Structure of species abundance distribution at parallel boundary sides

To continue the species abundance distribution analysis, let us consider expression (19) in more detail. Because the functions $\frac{1}{2}\frac{\partial D_{pp}}{\partial x_p} - V_p$ in (19) are non-increasing at the boundaries with respect to $x_q$, we can conclude the following:

1) if $x^0 > 0$, then $\frac{\partial p}{\partial x_p} < 0$ at $\{x_p = 0\} \cap \{x_q < x^0\}$, and if $x^0 < J$, then $\frac{\partial p}{\partial x_p} > 0$ at $\{x_p = 0\} \cap \{x_q > x^0\}$;

2) if $x^1 > 0$, then $\frac{\partial p}{\partial x_p} < 0$ at $\{x_p = J\} \cap \{x_q < x^1\}$, and if $x^1 < J$, then $\frac{\partial p}{\partial x_p} > 0$ at $\{x_p = J\} \cap \{x_q > x^1\}$,

where $q = 2$ if $p = 1$ and $q = 1$ if $p = 2$.

Based on the statements 1) and 2), a classification of the species abundance distributions at the boundary abundances $x_p = 0$ and $x_p = J$ with respect to the abundances $x^0$ and $x^1$, where the mixed boundary conditions (17) degenerate to the zero flux boundary conditions, is straightforward. The possible cases for the behavior of species abundance distributions at the boundaries are distinguished with respect to 9 different locations of the abundances $x^0$ and $x^1$ in the intervals: $(-\infty,0)$, $[0,J)$ and $[J,+\infty)$. Figure 4.1 shows the shapes of two contours of the species abundance distribution on the boundary sides $x_p = 0$ (lover curve) and $x_p = J$ (upper curve).

Further the species abundance distributions classification is performed separately for species with small and large metacomunity relative abundances, $\omega_i < 1/2$ and $\omega_i \geq 1/2$, respectively. It follows directly from Table 4.1, that if $\omega_i < 1/2$ then there are only 6 possible combinations for $x^0$ and $x^1$, these are cases (*i*)-(*iii*), (*v*), (*vi*) and (*ix*) in Figure 4.1. On the other hand, if $\omega_i \geq 1/2$ then there are also 6 possible combinations for $x^0$ and $x^1$ , these are cases (*i*), (*iv*), (*v*) and (*vii*)-(*ix*) in Figure 4.1.

In Table 4.1 the conditions for different types of species abundance distribution at the boundary abundances $x_p = 0$ and $x_p = J$ are given using linear relationships:

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

$$v_\omega^J(m^m, m^l) = m^m(2\omega(J-1)+1) + m^l(2J-1),$$

which involve the immigration probabilities $m^m$ and $m^l$, the metacommunity relative abundance $\omega_i$ and the size of local communities $J$. The ranges of the immigration probabilities $m^m$ and $m^l$ for possible types of species abundance distribution at $x_p = 0$ and $x_p = J$ are shown in Figure 4.2 for $0 \leq \omega_i < 1/2$, $\omega_i = 1/2$ and $1/2 < \omega_i \leq 1$. These ranges are separated using the lines:

$$w_{\omega_i}^J(m^m, m^l) = 2J/(J+1), \qquad w_{1-\omega_i}^J(m^m, m^l) = 2J/(J+1),$$

$$v_{\omega_i}^J(m^m, m^l) = 2J/(J+1), \qquad v_{1-\omega_i}^J(m^m, m^l) = 2J/(J+1). \qquad (20)$$

Note that if the local communities are isolated from the metacommunity, i.e., $m^m = 0$, the type of the species abundance distribution differs for the values of the immigration probability between local communities $m^l$ smaller and larger of $m^l(v) = \dfrac{m^l(w)}{2J-1}$, where $m^l(w) = \dfrac{2J}{J+1} \approx 2$. Similarly, if the local communities are isolated from each other, $m^l = 0$, the type of the species abundance distribution depends on the values $m^m(\omega_i) = \dfrac{2J}{(J+1)(2\omega_i(J-1)+1)}$ and

$m^m(1-\omega_i)=\dfrac{2J}{(J+1)(2(1-\omega_i)(J-1)+1)}$ for the immigration probability from the metacommunity $m^m$, see Figure 4.2.

Note that the model for species abundance dynamics in two local communities (2) requires that the sum of nonnegative immigration probabilities $m^m$ and $m^l$ be less or equal to one. This inequality constraint yields oftentimes reduction in the number of possible combinations for the species abundance distributions at the boundary abundances $x_p = 0$ and $x_p = J$, see Figure 4.3. For example, in the case when $\omega_i$ is very small, i.e., $0 \le \omega_i \le \dfrac{1}{2(J+1)}$, Figure 4.3 shows that the combination (*i*) at the boundaries $x_p = 0$ and $x_p = J$ is not feasible. Similarly, it can be inferred from Figure 4.2 for $\omega_i > 1/2$ that this combination is also not feasible when the metacommunity relative abundance is large, i.e., $\omega_i \ge 1-\dfrac{1}{2(J+1)}$. Therefore, the combination (*i*) is possible only for the following metacommunity relative abundances

$$\frac{1}{2(J+1)} < \omega_i < 1-\frac{1}{2(J+1)}. \tag{21}$$

It worth to note the important influence of the relationship between the metacommunity relative abundance and the size of the local community in determining possible combinations for the species abundance distributions at the boundary abundances $x_p = 0$ and $x_p = J$. For example, the combination (*i*) is only possible when the size of the local community is enough large, that is when $J > \dfrac{1}{2\min\{\omega_i, 1-\omega_i\}} - 1$. (see inequality (21))

Moreover, note that the type of species abundance behavior at the boundaries $x_p = 0$ and $x_p = J$ varies significantly with the sizes of local community $J$, see Eqs. (20). For example, for $\omega_i = 0.2$, $m^m = 0.05$ and $m^l = 0.05$ we observe that with increase in the size of local community $J$ the combination (*ix*) with $J = 10$ switches first to the combination (*vi*) with $J = 15$ then to (*v*) with $J = 20$, (*ii*) with $J = 50$ and, finally, to (*i*) with $J = 100$. Another example illustrates different sequence of species abundance combinations at the boundary for variable $J$, i.e., for $\omega_i = 0.2$, $m^m = 0.05$ and $m^l = 0.01$ we observe that the combination (*ix*) with $J = 10$ switches first to the combination (*vi*) with $J = 20$, then to (*iii*) with $J = 30$, (*ii*) with $J = 50$ and, finally, to (*i*) with $J = 100$.

### 4.4.3 Classification of the species abundance dynamics in the local communities

When the species is extinct or monodominant in one local community, then the type of species abundance distribution in another local community defines the joint species abundance distribution for both local communities. Hereafter we will refer to different types of joint species abundance distributions as the scenarios of species abundance dynamics in two local communities. Of course, the number for the scenario of the species abundance dynamics will be defined based on the number of the type for species abundance distribution at the boundary abundances. Since all 9 types of species abundance behavior at both pairs of the parallel boundary sides of the abundance domain $\Omega$ are not feasible for any values of model parameters (immigration probabilities, metacommunity relative abundance and the size of local communities), the number of possible scenarios for the species abundance is also less than 9. More advanced analysis reveals that there are only 3 possible scenarios for species abundance dynamics in two local communities for $\omega_i = 1/2$, 6 possible scenarios for $0 < \left|\omega_i - \frac{1}{2}\right| < \frac{J}{2(J+1)}$, and 5 possible scenarios for $\left|\omega_i - \frac{1}{2}\right| \geq \frac{J}{2(J+1)}$.

## 4.5 Sensitivity analysis. Examples

In this section we analyze the equilibrium species abundance distributions. Specifically, we: (a) investigate in great detail the equilibrium species abundance distributions for two local communities with the same frequencies of death events, $\mu_1 = \mu_2$, and (b) sketch the results for the two local communities with different frequencies of death events $\mu_1 \neq \mu_2$. Moreover, we also analyze the equilibrium species abundance distributions using the correlation coefficient between species abundances in two local communities.

### 4.5.1 Two local communities with the same frequencies of death events

Let us consider two local communities of size $J = 200$ individuals each that have the same frequencies of death events ($\mu_1 = \mu_2$). Further, assume that species of interest, say species $i$, has small relative abundance in the metacommunity, $\omega_i = 0.2 < 1/2$. The analysis of the common species ($\omega_i > 1/2$) can be provided in analogous manner.

It was mentioned in the previous section that there are only 6 possible scenarios for the species abundance dynamics in the case when the metacommunity relative abundance is smaller than $1/2$, these are scenarios (*i*)-(*iii*), (*v*), (*vi*) and (*ix*). To illustrate all these scenarios we have chosen the realistic values for the immigration probabilities in each scenario. For both local communities we showed the landscape and contour plots for the abundance density of species $i$ in Figure 4.4. Furthermore, we also showed the additive species abundance distributions in both local communities, see Figure 4.4. Note that in this experiment equilibrium species abundance distributions is independent of the equal values of the parameters $\mu_1$ and $\mu_2$, since these parameters specify the speed of the convergence to equilibrium species abundance distributions, and play a role of the time scales in the dynamics of the species abundances in the local communities. Thus, a constant value of 0.0001 for the parameters $\mu_1$ and $\mu_2$ was used in all experiments.

Let us now analyze all scenarios for species abundance distribution and dynamics in more detail.

Consider Scenario (*ix*) first. This scenario is characterized by low immigration from the metacommunity and between the local communities. Because of low immigration, the species abundance dynamics in local communities is very similar to the case with no immigration. Note that in the local communities which do not obtain immigrants from the metacommunity and from each other, the species dynamics are independent between two local communities and between each local community and the metacommunity. Such local communities are referred to as isolated local communities.

When analyzing isolated local communities Hubbell (2001) observed that species abundance dynamics in such communities possesses two absorbing states at zero abundance level and at the monodominance level. In the case of two local isolated communities considered in this chapter, we observe not two, but four absorbing states $(0,0)$, $(J,0)$, $(0,J)$ and $(J,J)$ for the species abundance dynamics. Because the immigration intensity is very small, the new immigrants appear in local communities very seldom, and the species abundance in local communities becomes stabilized at one of the four absorbing states most of time. Therefore, the effect of the small immigration on the species abundance distribution can be considered as a catastrophic event in local communities. As a result, for small immigration intensities, the species abundance combinations $(0,0)$, $(J,0)$, $(0,J)$ and $(J,J)$ have maximal probabilities. That is, the probabilities that the species will go extinct or become monodominant in these local communities are very high. Moreover, note that in the case of species abundance dynamics scenario (*ix*), the additive species abundance distribution in both local communities is significantly different from the species abundance distribution in each local community. From Figure 4.4 we can see that the additive species abundance distribution in both local communities is W-shaped and has local maximums not only at the species abundance levels 0 and $2J$, but also at abundance $J$. Note that when the additive species abundance distribution reaches level $J$, the species of interest is monodominant in one local community and extinct from the other local community.

Scenario (*vi*). When species immigrate to local communities from the metacommunity more often, or when they move from one local community to another more frequently, the species abundance dynamics distribution takes on a different shape than that of Scenario (*ix*). Specifically, if the species abundance is very small in one local community, then this species will have very small effect on the species abundance distribution in another local community. In this case, with increase in the immigration intensity from the metacommunity, the species abundance distribution in the second local community will be S-shaped (Babak, 2006). Otherwise, if the species is almost monodominant in one local community, its effect on the species abundance in another local community is large. As result, the species abundance distribution in the second local community will be still U-shaped as in Scenario (*ix*). When analyzing both local communities jointly, we can infer that the species abundance distribution has two local maximums at the abundances $(0,0)$ and $(J,J)$, despite the additive species abundance for both local communities is S-shaped, see Figure 4.4(*vi*). Thus, the probability that species will go extinct or become monodominate in both local communities is the highest.

Scenario (*v*). For Scenario (*v*) the species abundance distribution can take on two reverse shapes at the boundary of the abundance domain $\Omega$. If the species is not presented in one local community, its abundance in another local community is, as in Scenario (*vi*), S-shaped. If species is monodomimant in one local community, its abundance in another local community is reverse S-shaped. This shape of the species abundance distribution can be explained by increasing similarity of the local communities due to high local immigration intensities. Figure 4.4(*v*) shows the patterns of species abundance distribution with immigration probabilities larger than considered in Scenarios (*ix*) and (*vi*). One can clearly note from this figure that because of high immigration, the local communities are tightly connected and are very similar to each other. As result the species abundance combinations $(J,0)$ and $(0,J)$ are less probable in this scenario than in Scenarios (*ix*) and (*vi*). The additive species abundance dynamics in Scenario (*vi*) is S-shaped. As in Scenario (*vi*), the species has very high chance of extinction from both local communities or monodominance in both local communities.

Scenario (*iii*). The species abundance distribution for Scenario (*iii*) is shown in Figure 4.4(*iii*). This figure clearly shows that if the immigration from the metacommunity dominates the local immigration between communities, then the effect of one local community on another local community is not strong and, therefore, the species composition in both local communities are very similar to those in the metacommunity. As a result, the equilibrium species abundance distribution is S-Shaped at each side of the domain $\Omega$, its maximum is attained at the species abundance $(0,0)$, and its minimum is at $(J,J)$. The probability that species go extinct from both local communities is very high, while the probability of species monodominance in both communities is very low.

Scenario (*ii*). Similarly to Scenario (*iii*), the maximum of the equilibrium species abundance distribution in Scenario (*ii*) is attained at $(0,0)$, that is, the probability that the species will go extinct is the highest for this scenario. However, on the contrary to Scenario (*iii*), the equilibrium species abundance distribution is not always S-Shaped at the boundary values of the species abundances in this case. This is because of the strong impact of the local immigration from one local community to another. The role of local immigration is the best seen for the species abundance distribution in one local community if the species is monodominant in another local community. In this case the species abundance contour for a local community is reverse U-shaped. As in Scenarios (*iii*), (*v*) and (*vi*), the additive species abundance distribution in Scenario (*ii*) is S-shaped.

Scenario (*i*). The last possible scenario for the species abundance dynamics is Scenario (*i*). For this scenario we can observe that for large immigration probabilities, particularly for large $m^m$, new immigrants intensively move to the local communities from the metacommunity. As result, the species abundance distributions in local communities become more similar to those in the metacommunity. The species abundance probability density achieves maximum close to the species abundances $(\omega_i J, \omega_i J)$. This means that species of scenario (*i*) tends to persist for a long time in at least one local community. Note also that at the boundary levels of abundance in one local community, the species abundance distribution in another local community takes on reverse U-shape. Moreover, the additive species abundance distribution for both local communities is also reverse U-shaped.

Now let us consider the intermediate scenarios. In particular, the following four intermediate scenarios will be considered for $\omega_i < 1/2$, see Figures 4.2 and 4.3: Scenario (*i-ii-iii*) as an intermediate case for Scenarios (*i*), (*ii*) and (*iii*); Scenario (*iii-vi-ix*) as an intermediate case for Scenarios (*iii*), (*vi*) and (*ix*); Scenario (*v-vi-ix*) as an intermediate case for Scenarios (*v*), (*vi*) and (*ix*); and, finally, Scenario (*ii-iii-v-vi*) as an intermediate case for Scenarios (*ii*), (*iii*), (*v*) and (*vi*).

Because the probabilities of local immigration in Scenarios (*i-ii-iii*) and (*iii-vi-ix*) are zeros, the species dynamics in one local community in either of these scenarios is independent of its dynamics in another local community. Thus, the analysis of species abundance dynamics for each local community can be made separately, see (Babak, 2006).

For Scenario (*v-vi-ix*) the immigration probabilities from the metacommunity into local communities are zeros. Thus, because of no immigration from outside of the local communities, the species abundance dynamics in local communities has two absorbing states as in the case of only one local community (Hubbell, 2001; Babak, 2006). These absorbing states of species abundance are 0 and $2J$ corresponding to species extinction from both local communities and species monodomimance in both local communities, respectively.

From analysis of the boundary conditions given in Figure 4.1, we can conclude that the equilibrium species abundance distribution at the boundary sides $x_1 = 0$ and $x_2 = 0$ for intermediate Scenario (*ii-iii-v-vi*) is S-shaped. Moreover, we can also observe that the species abundance distribution at the boundaries $x_1 = J$ and $x_2 = J$ has zero gradients at both ends of the abundance intervals. Figure 4.5 shows the equilibrium species abundance for the intermediate values of the immigration probabilities $m^m = \dfrac{1}{(1-\omega_i)(J+1)}$ and $m^l = \dfrac{1-2\omega_i}{(1-\omega_i)(J+1)}$ calculated from Equations (11)-(13). From this figure one can clearly see, that species abundance distribution confirms to all conclusions made from the analysis of the boundary conditions using

Figure 4.1. It worth to note also that the maximal probability of the species abundance in intermediate Scenario (*ii-iii-v-vi*) is attained at the zero abundance level $(0,0)$, and the minimal is at the abundance combinations $(J,0)$ and $(0,J)$. Since Scenario (*ii-iii-v-vi*) is an intermediate case of Scenarios (*ii*), (*iii*), (*v*) and (*vi*), the additive species abundance distribution for both local communities is S-shaped, as it is in all of these scenarios. In general, the species dynamics also follows for intermediate scenario some average characteristics of Scenarios (*ii*), (*iii*), (*v*) and (*vi*). In particular, the chance of the species extinction for the Scenario (*ii-iii-v-vi*) is very high.

Note that for analysis of each individual Scenario (*i*), (*ii*), (*iii*), (*v*), (*vi*) or (*ix*) we can either create figures like Figure 4.4, or directly analyze the behavior of the species abundance distribution at the boundary of the domain $\Omega$ using Figure 4.1.

### 4.5.2 Non-isolated local communities of equal size with different frequencies of death events

Because the frequencies of the death events in local communities can be eliminated from boundary conditions (12), we can conclude that the type of species abundance distribution at the boundary of the domain $\Omega$ is independent of death frequencies, $\mu_1$ and $\mu_2$. Furthermore, note that despite the values of the species abundance distribution in the domain $\Omega$ depend on the parameters $\mu_1$ and $\mu_2$, the shape of this distribution (i.e., locations of maximum and minimum values, the directions of monotonicity) is defined only based on the type of boundary conditions.

Figure 4.6 shows an example of species abundance distribution in two local communities of the same size with the same immigration probabilities, but with $\mu_1/\mu_2 = 10$. As you can see different frequencies of death events, that is different values of $\mu_1$ and $\mu_2$, mainly influence the symmetry of species abundance distribution in the local communities.

### 4.5.3 Correlation between species abundances in two local communities

Correlation between species abundances in two local communities can be considered as a measure of similarity of local communities. It can be easily calculated from the probability density of species abundance in both local communities using equation (16). Figure 4.7 shows the plot of correlation between species abundances in two local communities as a function of immigration probabilities $m^m$ and $m^l$. From this figure, one can clearly see that for very small immigration probability from the metacommunity $m^m$, the correlation between species abundance in two local communities is close to 1, and for very small immigration probability between local communities $m^l$, the correlation between species abundance in two local communities is close to 0.

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

From Figure 4.7 we can also note that when the probability of immigration from the metacommunity is fixed, the correlation increases with increase in the immigration between local communities. This is because the similarity of species abundance dynamics in two local communities increases with increase in intensity of the immigration level between local communities. On the other hand, when the probability of immigration between local communities is fixed, the correlation between local comunities reduces with increase in the probability of immigration from the metacommunity. In this case the balance between local and global immigration processes is shifted towards the prevalence of the immigration from the metacommunity. Thus, less similarity in the species abundance composition for both local communities can be observed.

Analyzing different scenarios for species abundance dynamics, we noticed that for each scenario the range of possible correlation coefficients between species abundances in both local communities is large, it can be from 0 to 1. Thus, only based on the value of correlation between species abundances in local communities it is impossible to predict the type of species abundance dynamics in these two local communities. Therefore, we can conclude that similarity or dissimilarity of two local communities does not have a sensitive effect on the type of species abundance dynamics in these local communities.

Finally, we would like to note that the correlation between species abundances in two local communities can be closely approximated using the following formula

$$r_{12} \approx \frac{m^l}{m^m + m^l}. \qquad (22)$$

The conclusions made above for the correlation between species abundance in two local communities can be easily verified using this approximation.

## 4.6 Conclusions and discussion

In this chapter a model for species abundance dynamics in two local communities of equal size was formulated. The proposed model describes species dynamics in similar patches or islands connected to a large source of organisms – a metacommunity. The model for species abundance dynamics in two local communities of equal size is developed in line with the framework of Hubbell's neutral theory for species dynamics in zero-sum local community. The species in the proposed model are considered to be neutral, that is, individuals of different species are assumed to have the same birth-death-immigration characteristics and do not have trophic hierarchy.

To analyze the model for species abundance dynamics a continuous probabilistic approach was applied. Specifically, Kolmogorov-Fokker-Planck forward equation for the distribution of species abundance in two local communities was derived and analyzed. A similar continuous approach to species abundance dynamics was used for analysis of species abundance dynamics in one zero-sum local community (Babak, 2006). However, the continuous model for two local communities presented in this chapter is much more complicated due to increased dimensionality of the problem. Thus, it requires more thorough analysis.

A comprehensive analysis of species abundance distributions for two local communities at the equilibrium state, a state at which the species abundance dynamics is assumed to be stable in local communities, is provided in Section 4 of the chapter. For investigation of the equilibrium species abundance distribution, properties of boundary conditions were considered first. As a result of analysis of species abundances distributions at boundary levels, we obtained classification of species abundance dynamics in two local communities with respect to different species characteristics such as immigration intensity, species representation in the metacommunity and, of course, the size of local communities. Based on different ecological features such as species persistence, extinction and monodominance in one or both local communities, several different scenarios for species abundance dynamics were distinguished. Using information on the type of species abundance dynamics scenario in local communities, one can easily predict the development of species abundance in these local communities and take conservation actions to prevent species extinction if needed.

The sensitivity analysis of the model for species abundance dynamics in two local communities of equal size is confirmed by a case study of different species abundance scenarios in two equal local communities and local communities with different death rates.

Also in this chapter, the similarities of the species abundance dynamics in two local communities were investigated using the correlation coefficient between species abundances in both local communities. It was found that for a fixed probability of immigration from the metacommunity, the correlation increases with an increase in the immigration between local communities, and, vice versa, for a fixed probability of immigration between local communities, the correlation decreases with an increase in the immigration from the metacommunity. Moreover, from equation (22), we can infer that the correlation between species abundance dynamics in local communities is approximately constant for proportional values of the immigration probabilities $m^l / m^m = C$ and the correlation coefficient increases with respect to the coefficient of proportion $C$. Thus, higher similarity of the species abundance dynamics in two local communities is observed for larger values of the proportion between immigration probabilities $m^l / m^m$. However, the type (scenario) of the species abundance dynamics in local communities cannot be defined on the basis of similarity or dissimilarity between species abundance in two local communities, since the ranges of the correlation coefficient between species abundances in two local communities are large and overlap for different scenarios of species abundance dynamics.

We believe that the model for species abundance dynamics in two local communities proposed in this chapter allows us to understand more deeply the processes in local habitats or islands connected through immigration. The developed model can be considered as a link between spatially implicit and spatially explicit models of species abundance dynamics, since introduction of spatial characteristics requires discretization of ecological communities into two or more small component communities. We also hope that the results presented here will be useful for landscape ecology, particularly for the study of population dynamics in fragmented landscapes.

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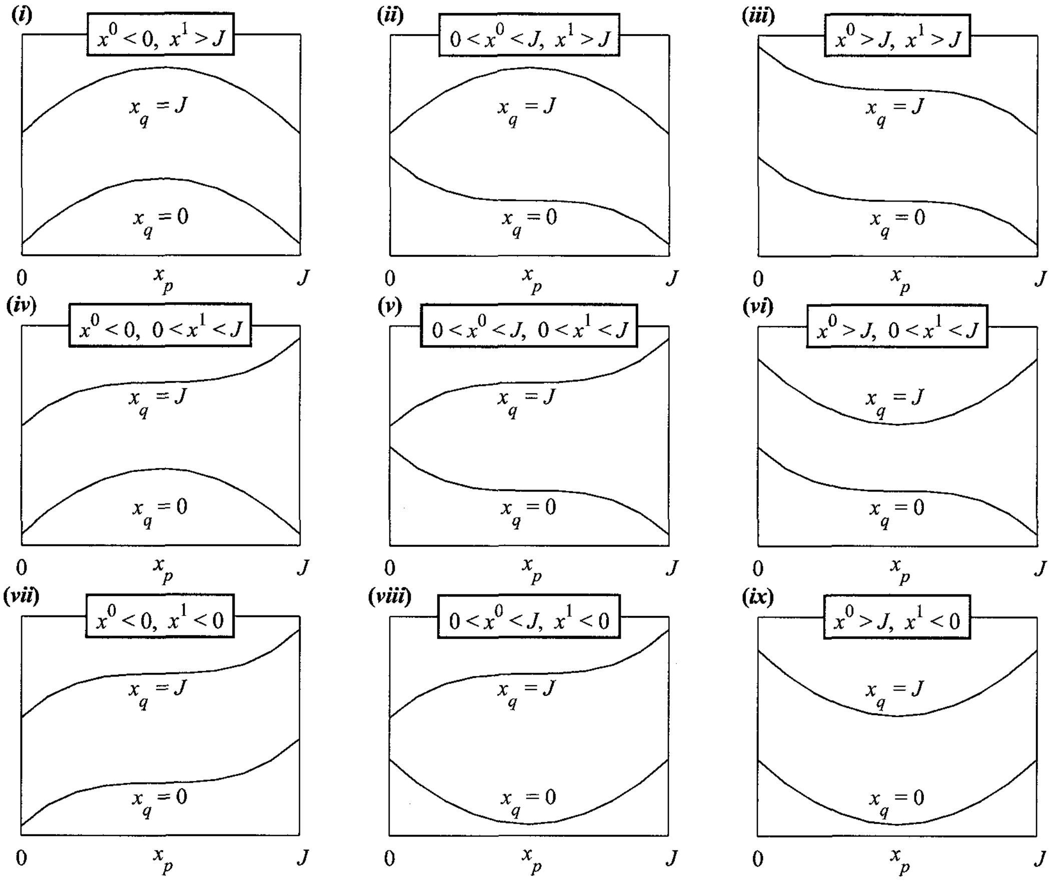

Figure 4.1: The shapes of the probability density of species abundance in the $p$ th local community if the species is absent $x_q = 0$ (lower line) and monodominant $x_q = J$ in the $q$ th local community. These shapes are constructed based on the values $x^0$ and $x^1$ with respect to location on the interval $[0, J)$. Possible combinations for $\omega_i < 1/2$ are in the upper triangle of the figure, i.e., cases (*i*)-(*iii*), (*v*), (*vi*) and (*ix*). Possible combinations for $\omega_i \geq 1/2$ are in the lower triangle of the figure, i.e., cases (*i*), (*iv*), (*v*) and (*vii*)-(*ix*).

Table 4.1: The conditions for parameters of the model required for each combination of values $x^0$ and $x^1$ specified by cases (*i*)-(*ix*). $w^J_\omega(m^m, m^l) = m^m(2\omega(J-1)+1)+m^l$ and $v^J_\omega(m^m, m^l) = m^m(2\omega(J-1)+1)+m^l(2J-1)$.

| Combination | Description | Conditions |
|---|---|---|
| (*i*) | $x^0 \le 0$<br>$J < x^1$ | $2J/(J+1) \le w^J_{\omega_i}(m^m, m^l)$<br>$2J/(J+1) < w^J_{1-\omega_i}(m^m, m^l)$ |
| (*ii*) | $0 < x^0 \le J$<br>$J < x^1$ | $w^J_{\omega_i}(m^m, m^l) < 2J/(J+1) \le v^J_{\omega_i}(m^m, m^l)$<br>$2J/(J+1) < w^J_{1-\omega_i}(m^m, m^l)$ |
| (*iii*) | $J < x^0$<br>$J < x^1$ | $v^J_{\omega_i}(m^m, m^l) < 2J/(J+1)$<br>$2J_p/(J_p+1) < w^{J_p}_{1-\omega_i}(m^m_p, m^l_p)$ |
| (*iv*) | $x^0 \le 0$<br>$0 < x^1 \le J$ | $2J/(J+1) \le w^J_{\omega_i}(m^m, m^l)$<br>$w^J_{1-\omega_i}(m^m, m^l) \le 2J/(J+1) < v^J_{1-\omega_i}(m^m, m^l)$ |
| (*v*) | $0 < x^0 \le J$<br>$0 < x^1 \le J$ | $w^J_{\omega_i}(m^m, m^l) < 2J/(J+1) \le v^J_{\omega_i}(m^m, m^l)$<br>$w^J_{1-\omega_i}(m^m, m^l) \le 2J/(J+1) < v^J_{1-\omega_i}(m^m, m^l)$ |
| (*vi*) | $J < x^0$<br>$0 < x^1 \le J$ | $v^J_{\omega_i}(m^m, m^l) < 2J/(J+1)$<br>$w^J_{1-\omega_i}(m^m, m^l) \le 2J/(J+1) < v^J_{1-\omega_i}(m^m, m^l)$ |
| (*vii*) | $x^0 \le 0$<br>$x^1 \le 0$ | $2J/(J+1) \le w^J_{\omega_i}(m^m, m^l)$<br>$v^J_{1-\omega_i}(m^m, m^l) \le 2J/(J+1)$ |
| (*viii*) | $0 < x^0 \le J$<br>$x^1 \le 0$ | $w^J_{\omega_i}(m^m, m^l) < 2J/(J+1) \le v^J_{\omega_i}(m^m, m^l)$<br>$v^J_{1-\omega_i}(m^m, m^l) \le 2J/(J+1)$ |
| (*ix*) | $J < x^0$<br>$x^1 \le 0$ | $v^J_{\omega_i}(m^m, m^l) < 2J/(J+1)$<br>$v^J_{1-\omega_i}(m^m, m^l) \le 2J/(J+1)$ |

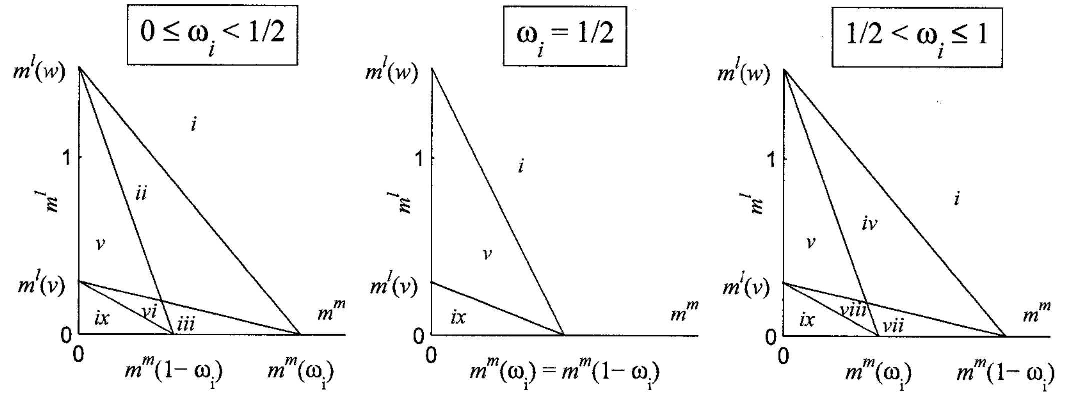

Figure 4.2: Illustration of different cases for species abundance distribution at the boundaries $x_q = 0$ and $x_q = J$ with respect to the values of immigration probabilities $m^m$ and $m^l$, $q = 3 - p$, $p = 1,2$. Three intervals for the metacommunity relative abundance of species $i$ are presented: $0 \le \omega_i < 1/2$, $\omega_i = 1/2$ and $1/2 < \omega_i \le 1$.

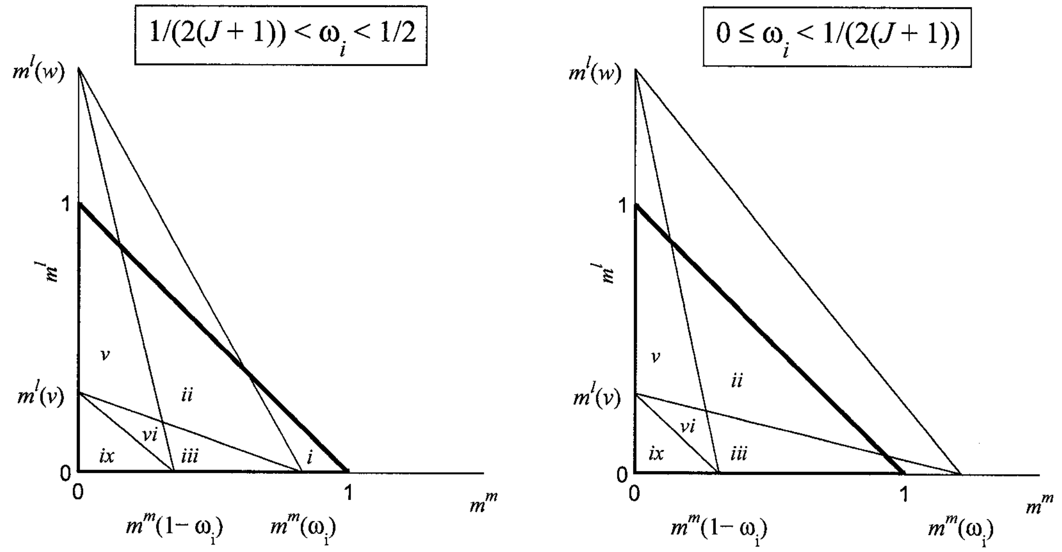

Figure 4.3: Illustration of different cases for species abundance distribution at the boundaries $x_q = 0$ and $x_q = J$ with respect to the values of immigration probabilities $m^m$ and $m^l$, $q = 3 - p$, $p = 1,2$, subject to the conditions $m^m + m^l \le 0$, and $m^m \ge 0$, $m^l \ge 0$. There are 6 possible scenarios if $1/(2(J+1)) < \omega_i < 1/2$, and only 5 possible combinations if $0 \le \omega_i < 1/(2(J+1))$.

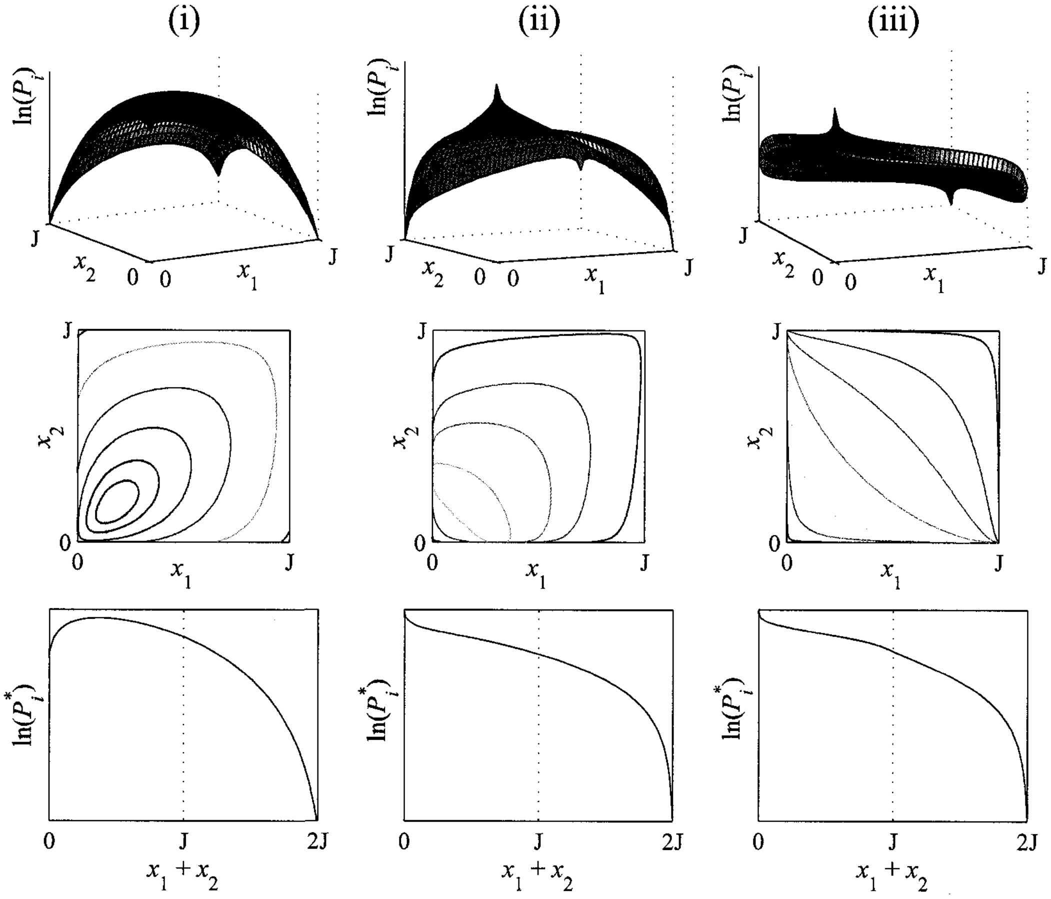

Figure 4.4: Illustration of possible scenarios for species abundance probability density in two equal local communities of size $J = 200$, and $\mu_1 = \mu_2$ with respect to different values of the immigration probabilities. The species metacommunity relative abundance is $\omega_i = 0.2 < 1/2$. Figures in the top row show the landscape log-plots and figures in the middle row show the contour plots for the equilibrium species abundance probability densities obtained using numerical approximations for problem (11)-(13). Figures in the bottom row show the additive equilibrium species abundance probability functions calculated using Equation (15).

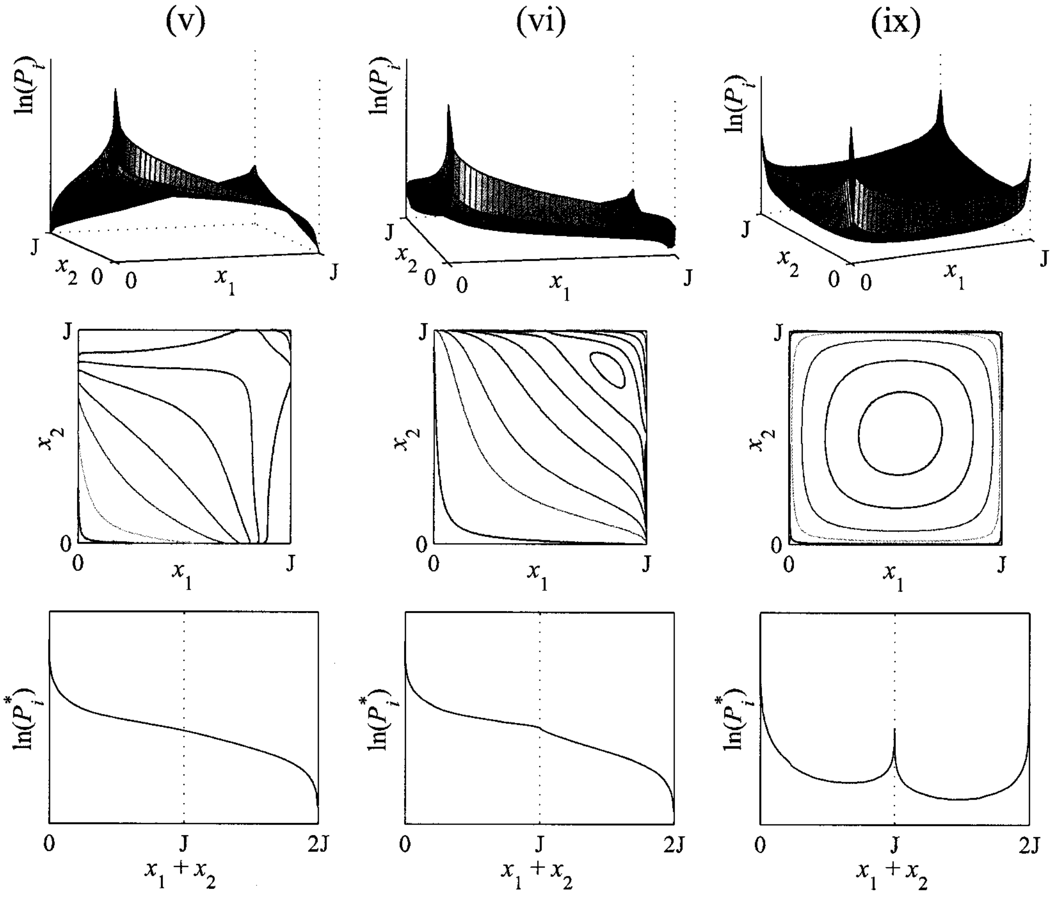

Figure 4.4: Cont. The values of the immigration probabilities are chosen to be the following: (*i*) $m^m = 0.1$, $m^l = 0.1$; (*ii*) $m^m = 0.01$, $m^l = 0.01$; (*iii*) $m^m = 0.01$, $m^l = 0.001$; (*v*) $m^m = 0.005$, $m^l = 0.005$; (*vi*) $m^m = 0.005$, $m^l = 0.002$; (*ix*) $m^m = 0.001$, $m^l = 0.001$.

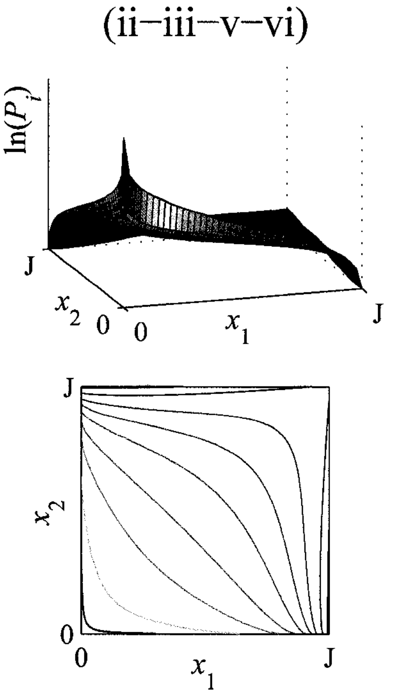

Figure 4.5: Illustration of the intermediate scenario (*ii-iii-v-vi*) for species abundance probability density in two local communities of size $J = 200$, $\omega_i = 0.2 < 1/2$ and $\mu_1 = \mu_2$. Upper figure shows the landscape log-plots and lower figure shows the contour plots for the equilibrium species abundance probability densities obtained using numerical approximations for problem (11)-(13). The values of the immigration probabilities are chosen to be: $m^m = \dfrac{1}{(1-\omega_i)(J+1)}$, $m^l = \dfrac{1-2\omega_i}{(1-\omega_i)(J+1)}$.

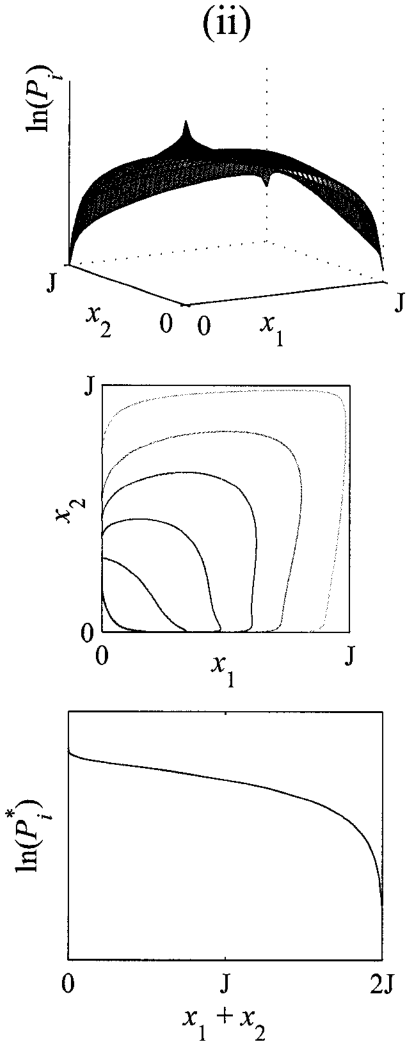

Figure 4.6: Illustration of the effect of different values of the parameters $\mu_1$ and $\mu_2$ ($\mu_1 / \mu_2 = 10$) on the species abundance probability density in two local communities of size $J = 200$ and immigration probabilities $m^m = 0.01$, $m^l = 0.01$. The species metacommunity relative abundance is $\omega_i = 0.2 < 1/2$. Upper figure shows the landscape log-plots and middle figure shows the contour plots for the equilibrium species abundance probability densities obtained using numerical approximations for problem (11)-(13). Lower figure shows the additive equilibrium species abundance probability functions calculated using Equation (15). The species abundance dynamics follows Scenario (*ii*) in both local communities, but the species abundance distribution is not symmetric as in the case when $\mu_1 = \mu_2$.

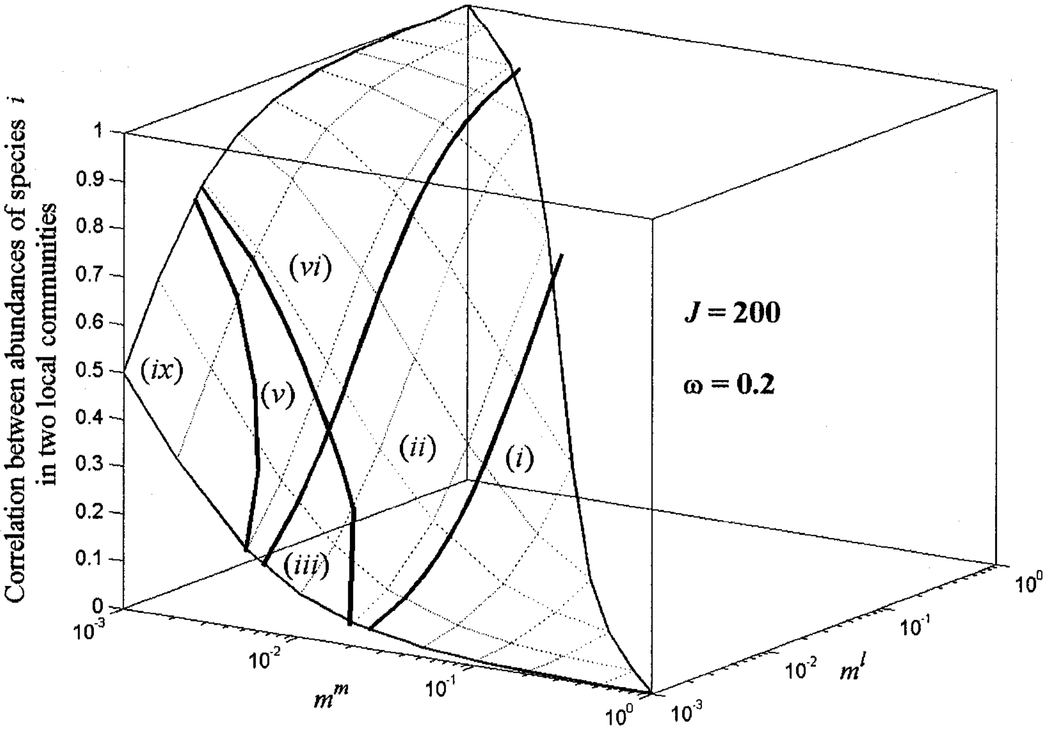

Figure 4.7: Correlation between abundance of species $i$ in two local communities as a function of probability of immigration from the metacommunity $m^m$ and from another local community $m^l$, $m^m + m^l \leq 1$. The size of local community $J = 200$, and the metacommunity species relative abundance $\omega_i = 0.2$. The surface is divided into the areas of the immigration probabilities from different types of species abundance dynamics represented by scenarios (i), (ii), (iii), (v), (vi) and (ix).

# Chapter 5

# Species extinction time and probability in two connected equal local communities

## 5.1 Introduction

A question that has important implications for the conservation of biodiversity in ecological communities is how the species extinction time and probability depend on such ecological processes as immigration (Lande et al. 2003, Alonso and McKane 2002, Gaggiotti 2003), reproduction (Ludwig 1996b, Hakoyama and Iwasa 2000, Moller 2003, Lande et.al. 2003, Engen et al. 2005), the size and spatial structure of ecological community (Keymer et al. 2000, Jablonski 2000, Alonso and McKane 2002, Engen et al. 2002, Ovaskainen and Hanski 2003).

To analyze the extinction time and probability various approaches were applied including statistical estimation (Solow 2005), maximum likelihood methods (Hakoyama and Iwasa 2000), Bayesian analysis (Solow 1993, Ludwig 1996b), Fourier series analysis (Sole et al. 1997, Newman and Eble 1999), time series analysis (Ludwig 1999, Hakoyama and Iwasa 2000), diffusion approximations (Lande et al. 2003, Ludwig 1996a, Grasman 1996, Nasell 1999, Engen et al. 2005), and simulation study (Mangel and Ludwig 1977, Grimm and Wissel 2004). Using these methods both spatially implicit and spatially explicit population models were investigated (Lande et al. 2003, Alonso and McKane 2002, Ovaskainen and Hanski 2003).

The extinction time and probability were studied for various population models. For example, probability of extinction in a stochastic competition was studied by Mangel and Ludwig (1977), the effect of demographic and environmental stochasticity and random catastrophes on extinction processes were investigated by Lande et al. (2003), Hakoyama and Iwasa (2000), Engen et al. (2005), effect of migration processes on the extinction dynamics was considered by Alonso and McKane (2002), Gaggiotti (2003), models with density dependence were studied by Lande et al. (2003), Hakoyama and Iwasa (2000), Bascompte (2003).

Relatively smaller attention was attracted to the study of extinction dynamics and estimation of extinction time and probability for neutral macroecological models.

Leigh (1981) determined that the average time to extinction under neutrality when a population size is bounded. Rosenzweig (1995) proposed a neutral model for the evolution of continental diversity and showed that increased diversity per se will cause increased extinction rates per species. Ricklefs (2003, 2006) suggested that drift is too slow to account for the turnover of species within a regional flora and other forces must act. Nee (2005) discussed the time scale for extinction of common species in a neutral community. Hubbell (2001) introduced the probability that a species will suffer the death of given number of individuals, showed that the time to fixation (local extinction or complete dominance) is inversely proportional to the death rate in the isolated local communities, established that the times to fixation and local extinction are approximately Gamma distributed, and calculated the average number of death in community until extinction of the given species using discrete Markov chain approach.

In this chapter the relationships between the extinction processes, and immigration and demographic processes are investigated for structured neutral local communities, using a neutral model for the species abundance dynamics in two equal local communities connected with each other and with the metacommunity through immigration. The investigation of species abundance dynamics for this model was performed in Chapter 4 based on the sensitivity analysis of the equilibrium species abundance distributions in two local communities with respect to immigration and demographic factors. Similar model for species abundance dynamics in two local communities was studied by Hubbell (2001) using discrete Markov Chain approach, and, therefore, was restricted only to small local communities. In Chapter 4 I used a continuous probabilistic approach to investigate the species abundance dynamics in two local communities, and proposed a realistic classification of species abundance behavior in local communities subject to different chances of species extinction, monodominance and persistence.

This chapter is addressed to the study of extinction time and probability of a species in two equal neutral local communities connected with each other and with the metacommunity by means of a continuous probabilistic approach. Using Kolmogorov-Fokker-Planck backward equation, I derive models for the species persistence probability in two local communities, and the average first time to species extinction. I consider two scenarios for species extinction: species extinction from one given local community, and species extinction from either the first or second local community. In addition, I calculate the probability of species extinction from one local community before the other local community for different species abundances in two local communities. Using this probability I can answer the question from each local community the species would most likely go extinct first. Finally, I make a comparison analysis of species extinction dynamics in two local communities and in one local community. This analysis gives us an example of comparison between species abundance dynamics in spatially structured ecological communities (ecological communities involving interaction between many different neighboring habitat patches) and unstructured ecological communities (ecological communities with no spatial factors).

This chapter is organized as follows. In Section 5.2, I review the formulation of the model for species abundance dynamics in two equal local communities connected with each other and to the metacommunity (see Chapter 4). In Section 5.3, the model for distribution of the first time to species extinction is derived using Kolmogorov-Fokker-Planck backward equation. Based on this model, the average first time to species extinction and higher moments of the first time to species extinction are calculated for two scenarios. In the first problem the extinction of the species is considered from one given local community (say from the first local community), and in the second problem the extinction of the species is considered from at least one local community (from either the first or second local community). In Section 5.4, the model for probability of species extinction from one local community before the species extinction from the other local community is developed. In Section 5.5, the sensitivity analysis for the average extinction time and the probability of extinction from one local community before the other local community is provided with respect to such ecological characteristics as immigration probability between local communities and immigration probability from the metacommunity. Finally, in Section 5.6, the comparison study is performed for the species extinction time from the local community connected only to the metacommunity, and for the species extinction time from the local community connected to both the other local community and the metacommunity.

## 5.2 Discrete model for species abundance dynamics in two local communities

The model for species abundance dynamics in two zero-sum local communities of the same size connected through immigration with each other and with the metacommunity is derived in Chapter 4. Denote the size of local communities by $J$, the number of individuals of species $i$ in the first and second local communities by $N_{1,i}$ and $N_{2,i}$, respectively. Then the change in the number of individuals of species $i$ per unit time step in $p^{\text{th}}$ local community, $p=1,2$, can be defined using the following transition probabilities

$$W_{p,i}(N_p-1\,|\,N_p,N_q)=\frac{N_p}{J}\left((1-m^m-m^l)\frac{J-N_p}{J-1}+m^m(1-\omega_i)+m^l\frac{J-N_q}{J}\right),$$

$$W_{p,i}(N_p+1\,|\,N_p,N_q)=\frac{J-N_p}{J}\left((1-m^m-m^l)\frac{N_p}{J-1}+m^m\omega_i+m^l\frac{N_q}{J}\right), \tag{1}$$

$$W_{p,i}(N_p\,|\,N_p,N_q)=1-W_{p,i}(N_p-1\,|\,N_p,N_q)-W_{p,i}(N_p+1\,|\,N_p,N_q),$$

where $q=\begin{cases}1: & p=2,\\ 2: & p=1;\end{cases}$ $N_r=N_{r,i}$, $r=1,2$; $\omega_i$ is the relative abundance of species $i$ in the metacommunity, $m^m$ is the probability that a death in a local community will be replaced by an immigrant from the metacommunity and $m^l$ is the probability that a death in a local community will be replaced by an immigrant from the other local community, $m = m^m + m^l$.

Further, we assume that species abundance dynamics in one local community is independent of species abundance dynamics in another local community. Then, the transition probabilities for the dynamics of species $i$ in both local communities can be defined as

$$W_i(N_1+\Delta_1, N_2+\Delta_2 \mid N_1, N_2) = W_{1,i}(N_1+\Delta_1 \mid N_1, N_2) \times W_{2,i}(N_2+\Delta_2 \mid N_2, N_1) \qquad (2)$$

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

To apply a continuous probabilistic technique to the analysis of the model for the species abundance dynamics in two local communities, we define the transition probabilities for the change $\Delta N_{p,i}$ in the number of individuals $N_{p,i}$ of the $i$th species in local community $p$, $p = 1,2$ per time step $\Delta t$ as

$$\begin{aligned} \Pr(\Delta N_{p,i} = \pm 1 \mid N_{p,i} = N_p, N_{q,i} = N_q) &= \mu_p \Delta t W_{p,i}(N_p \pm 1 \mid N_p, N_q), \\ \Pr(\Delta N_{p,i} = 0 \mid N_{p,i} = N_p, N_{q,i} = N_q) &= 1 - \Pr(\Delta N_{p,i} = 1 \mid N_{p,i} = N_p, N_{q,i} = N_q) \\ &\quad - \Pr(\Delta N_{p,i} = -1 \mid N_{p,i} = N_p, N_{q,i} = N_q), \end{aligned} \qquad (3)$$

where $\mu_p$ is the number of death events per unit time interval in local community $p$.

Then the joint transition probabilities for the change in the species abundance in both local communities are given by

$$\begin{aligned} &\Pr(\Delta N_{1,i} = \Delta_1, \Delta N_{2,i} = \Delta_2 \mid N_{1,i} = N_1, N_{2,i} = N_2) \\ &= \Pr(\Delta N_{1,i} = \Delta_1 \mid N_{1,i} = N_1, N_{2,i} = N_2) \times \Pr(\Delta N_{2,i} = \Delta_2 \mid N_{2,i} = N_2, N_{1,i} = N_1) \end{aligned} \qquad (4)$$

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

Let's define the change in the abundance of the $i$th species in both local communities per time step $\Delta t$ as a vector $\Delta N_i = (\Delta N_{1,i}, \Delta N_{2,i})$, where $\Delta N_{p,i} = N_{p,i}(t+\Delta t) - N_{p,i}(t)$, $p = 1,2$; and let $N_i = (N_{1,i}, N_{2,i})$ and $x = (x_1, x_2)$.

Because the species abundance in one local community per one time step $\Delta t$ can change only by one individual or remain the same, the variables $\Delta N_{p,i}$ attain only values -1,0 and 1. And, therefore, the mean and the second moment of the change in the abundance of the $i$th species per infinitely small time interval $\Delta t$ can be calculated as

$$V(x) = \begin{pmatrix} V_1(x) \\ V_2(x) \end{pmatrix} = \lim_{\Delta t \to 0} \frac{1}{\Delta t} \begin{pmatrix} E(\Delta N_{1,i} \mid N_i = x) \\ E(\Delta N_{2,i} \mid N_i = x) \end{pmatrix},$$

$$V_p(x)=\mu_p m^m\left(\omega_i-\frac{x_p}{J}\right)+\mu_p m^l\left(\frac{x_q}{J}-\frac{x_p}{J}\right), \tag{5}$$

$$D(x)=\begin{pmatrix} D_{11}(x) & D_{12}(x) \\ D_{21}(x) & D_{22}(x) \end{pmatrix}=\lim_{\Delta t\to 0}\frac{1}{\Delta t}\begin{pmatrix} E(\Delta N_{1,i}{}^2 \mid N_i=x) & E(\Delta N_{1,i}\Delta N_{2,i} \mid N_i=x) \\ E(\Delta N_{1,i}\Delta N_{2,i} \mid N_i=x) & E(\Delta N_{2,i}{}^2 \mid N_i=x) \end{pmatrix}$$

,

$$D_{pp}(x)=\mu_p\left(2(1-m^m-m^l)\frac{x_p(J-x_p)}{J(J-1)}+m^m(1-\omega_i)\frac{x_p}{J}+m^m\omega_i\frac{J-x_p}{J}+\right.$$

$$\left.+m^l\frac{J-x_q}{J}\frac{x_p}{J}+m^l\frac{x_q}{J}\frac{J-x_p}{J}\right),$$

$$D_{pq}(x)=0, \tag{6}$$

where $p=1,2$ and $q=\begin{cases}1: & p=2,\\ 2: & p=1.\end{cases}$

## 5.3 Distribution of persistence and extinction times

Let us now define the abundances $x_1$ and $x_2$ of species $i$ in the first and second local communities as continuous variables from interval $[0,J]$; and let $p_i(y,s\mid x,t)$ be the probability density that species $i$ has abundance $y=(y_1,y_2)$ in both local communities at time $s$ given abundance $x=(x_1,x_2)$ of species $i$ at time $t$, $t\le s$.

The probability that the abundance of species $i$ at time $t$ remains in the abundance domain $\tilde{\Omega}\subseteq\Omega=(0,J)\times(0,J)$ given the abundance $x=(x_1,x_2)\in\tilde{\Omega}$ of species $i$ at time 0 is:

$$G_i(x,t;\tilde{\Omega})=\iint_{\tilde{\Omega}} p_i(\xi,t\mid x,0)\mathrm{d}\xi . \tag{7}$$

This probability is a solution of the Kolmogorov backward equation (Gardiner, 1983)

$$\frac{\partial G_i}{\partial t}=\frac{1}{2}\left(D_{11}\frac{\partial^2 G_i}{\partial x_1{}^2}+D_{22}\frac{\partial^2 G_i}{\partial x_2{}^2}\right)+V_1\frac{\partial G_i}{\partial x_1}+V_2\frac{\partial G_i}{\partial x_2},\quad x\in\tilde{\Omega},\quad t>0, \tag{8}$$

where $V$ and $D$ are the first and second moments of the change in the abundance of species $i$ per time step $\Delta t$ as $\Delta t\to 0$ defined in (5) and (6).

Since it is assumed that the species abundance belongs to the abundance domain $\tilde{\Omega}$ at the initial time moment, say at time 0 (the probability that the species abundance belongs to the domain $\tilde{\Omega}$ is zero), the following initial condition is imposed

$$G_i(x,0) = 1, \quad x \in \tilde{\Omega}. \tag{9}$$

Depending on the ecological formulation of the problem we set either absorbing or reflecting boundary conditions. In general, let $\tilde{\Gamma}$ be the boundary of the species abundances domain $\tilde{\Omega}$, and let $\tilde{\Gamma} = \tilde{\Gamma}_{abs} \cup \tilde{\Gamma}_{ref}$, where $\tilde{\Gamma}_{abs}$ and $\tilde{\Gamma}_{ref}$ denote absorbing and reflecting parts of the boundary $\tilde{\Gamma}$, and $\varnothing = \tilde{\Gamma}_{abs} \cap \tilde{\Gamma}_{ref}$. Then on the absorbing boundary $\tilde{\Gamma}_{abs}$ of the abundance domain $\tilde{\Omega}$ we assume that

$$G_i = 0, \quad x \in \tilde{\Gamma}_{abs}, \quad t \geq 0, \tag{10}$$

and on the reflecting boundary $\tilde{\Gamma}_{ref}$, the boundary condition is

$$D_{11} \frac{\partial G_i}{\partial x_1} n_1 + D_{22} \frac{\partial G_i}{\partial x_2} n_2 = 0, \quad x \in \tilde{\Gamma}_{ref}, \quad t \geq 0, \tag{11}$$

where the vector $\vec{n} = (n_1, n_2)$ is the outward normal to the boundary of the domain $\tilde{\Omega}$ defined on $\tilde{\Gamma}_{ref}$.

Note that $G_i(x,t)$ defines the probability distribution of time by which species $i$ has not crossed the boundary $\tilde{\Gamma}_{abs}$ given the species abundance in both local communities $x = (x_1, x_2)$ at the initial time $t = 0$. Using this distribution we can easily calculate the probability that species $i$ will cross the boundary $\tilde{\Gamma}_{abs}$ by time $t$ as

$$F_i(x,t) = 1 - G_i(x,t).$$

We will use this probability to define the probability of species extinction, the mean and variance of the first passage time to species extinction etc.

Let us now consider the abundance domain $\Omega = (0,J) \times (0,J)$ in more detail. The boundary $\Gamma$ of this domain can be divided into four distinct regions $\Gamma = \Gamma^{0*} \cup \Gamma^{*1} \cup \Gamma^{1*} \cup \Gamma^{*0}$, such that $\Gamma^{0*} = \{0\} \times (0,J)$, $\Gamma^{*1} = (0,J) \times \{J\}$, $\Gamma^{1*} = \{J\} \times (0,J)$ and $\Gamma^{*0} = (0,J) \times \{0\}$. The outward normal vectors for each region of the boundary $\Gamma$ are: $\vec{n}^{0*} = (n_1^{0*}, n_2^{0*}) = (-1,0)$ for $\Gamma^{0*}$, $\vec{n}^{1*} = (n_1^{1*}, n_2^{1*}) = (1,0)$ for $\Gamma^{1*}$, $\vec{n}^{*0} = (n_1^{*0}, n_2^{*0}) = (0,-1)$ for $\Gamma^{*0}$, and $\vec{n}^{*1} = (n_1^{*1}, n_2^{*1}) = (0,1)$ for $\Gamma^{*1}$.

Two scenarios deserve special consideration here.

(1) *Extinction of species $i$ from either the first or second local community*

Let us denote by $G_i^{1\vee 2}(x,t)$ the probability that species $i$ has not gone extinct by time $t$ from any local community if at the initial time moment $t = 0$ its abundance was $x$. To define the boundary conditions for $G_i^{1\vee 2}$ note that the extinction of species $i$ from at least one local community occurs when its abundance reaches zero level in at least one local community, that is, the abundance of species $i$ reaches the boundary

$\Gamma_{*0} \cup \Gamma_{0*}$ of the abundance domain $\Omega$. In this case $\tilde{\Omega} = \Omega$, $\tilde{\Gamma}_{abs} = \Gamma_{*0} \cup \Gamma_{0*}$ and $\tilde{\Gamma}_{ref} = \Gamma_{*1} \cup \Gamma_{1*}$, and the boundary conditions for the probability $G_i^{1\vee 2}$ are the following

$$G_i^{1\vee 2} = 0, \quad x \in \Gamma_{*0} \cup \Gamma_{0*}, \qquad \frac{\partial G_i^{1\vee 2}}{\partial x_2} = 0, \quad x \in \Gamma_{*1}, \qquad \frac{\partial G_i^{1\vee 2}}{\partial x_1} = 0, \quad x \in \Gamma_{1*}, \quad t \geq 0. \tag{12}$$

(2) *Extinction of species i from one local community*

Let us consider extinction of species $i$ from only one local community. By $G_i^p(x,t)$ we denote the probability that species $i$ has not gone extinct by time $t$ from the $p^{\text{th}}$ local community, $p = 1,2$, if at the initial time moment $t = 0$ its abundance was $x$. Note that the extinction of the $i^{\text{th}}$ species from a local community occurs when its abundance reaches zero in this community, that is, the abundance of species $i$ reaches the boundary $\Gamma_{0*}$. Thus, $\tilde{\Omega} = \Omega$, $\tilde{\Gamma}_{abs} = \Gamma_{0*}$ and $\tilde{\Gamma}_{ref} = \Gamma_{1*} \cup \Gamma_{*0} \cup \Gamma_{*1}$. Then the boundary conditions for $G_i^1$ are the following

$$G_i^1 = 0, \quad x \in \Gamma_{0*}, \qquad \frac{\partial G_i^1}{\partial x_2} = 0, \quad x \in \Gamma_{*0} \cup \Gamma_{*1}, \qquad \frac{\partial G_i^1}{\partial x_1} = 0, \quad x \in \Gamma_{1*}; \quad t \geq 0. \tag{13}$$

Similarly we can define the boundary conditions for the problem of extinction of species $i$ from the second local community. In that case $\tilde{\Omega} = \Omega$, $\tilde{\Gamma}_{abs} = \Gamma_{*0}$, $\tilde{\Gamma}_{ref} = \Gamma_{1*} \cup \Gamma_{0*} \cup \Gamma_{*1}$ and

$$G_i^2 = 0, \quad x \in \Gamma_{*0}, \qquad \frac{\partial G_i^2}{\partial x_2} = 0, \quad x \in \Gamma_{*1}, \qquad \frac{\partial G_i^2}{\partial x_1} = 0, \quad x \in \Gamma_{0*} \cup \Gamma_{1*}; \quad t \geq 0. \tag{14}$$

Based on the probability that the abundance of species $i$ at time $t$ remains in the abundance domain $\tilde{\Omega}$ given the abundance $x = (x_1, x_2) \in \tilde{\Omega}$ of species $i$ at time 0, we can easily calculate the mean and higher moments of the first passage time to the boundary $\tilde{\Gamma}_{abs}$ of the abundance domain $\tilde{\Omega}$. The mean $T_i^1$ of the first passage time to the boundary $\tilde{\Gamma}_{abs}$ is calculated from the equation

$$\frac{1}{2}\left( D_{11} \frac{\partial^2 T_i^1}{\partial x_1^{\,2}} + D_{22} \frac{\partial^2 T_i^1}{\partial x_2^{\,2}} \right) + V_1 \frac{\partial T_i^1}{\partial x_1} + V_2 \frac{\partial T_i^1}{\partial x_2} = -1, \quad x \in \tilde{\Omega}, \tag{15}$$

and the $k^{\text{th}}$ moment $T_i^k$ of the first passage time is calculated from the equation

$$\frac{1}{2}\left( D_{11} \frac{\partial^2 T_i^k}{\partial x_1^{\,2}} + D_{22} \frac{\partial^2 T_i^k}{\partial x_2^{\,2}} \right) + V_1 \frac{\partial T_i^k}{\partial x_1} + V_2 \frac{\partial T_i^k}{\partial x_2} = -T_i^{k-1}, \quad x \in \tilde{\Omega}. \tag{16}$$

These equations are supplemented with the absorbing boundary condition (10) on $\tilde{\Gamma}_{abs}$ and reflecting boundary conditions (11) on $\tilde{\Gamma}_{ref}$. For each example given in

Section 5.3 the boundary conditions (10) and (11) can be detailed in the same form, see Equations (12)-(14).

## 5.4 Probability of species extinction from one local community before the other local community

Another important problem in conservation biology is in which community a species will go locally extinct first, and how the species abundance in the local communities affects the probability of species extinction from each local community. To address this problem we denote by $Q_i^k$ the probability of extinction of species $i$ from the $p^{\text{th}}$ local community before its extinction from the $q^{\text{th}}$ local community, where $p = 1,2$ and $q = \begin{cases} 1: & p = 2, \\ 2: & p = 1. \end{cases}$ Then the probability that species $i$ goes extinct from the first local community before the second local community can be calculated from the following equation

$$\frac{1}{2}\left( D_{11}\frac{\partial^2 Q_i^1}{\partial x_1{}^2} + D_{22}\frac{\partial^2 Q_i^1}{\partial x_2{}^2} \right) + V_1\frac{\partial Q_i^1}{\partial x_1} + V_2\frac{\partial Q_i^1}{\partial x_2} = 0, \quad x \in \Omega, \tag{17}$$

Since the abundance level $x_1 = 0$ is attained when the species is extinct from the first local community, the probability of extinction at this abundance level is 1, and, therefore, the boundary condition at $\Gamma_{0*}$ is the following

$$Q_i^1 = 1, \quad x \in \Gamma_{0*}. \tag{18}$$

On the other hand, the abundance level $x_2 = 0$ is attained when the species is extinct from the second local community, and the probability of extinction at this abundance level is 0

$$Q_i^1 = 0, \quad x \in \Gamma_{*0}. \tag{19}$$

At the boundary $\Gamma_{1*} \cup \Gamma_{*1}$ we impose the reflecting boundary conditions in the form

$$\frac{\partial Q_i^1}{\partial x_2} = 0, \quad x \in \Gamma_{*1}, \qquad \frac{\partial Q_i^1}{\partial x_1} = 0, \quad x \in \Gamma_{1*}. \tag{20}$$

Note that for $Q_i^2$ only the boundary conditions (18) and (19) are reversed.

Similarly to the problem of the probability of extinction event in one local community before the extinction event in the other local community, we can consider the problem about the probability of extinction in one local community versus the probability of monodominance in the same or in the other local community. For these problems we need only to modify boundary conditions (18)-(20).

## 5.5 Sensitivity analysis

In this section the average first time to species extinction in the local communities is studied subject to different immigration probabilities from the metacommunity $m^m$ and the immigration probabilities between local communities $m^l$. The study of the first time to extinction is also supplemented with the analysis of the probability of species extinction in one local community before its extinction from the other local community.

To perform the sensitivity analysis for the time to species extinction from the local community let us first recall the classification of species abundance dynamics in two local communities. According to this classification we distinguished six different scenarios of the species abundance dynamics in two local communities when the species abundance in the metacommunity is relatively small, that is $\omega_i < 0.5$ (see Chapter 4):

Scenario (i). The species is highly persistent in the local communities, that is, its chance of extinction or monodominance in each or in both local communities is very small;

Scenario (ii). The species has very high chance of extinction and very small chance of monodominance in one local community when it is absent from the other local community. However, when the species is monodominant in one local community its chance of extinction and monodominance in the other local community is very small;

Scenario (iii). The species has very high chance of extinction and very small chance of monodominance in one local community regardless of the species abundance in the other local community;

Scenario (v). The species has very high chance of extinction and very small chance of monodominance in one local community when it is absent from the other local community, and the species has very small chance of extinction and very high chance of monodominance in each local community when it is monodominant in the other local community;

Scenario (vi). The species has very high chance of extinction and very small chance of monodominance in one local community when it is absent from the other local community, and the species has very high chance of extinction and monodominance in one local community when it is monodominant in the other local community;

Scenario (ix). The species is, most of the time, extinct or monodominant in each local community, that is, it has very high chance of extinction and monodominance in local communities.

The sensitivity analysis for the mean first extinction time of species from local communities is performed in accordance to the above species abundance dynamics classification. Figure 5.1 illustrates for each species abundance scenario the first extinction time of species from the first local community, the probability of species extinction from the first local community before its extinction from the second local community, and also the mean first extinction time of species from either local community.

For Scenario (i) of the species abundance dynamics, the mean first time to species extinction from the first local community is very large, and this time is almost independent of the initial species abundance in the local communities; moreover, the mean first time to species extinction from the first or second local community is also large and independent of the initial species abundances in two local communities. This shows that for Scenario (i) the species is highly persistent in the two local communities regardless of its abundance in both of them. The plot for the probability of species extinction from the first local community before its extinction from the second local community shows that the extinction of the species is equally probable from the first and the second local community regardless of the species initial abundance.

Since for Scenario (ii) the species is still highly persistent in the first local community if it is monodominant in the second local community, the average first time to extinction of the species from the first local community in this case is very high and this time is almost independent of the species initial abundance in the first local community. However, if the species has low abundance in the second local community the average first time to extinction from the first local community increases significantly with respect to the species abundance in it. Figure 5.1 (ii) shows that the probability of the species extinction from the first local community before its extinction from the second local community is almost 1/2 if the species is highly abundant or monodominant in the second local community, and this probability decreases significantly if the species is almost extinct from the second local community. The above analysis demonstrates that for Scenario (ii) the role of the immigration between local communities is very high; therefore, the species abundance level in one local community has large effect on the species abundance dynamics, the species extinction time and probability in the other local community.

For Scenario (iii) the mean first time to extinction of the species from the first local community is almost independent of the species abundance in the second local community, and the species has significantly higher chance to extinction from the local community in which its abundance is smaller, see Figure 5.1(iii). Therefore, the prevalent role on the species abundance dynamics and extinction in this scenario plays the immigration from the metacommunity.

For Scenarios (v), (vi) and (ix) the mean first time to species extinction from the first local community is significantly larger if the species has higher abundance in the second local community. This characteristic shows that the effect of immigration between local communities plays an important role on the species abundance dynamics and species extinction. Also, it is worth noting from Figures 5.1 (v, vi, ix) that for Scenario (ix) the mean first time to extinction from the first local community increases almost linearly with respect to the species initial abundance in it, however, for Scenarios (v) and (vi) this relationship is nonlinear. In Scenario (ix) the mean first time to extinction from the first or second local community increases also almost linearly with respect to the species initial abundance in the local communities.

## 5.6 Comparison of extinction time in local community connected only to metacommunity and connected to both metacommunity and other local community

In this section the effect of the immigration intensity between local communities $m^l$ on the mean first time to species extinction from one local community is investigated. The mean first time to species extinction from one local community connected to the metacommunity and the other local community is compared to the mean first time to species extinction from one local community connected only to the metacommunity. Note that the species extinction time in the model for one local community connected only to the metacommunity was examined using the continuous probabilistic approach in (Babak 2006).

Figures 5.2 (a,b,c) demonstrate the plots of the mean first time to species extinction from the local community for three different values of the immigration probability from the metacommunity $m^m$. In the case of two connected local communities these figures illustrate the mean first time to species extinction from the first local community calculated for different initial species abundances in the first local community as an averaged value for all possible initial species abundances in the second local community. Figures 5.2 (a,b,c) clearly show that the mean first time to species extinction from one local community connected with the other local community and with the metacommunity converges to the mean first time to species extinction from one local community connected only to the metacommunity as the immigration probability between local communities $m^l$ tends to zero. Moreover, the mean first time to species extinction from the local community connected to both the metacommunity and the other local community is almost always larger than the mean first time to species extinction from the local community connected only to the metacommunity.

Figure 5.2 (a) shows the average first time to species extinction from one local community for high immigration probability from the metacommunity, $m^m = 0.1$. In this case the species abundance dynamics is typical for Scenario (i) for all values of $m^l$. Therefore, the behavior of the average first time to species extinction with respect to the initial species abundance in the local community is similar for different $m^l$. Specifically, the average extinction time is almost independent on the initial species abundance in the local community. This behavior of the average first time to extinction is typical for highly persistent species in the local community, since the extinction time and probability of extinction for such species are almost independent of the species initial abundance.

Figure 5.2 (b) shows the average first time to extinction from one local community for intermediate immigration probability from the metacommunity, $m^m = 0.01$. We know that for such value of the immigration probability $m^m$, the immigration probability between local communities $m^l$ can significantly change the species abundance dynamics scenario in the local community (see Chapter 4) as well as the structure of the average first time to species extinction (see Figure 5.2 (b)). Let us examine the effect of $m^l$ on the extinction time and probability in detail.

For the values of the immigration probability $m^l$ larger than 0.003 the species abundance dynamics is typical for Scenario (ii). For this scenario the species has very high chance of extinction and very small chance of monodominance in the local community when it is absent from the other local community, and very small chance of extinction or monodominance in the local community when the species is monodominant in the other local community. In this case the average first time to extinction increases almost linearly with respect to the non-zero initial species abundance in the local community.

For the values of the immigration probability $m^l$ smaller than 0.003 the species abundance dynamics is typical for Scenario (iii). For this scenario the species has very high chance of extinction and very small chance of monodominance in the local community regardless of the species abundance in the other local community. In this case the average first time to species extinction increases nonlinearly with respect to the species initial abundance in the local community, thus the initial species abundance plays a very important role on the species persistence in the local community.

Finally, Figure 5.2 (c) shows the effect of the immigration probability between local communities $m^l$ on the average first time to species extinction for very small immigration probability from the metacommunity, $m^m = 0.004$. As in the previous example (Figure 5.2(b)) the species abundance dynamics scenario varies with respect to the value of the immigration probability between local communities $m^l$. For very large immigration probabilities $m^l$ ($m^l > 0.71$), the species abundance dynamics is typical for Scenario (ii). In this case the average extinction time from the local community is large and increases almost linearly with respect to the species initial abundance, therefore the species is highly persistent in the local community.

For very small immigration probabilities $m^l$ ($m^l < 0.002$), the species abundance dynamics is representative for Scenario (ix) with very high chances of species extinction or monodominance in the local communities. Therefore, due to high possibility of either species extinction or monodominance, the average first time to species extinction from the local community increases almost linearly with respect to the initial species abundance. It is worth noting that only in the case of Scenario (ix) the average first time to species extinction decreases with respect to the immigration probability $m^l$. This counter-intuitive behavior of the species extinction time can be explained by the fact that for Scenario (ix) the chance of species monodominance in one local community is larger for smaller immigration probability between local communities $m^l$. Since for the monodominant species in the local community the time to extinction is larger than for non-monodominant species, the increase in the probability of species monodominance increases the time that the species abundance remains close to the monodominance level, and therefore, increases the time to species extinction from the local community.

We now consider the average first time to species extinction for intermediate values of the immigration probability $m^l$, $0.002 < m^l < 0.71$. In this case the species abundance dynamics is typical for Scenario (v) if $0.004 < m^l < 0.71$, and for Scenario (vi) if $0.002 < m^l < 0.004$.

For these scenarios the species has very high chance of extinction and very small chance of monodominance in the local community if the species abundance is low in the other local community, and the chance of species monodominance in the local community is high when the species is monodominant in the other local community. The structure of the average extinction time is not stable for these intermediate scenarios. For smaller values of $m^l$ from the considered interval the average first time to extinction increases gradually with respect to the initial species abundance in the local community, whereas for larger values of $m^l$ the average first time to extinction increases sharply for small initial species abundances, and is almost linear for larger initial species abundances.

## 5.7 Conclusions and discussion

In this chapter the extinction time and probability were investigated for a species in two equal local communities connected with each other and with the metacommunity through immigration. Using Kolmogorov-Fokker-Planck backward equation the models for:

- the persistence probability of a species in two local communities,
- the average first time to extinction of a species from one local community,
- the average first time to extinction of a species from the first or second local community, and
- the probability that a species will go extinct from one local community before its extinction from the other local community

were derived and analyzed. Similar continuous probabilistic approach to the above problems was used for analysis of species abundance dynamics in one zero-sum local community (Babak, 2006). However, the continuous model for two local communities presented in this paper is much more complicated due to increased dimensionality of the problem.

The sensitivity analysis of the average first time to species extinction from the first local community, the probability of species extinction from the first local community before the second local community, and the average first time to species extinction from at least one local community is provided in Section 5.5. This analysis is performed subject to the type of species abundance dynamics in two equal local communities developed in Chapter 4. It was distinguished that for different species abundance dynamics scenario in two equal local communities, the structure of the average first time to species extinction varies significantly. Specifically, if the local communities connected closely to the metacommunity (high immigration probability $m^m$, Scenario (i)), then the first time to species extinction is almost independent of the initial species abundance in the local communities, and the species has the same chance of extinction from the first and second local communities regardless of the species initial abundances in them. This character of the species extinction time and probability confirms that in the case of Scenario (i) the species is highly persistent.

For smaller immigration probabilities from the metacommunity $m^m$, the average first time to extinction of a species is more sensitive to the species initial abundance in the local communities. In such case the level of connection between the local communities (the immigration probability between local communities $m^l$) plays more important role on the species abundance dynamics in the local communities and on the species extinction time. Therefore, the species in the local communities need more careful treatment for conservation purposes. For example if the immigration probabilities $m^m$ and $m^l$ are very small and the local communities are very weakly connected with each other and with the metacommunity (Scenarios (vi) and (ix)), the average first time to species extinction from one local community is almost proportional to the initial species abundance in this local community, and, therefore, the species with lower abundances are much more vulnerable than the species with higher abundances.

It is worth noting that from the sensitivity analysis of the species extinction time and probability presented in Section 5.5, one can easily predict the development of species abundance in two local communities with respect to the level of connectedness of local communities with each other and with the metacommunity.

The sensitivity analysis clearly illustrates the effect of species abundance, species fraction in the metacommunity and immigration probabilities on the extinction dynamics of a given species in local communities. This analysis is particularly important for the population viability analysis of rare species. The analysis shows that the rare species are not necessary at high risk of extinction. For example, when local communities are closely connected to the metacommunity, the persistence time (mean time to extinction) for rare species is almost the same as for common species. Therefore, the extinction risk of rare species in this case is also close to the extinction risk of common species. However, if local communities are weakly connected to the metacommunity, the risk of extinction of rare species is much higher than the risk of extinction of common species. In this case the rare species are potential candidates for conservation actions.

Also in this chapter (Section 5.6), the comparison study of the species extinction time in two local communities and in one local community was performed. It was noted that in most cases the average first time to species extinction from one local community connected only to the metacommunity is smaller than the average first time to species extinction from one local community connected to both the metacommunity and the other local community, see Figures 5.2(a-c). This property shows the effect of the spatial structure of living communities on the species persistence in them. Specifically, in living communities involving more complex structure of interactions with other living communities or sources of organisms in the ecosystem the species persistence is higher than in living communities connected only to one source of living organisms.

It was also observed from the comparison analysis that the average first time to species extinction from the local community very weakly connected to the other local community is very close to the average first time to species extinction from one local community isolated from the other local community. This rather obvious observation states that if the local communities are weakly connected ($m^l$ is very small) then the effect of the species abundance in one local community on the species extinction time, probability and distribution in the other local community is negligible. Therefore, the species abundance dynamics in two weakly connected equal local communities can be easily obtained based on the study of the species abundance dynamics in one local community (Hubbell 2001; Babak 2006).

Finally, the models for the species extinction time and extinction in two local communities proposed in this chapter would allow us to understand more deeply the effect of the spatially structured habitats on the species persistence and abundance dynamics. The knowledge about the structure of the interactions between living habitats or communities, the intensity of immigration processes between them and the species composition in connected habitats can help to determine conservation actions to prevent species extinction (Kareiva 1987, Doak et al. 1992, Hall and Caswell 1999, Johnson et al. 2004). The analysis of the model for species abundance dynamics in two local communities clearly shows that even simple spatial structure of living habitats can significantly influence the species persistence and species composition in local communities.

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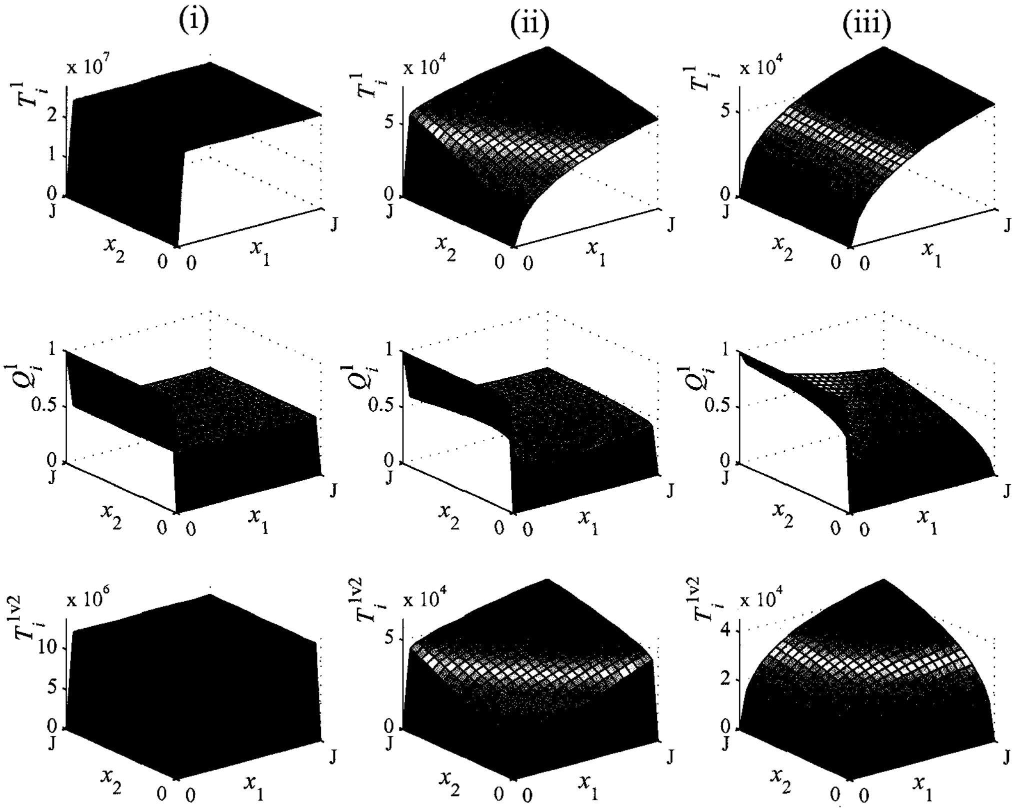


Figure 5.1: Effect of the type of species abundance dynamics scenario on species abundance evolution in the two equal local communities of size $J = 200$. The numbers of death events per unit time interval in local communities are $\mu_1 = \mu_2 = 1$. The species metacommunity relative abundance is $\omega_i = 0.2 < 1/2$. Figures in the top row show the mean first time to species extinction in the first local community calculated using Eq. (16) with boundary conditions in the form (14); figures in the middle row show the probability of extinction of the species from the first local community before the second local community calculated using Eqs. (18)-(21); and figures in the bottom row show the mean first time to species extinction either from the first local community or from the second local community calculated using Eq. (16) with boundary conditions in the form (13).

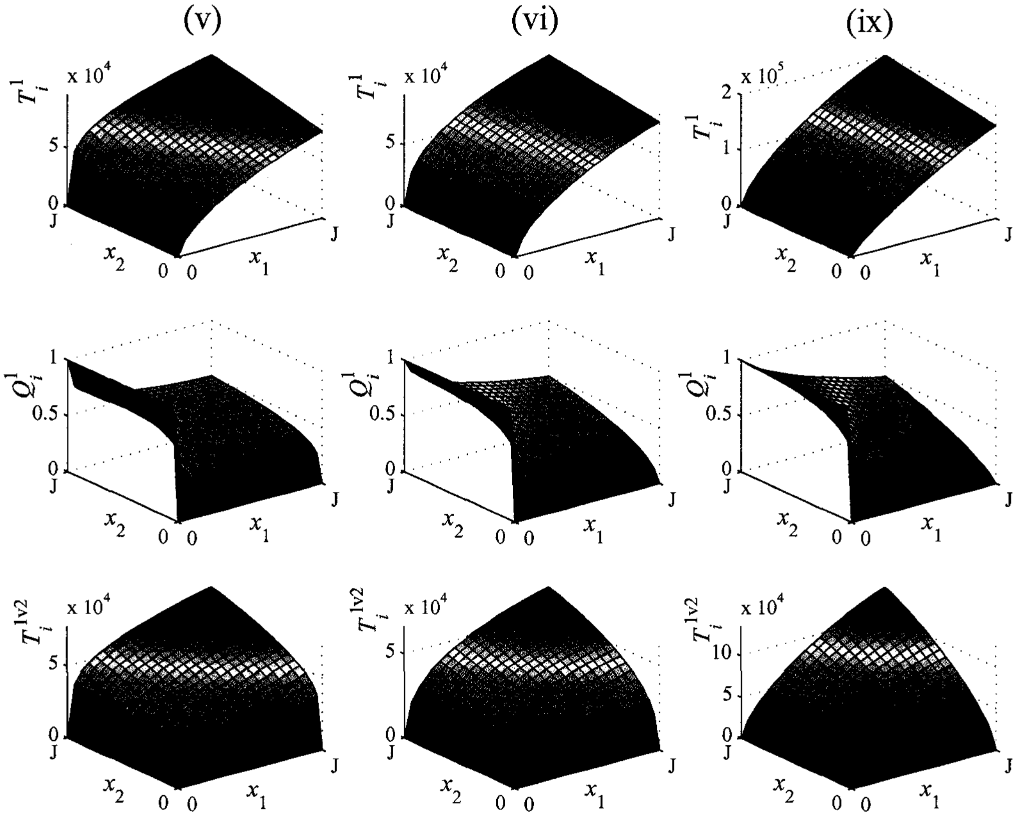
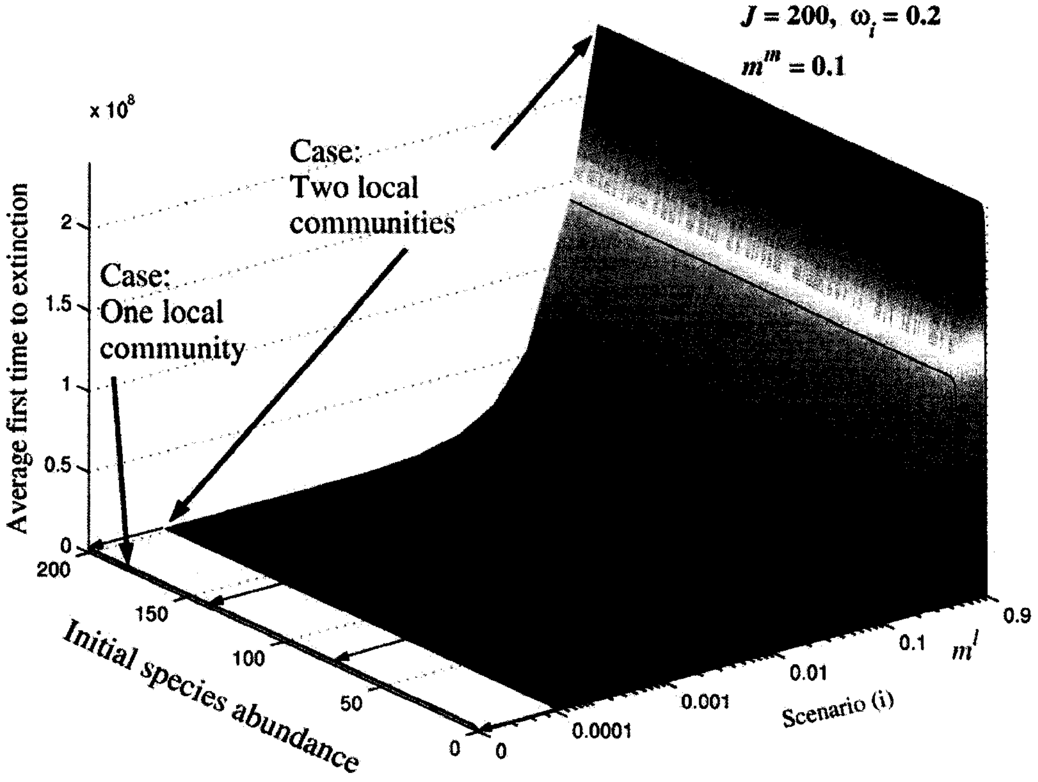
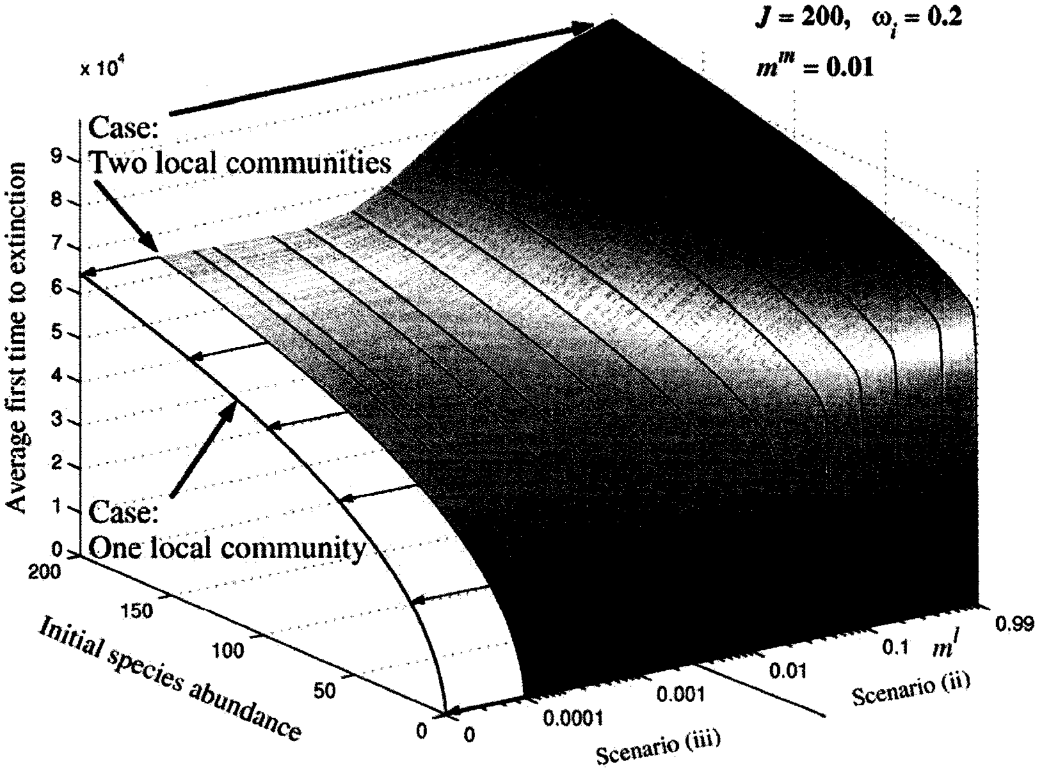


Figure 5.1: Cont. The values of the immigration probabilities are chosen to be the following: (*i*) $m^m = 0.1$, $m^l = 0.1$; (*ii*) $m^m = 0.01$, $m^l = 0.01$; (*iii*) $m^m = 0.01$, $m^l = 0.001$; (*v*) $m^m = 0.005$, $m^l = 0.005$; (*vi*) $m^m = 0.005$, $m^l = 0.002$; (*ix*) $m^m = 0.001$, $m^l = 0.001$.



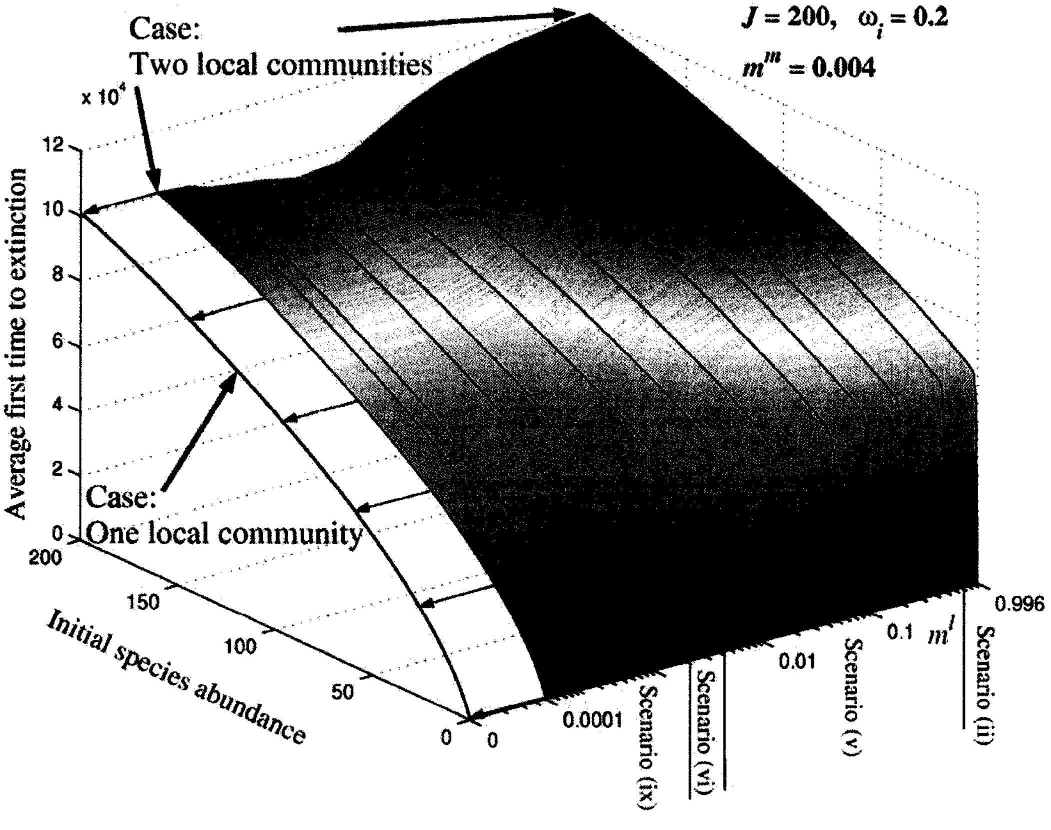
(a)

Figure 5.2: Effect of the immigration probability $m^l$ on the average first time to extinction in the first local community, and comparison of the average times to extinction in one local community connected only to the metacommunity (Hubbell's zero-sum model for local community) and in one local community connected to both the metacommunity and the other local community of the same size. (a) $m^m = 0.1$ (Scenario (i) for all values of $m^l$); (b) $m^m = 0.01$ (Scenario (iii) for $m^l < 0.003$ and Scenario (ii) for $m^l > 0.003$); (c) $m^m = 0.001$ (Scenario (ix) for $m^l < 0.002$ and Scenario (v) for $0.002 < m^l < 0.0045$, Scenario (vi) for $0.0045 < m^l < 0.71$ and Scenario (ii) for $m^l > 0.71$). The size of the local community is $J = 200$, and the metacommunity relative abundance of species $i$ is $\omega_i = 0.2$.



(b)

Figure 5.2: Cont.



(c)

Figure 5.2: Cont.

# Chapter 6

# Analysis of species abundance distribution in two semi-isolated local communities

## 6.1 Introduction

The biodiversity and species dynamics in complex ecological systems was investigated on different levels of organization from small open communities, components of all living systems, to all closed networks of open local communities (MacArthur and Wilson 1967; Hubbell 2001; Hanski and Gilpin 1997). Understanding the mechanisms of species abundance dynamics on all different levels of community organization is of high concern in viability analysis and ecosystem management and restoration (Primack 2002). The research on this matter dates back to works of Fisher et al. (1943) and Preston (1948). Since that time many different models for species abundance dynamics were proposed based on different biological principles (MacArthur 1957; 1960; Bulmer 1974; May 1975; Caswell 1976; Sugihara 1980; Engen & Lande 1996).

One of the newest and most controversial biological principles is the principle of neutrality for community organization which consists in assuming no differences between individuals of different species and no trophic hierarchy of community (Hubbell 2001; Gaston & Chown 2005). Using the principle of neutrality, Hubbell (2001) predicted the existence of new statistical distribution of relative species abundance, called the zero-sum multinomial and explained species area relationships. The zero-sum multinomial distribution was derived for communities which fulfill the zero-sum principle. This principle states that the sum of all changes in abundances is always zero, that is, the total number of individuals in the community is a conserved quantity (Hubbell 2001).

The analytical formalization of Hubbell's neutral theory was proposed for two types of living communities with respect to their isolation or connectedness to other living communities through immigration processes. The closed living communities, also called metacommunities, are considered as such evolutionary biogeographic units in which species can generate, live and go extinct (Hu et al. 2006). The opened living (local) communities in contrast to the metacommunities obtain new individuals through immigration from other communities or from the metacommunity. Metacommunities can be subdivided into several opened local communities linked by dispersal of species.

The dynamics of species abundances in local community depends on species representation in the metacommunity, on the intensity of immigration from the metacommunity and, of course, on the size of local community. To formulate the model for species abundance dynamics, Hubbell defined the change in the number of individuals of species $i$ per unit time step using the transition probabilities for the species abundances. If we denote the number of individuals of the $i$th species in a local community by $N_i$ and the size of local community by $J$. Then, the respective transition probabilities for abundance of species $i$ per unit time step are (Hubbell 1997, 2001)

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

where $\omega_i$ is the fractional metacommunity relative species abundance of the $i$th species, and $m$ is the probability that a death in the local community will be replaced by an immigrant (Hubbell, 1997; 2001). The total size of the local community $J$ can be represented as a sum of all species abundances $J = \sum_{i=1}^{S} N_i$, where $S$ denotes the total number species.

Based on the assumption of neutrality and the zero-sum principle, Hubbell (2001) also proposed a model for species abundance dynamics in two equal local communities connected with each other and with the metacommunity through immigration. This model was formulated by modifying the model for one local community. For analysis of the proposed model for two equal local communities Hubbell applied a discrete Markov Chain approach (Hubbell 2001). Using this approach Hubbell obtained the equilibrium abundance distribution for one species and compared the species abundances in two local communities using the covariance coefficient. However, in the view of high computation difficulty of the discrete approach, the study of Hubbell's model for species abundance dynamics in two local communities is restricted only to very small local communities.

In this chapter we propose a new spatially implicit model for species abundance dynamics in two semi-isolated local communities, i.e., two islands or habitats in the global ecological network of living communities. Though, the proposed model is spatially implicit, it can be considered as a link between spatially implicit and spatially explicit models for species abundance dynamics. This is because the connected with each other local communities are positioned in the global ecological network of living communities in such way that only one of them can obtain immigrants directly from the rest of the ecological system. Such positioning is, for example, typical for the local communities located close to the boundary of the ecological system or metacommunity.

The model for species abundance dynamics in two local communities proposed in this chapter is constructed within the framework of the Hubbell's zero-sum neutral theory for local communities. That is, the local communities are assumed to satisfy the zero-sum principle and the species are considered to be neutral. The developed model for two semi-isolated local communities is analyzed using continuous probabilistic technique. This technique allowed us not only to derive the species abundance distribution for local communities of any size, but also to make a classification of the species abundance dynamics in two semi-isolated local communities with respect to immigration intensities, species abundance in the metacommunity and size of local communities.

The chapter is organized as follows. In Section 6.2, we will propose a discrete model for species abundance dynamics in two semi-isolated local communities. In Section 6.3, we modify this discrete model to formulate a continuous model for probability density of species abundances in two semi-isolated local communities using Kolmogorov-Fokker-Planck forward equation. In this section we also derive the models for species abundance distributions in two equilibrium local communities, for marginal species abundance distribution for each local community and for additive species abundance distribution in both local communities. In Section 6.4, we analyze the model for equilibrium species abundance distributions in two local communities, and make a classification of species abundance dynamics in two local communities. According to this classification we distinguish realistic scenarios for species abundance dynamics in two local communities with respect to the immigration probability, species metacommunity relative abundance and size of local communities. And, finally, in Sections 6.5 and 6.6, we present several examples for possible scenarios of species abundance dynamics in two semi-isolated local communities, and discuss the ecological motives underlying each of these scenarios.

## 6.2 Formulation of discrete model for species abundance dynamics in two local communities

Let us consider two zero-sum local communities of the same size connected with each other and with the metacommunity - a large reservoir of organisms of different species with unchanged species abundance fractions. Assume that the local communities are semi-isolated from the metacommunity, that is, only one of the two local communities, say, the first local community, can obtain immigrants from the metacommunity. Further, we will refer to the first local community as non-isolated local community, and to the second local community as semi-isolated local community.

A discrete model for species abundance dynamics in two zero-sum local communities of the same size is formulated as follows. Let denote the size of local communities by $J$, and the number of individuals of species $i$ in the first and second local communities by $N_{1,i}$ and $N_{2,i}$, respectively. Then the change in the number of individuals of species $i$ per unit time step in the first (non-isolated) local community can be defined using the following transition probabilities

$$W_{1,i}(N_1 - 1 \mid N_1, N_2) = \frac{N_1}{J}\left((1 - m^m - m^l)\frac{J - N_1}{J - 1} + m^m(1 - \omega_i) + m^l\frac{J - N_2}{J}\right),$$

$$W_{1,i}(N_1 + 1 \mid N_1, N_2) = \frac{J - N_1}{J}\left((1 - m^m - m^l)\frac{N_1}{J - 1} + m^m\omega_i + m^l\frac{N_2}{J}\right), \qquad (2)$$

$$W_{1,i}(N_1 \mid N_1, N_2) = 1 - W_{1,i}(N_1 - 1 \mid N_1, N_2) - W_{1,i}(N_1 + 1 \mid N_1, N_2),$$

where $N_r = N_{r,i}$, $r = 1,2$; $\omega_i$ is a fractional metacommunity relative species abundance of species $i$, $m^m$ is the probability that a death in the first local community will be replaced by an immigrant from the metacommunity and $m^l$ is the probability that a death in a local community will be replaced by an immigrant from another local community, $m = m^m + m^l$.

The change in the number of individuals of species $i$ per unit time step in the second (semi-isolated) local community is defined similarly using the following transition probabilities

$$W_{2,i}(N_2 - 1 \mid N_1, N_2) = \frac{N_2}{J}\left((1 - m^l)\frac{J - N_2}{J - 1} + m^l\frac{J - N_1}{J}\right),$$

$$W_{2,i}(N_2 + 1 \mid N_1, N_2) = \frac{J - N_2}{J}\left((1 - m^l)\frac{N_2}{J - 1} + m^l\frac{N_1}{J}\right), \qquad (3)$$

$$W_{2,i}(N_2 \mid N_1, N_2) = 1 - W_{2,i}(N_2 - 1 \mid N_1, N_2) - W_{2,i}(N_2 + 1 \mid N_1, N_2).$$

The transition probabilities given by expressions (2) and (3) can be explained as follows. The fractions $\frac{N_p}{J}$ and $\frac{J - N_p}{J}$ in the transition probabilities $W_{p,i}(N_p - 1 \mid N_p, N_q)$ and $W_{p,i}(N_p + 1 \mid N_p, N_q)$, respectively, account for death of one individual in species $i$ and one individual in other species. The numbers $(1 - m^m - m^l)\frac{N_1}{J - 1}$, $(1 - m^m - m^l)\frac{J - N_1}{J - 1}$ and $(1 - m^l)\frac{N_2}{J - 1}$, $(1 - m^l)\frac{J - N_2}{J - 1}$ define the probabilities of birth in the first and second local communities, respectively. The probabilities of immigration from the metacommunity into the first local community of an individual of species $i$ and an individual of other species are given by $m^m\omega_i$ and $m^m(1 - \omega_i)$, respectively. Finally, the numbers $m^l\frac{N_q}{J}$ and $m^l\frac{J - N_q}{J}$ define the probabilities of immigration from local community $q$ into local community $p$ of an individual of species $i$ and an individual of other species, $q = \begin{cases} 1: & p = 2, \\ 2: & p = 1. \end{cases}$

Moreover, if we assume that the species abundance dynamics in one local community is independent of the species abundance dynamics in another local community. Then, the transition probabilities for dynamics of species $i$ in both local communities are defined as follows

$$W_i(N_1 + \Delta_1, N_2 + \Delta_2 \mid N_1, N_2) = W_{1,i}(N_1 + \Delta_1 \mid N_1, N_2) \times W_{2,i}(N_2 + \Delta_2 \mid N_1, N_2) \tag{4}$$

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

## 6.3 Continuous probabilistic approach

### 6.3.1 Model for species abundance dynamics in two local communities

In order to derive the continuous model for species abundance distribution in two zero-sum local communities, we define the transition probabilities for the change $\Delta N_{p,i}$ of the number of individuals $N_{p,i}$ of the $i$th species in local community $p$, $p = 1,2$ per time step $\Delta t$ as

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

$$\begin{aligned} \Pr(\Delta N_{p,i} = 0 \mid N_{p,i} = N_p, N_{q,i} = N_q) = 1 - \Pr(\Delta N_{p,i} = 1 \mid N_{p,i} = N_p, N_{q,i} = N_q) \\ - \Pr(\Delta N_{p,i} = -1 \mid N_{p,i} = N_p, N_{q,i} = N_q), \end{aligned} \tag{5}$$

where $\mu_p$ is the number of death events per unit time interval in local community $p$.

Then the joint transition probabilities for the change in the species abundance in both local communities are the following

$$\begin{aligned} &\Pr(\Delta N_{1,i} = \Delta_1, \Delta N_{2,i} = \Delta_2 \mid N_{1,i} = N_1, N_{2,i} = N_2) \\ &= \Pr(N_{1,i} = \Delta_1 \mid N_{1,i} = N_1, N_{2,i} = N_2) \times \Pr(N_{2,i} = \Delta_2 \mid N_{2,i} = N_2, N_{1,i} = N_1) \end{aligned} \tag{6}$$

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

## 6.3.2 Dynamics of species abundance distribution. Kolmogorov-Fokker-Planck forward equation

Let us define the change in the abundance of the $i$th species in both local communities per time step $\Delta t$ as a vector $\Delta N_i = (\Delta N_{1,i}, \Delta N_{2,i})$, where $\Delta N_{p,i} = N_{p,i}(t+\Delta t) - N_{p,i}(t)$, $p = 1,2$; and let $N_i = (N_{1,i}, N_{2,i})$ and $x = (x_1, x_2)$.

Because the species abundance in one local community per one time step $\Delta t$ changes only by one individual or remain the same, the variables $\Delta N_{p,i}$ can attain only values -1,0 and 1. And therefore the mean and the second moment of the change in the abundance of the $i$th species per infinitely small time interval $\Delta t$ can be calculated as

$$V(x) = \begin{pmatrix} V_1(x) \\ V_2(x) \end{pmatrix} = \lim_{\Delta t \to 0} \frac{1}{\Delta t} \begin{pmatrix} E(\Delta N_{1,i} \mid N_i = x) \\ E(\Delta N_{2,i} \mid N_i = x) \end{pmatrix},$$

$$D(x) = \begin{pmatrix} D_{11}(x) & D_{12}(x) \\ D_{21}(x) & D_{22}(x) \end{pmatrix} = \lim_{\Delta t \to 0} \frac{1}{\Delta t} \begin{pmatrix} E(\Delta N_{1,i}{}^2 \mid N_i = x) & E(\Delta N_{1,i} \Delta N_{2,i} \mid N_i = x) \\ E(\Delta N_{1,i} \Delta N_{2,i} \mid N_i = x) & E(\Delta N_{2,i}{}^2 \mid N_i = x) \end{pmatrix},$$

where

$$V_1(x) = \mu_1 m^m \left( \omega_i - \frac{x_1}{J} \right) + \mu_1 m^l \left( \frac{x_2}{J} - \frac{x_1}{J} \right), \quad V_2(x) = \mu_2 m^l \left( \frac{x_1}{J} - \frac{x_2}{J} \right);$$

$$D_{11}(x) =$$

$$\mu_1 \left( 2(1 - m^m - m^l) \frac{x_1(J - x_1)}{J(J-1)} + m^m (1 - \omega_i) \frac{x_1}{J} + m^m \omega_i \frac{J - x_1}{J} + m^l \frac{J - x_2}{J} \frac{x_1}{J} + m^l \frac{x_2}{J} \frac{J - x_1}{J} \right),$$

$$D_{22}(x) = \mu_2 \left( 2(1 - m^l) \frac{x_2(J - x_2)}{J(J-1)} + m^l \frac{J - x_1}{J} \frac{x_2}{J} + m^l \frac{x_1}{J} \frac{J - x_2}{J} \right), \; D_{12}(x) = D_{21}(x) = 0 \, .(7)$$

Let us now define the abundances $x_1$ and $x_2$ of the $i$th species in the first and second local communities as continuous variables allowing any real values from the interval $[0, J]$. Then the conditional probability, $p(x,t)$, that the $i$th species has abundances $x_1$ and $x_2$ in the first and second local community at time $t$ satisfies the following Kolmogorov-Fokker-Planck forward equation

$$\frac{\partial p}{\partial t} = \frac{1}{2} \left( \frac{\partial^2 D_{11} p}{\partial x_1{}^2} + \frac{\partial^2 D_{22} p}{\partial x_2{}^2} \right) - \frac{\partial V_1 p}{\partial x_1} - \frac{\partial V_2 p}{\partial x_2}, \quad x = (x_1, x_2) \in \Omega = (0, J) \times (0, J), \quad t > \tau, \; (8)$$

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

Equation (8) is supplemented with the initial condition defining $p^0(x)$, the probability density of the $i$th species abundances $x_1$ and $x_2$ in the two local communities at the initial time moment $t = \tau$

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

and the natural boundary conditions

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

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

$$\iint\limits_{\Omega} p(x,\tau)\,\mathrm{d}x_1\mathrm{d}x_2 = \iint\limits_{\Omega} p^0(x)\,\mathrm{d}x_1\mathrm{d}x_2 = 1, \quad \text{for all } t \geq \tau. \tag{11}$$

In order to define the natural boundary conditions (10) more precisely, we need to specify the boundary $\Gamma$ of the abundance domain $\Omega = (0,J)\times(0,J)$ and the outward normal vectors $\vec{n}$ at each boundary abundance of $\Omega$.

It is clear that the abundance boundary $\Gamma$ consists of four parts $\Gamma = \Gamma^{0*} \cup \Gamma^{*1} \cup \Gamma^{1*} \cup \Gamma^{*0}$, where $\Gamma^{0*} = \{0\}\times(0,J)$, $\Gamma^{*1} = (0,J)\times\{J\}$, $\Gamma^{1*} = \{J\}\times(0,J)$ and $\Gamma^{*0} = (0,J)\times\{0\}$. Therefore the outward normal vectors are given by $\vec{n}^{0*} = (n_1^{0*}, n_2^{0*}) = (-1,0)$ for $\Gamma^{0*}$, $\vec{n}^{1*} = (n_1^{1*}, n_2^{1*}) = (1,0)$ for $\Gamma^{1*}$, $\vec{n}^{*0} = (n_1^{*0}, n_2^{*0}) = (0,-1)$ for $\Gamma^{*0}$, and $\vec{n}^{*1} = (n_1^{*1}, n_2^{*1}) = (0,1)$ for $\Gamma^{*1}$.

Then the boundary conditions (10) for each part of the boundary separately can be rewritten as follows

$$\frac{1}{2}\frac{\partial D_{11}p}{\partial x_1} - V_1 p = 0, \quad x \in \Gamma^{0*} \cup \Gamma^{1*}, \qquad \frac{1}{2}\frac{\partial D_{22}p}{\partial x_2} - V_2 p = 0, \quad x \in \Gamma^{*0} \cup \Gamma^{*1}. \tag{10'}$$

### 6.3.3 Equilibrium species abundance distribution in two local communities

Equilibrium species abundance distribution is an important tool for studying species abundance dynamics in local communities. It can be considered as a long time limit of species abundance distribution in local communities or as a stabilized species abundance distribution in absence of external factors or model perturbations.

It follows from model (8)-(11) for the dynamics of the abundance density of species $i$, that the equilibrium (steady state) abundance density of species $i$ in two local communities fulfils the following elliptic differential equation

$$0=\frac{1}{2}\left(\frac{\partial^2 D_{11}P}{\partial x_1{}^2}+\frac{\partial^2 D_{22}P}{\partial x_2{}^2}\right)-\frac{\partial V_1 P}{\partial x_1}-\frac{\partial V_2 P}{\partial x_2}, \quad x\in\Omega, \tag{12}$$

and boundary conditions (10) or (10') with the total probability over domain $\Omega$ equal to 1 (see also Eq.(11)).

## 6.3.4 Marginal species abundance distribution in one local community

The marginal species abundance distribution is used for comparison of the species abundance distribution in one of the two local communities and in both local communities.

The formulae for the marginal species abundance distribution can be easily obtained using the following expression for the $q$ th local community

$$p_q(x_q,t)=\int_0^J p(x_1,x_2,t)dx_p\,, \quad x_q\in(0,J) \tag{13}$$

where $q=\begin{cases}1: & p=2,\\ 2: & p=1.\end{cases}$

## 6.3.5 Additive species abundance distribution in both local communities

Another problem of interest for community ecologists is the species abundance distribution in both local communities, that is the distribution of $x_1+x_2$. Based on this distribution a comparison study of the abundance distributions in each local community and in the merged two local communities can be performed.

The species abundance distribution in both local communities can be defined as

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

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

## 6.3.6 Correlation between species abundances in two local communities

One of the important characteristics of the relationship between species abundance distributions in two local communities is the magnitude of their correlation. In order to define it, we derive first the formulae for the covariance and variances of the species abundances in local communities

$$Cov(N_{1,i},N_{2,i}) = \iint\limits_{\Omega}(x_1 - E(N_{p,i}))(x_2 - E(N_{p,i}))p(x_1,x_2,t)dx_1dx_2\,, \tag{15}$$

$$Var(N_{p,i}) = \iint\limits_{\Omega}(x_p - E(N_{p,i}))(x_p - E(N_{p,i}))p(x_1,x_2,t)dx_1dx_2\,,\ p = 1,2\,;$$

where

$$E(N_{p,i}) = \iint\limits_{\Omega} x_p p(x_1,x_2,t)dx_1dx_2\,,\ p = 1,2\,;$$

Then, the correlation coefficient is found as

$$r_{12} = \frac{Cov(N_{1,i},N_{2,i})}{\sqrt{Var(N_{1,i})Var(N_{2,i})}}\,. \tag{16}$$

# 6.4 Analysis of the model

## 6.4.1 Analysis of the boundary conditions for the species abundance density function

A change in species abundance distribution with respect to different values of the immigration probabilities, the species metacommunity relative abundance, the community sizes and the number of death events per unit time interval can be investigated by imposing different boundary condition on equation (8) or (12).

First we consider mixed boundary conditions (10) (or (10')). These boundary conditions can be rewritten as

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

$$\frac{1}{2}D_{22}\frac{\partial p}{\partial x_2} + \left(\frac{1}{2}\frac{\partial D_{22}}{\partial x_2} - V_2\right)p = 0, \quad x \in \Gamma^{*0} \cup \Gamma^{*1}. \tag{10''}$$

The critical boundary abundances at which the mixed boundary conditions degenerate to the zero flux boundary conditions are found by solving the following equations

$$\left.\frac{1}{2}\frac{\partial D_{pp}}{\partial x_p} - V_p\right|_{x_p=0} = 0, \qquad \left.\frac{1}{2}\frac{\partial D_{pp}}{\partial x_p} - V_p\right|_{x_p=J} = 0, \qquad p = 1,2\,, \tag{17}$$

where

$$\frac{1}{2}\frac{\partial D_{11}p}{\partial x_1}-V_1p=$$
$$\mu_1\left(\frac{(m^m+m^l)(J+1)-2}{J(J-1)}x_1-m^l\frac{J+1}{J^2}x_2+\frac{1}{J-1}-\left(\frac{(m^m+m^l)}{2(J-1)}+m^m\omega_i\right)\frac{J+1}{J}\right),$$

$$\frac{1}{2}\frac{\partial D_{22}p}{\partial x_2}-V_2p=\mu_2\left(\frac{m^l(J+1)-2}{J(J-1)}x_2-m^l\frac{J+1}{J^2}x_1+\frac{1}{J-1}-m^l\frac{J+1}{2J(J-1)}\right)\qquad(18)$$

are non-increasing functions with respect to $x_2$ and $x_1$, respectively.

Note that the zero flux boundary conditions, also known as Neumann Boundary conditions, imply zero gradient of the probability of species abundances at the boundary abundances.

After substitution of Eq. (18) into Eq. (17), we obtain the following formulae for calculation of the boundary critical abundances $(0,x_2^0)$, $(J,x_2^J)$, $(x_1^0,0)$ and $(x_1^J,J)$ where the respective boundary conditions given by equations (10'') degenerate to the zero flux boundary conditions

$$x_2^0=\left(\frac{1-(m^m+m^l)}{m^l}\frac{J^2}{(J-1)(J+1)}+\frac{m^m+m^l}{2m^l}\frac{J}{J+1}\right)-\omega_i\frac{m^m}{m^l}J,$$

$$x_2^J=-\left(\frac{1-(m^m+m^l)}{m^l}\frac{J^2}{(J-1)(J+1)}+\frac{m^m+m^l}{2m^l}\frac{J}{J+1}\right)+J+(1-\omega_i)\frac{m^m}{m^l}J,$$

$$x_1^0=\left(\frac{1-m^l}{m^l}\frac{J^2}{(J-1)(J+1)}+\frac{J}{2(J+1)}\right),\quad x_1^J=J-\left(\frac{1-m^l}{m^l}\frac{J^2}{(J-1)(J+1)}+\frac{J}{2(J+1)}\right).\qquad(19)$$

For large local communities, the above formulae can be simplified to the subsequent

$$x_2^0=\left(\frac{1}{m^l}-\frac{m^m+m^l}{2m^l}\right)-\omega_i\frac{m^m}{m^l}J,\qquad x_2^J=-\left(\frac{1}{m^l}-\frac{m^m+m^l}{2m^l}\right)+J+(1-\omega_i)\frac{m^m}{m^l}J,$$

$$x_1^0=\left(\frac{1-m^l}{m^l}+\frac{1}{2}\right),\qquad x_1^J=J-\left(\frac{1-m^l}{m^l}+\frac{1}{2}\right).\qquad(20)$$

## 6.4.2 Structure of species abundance distribution in the semi-isolated local community

Let us first consider the behavior of the species abundance distribution in the semi-isolated (second) local community when the species is extinct or monodominant in the first local community. Since the function $\frac{1}{2}\frac{\partial D_{22}}{\partial x_2}-V_2$ in (18) is non-increasing with respect to $x_1$, we can infer that if the critical value $x_1^0$ of the species abundance can be reached in the first local community, i.e., $x_1^0 < J$, then the derivative $\frac{\partial p}{\partial x_2}$ is negative at the abundance levels (0,0) and $(0,J)$, and $\frac{\partial p}{\partial x_2}$ is positive at the abundance levels ($J$,0) and $(J,J)$. Similarly, if the critical species abundance value $x_1^0$ cannot be reached in the first local community, i.e., $x_1^0 > J$, then the derivative $\frac{\partial p}{\partial x_2}$ is negative at the abundance levels (0,0) and ($J$,0), and $\frac{\partial p}{\partial x_2}$ is positive at the abundance levels $(0,J)$ and $(J,J)$. The signs of the derivative $\frac{\partial p}{\partial x_2}$ at the corner abundances define the two types of the structure for the species abundance distribution in the second local community when the species is absent or monodominant in the first local community. These species abundance distributions are either U-shaped or S-shaped as shown in Figure 6.1.

The U-shaped species abundance distribution in the second local community, when the species abundance in the first local community is equal to 0 or $J$, describes that most of the time the species abundance in the second local community is at levels 0 or $J$. In this case the species has very high chance of extinction or monodominance in the second local community.

When the species abundance distribution in the second local community is S-shaped, the species abundance is most of time at the abundance level 0, and the probability that the species abundance riches the level $J$ is very small. Thus, the species with S-shaped species abundance distribution in the second local community has very high chance to extinction and very small chance of monodominance, when the species abundance in the first local community is equal to 0 or $J$.

### 6.4.3 Structure of species abundance distribution in the non isolated local community

The source for new individuals in the first local community is larger than in the second local community, since the first local community obtains new immigrants not only from the second local community, but also from the metacommunity. As result, the number of different structures for the species abundance distribution in the first local community at the boundary species abundances in the second local community is larger than the number of structures of the species abundance distribution in the second local community at the boundary species abundances in the first local community.

To describe possible cases for the species abundance distribution in the first local community, let us consider the non-increasing function $\frac{1}{2}\frac{\partial D_{11}}{\partial x_1} - V_1$ in (18) with respect to $x_2$ for the two values of the species abundance in the first local community $x_1 = 0$ and $x_1 = J$.

The signs of $\frac{1}{2}\frac{\partial D_{11}}{\partial x_1} - V_1$ at the boundary abundances (0,0) and ($J$,0) define the type of the species abundance in the first local community when the species is absent in the second local community. Similarly, the signs of $\frac{1}{2}\frac{\partial D_{11}}{\partial x_1} - V_1$ at the boundary abundances $(0,J)$ and $(J,J)$ define the type of the species abundance in the first local community when the species is monodominant in the second local community. To define the sign of the $\frac{1}{2}\frac{\partial D_{11}}{\partial x_1} - V_1$ at the boundary abundances we consider the values of $x_2^0$ and $x_2^J$ at which the function $\frac{1}{2}\frac{\partial D_{11}}{\partial x_1} - V_1$ degenerate to zero. For example, if $x_2^0 < 0$, then $\frac{1}{2}\frac{\partial D_{11}p}{\partial x_1} - V_1 p < 0$ and $\frac{\partial p}{\partial x_1} > 0$ at (0,0) and $(0,J)$, thus we can conclude that the probability of species abundance increases for small species abundances in the first local community when the species is absent or monodominant in the second local community. If $x_2^0 > J$, then $\frac{\partial p}{\partial x_1} < 0$ at (0,0) and $(0,J)$, and the probability of species abundance decreases for small species abundances in the first local community when the species is absent or monodominant in the second local community. Finally, if $0 < x_2^0 < J$, then $\frac{\partial p}{\partial x_1} < 0$ at (0,0) and $\frac{\partial p}{\partial x_1} > 0$ at $(0,J)$, thus the probability of species abundance decreases for small species abundances in the first local community when the species is absent in the second local community, and it increases for small species abundances in the first local community when the species is monodominant in the second local community.

Similar conclusions with respect to behavior of the species abundance distribution for the large species abundances in the first local community at the boundary abundances $x_0 = 0$ and $x_2 = J$ can be made from location of the abundance value $x_2^J$ with respect to the three intervals $(-\infty,0)$, $[0,J)$ and $[J,+\infty)$.

In total, 9 locations are possible for the pair $x_2^0$ and $x_2^J$ with respect to critical abundances 0 and $J$. The respective types for the species abundance distribution in the first local community, when the species is absent and monodominant in the second local community, are illustrated in Figure 6.2.

Note that due to constraint on the sum of nonnegative immigration probabilities $m^m$ and $m^l$ (this sum cannot exceed 1), for each values of the metacommunity relative abundance $\omega_i$ and the size of local communities $J$ the number of possible types for species abundance distribution in the first local community is smaller than 9. For example, in the case when $0 \le \omega_i < 1/2$, the types (*ii*), (*iii*), (*v*), (*vi*) and (*ix*) for species abundance distribution in the first local community when $x_2 = 0$ and $x_2 = J$ are always possible, furthermore, in addition to these species abundance types the type (*i*) is possible for $\frac{1}{2(J+1)} < \omega_i < \frac{1}{2}$. Similarly, for $1/2 < \omega_i \le 1$, the types (*iv*), (*v*), (*vii*), (*vii*) and (*ix*) for species abundance distribution in the first local community are always possible, and, in addition to these types the type (*i*) is possible for $\frac{1}{2} < \omega_i < 1 - \frac{1}{2(J+1)}$. If $\omega_i = 1/2$, the 3 possible types of species abundance distribution in the first local community are (*i*), (*v*) and (*ix*).

The local community size plays also a critical rule in determining possible combinations for the species abundance distributions in the first local community at the boundary abundances $x_2 = 0$ and $x_2 = J$. For example, the combination (*i*) is only possible when the size of the local community is large enough, that is when $J > \frac{1}{2\min\{\omega_i, 1-\omega_i\}} - 1$.

## 6.4.4 Classification of the species abundance dynamics in both local communities

Based on the previous analysis of species abundance distribution types in one local community when the species is absent or monodominant in the other local community we can define the type of the joint species abundance distribution for both local communities.

Hereafter, we will refer to different types of joint species abundance distributions as the scenarios for species abundance dynamics in two local communities. The number of the scenario for the species abundance dynamics will be defined based on both, the number of the type for species abundance distribution in the first local community when the species is absent or monodominant in the second local community, and the number of the type for species abundance distribution in the second local community when when the species is absent or monodominant in the first local community.

Which scenario for the species abundance dynamics is observed in two local communities depends on the values of the immigration probabilities $m^l$ and $m^m$, the species metacommunity relative abundance $\omega_i$ and on the size of local communities $J$. Table 6.1 states the conditions on the parameters of the continuous model required for each possible species abundance dynamics scenario to be attained. Based on this table, the number of the species abundance scenario can be defined easily from the values of $m^l$, $m^m$, $\omega_i$ and $J$.

Figures 6.3 illustrate all possible species abundance scenarios with respect to the metacommunity relative abundance. The permissible regions for the immigration probabilities $m^{m}$ and $m^{l}$ in Figure 6.3 are shown using the triangles with the vertices (0,0), (0,1) and (1,0). Such shape of the permissible region for $m^{m}$ and $m^{l}$ is dictated by the constraint that the sum of the nonnegative immigration probabilities cannot exceed 1. The permissible triangles are divided into two parts by the horizontal dashed line $m^{l} = m_J^{l}$, where $m_J^{l} = \dfrac{2J}{(2J-1)(J+1)}$. This line defines the type of the species abundance distribution in the second local community $i_2$. Specifically, if the pair of immigration probabilities $(m^{m}, m^{l})$ belongs to upper sub-triangle, or $m^{l} > m_J^{l}$, then $i_2 = (v)$; otherwise, if $(m^{m}, m^{l})$ belongs to lower sub-domain of the permissible triangle, or $m^{l} < m_J^{l}$, then $i_2 = (ix)$.

The upper and lower sub-domains of the permissible triangles for the immigration probabilities are further divided into smaller parts using the lines $m^{m}(2\omega_i(J-1)+1)+m^{l} = 2J/(J+1)$, $m^{m}(2(1-\omega_i)(J-1)+1)+m^{l} = 2J/(J+1)$, $m^{m}(2\omega_i(J-1)+1)+m^{l}(2J-1) = 2J/(J+1)$ and $m^{m}(2(1-\omega_i)(J-1)+1)+m^{l}(2J-1) = 2J/(J+1)$. The resulting parts define the type of the species abundance distribution in the first local community $i_1$ on the basis of the value of the pair $(m^{m}, m^{l})$. As it is shown in Figures 6.3, not all types $i_1$ are possible for the fixed values of the metacommunity relative abundance $\omega_i$ and the size of local communities $J$. For example, if the type of the species abundance distribution in the second local community $i_2$ is (*v*), then for $\omega_i \le \omega^{J,2} = \dfrac{2J-1}{2(J-1)(2J+1)}$, the type $i_1$ can only be either (*v*) or (*ii*); for $\omega^{J,2} < \omega_i < 1/2$, $i_1$ can only be (*v*), (*ii*) or (*i*); for $\omega_i = 1/2$, $i_1$ can only be (*v*) or (*i*); for $1/2 < \omega_i < 1-\omega^{J,2}$, $i_1$ can only be (*v*), (*iv*) or (*i*); and for $\omega_i \ge 1-\omega^{J,2}$, the type $i_1$ can only be either (*v*) or (*iv*). Similarly, if the type of the species abundance distribution in the second local community $i_2$ is (*ix*), then for $\omega_i \le \omega^{J,1} = \dfrac{1}{2(J+1)}$, the five possible types for $i_1$ are (*ii*), (*iii*), (*v*), (*vi*) and (*ix*); for $\omega^{J,1} < \omega_i < 1/2$, the six possible types for $i_1$ are (*i*), (*ii*), (*iii*), (*v*), (*vi*) and (*ix*); for $\omega_i = 1/2$, $i_1$ can only be (*i*) or (*v*) or (*ix*); for $1/2 < \omega_i < 1-\omega^{J,1}$, the six possible types for $i_1$ are (*i*), (*iv*), (*v*), (*vii*), (*viii*) and (*ix*); and, finally, for $\omega_i \ge 1-\omega^{J,1}$, the only possible types for $i_1$ are (*iv*), (*v*), (*vii*), (*viii*) and (*ix*).

Finally, let us note that the maximal number of all possible scenarios is 9: three species abundance scenarios for $i_2 = (ix)$ and six species abundance scenarios for $i_2 = (v)$. The minimal number of scenarios in two local communities is 7. All these scenarios can easy distinguished from Figures 6.3.

## 6.5 Sensitivity analysis

In this section we will analyze different scenarios for the species abundance dynamics in two semi-isolated local communities using the equilibrium species abundance probability density in the two local communities (landscape and contour plots), the equilibrium marginal species abundance probability densities for each local community and the additive marginal species abundance probability densities for joint local communities, see Figure 6.4. Based on the correlation coefficient between species abundances in two local communities, we will also discuss the similarities between species abundance dynamics in two local communities, see Figure 6.5.

### 6.5.1 Analysis of different species abundance dynamics scenarios

Let us study the abundance dynamics of a particular species, say species $i$, in two local communities of size $J = 200$, using the analysis of the equilibrium species abundance distributions. We assume that the frequencies of death events in both local communities are equal, i.e., $\mu_1 = \mu_2$. Since the values of the equal frequencies of death events in two local communities play only a role of the time scales in the dynamics of the species abundances in the local communities, and they specify the speed of the convergence to equilibrium species abundance distributions, the equilibrium species abundance distribution is independent of the values of parameters $\mu_1$ and $\mu_2$. Thus, in all experiments we will use a constant value of 0.0001 for the parameters $\mu_1$ and $\mu_2$.

In our study we consider only the case when species $i$ has small relative abundance in the metacommunity, that is, $\omega_i = 0.2 < 1/2$. The analysis of the species abundance dynamics for common species ($\omega_i > 1/2$) can be provided in analogous manner.

It was already mentioned in the previous section that the maximal number of possible scenarios for the species abundance dynamics in the case when the metacommunity relative abundance is smaller than 1/2 is 9, these are scenarios (*i,ix*), (*ii,ix*), (*iii,ix*), (*v,ix*), (*vi,ix*), (*ix,ix*), (*i,v*), (*ii,v*) and (*v,v*). To illustrate all these scenarios the realistic values for the immigration probabilities are chosen.

Since the species in the second semi-isolated local community has only two possible structures of the species abundance distribution, we divide all possible species abundance dynamics scenarios into two groups: (*i,ix*), (*ii,ix*), (*iii,ix*), (*v,ix*), (*vi,ix*) and (*ix,ix*) with the species abundance distribution in the second local community of type (*ix*); and (*i,v*), (*ii,v*) and (*v,v*) with the species abundance distribution in the second local community of type (*v*). Each of these groups of scenarios will be examined separately.

Let us start the analysis of the species abundance dynamics in the two local communities from the case when the local communities are weakly connected, that is, when the immigration probability between local communities $m^l$ is small. The possible scenarios for the species abundance dynamics then are scenarios (*i,ix*), (*ii,ix*), (*iii,ix*), (*v,ix*), (*vi,ix*) and (*ix,ix*). For these scenarios, the common type (*ix*) of the species abundance distribution in the second local community is characterized by the U-shaped form when the species is absent or monodominant in the first local community. That is, the species in the second local community has high chance to either go extinct or become monodominant. Note that for this group of species abundance dynamics scenarios, the structure of the species abundance distribution in the first local community can vary between types (*i*), (*ii*), (*iii*), (*v*), (*vi*) and (*ix*).

We begin our analysis of each scenario in the first group composed of scenarios (*i,ix*), (*ii,ix*), (*iii,ix*), (*v,ix*), (*vi,ix*) and (*ix,ix*) from scenario (*ix,ix*) which is associated with small probabilities of immigration $m^m$ and $m^l$.

For scenario (*ix,ix*) all boundary species abundance distributions are U-shaped, see Figures 6.1 and 6.2. Thus, the maximal probability of the species abundances is achieved at the abundance levels $(0,0)$, $(J,0)$, $(0,J)$ and $(J,J)$, and the minimal probability is achieved inside of the abundance domain $\Omega$, see Figure 6.4. This type of the species abundance for scenario (*ix,ix*) can be explained using high similarity of the species abundance for this scenario to the case of the species abundance dynamics in two isolated local communities, that is, in local communities which neither obtain new immigrants from the metacommunity nor interchange immigrants between each other. Specifically, the similarity follows from the fact that if the immigration intensities are very small, new immigrants appear in local communities of scenario (*ix,ix*) very seldom, and the time interval between immigration events is very large. Thus, the species abundance dynamics for scenario (*ix,ix*) is the same as in isolated local communities.

It is known from analysis of species abundance dynamics in one isolated zero-sum local community that the species abundance dynamics in such local community possess two absorbing states at zero abundance level and at the monodominance level (Hubbell 2001). For the two local isolated communities species abundance dynamics is much more complicated, it has four absorbing states $(0,0)$, $(J,0)$, $(0,J)$ and $(J,J)$. As result the probability that the species abundance will achieve one of these absorbing states and remain there equals 1. Because in scenario (*ix,ix*), the immigration intensity is very small, the species abundance combinations $(0,0)$, $(J,0)$, $(0,J)$ and $(J,J)$ are also most probable among all possible species abundance combinations from the domain $\Omega$. Thus, the probability that the species will go extinct or become monodominant in such local communities is very high and, therefore, the species abundance distribution at the boundary of the abundance domain $\Omega$ is U-shaped. Note that Figures 6.4 for scenario (*ix,ix*) show that the equilibrium marginal species abundance probability densities for each local community are also U-shaped. However, the additive species abundance distribution in both local communities for this scenario is significantly different from both marginal species abundance distributions. Specifically, the additive species abundance distribution in both local communities is W-shaped and has local maximums not only at the species abundance levels 0 and $2J$, but also at abundance level $J$. Note that when the additive species abundance distribution reaches level $J$, the species of interest is monodominant in one local community and absent in the other local community.

Similar species abundance dynamics to discussed above is observed for scenario *(vi,ix)* which is characterized by higher probability of imigration probability from the metacommunity than for scenario *(ix,ix)*. For this scenario the species abundance in the first local community when the species is absent in the second local community is S-shaped. Thus, the probability that species monodominate in the first local community and go extinct in the second local community is significantly lower than in scenario *(ix,ix)*. As result, the additive species abundance distribution plot for scenario *(vi,ix)* shows that the probability of the species abundance at the abundance level $J$ is significantly smaller than for scenario *(ix,ix)*. However, as in scenario *(ix,ix)* the marginal species abundance distributions are still U-shaped and the species abundances $(0,0)$, $(0,J)$ and $(J,J)$ have maximal probabilities, see Figures 6.4.

Now let us consider scenario *(v,ix)* for which the local communities are more closely connected with each other than in scenario *(vi,ix)*. The species abundance distribution in this case for the first local community becomes reverse S-shaped, that is the chance of the species extinction in the first local community when the species is monodominant in the second local community is much lower than for scenario *(vi,ix)*. Furthermore, the probability of the additive abundance $J$ for scenario *(v,ix)* is smaller than for scenarios *(vi,ix)* and *(ix,ix)* and the additive species abundance probability density as result becomes almost U-shaped. Note, however, that for scenario *(v,ix)* the maximal probability is still achieved at the boundary abundance levels $(0,0)$ and $(J,J)$, and the marginal species abundance distributions are still U-shaped as in scenarios *(vi,ix)* and *(ix,ix)*, see Figures 6.4 .

The structure of the species abundance distributions for scenarios *(iii,ix)* and *(ii,ix)* can be described using the same species abundance distribution contours at the boundary abundances $x_1 = 0$, $x_1 = J$ and $x_2 = 0$ as fo scenarios *(v,ix)* and *(vi,ix)*. Moreover, for scenarios *(iii,ix)* and *(ii,ix)*, the marginal species abundance distributions in the two local communities are the same, that is, in the first local community the marginal species abundance distribution as for scenarios *(iii,ix)* and *(ii,ix)* is S-shaped and in the second local community it is U-shaped. Note, however, that the species abundance dynamics in the first local community when the species is monodominant in the second local community is S-shaped for Scenario *(iii,ix)* and reverse U-shaped for Scenario *(ii,ix)*.

On the contrary to scenario *(v,ix)*, for scenario *(iii,ix)*, the immigration process from the metacommunity dominates the immigration process between local communities. Thus, due to high number of new immigrants of different species from the metacommunity, the species monodominance in the first local community becomes less probable than for scenarios *(v,ix)*, *(vi,ix)* and *(ix,ix)*. But, the immigration intensity from the metacommunity is still too low to prevent high chance of the species extinction from the first local community.

In scenario (*ii,ix*), immigration between local community balances immigration from the metacommunity. Then due to high rate of the immigrantion between local communities, the probability of species extinction from the first local community becomes smaller when species is monodominant in the second local community. Thus, species in the first local community has higher chance of persistence when species is monodominant in the second local community.

For both scenarios (*ii,ix*) and (*iii,ix*), the additive species abundance distribution inr both local communities attains it maximal value at the zero abundance and minimal value at the abundance level $2J$. However, the probability of additive species abundance at the level $J$ for scenario (*iii,ix*) is higher than for scenario (*ii,ix*). Note also that the shape of the additive species abundance distribution in the case of scenario (*ii,ix*) is a combination of U and S shapes, and for scenario (*iii,ix*) it is a combination of U and reverse U shapes, see Figures 6.4.

For the last possible scenario in the first group, scenario (*i,ix*), the immigration probability from the metacommunity is large. As result, due to higher species turnover in the first local community the probability of the species extinction from the first local community is smaller than the probability of species persistence. The species abundance distribution in the first local community attains properties of type (*i*), that is, the species abundance distribution in the first local community is reverse U-shaped when the species is absent and monodominant in the second local community, see Figure 6.4. Furthermore, the marginal species abundance distribution in the first local community is also reverse U-shaped, whereas in the second local community it is U-shaped. The shape of the additive species abundance distribution is also closer to the reverse U shape. This means that the species is highly persistent not only in the first local community connected to the metacommunity, but also in both local communities.

Now let us consider the second group of species abundance dynamics scenarios, that is, scenarios (*i,v*), (*ii,v*) and (*v,v*). For all these scenarios, the species abundance distribution in the second (semi-isolated) local community is S-shaped when the species is absent in the first local community, and is always reverse S-shaped when the species is monodominant in the first local community. Moreover, note that for all scenarios of the second group characteristic is that the first local community impacts significantly the species abundance dynamics in the second local communities. Specifically, when the species is of zero or low abundance in the first local community, the rate of the species extinction from the second local community is the highest, and when the species is monodominant in the first local community, the rate of species extinction from the second local community is the lowest.

For scenario (*v,v*), the probability of the immigration from the metacommunity into the first local community is smaller than in scenarios (*i,v*) and (*ii,v*). The species abundance distribution in the first local community is of type (*v*), that is, it is S-shaped when the species is absent from the second local community and reverse S-shaped when the species is monodominant in the second local community. Thus, since the species abundance in both local communities is most of the time close to abundance levels (0,0) and $(J,J)$, the chance of species extinction and monodominance in both local communities is very high. This can be also confirmed by the landscape plot of species abundance distribution in both local communities and from the U-shaped plot of additive species abundance distribution, see Figure 6.4. Moreover, note from Figure 6.4 which shows the marginal species abundance distributions for both local communities that probability of species extinction from one local community and monodominance in the other local community is also relatively high.

For scenario *(ii,v)* we can observe that when the immigration from the metacommunity increases, the species abundance dynamics starts to change in the first local community when the species is monodominant in the second local community. The shape of the species abundance distribution in the first local community when $x_2 = J$ is reverse U-shaped, and the marginal species abundance distribution in this local community becomes is S-shaped, see Figure 6.4. As a result of higher rate of immigration of other species in the first local community, the probability of species monodominance in it decreases significantly in comparison to scenario *(v,v)*. However, because the intensity of immigration is relatively small, species extinction from the first local community as well as from both local communities is observed. The S-shaped plot for additive species abundance distribution also shows that the chance of species monodominance in both local communities is much lower than the species extinction from both of them, see Figure 6.4.

For the last scenario *(i,v)* in second group, the rate of immigration from the metacommunity is very high. This affects both local communities in such a way that species becomes highly persistent in both of local communities. Figure 6.4 show the reverse U-shaped marginal and additive species abundance distributions as well as the landscape and contour plots characteristic for local communities in which species are most of time present in both local communities; and for which the chance of species extinction is very small.

### 6.5.2 Correlation between species abundances in two local communities

The similarity between species abundance dynamics in two local communities can be evaluated using correlation coefficient between them. This correlation coefficient can be easily calculated from the probability density of species abundances in both local communities using equation (16).

Figure 6.5 shows the plot of correlation between species abundances in two local communities as a function of immigration probabilities $m^m$ and $m^l$. From this figure, one can clearly see that for very small probability of immigration from the metacommunity $m^m$, the correlation between species abundance in two local communities is close to 1, and for very small probability of immigration between local communities $m^l$, the correlation between species abundances in two local communities is close to 0.

To explain high correlation between species abundances in two local communities for small values of immigration probability $m^m$, let us consider the limiting case for the immigration from the metacommunity, that is, consider local communities with no immigration from the metacommunity. Similarly to the case of only one local community considered in (Hubbell, 2001; Babak, 2006), for isolated local communities from the metacommunity ($m^m = 0$) the abundance dynamics for species possesses two absorbing states corresponding to either extinction of the species from both local communities, or monodominance in them. When the species abundance in both local communities becomes equal to (0,0) or $(J,J)$, the correlation coefficient between species abundances in such two deterministic local communities is equal to 1, that is, there is a perfect linear correlation between local communities. If the local communities are very weakly connected to the metacommunity, i.e., $m^m$ is very small, the analogous patterns of the species abundance dynamics are observed to the case when $m^m = 0$, and, therefore, the correlation coefficient between species abundances in both local communities is close to 1.

Small correlation between species abundances in two local communities can be explained by considering mutually isolated local communities, i.e., $m^l = 0$. In the mutually isolated local communities the species abundance dynamics in the semi-isolated (second) local community possesses two absorbing states at the levels 0 and $J$, and the species abundance dynamics in the non-isolated (first) local community is independent of the species abundance dynamics in the semi-isolated local community. Thus, when $m^l = 0$, the species abundances in the local communities are changing independently each of other. As result, the correlation between species abundances is zero. If the connection between local communities is very weak, the species abundance dynamics in one local community is almost independent in the other local community. Thus, the correlation coefficient in this case is very small.

From Figure 6.5 we can also conclude that when the probability of immigration from the metacommunity is fixed, the correlation increases with increase in the immigration between local communities. This is because the similarity of species abundance dynamics in two local communities increases with increase in the intensity of immigration between local communities. On the other hand, when the probability of immigration between local communities is fixed, the correlation between local communities reduces with increase in the immigration from the metacommunity. This is due to the fact that balance between local and global immigration processes is shifted towards the prevalence of the immigration from the metacommunity, resulting in less similarity in the species abundance composition for both local communities.

In general, when analyzing different scenarios for species abundance dynamics, we, however, noticed that for each scenario the range of possible correlation coefficients between species abundances in two local communities is large. The values of the correlation coefficient for the same scenario can even vary from 0 to 1, for example, this is observed for scenarios (*ix,ix*) and (*vi,ix*) with $\omega_i < 1/2$; and for scenarios (*ix,ix*) and (*viii,ix*) with $\omega_i > 1/2$. Thus, only based on the value of correlation between species abundances in local communities it is impossible to predict the type of species abundance dynamics in these local communities. However, some analysis of the similarity between species abundance dynamics in two local communities with respect to for different scenarios can be performed. For example, if $\omega_i < 1/2$ we can note that the value of the correlation coefficient is high and the species abundance structures in the local communities are more similar to each other for scenarios $(v, v)$ and $(v, ix)$ than for scenario $(iii, ix)$.

## 6.6 Conclusions and discussion

In this chapter we have proposed a new model for species abundance dynamics in two local communities. The local communities under investigation are connected to each other and semi-isolated from the metacommunity, that is, only one of the local communities obtains immigrants from the metacommunity directly. The metacommunity is thought as a large source of organisms of different species with constant fractions of species abundances. The model is formulated in accordance with specifications set up by Hubbell theory for species abundance dynamics in zero-sum local community. The species in the proposed model are considered to be neutral, that is, individuals of different species are assumed to have the same birth-death-immigration characteristics and no trophic hierarchy.

To analyze the model for species abundance dynamics we applied a continuous probabilistic approach based on the Kolmogorov-Fokker-Planck forward equation for the distribution of species abundances in two local communities. Note that similar approach was used for analysis of species abundance dynamics in one zero-sum local community (Babak, 2006); however, for two local communities the model has higher dimensionality, and requires more thorough analysis than the model for only one local community.

The main objective of this chapter was to analyze the species abundance dynamics based on the equilibrium state of the species abundance distribution in two local communities. Under the equilibrium state of the species abundances in two local communities the long time behavior of the species abundances can be understood.

The investigation of the equilibrium species abundance distribution we started from considering the properties of the boundary conditions for the steady state problem of the Kolmogorov-Fokker-Planck forward model. We first investigated the effect of the species abundance in one local community on the species abundance distribution in the other local community, particularly, for each local community we found such values of the species abundance that the change in the species abundance distribution in the other connected local community is not significant when the species is absent or monodominant in it. The outcome of the analysis of the species abundances distributions at the boundary levels was a realistic classification of the species abundance distributions in both local communities with respect to different ecological characteristics such as immigration probabilities, species representation in the metacommunity and, of course, the size of local communities. Based on different types of the species abundance distribution in the local communities, we defined several scenarios of the species abundance dynamics in both local communities. Different scenarios of species abundance dynamics were distinguished with respect to such ecological characteristics as species persistence, extinction and monodominance in one or both local communities. Such characterization of species abundance dynamics in local communities allowed us to predict the species abundance in local communities and also to define the needs in conservation actions to prevent species extinction.

In this chapter, similarities of species abundance dynamics in two local communities were investigated using correlation coefficient between species abundances in both local communities. It was found that for fixed probability of immigration from the metacommunity, the correlation increases with increase in the rate of immigration between local communities; whereas, for fixed probability of immigration between local communities, the correlation decreases with increase in the immigration from the metacommunity. It was also observed that the type of species abundance dynamics in both local communities cannot be determined based on similarity or dissimilarity between species abundance in two local communities, since the ranges of the correlation coefficients overlap for most of the species abundance scenarios.

To sum up, the chapter we would like to underline that the model for species abundance dynamics in two semi-isolated local communities proposed in this chapter allow to understand more deeply the processes in connected through immigration local habitats or islands. This model can be considered as a link between spatially implicit and spatially explicit models of species abundance dynamics, since introduction of spatial characteristics requires discretization of ecological communities or habitats into two or more small component parts. The proposed model is applicable to the case when a large living habitat can be divided into a network of small local habitats, which contains two types of communities: non-isolated communities connected with all other habitats in the network through immigration process and partially (semi-) isolated communities connected only to some other but not all communities in the network. We are confident that the results presented here will be useful for landscape ecology, particularly for the study of population dynamics in fragmented landscapes, and conservation management.

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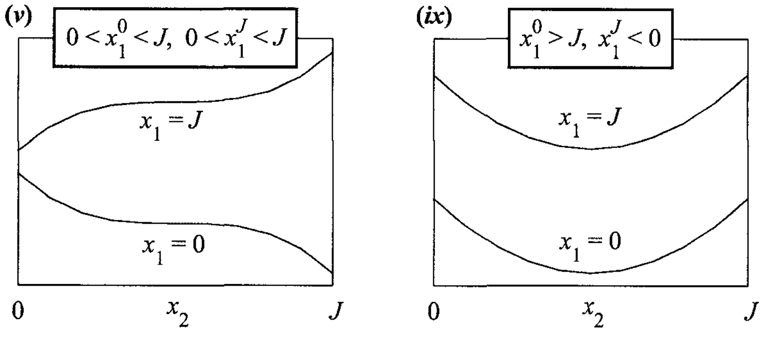

Figure 6.1: The shapes of the probability density of species abundance in the second (semi-isolated) local community if the species is absent $x_1 = 0$ (lower line) and monodominant $x_2 = J$ in the first local community. These shapes are constructed based on the values $x_1^0$ and $x_1^J$ with respect to location on the interval $[0, J)$. Possible combinations $(v)$ and $(ix)$ are independent of the value of the metacommunity relative abundance $\omega_i$.

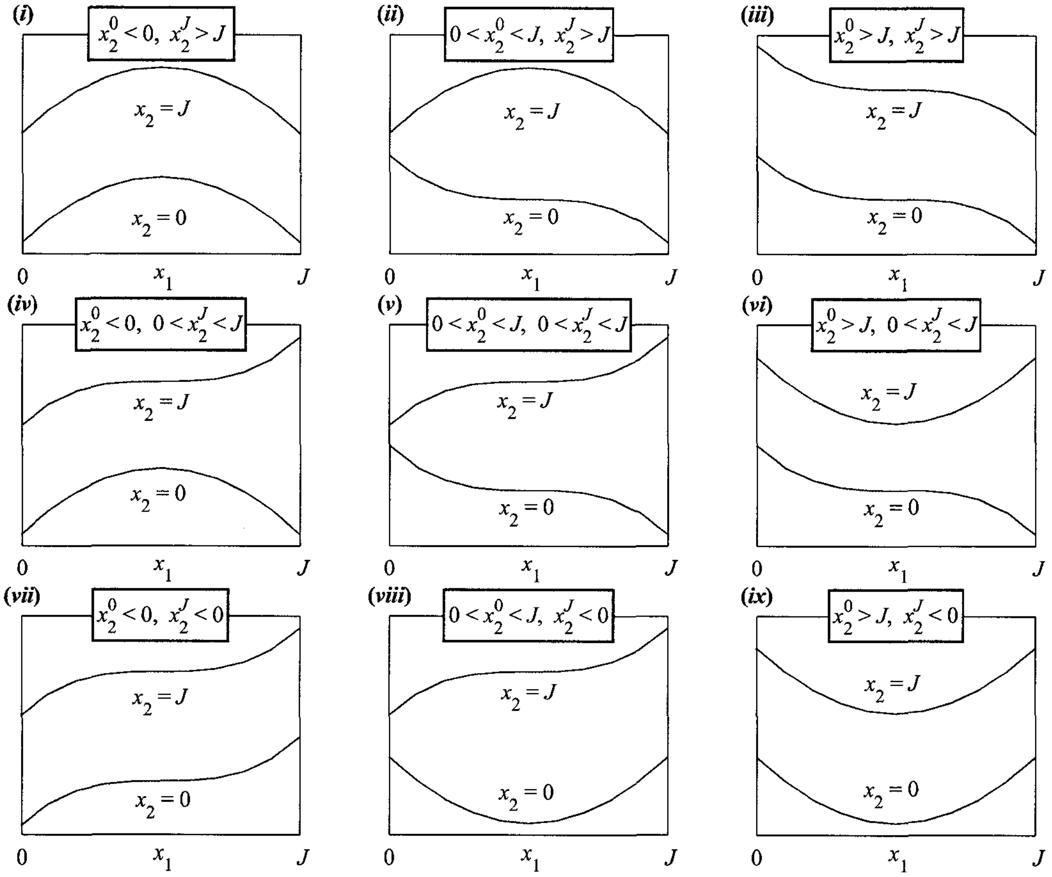

Figure 6.2: The shapes of the probability density of species abundance in the first (non-isolated) local community if the species is absent $x_2 = 0$ (lower line) and monodominant $x_2 = J$ in the second local community. These shapes are constructed based on the values $x_2^0$ and $x_2^J$ with respect to location on the interval $[0, J)$. Possible combinations for $\omega_i < 1/2$ are in the upper triangle of the figure, i.e., cases (*i*)-(*iii*), (*v*), (*vi*) and (*ix*). Possible combinations for $\omega_i \geq 1/2$ are in the lower triangle of the figure, i.e., cases (*i*), (*iv*), (*v*) and (*vii*)-(*ix*).

Table 6.1: The conditions for parameters of the model required for each possible species abundance dynamics scenario. Here $m_J^l = \frac{2J}{(2J-1)(J+1)}$ and

$$m_{J,\omega}^m(m^l) = \frac{\frac{2J}{J+1} - m^l}{2\omega(J-1)+1}.$$

| | Community 2 | | Community 1 | |
|---|---|---|---|---|
| Scenario | Type | Condition | Type | Condition |
| $(i,v)$ | $(v)$ | $m^l > m_J^l$ | $(i)$ | $m^m > \max\{m_{J,\omega_i}^m(m^l), m_{J,1-\omega_i}^m(m^l)\}$ |
| $(ii,v)$ | | | $(ii)$ | $m_{J,1-\omega_i}^m(m^l) < m^m < m_{J,\omega_i}^m(m^l)$ |
| $(iv,v)$ | | | $(iv)$ | $m_{J,\omega_i}^m(m^l) < m^m < m_{J,1-\omega_i}^m(m^l)$ |
| $(v,v)$ | | | $(v)$ | $m^m < \min\{m_{J,\omega_i}^m(m^l), m_{J,1-\omega_i}^m(m^l)\}$ |
| $(i,ix)$ | $(ix)$ | $m^l < m_J^l$ | $(i)$ | $m^m > \max\{m_{J,\omega_i}^m(m^l), m_{J,1-\omega_i}^m(m^l)\}$ |
| $(ii,ix)$ | | | $(ii)$ | $\max\left\{m_{J,1-\omega_i}^m(m^l), m_{J,\omega_i}^m((2J-1)m^l)\right\} < m^m < m_{J,\omega_i}^m(m^l)$ |
| $(iii,ix)$ | | | $(iii)$ | $m_{J,1-\omega_i}^m(m^l) < m^m < m_{J,\omega_i}^m((2J-1)m^l)$ |
| $(iv,ix)$ | | | $(iv)$ | $\max\left\{m_{J,\omega_i}^m(m^l), m_{J,1-\omega_i}^m((2J-1)m^l)\right\} < m^m < m_{J,1-\omega_i}^m(m^l)$ |
| $(v,ix)$ | | | $(v)$ | $\max\{m_{J,\omega_i}^m((2J-1)m^l), m_{J,1-\omega_i}^m((2J-1)m^l)\} < m^m$<br>$< \max\{m_{J,\omega_i}^m(m^l), m_{J,1-\omega_i}^m(m^l)\}$ |
| $(vi,ix)$ | | | $(vi)$ | $m_{J,1-\omega_i}^m((2J-1)m^l) < m^m <$<br>$< \min\left\{m_{J,1-\omega_i}^m(m^l), m_{J,\omega_i}^m((2J-1)m^l)\right\}$ |
| $(vii,ix)$ | | | $(vii)$ | $m_{J,\omega_i}^m(m^l) < m^m < m_{J,1-\omega_i}^m((2J-1)m^l)$ |
| $(viii,ix)$ | | | $(viii)$ | $m_{J,\omega_i}^m((2J-1)m^l) < m^m <$<br>$< \min\left\{m_{J,\omega_i}^m(m^l), m_{J,1-\omega_i}^m((2J-1)m^l)\right\}$ |
| $(ix,ix)$ | | | $(ix)$ | $m^m < \min\{m_{J,\omega_i}^m((2J-1)m^l), m_{J,1-\omega_i}^m((2J-1)m^l)\}$ |

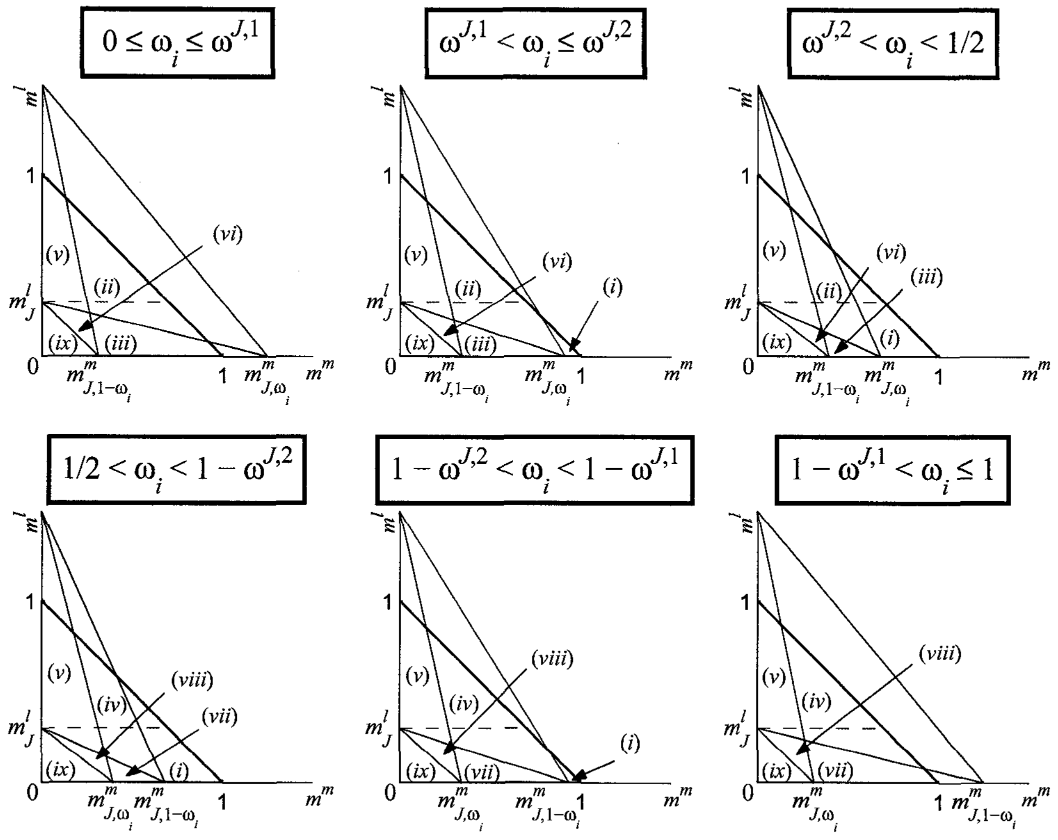

Figure 6.3: The effect of the metacommunity relative abundance $\omega_i$ on possible type $(i_1, i_2)$ of the species abundance density in both local communities based on the types of the species abundance distribution in each local community given the species is absent or monodominant in the other local community. The horizontal dashed line splits the two possible types $i_2 = (v)$ and $i_2 = (ix)$ of the species abundance distributions in the second local community when the species is absent or monodominant in the first local community, that is, $i_2 = (v)$ if $m^l > m^l_J$, and $i_2 = (ix)$ if $m^l < m^l_J$, where $m^l_J = \dfrac{2J}{(2J-1)(J+1)}$.

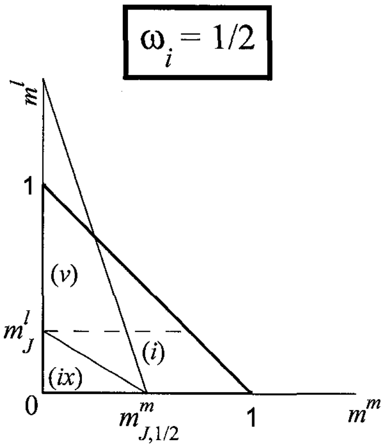

Figure 6.3. Cont. The possible type of the species abundance distribution in the first local community $T_1$ when the species is absent or monodominant in the second local community are restricted by the sum of the nonnegative values of the immigration probabilities $m^m$ and $m^l$ which is not larger than 1 and are defined separately with respect to the value $T_2$, or either the pair $(m^m, m^l)$ is above or below the line $m^l = \frac{2J}{(2J-1)(J+1)}$. The range of the metacommunity relative abundance $\omega_i$ is divided into seven parts with respect to the values $\omega^{J,1} = \frac{1}{2(J+1)}$ and $\omega^{J,2} = \frac{2J-1}{2(J-1)(2J+1)}$. The intermediate values of the immigration probability $m^m$ when $m^l = 0$ are defined using the relationship $m^m_{J,\omega} = \frac{2J}{(2\omega(J-1)+1)(J+1)}$.

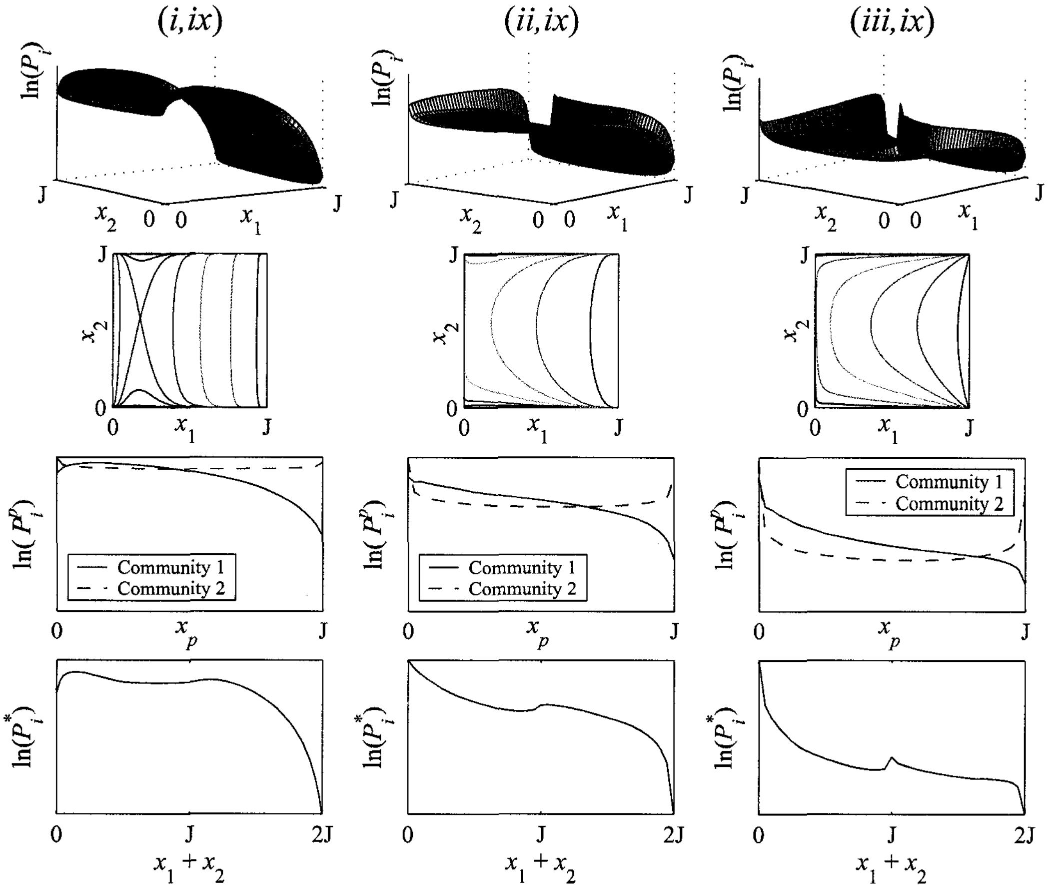

Figure 6.4:. Illustration of possible scenarios for species abundance probability density in two semi-isolated local communities with respect to different values of the immigration probabilities $m^m$ and $m^l$. The local communities are of the size $J = 200$ with the same frequencies of the death events $\mu_1 = \mu_2$. The species metacommunity relative abundance is $\omega_i = 0.2 < 1/2$. Figures in the first row show the landscape log-plots and figures in the second row show the contour plots for the equilibrium species abundance probability densities obtained using numerical approximations for problem (11)-(13). The values of the immigration probabilities are chosen to be the following: $(i,ix)$ $m^m = 0.1$, $m^l = 0.002$; $(ii,ix)$ $m^m = 0.02$, $m^l = 0.002$; $(iii,ix)$ $m^m = 0.01$, $m^l = 0.002$.

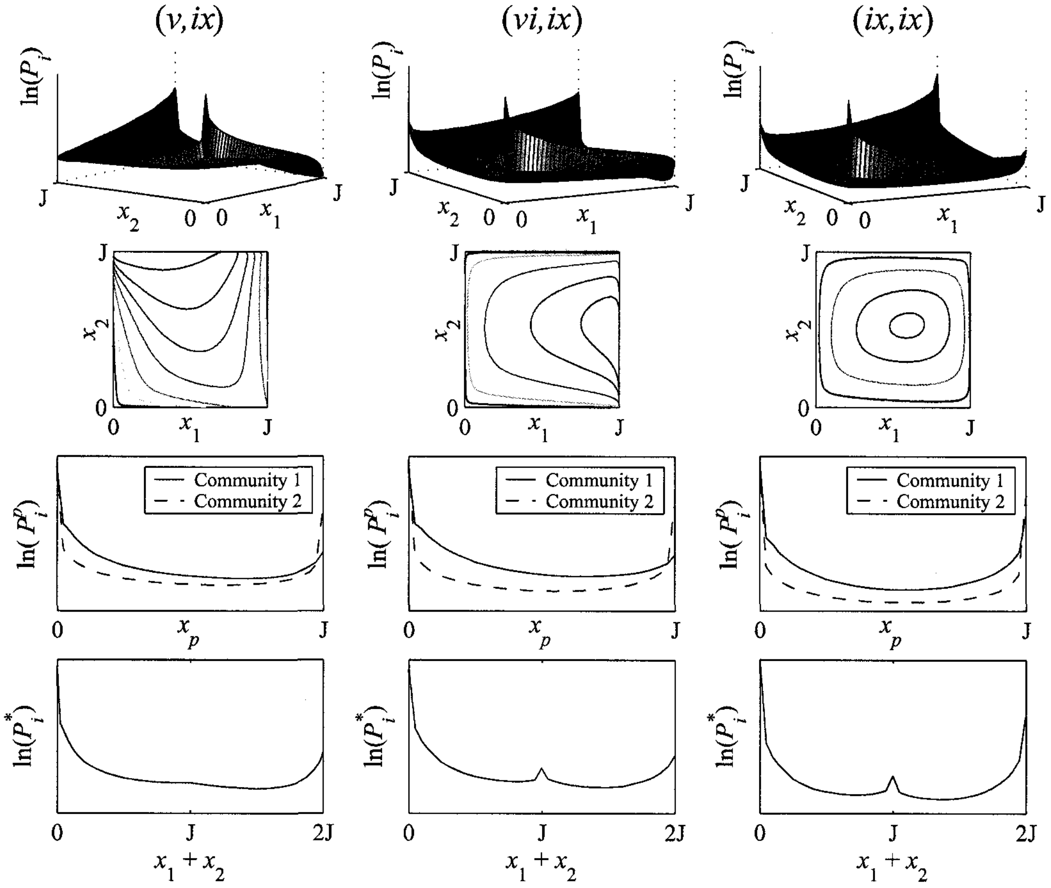

Figure 6.4: Cont. Figures in the third row show the equilibrium marginal probability density functions for the species abundance in the first and second local communities and figures in the forth row show the additive equilibrium species abundance probability functions calculated using Equation (15). The values of the immigration probabilities are chosen to be the following: $(v,ix)$ $m^m = 0.005$, $m^l = 0.0045$; $(vi,ix)$ $m^m = 0.005$, $m^l = 0.002$; $(ix,ix)$ $m^m = 0.002$, $m^l = 0.002$.

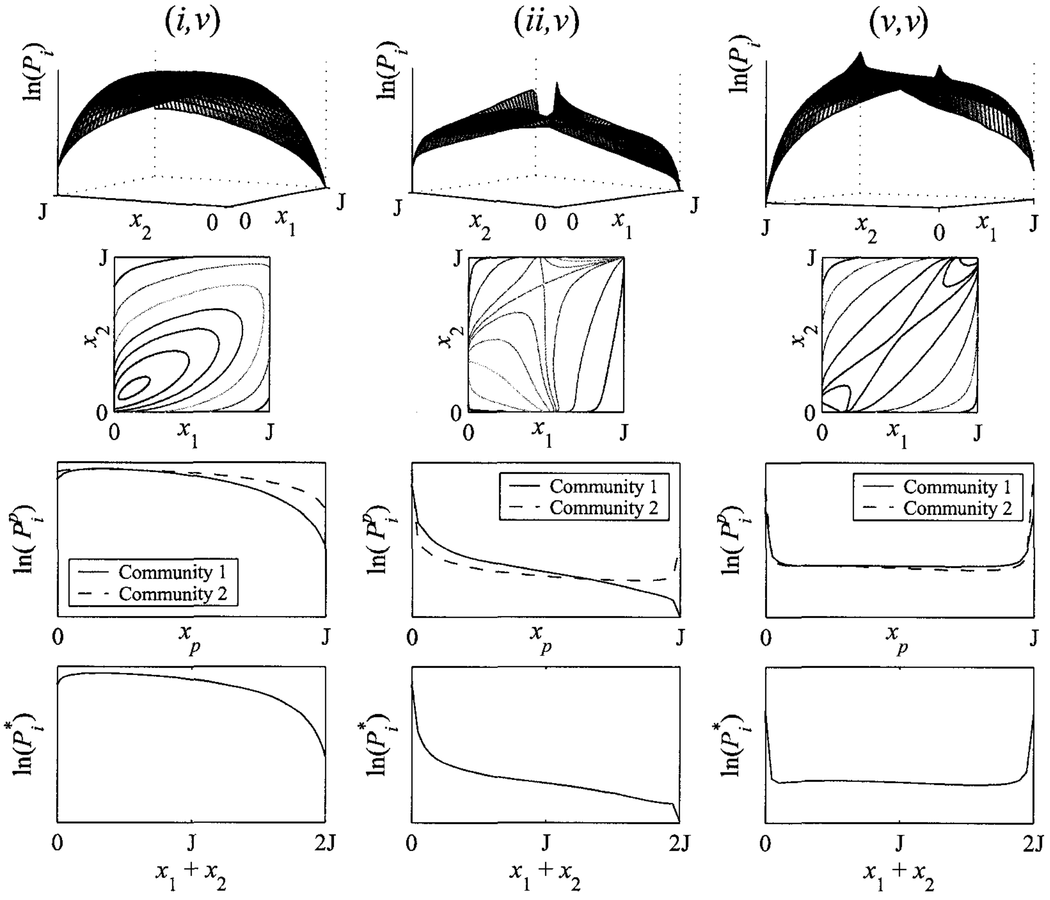

Figure 6.4: Cont. The values of the immigration probabilities are chosen to be the following: (*i*,*v*) $m^m = 0.1$, $m^l = 0.1$; (*ii*,*v*) $m^m = 0.01$, $m^l = 0.01$; (*v*,*v*) $m^m = 0.005$, $m^l = 0.05$.

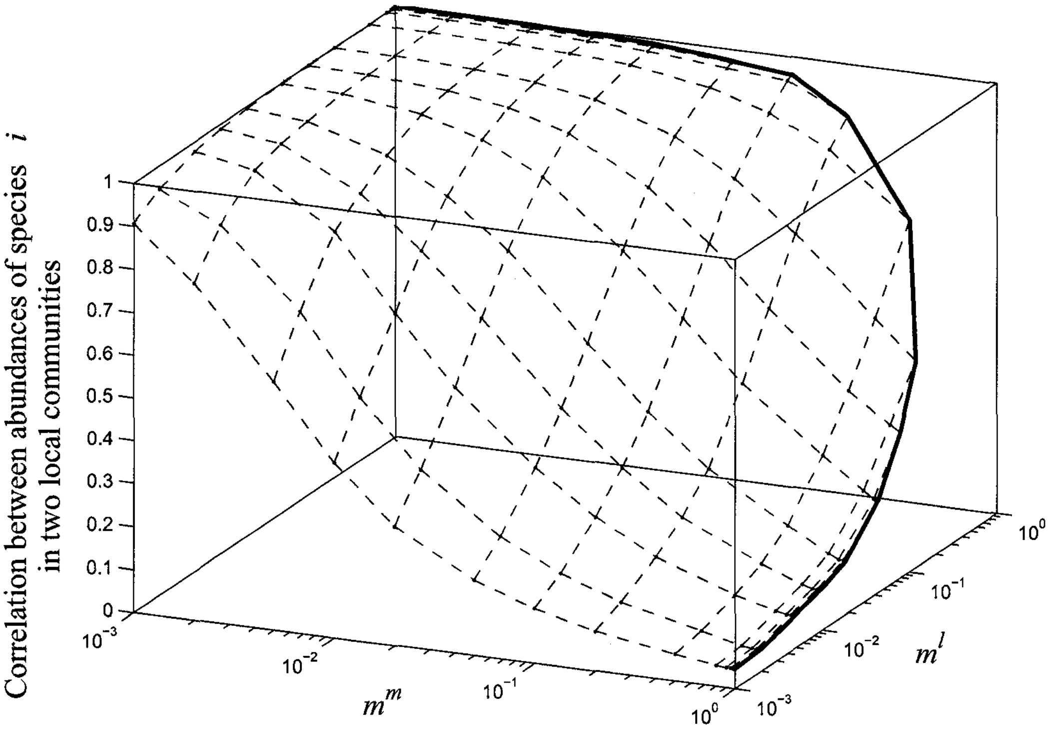

Figure 6.5: Correlation between abundance of species $i$ in two semi-isolated local communities as a function of probability of immigration from the metacommunity $m^m$ and from another local community $m^l$, $m^m + m^l \leq 1$. The size of local community $J = 200$ and the metacommunity species relative abundance $\omega_i = 0.2$.

# Chapter 7

# Species extinction time and probability in two semi-isolated local communities

## 7.1 Introduction

Neutral theory may be used to provide general insights into how species respond to spatially structured and nonhomogeneous habitats (Chave and Leigh Jr. 2002, Ovaskainen and Hanski 2003, Sole et al. 2004, Gilbert et al. 2006). The effect of spatial structure on the species distribution in living communities can be measured using different biodiversity indices (Chave and Leigh Jr. 2002, Condit et al. 2002, Borda-de Agua et al. 2002). Another important group of quantities for measure of the species dynamics in living communities is related to extinction processes (Hubbell 2001, Lande et al. 2003, Ginzburg et al. 1982, Grimm and Wissel 2004, etc.). This group of measures includes extinction time [mean variance, distribution] (Lande et al. 2003, Newman et al. 2004), probability of extinction [risk of extinction] (Lande 1993), extinction thresholds (Keymer et al. 2000, Ovaskainen and Hanski 2003), and persistence probability (Grimm and Wissel 2004).

Several various analytic, numerical and statistic methods were applied for analysis of extinction processes in living communities, including parametric and non-parametric estimation (Solow 2005), maximum likelihood methods (Ludwig 1996a), Bayesian analysis (Solow 1993, Ludwig 1996b), Fourier series analysis (Newman and Eble 1999), time series analysis (Hakoyama and Iwasa 2000), diffusion approximations (Lande et al. 2003). However, relatively smaller attention was addressed to investigation of extinction processes in neutral theory (Leigh 1981, Hubbell 2001, Ricklefs 2003, 2006, Nee 2005, Rosenzweig 1995).

In this chapter the relationships between the extinction processes, and immigration and demographic processes are investigated for structured neutral local communities, using a neutral model for the species abundance dynamics in two semi-isolated local communities, that is, such local communities that are connected with each other but only one of local communities is connected to the metacommunity through immigration. The investigation of species abundance dynamics for this model was performed in Chapter 6 based on the sensitivity analysis of the equilibrium species abundance distributions in two local communities with respect to immigration and demographic factors. In Chapter 6, a continuous probabilistic approach was used to investigate the species abundance dynamics in two local communities, and proposed a realistic classification of species abundance behavior in local communities subject to different chances of species extinction, monodominance and persistence.

This chapter is addressed to the study of extinction time and probability of species in two semi-isolated local communities of the same size by means of a continuous probabilistic approach. Using Kolmogorov-Fokker-Planck backward equation, I derive models for the species persistence probability in two local communities, and the average first time to species extinction. I consider two scenarios for species extinction: species extinction from one given local community (from only non-isolated or only semi-isolated local community), and species extinction from either the non-isolated or semi-isolated local community. In addition, I calculate the probability of species extinction from one local community before the other local community for different species abundances in two local communities. Using this probability I can answer the question from each local community the species would most likely go extinct first. Finally, I make a comparison analysis of species extinction dynamics in two local communities and in one local community. This analysis gives us an example of comparison between species abundance dynamics in spatially structured ecological communities (ecological communities involving interaction between many different neighboring habitat patches) and unstructured ecological communities (ecological communities with no spatial factors). The main question of this comparison study is whether spatial structure or more complex geometry of habitat interactions (Thrall et al. 2003, Park et al. 2002, Wiegand et al. 2002, McCarthy 1996, Lehtinen et al. 2003) has and important effect on the species persistence in local community.

This chapter is organized as follows. In Section 7.2, I recall the formulation of the model for species abundance dynamics in two semi-isolated local communities, that is, such connected with each other local communities that only one of them is connected to the metacommunity through immigration (see Chapter 6). In Section 7.3, the model for distribution of the first time to species extinction is derived using Kolmogorov-Fokker-Planck backward equation. Based on this model, the average first time to species extinction and higher moments of the first time to species extinction are calculated for two problems. In the first problem the extinction of the species is considered from only non-isolated local community or from only semi-isolated local community, and in the second problem the extinction of the species is considered from either semi-isolated or non-isolated local community. In Section 7.4, the model for probability of species extinction from one local community before the species extinction from the other local community is developed. In Section 7.5, the sensitivity analysis for the average extinction time and the probability of extinction from one local community before the other local community is provided with respect to such ecological characteristics as immigration probability between local communities and immigration probability from the metacommunity. Finally, in Section 7.6, the comparison study is performed for the time to species extinction from the non-isolated local community (connected to both the other local community and to the metacommunity), the time to species extinction from semi-isolated local community (connected only to the other local community) and the time to species extinction from the local community connected only to the metacommunity.

## 7.2 Discrete model for species abundance dynamics in two semi-isolated local communities

The model for species abundance dynamics in two semi-isolated local communities of the same size connected through immigration with each other and with the metacommunity is derived in Chapter 6. In this model the local communities are semi-isolated from the metacommunity, that is, only one of the two local communities, say, the first local community, can obtain immigrants from the metacommunity. Further, we will refer to the first local community as non-isolated local community, and to the second local community as semi-isolated local community. The discrete model for species abundance dynamics in this case is formulated as follows.

Let denote the size of local communities by $J$, and the number of individuals of species $i$ in the first and second local communities by $N_{1,i}$ and $N_{2,i}$, respectively. Then the change in the number of individuals of species $i$ per unit time step in the first (non-isolated) local community is defined using the following transition probabilities

$$\begin{aligned} W_{1,i}(N_1-1\,|\,N_1,N_2) &= \frac{N_1}{J}\left((1-m^m-m^l)\frac{J-N_1}{J-1}+m^m(1-\omega_i)+m^l\frac{J-N_2}{J}\right), \\ W_{1,i}(N_1+1\,|\,N_1,N_2) &= \frac{J-N_1}{J}\left((1-m^m-m^l)\frac{N_1}{J-1}+m^m\omega_i+m^l\frac{N_2}{J}\right), \\ W_{1,i}(N_1\,|\,N_1,N_2) &= 1-W_{1,i}(N_1-1\,|\,N_1,N_2)-W_{1,i}(N_1+1\,|\,N_1,N_2), \end{aligned} \tag{1}$$

where $N_r = N_{r,i}$, $r = 1,2$; $\omega_i$ is a fractional metacommunity relative species abundance of species $i$, $m^m$ is the probability that a death in the first local community will be replaced by an immigrant from the metacommunity and $m^l$ is the probability that a death in a local community will be replaced by an immigrant from another local community, $m = m^m + m^l$.

The change in the number of individuals of species $i$ per unit time step in the second (semi-isolated) local community is defined similarly using the following transition probabilities

$$
\begin{aligned}
&W_{2,i}(N_2-1\mid N_1,N_2)=\frac{N_2}{J}\left((1-m^l)\frac{J-N_2}{J-1}+m^l\frac{J-N_1}{J}\right),\\
&W_{2,i}(N_2+1\mid N_1,N_2)=\frac{J-N_2}{J}\left((1-m^l)\frac{N_2}{J-1}+m^l\frac{N_1}{J}\right),\\
&W_{2,i}(N_2\mid N_1,N_2)=1-W_{2,i}(N_2-1\mid N_1,N_2)-W_{2,i}(N_2+1\mid N_1,N_2).
\end{aligned}
\tag{2}
$$

Moreover, if we assume that the species abundance dynamics in one local community is independent of the species abundance dynamics in another local community. Then, the transition probabilities for dynamics of species $i$ in both local communities are defined as follows

$$
W_i(N_1+\Delta_1,N_2+\Delta_2\mid N_1,N_2)=W_{1,i}(N_1+\Delta_1\mid N_1,N_2)\times W_{2,i}(N_2+\Delta_2\mid N_1,N_2) \tag{3}
$$

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

In order to derive the continuous model for species abundance distribution in two zero-sum local communities, we define the transition probabilities for the change $\Delta N_{p,i}$ of the number of individuals $N_{p,i}$ of the $i$th species in local community $p$, $p=1,2$ per time step $\Delta t$ as

$$
\begin{aligned}
&\Pr\left(\Delta N_{p,i}=\pm1\mid N_{p,i}=N_p,N_{q,i}=N_q\right)=\mu_p\Delta t W_{p,i}\left(N_p\pm1\mid N_p,N_q\right),\\
&\Pr\left(\Delta N_{p,i}=0\mid N_{p,i}=N_p,N_{q,i}=N_q\right)=1-\Pr\left(\Delta N_{p,i}=1\mid N_{p,i}=N_p,N_{q,i}=N_q\right)\\
&\qquad\qquad\qquad\qquad\qquad\qquad\qquad-\Pr\left(\Delta N_{p,i}=-1\mid N_{p,i}=N_p,N_{q,i}=N_q\right),
\end{aligned}
\tag{4}
$$

where $\mu_p$ is the number of death events per unit time interval in local community $p$.

Then the joint transition probabilities for the change in the species abundance in both local communities are the following

$$
\begin{aligned}
&\Pr\left(\Delta N_{1,i}=\Delta_1,\Delta N_{2,i}=\Delta_2\mid N_{1,i}=N_1,N_{2,i}=N_2\right)\\
&\quad=\Pr\left(N_{1,i}=\Delta_1\mid N_{1,i}=N_1,N_{2,i}=N_2\right)\times\Pr\left(N_{2,i}=\Delta_2\mid N_{2,i}=N_2,N_{1,i}=N_1\right)
\end{aligned}
\tag{5}
$$

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

Let us denote the change in the abundance of the $i$th species in both local communities per time step $\Delta t$ as a vector $\Delta N_i=(\Delta N_{1,i},\Delta N_{2,i})$, where $\Delta N_{p,i}=N_{p,i}(t+\Delta t)-N_{p,i}(t)$, $p=1,2$; and let $N_i=(N_{1,i},N_{2,i})$ and $x=(x_1,x_2)$.

Because the species abundance in one local community per one time step $\Delta t$ changes only by one individual or remain the same, the variables $\Delta N_{p,i}$ can attain only values -1,0 and 1. And therefore the mean and the second moment of the change in the abundance of the $i$th species per infinitely small time interval $\Delta t$ can be calculated as

$$
V(x)=\begin{pmatrix}V_1(x)\\V_2(x)\end{pmatrix}=\lim_{\Delta t\to0}\frac{1}{\Delta t}\begin{pmatrix}E(\Delta N_{1,i}\mid N_i=x)\\E(\Delta N_{2,i}\mid N_i=x)\end{pmatrix},
$$

$$D(x)=\begin{pmatrix} D_{11}(x) & D_{12}(x) \\ D_{21}(x) & D_{22}(x) \end{pmatrix} = \lim_{\Delta t\to 0}\frac{1}{\Delta t}\begin{pmatrix} E(\Delta N_{1,i}{}^2 \mid N_i = x) & E(\Delta N_{1,i}\Delta N_{2,i} \mid N_i = x) \\ E(\Delta N_{1,i}\Delta N_{2,i} \mid N_i = x) & E(\Delta N_{2,i}{}^2 \mid N_i = x) \end{pmatrix},$$

where

$$V_1(x) = \mu_1 m^m\left(\omega_i - \frac{x_1}{J}\right) + \mu_1 m^l\left(\frac{x_2}{J} - \frac{x_1}{J}\right), \qquad V_2(x) = \mu_2 m^l\left(\frac{x_1}{J} - \frac{x_2}{J}\right); \tag{6}$$

$$D_{11}(x) = \mu_1\left( 2(1-m^m-m^l)\frac{x_1(J-x_1)}{J(J-1)} + m^m(1-\omega_i)\frac{x_1}{J} + m^m\omega_i\frac{J-x_1}{J} + \right.$$
$$\left. + m^l\frac{J-x_2}{J}\frac{x_1}{J} + m^l\frac{x_2}{J}\frac{J-x_1}{J}\right),$$

$$D_{22}(x) = \mu_2\left( 2(1-m^l)\frac{x_2(J-x_2)}{J(J-1)} + m^l\frac{J-x_1}{J}\frac{x_2}{J} + m^l\frac{x_1}{J}\frac{J-x_2}{J}\right),$$

$$D_{12}(x) = D_{21}(x) = 0\,. \tag{7}$$

## 7.3 Distribution of Persistence and extinction times. Kolmogorov-Fokker-Planck backward equation

Let us now define the abundances $x_1$ and $x_2$ of species $i$ in the first (non-isolated) and second (semi-isolated) local communities as a continuous variables allowing any real values from the interval $[0,J]$; and let $p_i(y,s\mid x,t)$ be the probability density that species $i$ has abundance $y=(y_1,y_2)$ in both local communities at time $s$ given the abundance $x=(x_1,x_2)$ of species $i$ at time $t$, $t\le s$.

Then we can define the probability,

$$G_i(x,t;\tilde{\Omega}) = \iint_{\tilde{\Omega}} p_i(\xi,t\mid x,0)\mathrm{d}\xi\,, \tag{8}$$

that the abundance of species $i$ at time $t$ remains in the abundance domain $\tilde{\Omega}\subseteq\Omega=(0,J)\times(0,J)$ given the abundance $x=(x_1,x_2)\in\tilde{\Omega}$ of species $i$ at time 0, as a solution of the Kolmogorov backward equation (Gardiner, 1983)

$$\frac{\partial G_i}{\partial t} = \frac{1}{2}\left(D_{11}\frac{\partial^2 G_i}{\partial x_1{}^2} + D_{22}\frac{\partial^2 G_i}{\partial x_2{}^2}\right) + V_1\frac{\partial G_i}{\partial x_1} + V_2\frac{\partial G_i}{\partial x_2}, \quad x\in\tilde{\Omega}, \quad t>0, \tag{9}$$

where $V$ and $D$ are the first and second moments of the change in the abundance of species $i$ per time step $\Delta t$ as $\Delta t\to 0$ defined in (6) and (7).

Since at the initial time moment, say at time 0, the species abundance in both local communities belongs to the abundance domain $\tilde{\Omega}$ (the probability that the species abundance belongs to the domain $\tilde{\Omega}$ is 1), the following initial condition is imposed

$$G_i(x,0) = 1, \quad x \in \tilde{\Omega}. \tag{10}$$

Depending on the ecological formulation of the problem we set either absorbing or reflecting boundary conditions. In general, let $\tilde{\Gamma}$ be the boundary of the species abundances domain $\tilde{\Omega}$, and let $\tilde{\Gamma} = \tilde{\Gamma}_{abs} \cup \tilde{\Gamma}_{ref}$, where $\tilde{\Gamma}_{abs}$ and $\tilde{\Gamma}_{ref}$ denote absorbing and reflecting parts of the boundary $\tilde{\Gamma}$, and $\varnothing = \tilde{\Gamma}_{abs} \cap \tilde{\Gamma}_{ref}$. Then at the absorbing boundary $\tilde{\Gamma}_{abs}$ of the abundance domain $\tilde{\Omega}$ we assume that

$$G_i = 0, \quad x \in \tilde{\Gamma}_{abs}, \quad t \geq 0, \tag{11}$$

and at the reflecting boundary $\tilde{\Gamma}_{ref}$, the boundary condition is

$$D_{11}\frac{\partial G_i}{\partial x_1}n_1 + D_{22}\frac{\partial G_i}{\partial x_2}n_2 = 0, \quad x \in \tilde{\Gamma}_{ref}, \quad t \geq 0, \tag{12}$$

where the vector $\vec{n} = (n_1, n_2)$ is the outward normal to the boundary of the domain $\tilde{\Omega}$ defined on $\tilde{\Gamma}_{ref}$.

Note that $G_i(x,t)$ defines the probability distribution of time by which species $i$ has not crossed the boundary $\tilde{\Gamma}_{abs}$ given the species abundance in both local communities $x = (x_1, x_2)$ at the initial time $t = 0$. Using this distribution we can easily calculate the probability that species $i$ will cross the boundary $\tilde{\Gamma}_{abs}$ by time $t$ as

$$F_i(x,t) = 1 - G_i(x,t). \tag{13}$$

This probability we will use to define the probability of species extinction, the mean and variance of the first passage time to species extinction etc.

Let us now consider the abundance domain $\Omega = (0,J) \times (0,J)$ in more detail. The boundary $\Gamma$ of this domain can be divided into four distinct parts $\Gamma = \Gamma^{0*} \cup \Gamma^{*1} \cup \Gamma^{1*} \cup \Gamma^{*0}$, such that $\Gamma^{0*} = \{0\} \times (0,J)$, $\Gamma^{*1} = (0,J) \times \{J\}$, $\Gamma^{1*} = \{J\} \times (0,J)$ and $\Gamma^{*0} = (0,J) \times \{0\}$. The outward normal vectors for each part of the boundary $\Gamma$ are the following: $\vec{n}^{0*} = (n_1^{0*}, n_2^{0*}) = (-1,0)$ for $\Gamma^{0*}$, $\vec{n}^{1*} = (n_1^{1*}, n_2^{1*}) = (1,0)$ for $\Gamma^{1*}$, $\vec{n}^{*0} = (n_1^{*0}, n_2^{*0}) = (0,-1)$ for $\Gamma^{*0}$, and $\vec{n}^{*1} = (n_1^{*1}, n_2^{*1}) = (0,1)$ for $\Gamma^{*1}$.

The following examples of the species abundance dynamics in two local communities can be considered.

(1) *Extinction of species $i$ from at least one local community*

Let us denote by $G_i^{1\vee2}(x,t)$ the probability that species $i$ has not gone extinct by time $t$ from any local community if at the initial time moment $t=0$ its abundance was $x$. To define the boundary conditions for $G_i^{1\vee2}$ note that the extinction of species $i$ from at least one local community occurs when its abundance reaches zero level in at least one local community, that is, the abundance of species $i$ reaches the boundary $\Gamma_{*0} \cup \Gamma_{0*}$ of the abundance domain $\Omega$. In this case $\tilde{\Omega}=\Omega$, $\tilde{\Gamma}_{abs}=\Gamma_{*0} \cup \Gamma_{0*}$ and $\tilde{\Gamma}_{ref}=\Gamma_{*1} \cup \Gamma_{1*}$, and the boundary conditions for the probability $G_i^{1\vee2}$ are the following

$$G_i^{1\vee2}=0, \quad x \in \Gamma_{*0} \cup \Gamma_{0*}, \qquad \frac{\partial G_i^{1\vee2}}{\partial x_2}=0, \quad x \in \Gamma_{*1}, \qquad \frac{\partial G_i^{1\vee2}}{\partial x_1}=0, \quad x \in \Gamma_{1*}, \quad t \geq 0. \tag{14}$$

(2) *Extinction of species i from the first (non-isolated) local community*

Let us consider extinction of species $i$ from only one local community. By $G_i^p(x,t)$ we denote the probability that species $i$ has not gone extinct by time $t$ from the $p$th local community, $p=1,2$, if at the initial time moment $t=0$ its abundance was $x$. Note that the extinction of the $i$th species from the first local community occurs when its abundance reaches zero level in this community, that is, the abundance of species $i$ reaches the boundary $\Gamma_{0*}$. Thus, $\tilde{\Omega}=\Omega$, $\tilde{\Gamma}_{abs}=\Gamma_{0*}$ and $\tilde{\Gamma}_{ref}=\Gamma_{1*} \cup \Gamma_{*0} \cup \Gamma_{*1}$. Then the boundary conditions for $G_i^1$ are the following

$$G_i^1=0, \quad x \in \Gamma_{0*}, \qquad \frac{\partial G_i^1}{\partial x_2}=0, \quad x \in \Gamma_{*0} \cup \Gamma_{*1}, \qquad \frac{\partial G_i^1}{\partial x_1}=0, \quad x \in \Gamma_{1*}; \quad t \geq 0. \tag{15}$$

(3) *Extinction of species i from the second (semi-isolated) local community*

Similarly to the problem of extinction from the first local community, we can define the boundary conditions for the problem of extinction of species $i$ from the second (semi-isolated) local community. In that case $\tilde{\Omega}=\Omega$, $\tilde{\Gamma}_{abs}=\Gamma_{*0}$, $\tilde{\Gamma}_{ref}=\Gamma_{1*} \cup \Gamma_{0*} \cup \Gamma_{*1}$ and

$$G_i^2=0, \quad x \in \Gamma_{*0}, \qquad \frac{\partial G_i^2}{\partial x_2}=0, \quad x \in \Gamma_{*1}, \qquad \frac{\partial G_i^2}{\partial x_1}=0, \quad x \in \Gamma_{0*} \cup \Gamma_{1*}; \quad t \geq 0. \tag{16}$$

Based on the probability that the abundance of species $i$ at time $t$ remains in the abundance domain $\tilde{\Omega}$ given the abundance $x=(x_1,x_2) \in \tilde{\Omega}$ of species $i$ at time 0, we can easily calculate the mean and higher moments of the first passage time to the boundary $\tilde{\Gamma}_{abs}$ of the abundance domain $\tilde{\Omega}$. The mean $T_i^1$ of the first passage time to the boundary $\tilde{\Gamma}_{abs}$ is calculated from the equation

$$\frac{1}{2}\left(D_{11}\frac{\partial^2 T_i^1}{\partial x_1{}^2}+D_{22}\frac{\partial^2 T_i^1}{\partial x_2{}^2}\right)+V_1\frac{\partial T_i^1}{\partial x_1}+V_2\frac{\partial T_i^1}{\partial x_2}=-1, \quad x \in \tilde{\Omega}, \tag{17}$$

and the $k$ th moment $T_i^k$ of the first passage time is calculated from the equation

$$\frac{1}{2}\left(D_{11}\frac{\partial^2 T_i^k}{\partial x_1^{\ 2}}+D_{22}\frac{\partial^2 T_i^k}{\partial x_2^{\ 2}}\right)+V_1\frac{\partial T_i^k}{\partial x_1}+V_2\frac{\partial T_i^k}{\partial x_2}=-T_i^{k-1},\quad x\in\tilde{\Omega}. \tag{18}$$

These equations are supplemented with the absorbing boundary condition (11) on $\tilde{\Gamma}_{abs}$ and reflecting boundary conditions (12) on $\tilde{\Gamma}_{ref}$. For each example given in Section 7.3 the boundary conditions (11) and (12) can be detailed in the same form, see Equations (14)-(16).

## 7.4 Probability of species extinction from one local community before its extinction from the other local community

Another important problem in conservation biology is in which community the species will go locally extinct first. To address this problem we denote by $Q_i^k$ the probability of extinction of species $i$ from the $p$ th local community before its extinction from the $q$ th local community, where $p=1,2$ and $q=\begin{cases}1: & p=2,\\ 2: & p=1.\end{cases}$ Then the probability that species $i$ goes extinct from the first (non-isolated) local community before the second (semi-isolated) local community can be calculated from the following equation

$$\frac{1}{2}\left(D_{11}\frac{\partial^2 Q_i^1}{\partial x_1^{\ 2}}+D_{22}\frac{\partial^2 Q_i^1}{\partial x_2^{\ 2}}\right)+V_1\frac{\partial Q_i^1}{\partial x_1}+V_2\frac{\partial Q_i^1}{\partial x_2}=0,\quad x\in\Omega, \tag{19}$$

Since the abundance level $x_1=0$ is attained when the species is extinct from the first (non-isolated) local community, the probability of extinction at this abundance level is 1, and, therefore, the boundary condition at $\Gamma_{0*}$ is the following

$$Q_i^1=1,\quad x\in\Gamma_{0*}. \tag{20}$$

On the other hand, the abundance level $x_2=0$ is attained when the species is extinct from the second (semi-isolated) local community, and the probability of extinction at this abundance level is 0

$$Q_i^1=0,\quad x\in\Gamma_{*0}. \tag{21}$$

At the boundary $\Gamma_{1*}\cup\Gamma_{*1}$ we impose the reflecting boundary conditions in the form

$$\frac{\partial Q_i^1}{\partial x_2}=0,\quad x\in\Gamma_{*1},\qquad \frac{\partial Q_i^1}{\partial x_1}=0,\quad x\in\Gamma_{1*}. \tag{22}$$

Note that for $Q_i^2$ only the boundary conditions (20) and (21) are reversed. The other way to calculate $Q_i^2$ is based on the following relationship

$$Q_i^1 + Q_i^2 = 1. \tag{23}$$

Similarly to the problem of the probability of extinction event in one local community before the extinction event in the other local community, we can consider the problem about the probability of extinction in one local community versus the probability of monodominance in the same or in the other local community. For these problems we need only to modify boundary conditions (20)-(22).

## 7.5 Sensitivity analysis

In this section the effect of the immigration probability from the metacommunity $m^m$ and the immigration probability between local communities $m^l$ on the average first time to species extinction in the local communities and on the probability of species extinction from one local community before its extinction from the other local community will be examined.

To perform the sensitivity analysis for the time to species extinction from the local community let us first recall the classification of species abundance dynamics in two semi-isolated local communities. According to this classification we distinguished nine different scenarios of the species abundance dynamics in two local communities when the species abundance in the metacommunity is relatively small, that is $\omega_i < 0.5$ (see Chapter 6). Different species abundance scenarios in two local communities are derived based on the type of the species abundance distribution in each local community.

From analysis presented in Chapter 6, it is possible to distinguish two groups of the species abundance dynamics scenarios with respect to the type of the species abundance distribution in the second (semi-isolated) local community. The first group of the species abundance dynamics scenarios includes Scenarios (i,ix), (ii,ix), (iii,ix), (v,ix), (vi,ix) and (ix,ix). For all these scenarios the chance of species extinction or monodominance in the second local community is very high. The second group of the species abundance dynamics scenarios includes Scenarios (i,v), (ii,v) and (v,v). For these scenarios the chance of species extinction from the second local community is very high if the species has low abundance in the first local community, and the chance of species monodominance in the second local community is very high if the species has high (close to monodominant level) abundance in the first local community.

With respect to the behavior of the species in the first (non-isolated) local community the species abundance scenarios can be characterized as follows:

Scenarios (i,ix) and (i,v). The species is highly persistent in the first local community, that is, the probabilities of the species extinction and monodominance in this local community are very small.

Scenarios (ii,ix) and (ii,v). If the species abundance in the second local community is very high then the species is highly persistent in the first local community; and if the species abundance in the second local community is very small then the species has very high chance of extinction from the first local community.

Scenarios (v,ix) and (v,v). If the species abundance in the second local community is very high then the species has very high chance of monodominance in the first local community; however, if the species abundance in the second local community is very small then the species has very high chance of extinction from the first local community.

Scenario (iii,ix). The species has very high chance of extinction and very small chance of monodominance in the first local community regardless its abundance in the second local community.

Scenario (ix,ix). The species has very high chance of extinction or monodominance in the first local community regardless its abundance in the second local community.

Scenario (vi,ix). The species has very high chance of extinction in the first local community regardless its abundance in the second local community, and the chance of species monodominance in the first local community is very high only if the species is highly abundant or monodominant in the second local community.

The sensitivity analysis for the mean first time of species extinction from local communities is performed in accordance to the above species abundance dynamics classification. For each species abundance scenario, Figure 7.1 illustrates the average first extinction time of species from the first (non-isolated) local community, the average first extinction time of species from the second (semi-isolated) local community, the probability of species extinction from the first (non-isolated) local community before its extinction from the second (semi-isolated) local community, and also the average first extinction time of species from either the first local community or the second local community.

Let us start to analyze the extinction time and probability from Scenarios (i,ix) and (i,v). Figures 7.1 (i,ix) and 7.1 (i,v) show that for these scenarios the average first time to species extinction from the first local community is very large and this time is almost independent of the initial species abundance in both local communities, moreover, the probability of species extinction from the first local community before its extinction from the second local community is very small. As a result, the species in the first local community from these scenarios are highly persistent. The average first time to species extinction from the second local community is different for Scenarios (i,ix) and (i,v). Specifically, for Scenario (i,ix) the role of the immigration probability between local communities is very small, therefore, the second local community is almost completely isolated, and the species is extinct or monodominant most of the time in this local community. The average time to species extinction from the second local community is almost proportional to the species abundance in it. Since the local communities are very weakly connected, the average time to species extinction from the second local community is independent of the species abundance in the first local community. The plot for the average first time to species extinction from at least one local community for Scenario (i,ix) shows that this time increases with respect to the initial species abundance in the second local community, and is almost independent of the initial species abundance in the first local community. In contrast, for Scenario (v,ix) the role of the immigration probability between local communities is large and the species abundance in the first local community has strong effect on the species persistence in the second local community. As a result the average first time to species extinction from the second local community is almost independent of the initial species abundance except the case when the initial species abundance in the first local community is small. The species is still highly persistent in the second local community, however, the average first time to species extinction from the second local community is much smaller than from the first local community, and the probability of extinction from the second local community is much higher than the probability of extinction from the first local community. Finally, for Scenario (v,ix) the plot of the average first time to species extinction from either the first or second local community indicates that this time to extinction is almost independent of the initial species abundance in the local communities.

Let us now consider Scenarios (ii,ix) and (ii,v). For these scenarios the immigration probability from the metacommunity is relatively high, however, the role of the immigration between local communities cannot be neglected. Figures for the average first time to species extinction from the first local community clearly indicate dependence of this time on the initial species abundances in both local communities. These figures also show that the structure of the average first time to species extinction from the first local community is very similar for Scenarios (ii,ix) and (ii,v), and the average first time to extinction from the first local community is relatively large for all non-zero initial species abundances in this local community. However, the average first time to species extinction from the second local community is different for Scenarios (ii,ix) and (ii,v) as a result of different types of the species abundance distributions in the second (semi-isolated) local community. Since for Scenario (ii,ix) the local communities are very weakly connected, the average first time to species extinction from the second local community is almost independent of the initial species abundance in the first local community. In contrast, for Scenario (ii,v) this time is obviously related to the species abundance in both local communities. It also worth noting that for Scenario (ii,v) the probability of species extinction from the first local community is smaller than the probability of species extinction from the second local community; however, for Scenario (ii,ix) this probability is clearly dependent on the initial species abundance in the second local community. The average first time to species extinction from either the first or second local community is much higher for Scenario (ii,v) than for Scenario (ii,ix); moreover, this time has different structure of dependence on the initial species abundances in local communities for these scenarios. Specifically, in the case of

Scenario (ii,ix) the average first time to species extinction from either the first or second local community is clearly asymmetric with respect to the initial species abundances in the local communities, whereas for Scenario (ii,v) higher symmetry of this time to species extinction is observed with respect to species abundances $(x_1, x_2) = (a, b)$ and $(x_1, x_2) = (b, a)$ in local communities.

The structure of the extinction time and probability for Scenario (iii,ix) is very similar to those for Scenario (ii,ix). For Scenario (iii,ix) the immigration probability between local communities is small, and the immigration from the metacommunity also dominates over the immigration between local communities. As a result, the average first time to species extinction from the second local community is almost independent on the species abundance in the first local community. It is worth to notice that the value of the time to species extinction for Scenario (iii,ix) is smaller than for Scenario (ii,ix), that is species would go extinct faster in the case of the species abundance dynamics from Scenario (iii,ix) than from Scenario (ii,ix).

In spite of the immigration intensities for Scenarios (v,ix), (vi,ix) and (ix,ix) are small, the role of the immigration probabilities for these species abundance dynamics scenarios is almost equally important for species extinction time and probability. For Scenario (ix,ix) the species has very high chance of monodominance in one or both local communities and the species abundance can remain at the monodominance level for relatively long time. Therefore, the average first time to species extinction in the case of Scenario (ix,ix) is relatively larger than for Scenarios (v,ix) and (vi,ix) with smaller chance of species monodominance in the local communities. It worth noting that, whereas the average first time to species extinction from the first local community is larger for Scenario (v,ix) than for Scenario (vi,ix), the average first time to species extinction from the second local community is smaller for Scenario (v,ix) than for Scenario (vi,ix).

Finally, let us consider Scenario (v,v). For this species abundance dynamics scenario the immigration between local communities dominates over the immigration from the metacommunity. Figures for the average first time of species extinction from the first local community and from the second local community clearly show that the species abundance in one local community has large effect on the time to extinction from the other local community. Moreover, for Scenario (v,v) the average first time to species extinction from the first local community is close to the average first time to species extinction from the second local community; however, the probability of extinction from the second (semi-isolated) local community is slightly larger than the probability of extinction from the first (non-isolated) local community.

## 7.6 Comparison of average first times to extinction from local community connected only to metacommunity and to both metacommunity and other local community

In this section the effect of the immigration probability between local communities $m^l$ on the mean first time to species extinction from the first (non-isolated) local community, and on the mean first time to species extinction from the second (semi-isolated) local community is studied. Furthermore, the comparison study of the species extinction time from the local community connected to both the metacommunity and the other local community and the species extinction time from the local community connected only to the metacommunity (Babak 2006) is provided.

Figures 7.2 (a,b,c) illustrate the plots of the mean first time to species extinction from the first (non-isolated) local community for three different values of the immigration probability from the metacommunity $m^m$. In the case of two connected local communities the mean first time to species extinction from the first local community is calculated for different initial species abundances in the first local community as an averaged value for all possible initial species abundances in the second (semi-isolated) local community. Figures 7.2 (a,b,c) clearly show that the mean first time to species extinction from the first local community connected with the second local community and with the metacommunity converges to the mean first time to species extinction from one local community connected only to the metacommunity as the immigration probability between local communities $m^l$ tends to zero. Moreover, the mean first time to species extinction from the local community connected to both the metacommunity and the other local community is larger than the mean first time to species extinction from the local community connected only to the metacommunity.

Figure 7.2 (a) shows the average first time to species extinction from the first (non-isolated) local community for high immigration probability from the metacommunity, $m^m = 0.1$. In this case the species abundance dynamics is typical for Scenario (i,ix) for $m^l < 0.005$ and for Scenario (i,v) otherwise. Since the species abundance distribution in the first local community is of the same type (i), the behavior of the average first time to species extinction from the first local community with respect to the initial species abundances is similar for different $m^l$. Specifically, the average extinction time is almost independent of the initial species abundance in the first local community. This behavior of the average first time to extinction is typical for highly persistent species in the local community, since the extinction time and probability of extinction for such species is almost independent of the species initial abundance.

Figure 7.2 (b) shows the average first time to extinction from the first local community for intermediate immigration probability from the metacommunity, $m^m = 0.01$. We know that for such value of the immigration probability $m^m$, the immigration probability between local communities $m^l$ can significantly change the species abundance dynamics scenario in the local community (see Chapter 6) as well as the structure of the average first time to species extinction (see Figure 7.2 (b)). Let us examine the effect of $m^l$ on the extinction time and probability in detail.

For the values of the immigration probability $m^l$ larger than 0.005 the species abundance dynamics is typical for Scenario (ii,v). For this scenario the species has very high chance of extinction and very small chance of monodominance in the first local community when it is absent from the second local community, and very small chance of extinction or monodominance in the first local community when the species is monodominant in the second local community. For Scenario (ii,v), the average first time to extinction from the first local community is large and increases almost linearly with respect to the non-zero initial species abundance in the local community. In this case a positive effect of the species abundance in the second local community on the average first time to species extinction from the first local community is observed due to close association between local communities.

For the values of the immigration probability $m^l$ smaller than 0.003 the species abundance dynamics is typical for Scenario (iii,ix). For this scenario the species has very high chance of extinction and very small chance of monodominance in the first (non-isolated) local community regardless of the species abundance in the second (semi-isolated) local community. In this case the average first time to species extinction increases nonlinearly with respect to the species initial abundance in the local community, therefore, the initial species abundance plays a very important role for the species persistence in the non-isolated local community.

For the intermediate values of the immigration probability $m^l$, $0.003 < m^l < 0.005$, the structure of the average first time to species extinction is gradually switching from the case with small immigration probability $m^l$ (Scenario ((iii,ix))) to the case with large immigration probability $m^l$ (Scenario ((ii,v))).

Figure 7.2 (c) shows the effect of the immigration probability between local communities $m^l$ on the average first time to species extinction from the first local community for very small immigration probability from the metacommunity, $m^m = 0.004$. As in the previous example (Figure 7.2(b)) the species abundance dynamics scenario varies with respect to the value of the immigration probability between local communities $m^l$. For very large immigration probabilities $m^l$ ($m^l > 0.71$), the species abundance dynamics is typical for Scenario (ii,v). In this case the average extinction time from the local community is large and increases almost linearly with respect to the species initial abundance, therefore the species is highly persistent in the local community, see also Figure 7.2 (b). For very small immigration probabilities $m^l$ ($m^l < 0.002$), the species abundance dynamics is representative for Scenario (ix,ix) with very high chances of species extinction or monodominance in the local communities. Therefore, for this scenario due to high possibility of either species extinction or monodominance, the average first time to species extinction from the local community increases almost linearly with respect to the initial species abundance.

Let us now consider the average first time to species extinction for intermediate values of the immigration probability $m^l$, $0.002 < m^l < 0.71$. In this case the species abundance dynamics is typical for Scenario (v,v) if $0.005 < m^l < 0.71$, Scenario (v,ix) if $0.004 < m^l < 0.005$ and for Scenario (vi,ix) if $0.002 < m^l < 0.004$. For these scenarios the species has very high chance of extinction and very small chance of monodominance in the first local community if the species abundance is low in the other local community, and the chance of species monodominance in the first local community is high when the species is monodominant in the other local community. The structure of the average extinction time is not stable for these intermediate scenarios. For smaller values of $m^l$ from the considered interval the average first time to extinction increases gradually with respect to the initial species abundance in the local community, whereas for larger values of $m^l$ the average first time to extinction increases sharply for small initial species abundances, and is almost linear for larger initial species abundances. It also worth noting that for Scenario (v,v) the average first time to species extinction from the first local community is much larger than for Scenarios (v,ix) and (vi,ix). Note also that for Scenario (v,v) the structure of the species extinction time is more similar to that for Scenario (ii,v) with very large immigration probabilities $m^l$, whereas for Scenarios (v,ix) and (vi,ix) the structure of the extinction time is more similar to that for Scenario (ix,ix) with very small immigration probabilities $m^l$.

Let us now consider the effect of the immigration probability between local communities $m^l$ on the average first time to species extinction from the second (semi-isolated) local community, see Figure 7.3. Figure 7.3 illustrates the extinction time from the second local community for high immigration probability from the metacommunity $m^m$, $m^m = 0.1$. For such value of $m^m$, the species abundance dynamics in local communities varies for different values of $m^l$, i.e., for closely connected local communities, $m^l > 0.005$ the species abundance dynamics is typical for Scenario (i,v), and for weakly connected local communities, $m^l < 0.005$ the species abundance dynamics is typical for Scenario (i,ix).

In the case of Scenario (i,v) the average first time to species extinction from the second local community is almost independent of the initial species abundance in this local community. Moreover, the extinction time from the second local community is increasing with respect to the immigration probability between local communities. This characteristic shows a positive effect of closely connected local communities on the average first extinction time. In the case of Scenario (i,ix) the average first time to species extinction from the second local community is almost proportional to the initial species abundance in the second local community. On the contrary to Scenario (i,v), the extinction time from the second local community is decreasing with respect to the immigration probability between local communities. Such behavior of the extinction time from the second local community for Scenario (i,ix) can be explained based on larger probability of species monodominance in the second local community for smaller immigration probability between local communities. Due to larger chance of species monodominance in the second local community and longer remaining time of the species at the monodominance level of abundance for smaller immigration probabilities $m^l$, the average first time to species extinction in the second local community decreases with respect to $m^l$ for Scenario (i,ix).

Finally, it also worth noting that the time to species extinction from semi-isolated local community connected only to the other local community but isolated from the metacommunity is much shorter then the time to species extinction from the local community connected only to the metacommunity.

## 7.7 Conclusions and discussion

In this chapter the extinction time and probability were investigated for a species in two semi-isolated local communities, that is, in the case when both local communities are connected with each other through immigration, but only one local community is connected with the metacommunity. Using Kolmogorov-Fokker-Planck backward equation the models for:

- the species persistence probability in two local communities,
- the average first time to species extinction from non-isolated and from semi-isolated local community,
- the average first time to species extinction from either non-isolated or semi-isolated local community, and
- the probability that the species will go extinct from one local community before its extinction from the other local community

were derived and analyzed. Note that similar continuous probabilistic approach to the above problems was used for analysis of species abundance dynamics in one zero-sum local community (Babak, 2006).

The sensitivity analysis of the average first time to species extinction from one community, the probability of species extinction from one local community before the other local community, and the average first time to species extinction from either local community is provided in Section 7.5. This analysis is performed subject to the type of species abundance dynamics in two semi-isolated local communities developed in Chapter 6. It was distinguished that for different species abundance dynamics scenarios in two semi-isolated local communities, the structure of the average first time to species extinction and the probability of extinction vary significantly. Specifically,

- the average first time to species extinction from the local community is larger if the local community is more closely connected to the metacommunity and/or to the other local commuity;
- the average first time to species extinction from the non-isolated local community is almost independent of the initial species abundance if the

immigration from the metacommunity is very high regardless of species abundance in the other, semi-isolated, local community;

- the average first time to species extinction from the semi-isolated local community is smaller than the average first time to species extinction from the non-isolated local community; therefore, the species goes extinct from the semi-isolated local community faster than from the non-isolated local community;
- if the non-isolated local community is closely connected to the metacommunity, the chance of species extinction from the semi-isolated local community is much larger than the chance of species extinction from the non-isolated local community, moreover, this chance is almost independent of the initial species abundance in both local communities;
- if the non-isolated local community is weakly connected to the metacommunity, then the average first time of species extinction from any one local community is strongly correlated to the species abundance in it, and the average first time of species extinction from either local community is strongly correlated to the species abundance in both of them.

From the comparison study of the species extinction times in two local communities and in one local community presented in Section 7.6, the following relationships for the extinction time can be established:

- the average first time to species extinction from the local community connected to both the other local community and to the metacommunity is larger than the average first time to species extinction from the local community connected only to the metacommunity, that is, the species is more persistent in the local community in spatially structured ecosystem;
- the average first time to species extinction from the local community connected to both the other local community and to the metacommunity converges to the average first time to species extinction from the local community connected only to the metacommunity as the immigration probability between local communities decreases;
- the average first time to species extinction from the local community connected only to the other non-isolated local community is smaller than the average first time to species extinction from the local community connected only to the metacommunity, that is, the species is more persistent in the local community connected directly to the large source of organisms (the metacommunity) than in the local community connected to small source of organisms (the other local community).

The presented results for the species abundance dynamics in two semi-isolated local communities show how the structure of living communities influences species persistence in living communities, species extinction dynamics and probability. The main message from the analysis of species extinction dynamics in two semi-isolated local communities is that the species extinction time and probability are highly influenced by the location of the local community in the ecological system.

Specifically, the species extinction time from the local community is positively related to the size of directly connected reservoirs of living organisms (living communities) and the number of such reservoirs.

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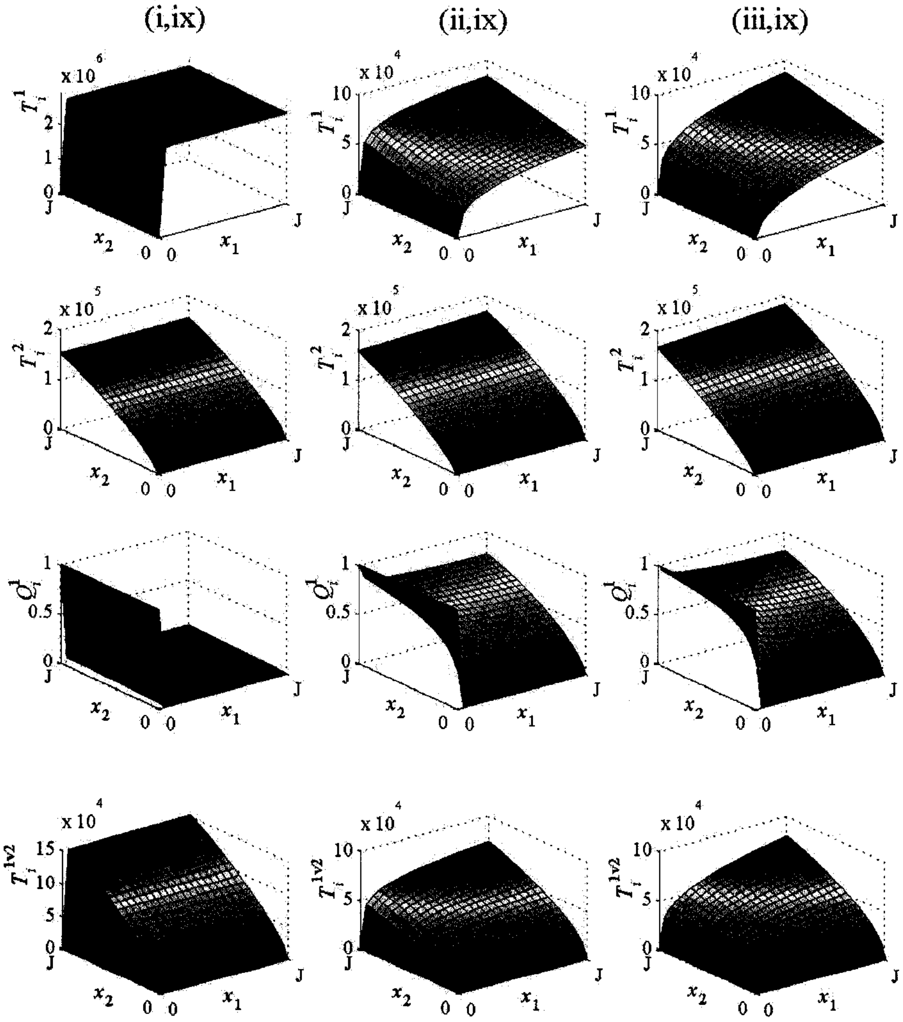


Figure 7.1: Effect of the type of species abundance dynamics scenario on species abundance evolution in the two semi-isolated local communities of size $J = 200$. The numbers of death events per unit time interval in local communities are $\mu_1 = \mu_2 = 1$. The species metacommunity relative abundance is $\omega_i = 0.2 < 1/2$. Figures in the 1-st row show the mean first time to species extinction in the first local community calculated using Eq. (17) with boundary conditions in the form (15); figures in the 2-rd row show the mean first time to species extinction in the second local community calculated using Eq. (17) with boundary conditions in the form (16).

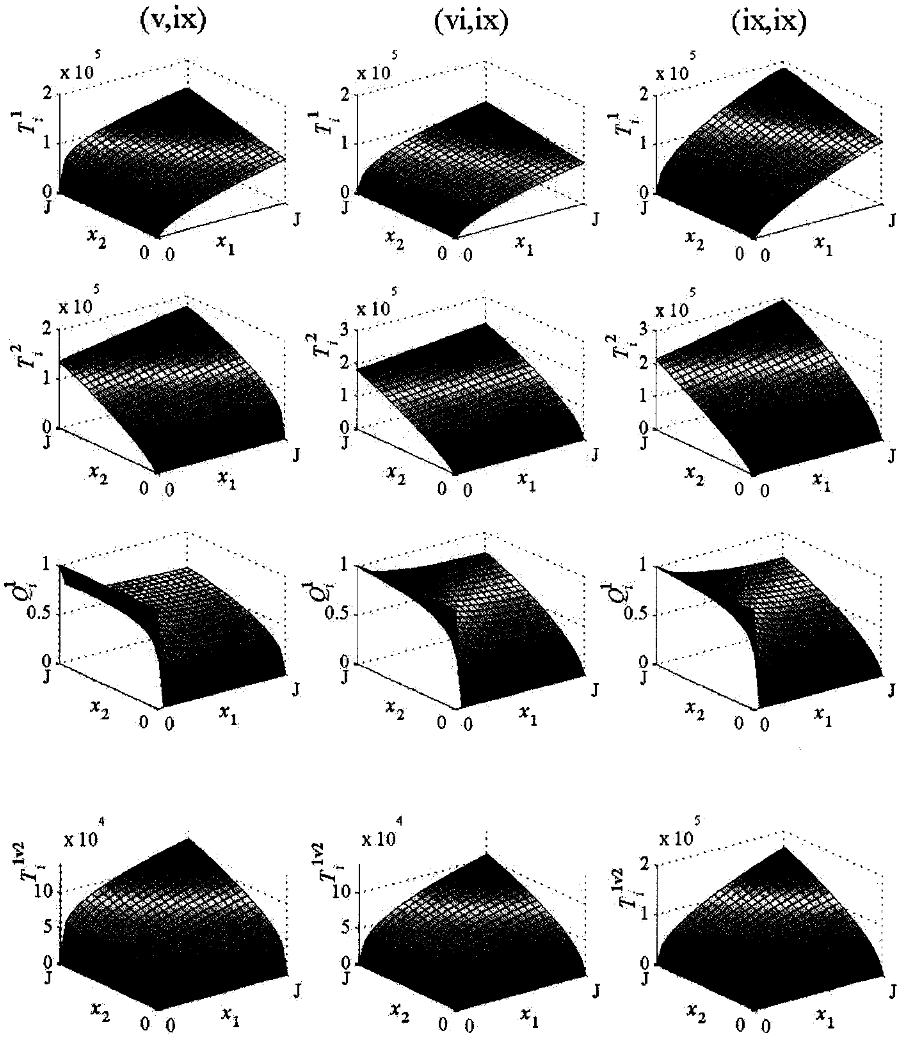


Figure 7.1: Cont. Figures in the 3-rd row show the probability of extinction of the species from the first local community before the second local community calculated using Eqs. (19)-(22); and figures in the 4-th row show the mean first time to species extinction either from the first local community or from the second local community calculated using Eq. (17) with boundary conditions in the form (14).

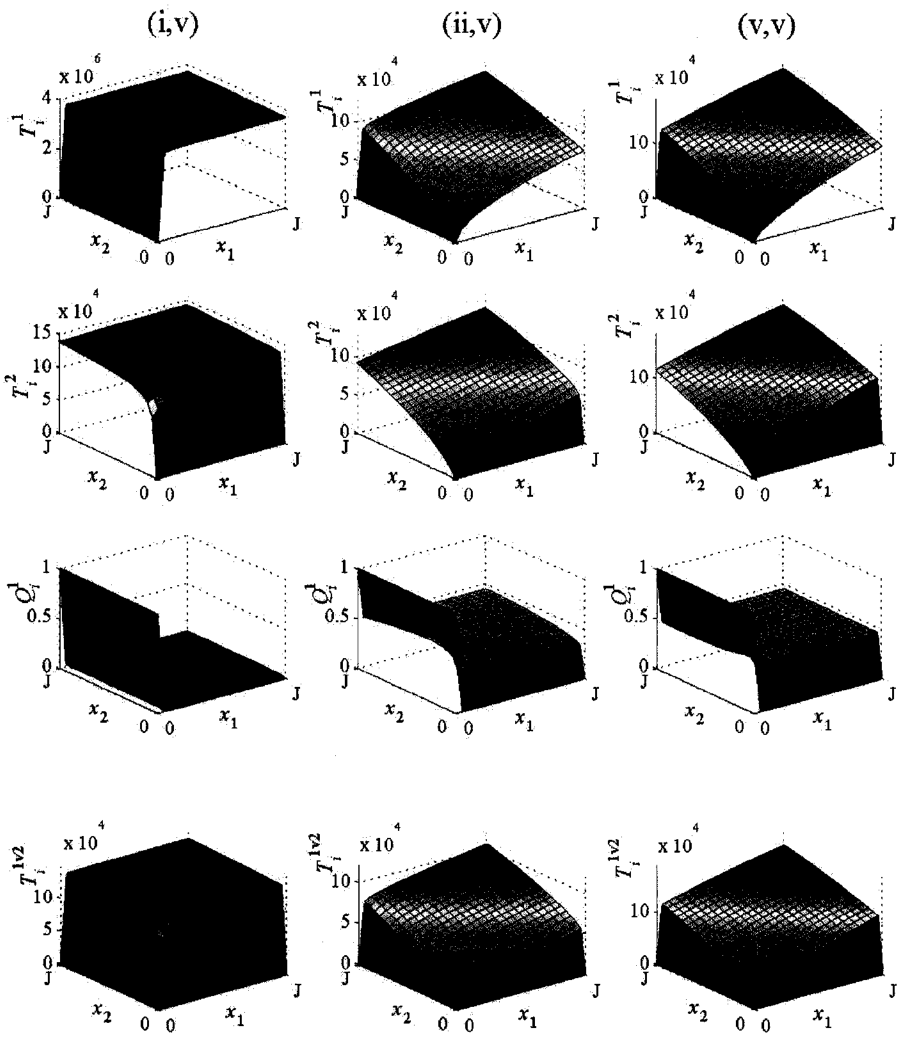
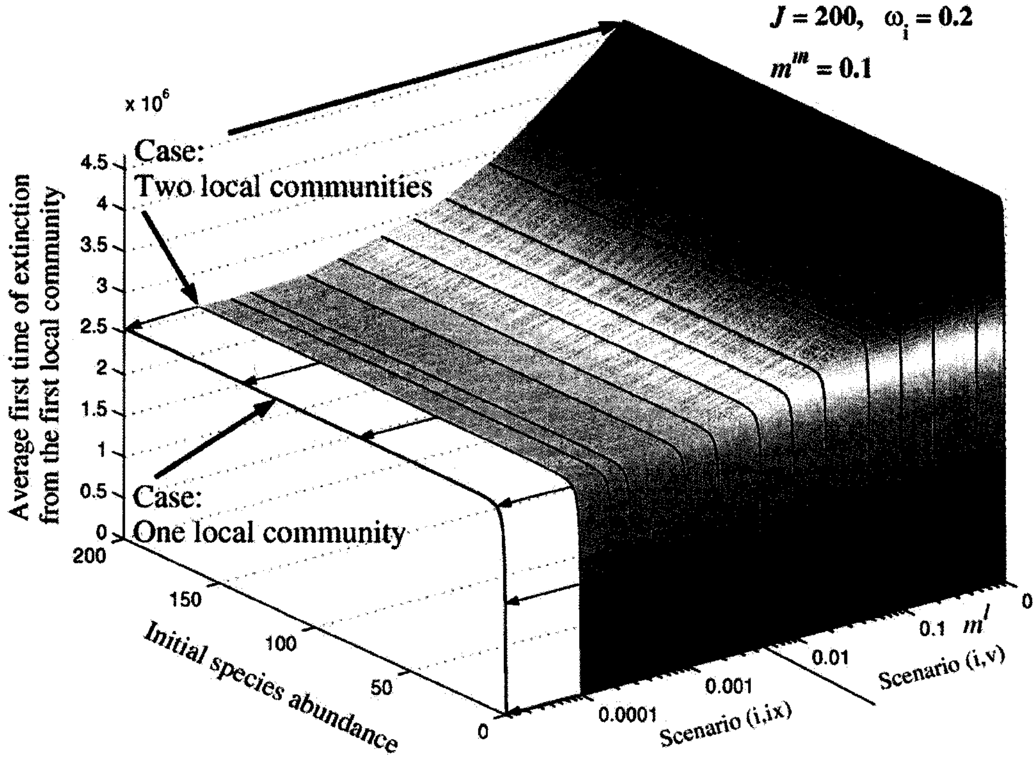
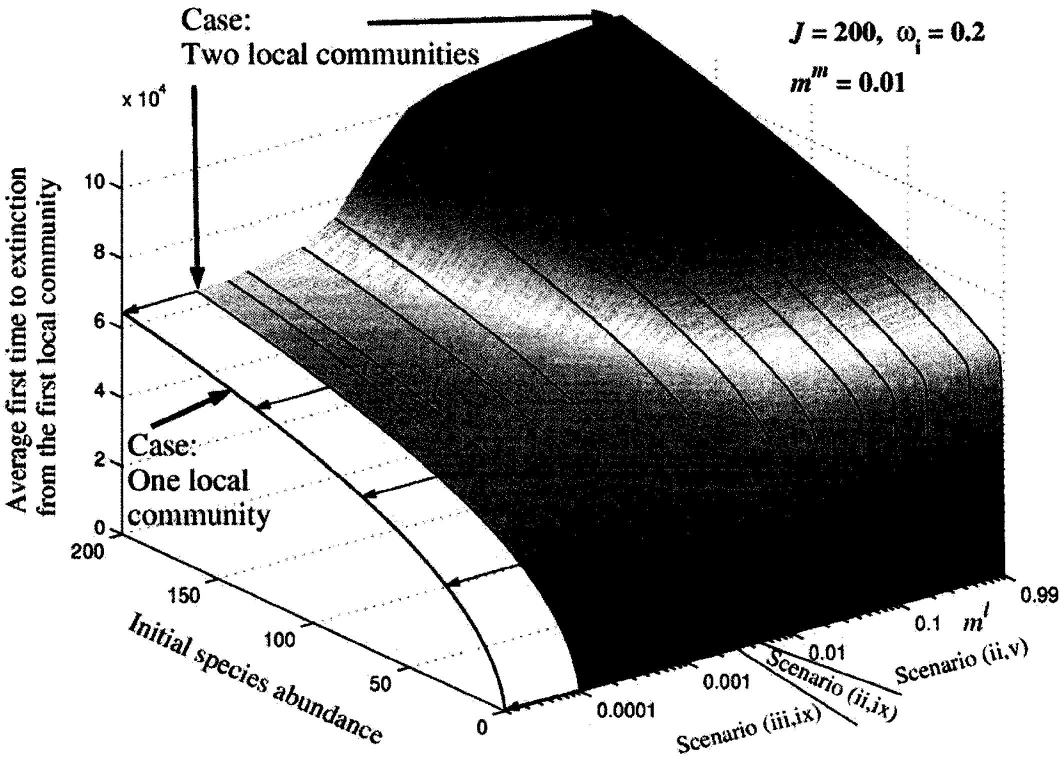


Figure 7.1: Cont. The values of the immigration probabilities are chosen to be the following: Scenario (*i,ix*) $m^m = 0.1$, $m^l = 0.002$; Scenario (*ii,ix*) $m^m = 0.02$, $m^l = 0.002$; Scenario (*iii,ix*) $m^m = 0.01$, $m^l = 0.002$; Scenario (*v,ix*) $m^m = 0.005$, $m^l = 0.0045$; Scenario (*vi,ix*) $m^m = 0.005$, $m^l = 0.002$; Scenario (*ix,ix*) $m^m = 0.002$, $m^l = 0.002$; Scenario (*i,v*) $m^m = 0.1$, $m^l = 0.1$; Scenario (*ii,v*) $m^m = 0.01$, $m^l = 0.01$; Scenario (*v,v*) $m^m = 0.005$, $m^l = 0.05$.



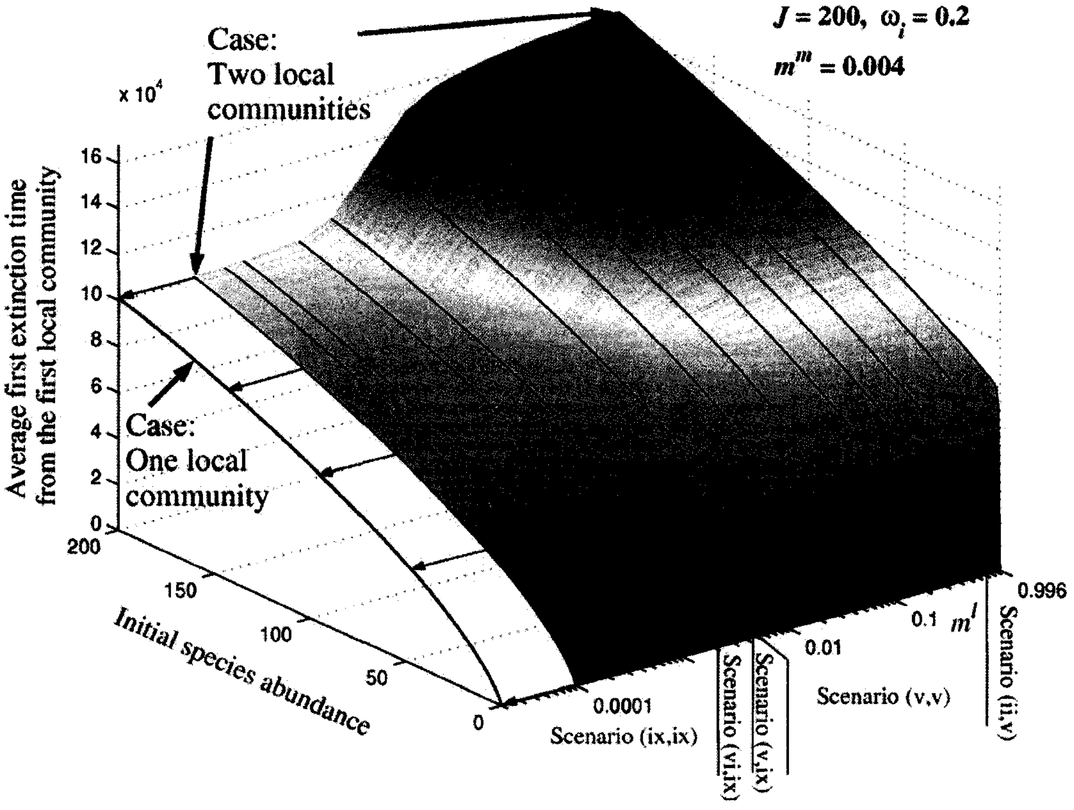
(a)

Figure 7.2: Effect of the immigration probability $m^l$ on the average first time to extinction in the first (non-isolated) local community, and comparison of the average times to extinction in one local community connected only to the metacommunity (Hubbell's zero-sum model for local community) and in one local community connected to both the metacommunity and the other local community of the same size. The size of the local community is $J = 200$, and the metacommunity relative abundance of species $i$ is $\omega_i = 0.2$. (a) $m^m = 0.1$ (Scenario (i,ix) for $m^l < 0.005$ and Scenario (i,v) for $m^l > 0.005$).



(b)

Figure 7.2: Cont. (b) $m^m = 0.01$ (Scenario (iii,ix) for $m^l < 0.003$, Scenario (ii,ix) for $0.003 < m^l < 0.005$ and Scenario (ii,v) for $m^l > 0.005$).



(c)

Figure 7.2: Cont. (c) $m^m = 0.004$ (Scenario (ix,ix) for $m^l < 0.002$, Scenario (vi,ix) for $0.002 < m^l < 0.0045$, Scenario (v,ix) for $0.0045 < m^l < 0.005$, Scenario (v,v) for $0.005 < m^l < 0.71$ and Scenario (ii,v) for $m^l > 0.71$).

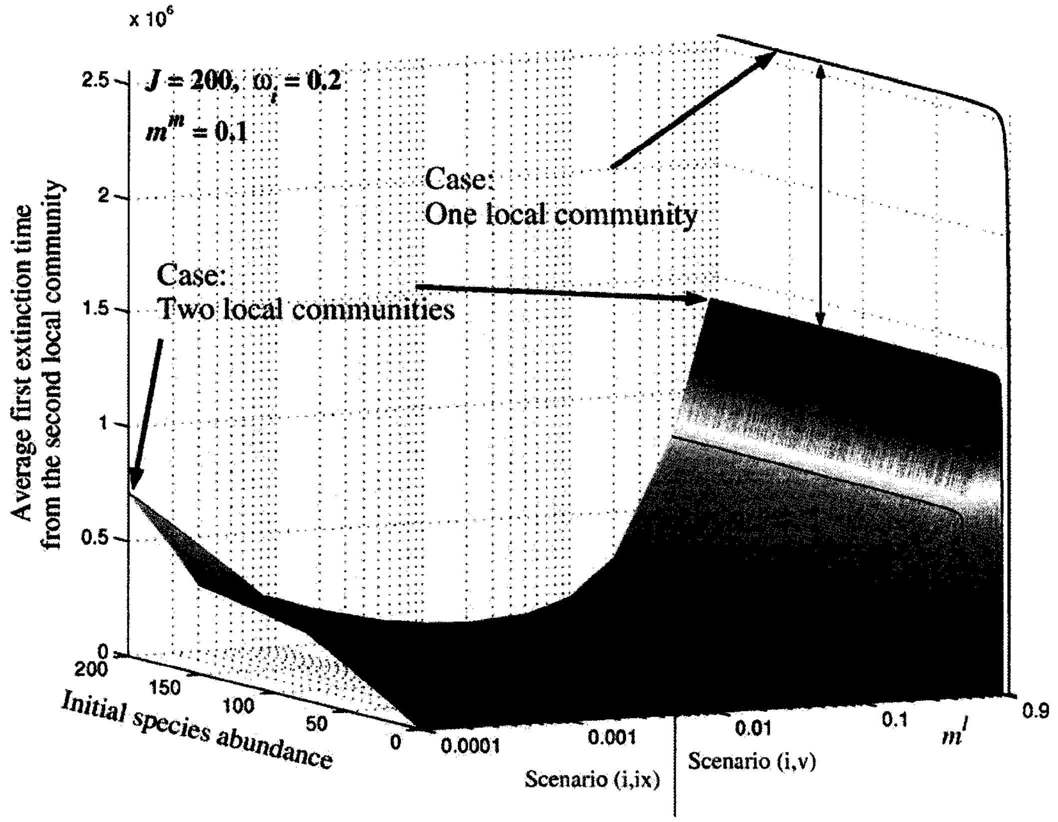


Figure 7.3: Effect of the immigration probability $m^l$ on the average first time to extinction in the second (semi-isolated) local community, and comparison of the average times to extinction in one local community connected only to the metacommunity (Hubbell's zero-sum model for local community) and in the semi-isolated local community connected to the other local community of the same size, but isolated from the metacommunity. The size of the local community is $J = 200$, and the metacommunity relative abundance of species $i$ is $\omega_i = 0.2$. $m^m = 0.1$ (Scenario (i,ix) for $m^l < 0.005$ and Scenario (i,v) for $m^l > 0.005$).

# Chapter 8
# General conclusions

The unified neutral theory of biodiversity and biogeography proposed by Hubbell (2001) aims to explain the species 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 only using discrete techniques such as Markov chain analysis (Hubbell 2001), master birth-death ordinary differential equations for the species abundance probability distribution (eg., Volkov et al. 2003, Vallade and Houchmandzadeh 2003, McKane et al. 2004) and using sampling analysis (eg., Alonso and McKane 2004, Etienne and Alonso 2005).

In this thesis (Chapter 2), I analyzed Hubbell's neutral model for species abundance dynamics in a local community using a continuous probabilistic approach. A continuous probabilistic 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 me the possibility not only to work with communities of any size, but also to derive such important quantities in conservation biology as the probability distributions of the persistence time and the first passage time to extinction and fixation. I also proposed a realistic classification for the species abundance dynamics in the local community with respect to the immigration intensity, species metacommunity relative abundance, and, of course, the size of the local community. The results of my analysis for the distribution of the extinction time were evaluated and verified through the simulation study of Hubbell's neutral zero-sum model. It was shown that for the species with large initial abundances, the distribution of the first passage time to extinction is very close to a Gamma distribution, as it was presumed by Hubbell (2001), but for the species with small initial abundance, the Gamma distribution does not produce a good fit to the first passage time to extinction.

The goal of the second part of my work (Chapters 3-7) was to analyze the effects of spatially structured habitat heterogeneities on the species abundance dynamics and extinction characteristics in zero-sum neutral local communities. I developed three macroecological models for species abundance dynamics in structured habitats. Specifically, I proposed the model for species abundance dynamics in a local community at the edge between two distinct ecological systems or metacommunities (Chapter 3, see also Figure 1.2), the model for species abundance dynamics in two local communities connected with each other and with the metacommunity through immigration (Chapters 4 and 5, see also Figure 1.3), and the model for species abundance dynamics in two local communities connected with each other but with only one of them connected to the metacommunity (Chapters 6 and 7, see also Figure 1.4). The developed models are designed to characterize real ecological situations. For example, grassland-forest transitions at small scale in British Columbia can be viewed as an example of the model for the edge effects between two distinct ecological systems (Bai et al. 2004). Stepping stone models of population structure and matrix stage structured models can be considered as an example for the species abundance dynamics models in two local communities (Kimura and Weiss 1964, Lutscher and Lewis 2004). The models for two local communities can be also used for description of the species structure on separated islands, or in different patches within the same living habitat (MacArthur and Wilson 1967, Formann 1995).

The models for the species abundance dynamics in structured ecological communities were analyzed using continuous probabilistic technique. This technique allowed us to:

- derive the models for the dynamics of species abundance distribution in local communities;
- develop the models for the equilibrium (steady-state) species abundance distribution in local communities;
- calculate indices of diversity and evenness (Simpson index, Shannon index, Simpson evenness index);
- calculate correlation between species abundances in two connected local communities;
- make a realistic classification of the species abundance dynamics in local communities with respect to the probabilities of species persistence, extinction and monodominance in local communities;
- derive the models for the probability of species persistence in a local community, and for the extinction risk - the probability of species extinction from a local community within a specified time interval;
- calculate the mean and variance of the time to species local extinction, the first passage time to species extinction;
- calculate the probability of species extinction from one local community before it becomes extinct from the other local community;
- perform sensitivity analyses of species abundance distributions and the time to species extinction with respect to immigration probabilities, frequency of death events, species fraction in the metacommunity and the size of the local community.

The main conclusions from the analysis of the models for structured ecological communities are the following:

- local communities at the edge maintain higher diversity and higher intensity of species interchange than those inside of homogeneous ecosystems (Chapter 3);
- the type of species abundance behavior in a local community can be predicted from knowledge about such parameters as the size of the local community, fraction of the species abundance in the metacommunity, immigration probabilities, death frequency and the location of the local community within an ecological network of living habitats (Chapters 3, 4 and 6);
- higher similarity of the species abundance dynamics in two local communities is observed for larger values of the immigration probability between local communities. Specifically, for fixed probability of immigration from the metacommunity, the correlation between species abundances in two local communities increases with an increase in the immigration between local communities, and, vice versa, for fixed probability of immigration between local communities, the correlation decreases with an increase in the immigration from the metacommunity (Chapters 4 and 6);
- the average first time to species extinction from a local community is larger if the local community is more closely connected to the metacommunity and/or to the other local commuity (Chapters 5 and 7);
- the time to species extinction and probability of species persistence are larger for local communities, which can obtain new immigrants from more than one source of organisms (Chapters 5 and 7); the size of external sources of organisms is positively related to the chance of species extinction and extinction time (Chapter 7).

Models developed in this thesis for species abundance dynamics in spatially structured local communities describe the processes in local communities connected through immigration with each other and with the metacommunity. These models for two local communities can be considered as a link between spatially implicit and spatially explicit models of species abundance dynamics. This is because introduction of spatial characteristics requires discretization of ecological communities into two or more smaller component communities.

In conclusion I would like to add that I strongly believe that a better, more mechanistic understanding of ecological communities is urgently needed in order to accurately predict spatial distribution and temporal dynamics of living species. The knowledge about such important ecological characteristics derived in this thesis as the time to species extinction, extinction risk, and type of species distribution in ecological communities is crucial for predicting the species abundance in local communities and also for defining the necessary approaches in conservation actions to prevent species extinction. I hope my research will not only contribute to such a basic ecological understanding of living communities, but will also enhance our ability to assess and manage human influences on them and to motivate further theoretical and empirical investigations. The results obtained in this thesis should be especially useful for landscape ecology, particularly for the study of population dynamics in fragmented landscapes.

# Bibliography

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