Limiting similarity and niche theory for structured populations

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J. Theor. Biol. *in press*

Abstract We develop the theory of limiting similarity and niche for structured populations with finite number of individual states (i-state). In line with a previously published theory for unstructured populations, the niche of a species is specified by the impact and sensitivity niche vectors. They describe the population's impact on and sensitivity towards the variables involved in the population regulation. Robust coexistence requires sufficient segregation of the impact, as well as of the sensitivity niche vectors. Connection between the population-level impact and sensitivity and the impact/sensitivity of the specific i-states is developed. Each i-state contributes to the impact of the population proportional to its frequency in the population. Sensitivity of the population is composed of the sensitivity of the rates of demographic transitions, weighted by the frequency and by the reproductive value of the initial and final i-states of the transition, respectively. Coexistence in a multi-patch environment is studied. This analysis is interpreted as spatial niche segregation.

Keywords: *regulation, limiting similarity, habitat segregation*

1 Introduction

Niche theory (Hutchinson, 1978) plays a central role in community ecology (Leibold, 1995). The underlying "Gause's principle" (Gause, 1934) has an axiomatic status (cf. Hardin, 1960). It mandates that species living together must differ to avoid competitive exclusion. This differentiation is considered as the segregation of the niches of the coexisting species (cf. Case, 2000, p. 368).

The nature and extent of the necessary segregation are of long-term interest. On the theory side MacArthur and Levins (1967); May and MacArthur (1972); May (1973, 1974); Vandermeer (1972, 1975); Abrams (1975) are the classic studies on limiting similarity; Abrams (1983, 1988); Chesson (2000b); Schwilk and Ackerly (2005); Abrams et al. (2008) are more recent ones. Stubbs and Wilson (2004); York (2007); Emery (2007) are examples from the vast empirical literature.

Our background study is Meszéna et al. (2006). It proved, that increasing similarity between the populations makes their coexistence less likely, more sensitive to external perturbations (see also Szabó and Meszéna, 2006; Barabás and Meszéna, submitted). The main limitation of this formalism was that it considered the populations to be homogeneous. In reality, individuals may belong to different states according to their age, size, developmental/physiological state or location. Conspecific individuals in different developmental states often assume different ecological roles, making the notion of the niche of a structured population non-trivial.

Spatial structure has a pronounced importance for niche theory also. Living in different habitats, under different environmental conditions, eliminates competitive exclusion, just like if they were consuming different resources, or differ in ecological function in any other way. These two essential ways of niche segregation will be referred to as habitat and functional segregation (cf. the "scenopoetic" and the "bionomic" niche axes of Hutchinson, 1978, p. 159). As different habitats are located at different places, description of a habitat-type niche segregation, unlike a functional one, necessitates to take into account the spatial structure of the populations in a heterogeneous environment.

Fortunately, there is a general mathematical way of handling any type of population structure. While the demographic parameters tend to differ in the different states, the long-term behavior of the population can be described by a single rate of increase, the leading eigenvalue of the dynamical matrix (Metz and Diekmann, 1986; Metz et al., 1992; Caswell, 2001). In this paper we establish niche theory of structured populations by connecting the population-level niche description to the description of the individual states. We will assume irreducibility, i.e. any individual states are reachable from any others. The more special case of spatial structure will receive special attention.

Section 2 develops the theory in general as well as for the spatial case. Section 3 studies the example case of a linear chain of habitats, as a model for niche segregation along an environmental gradient.

2 Theory

2.1 Limiting similarity for unstructured populations

In this subsection we recapitulate the theory of limiting similarity for unstructured populations form Meszéna et al. (2006).

First we note that an arbitrary coalition of competing populations is able to coexist if their parameters are fine-tuned to nullify their fitness-differences. The real question is whether the coexistence exists without this fine-tuning, i.e., for a wide range of parameters. We will asses this "robustness" of coexistence by introducing extra mortalities, acting upon each species separately. Robustness of coexistence will be measured by the range of extra mortalities that allow the coalition to coexist. If populations coexist only because their fitness-difference happens to be zero, such coexistence disappears when some of them experience an arbitrarily small additional mortality.

We will study coexistence of L species in a stable equilibrium point of their combined dynamics. The ith species is distinguished by the superscript $^{(i)}$. As a matter of definition, we assume that *all* interactions between the individuals (including the interference types) are channeled through D "regulating variables" collected into the D dimensional vector $\boldsymbol{I}$. As the population growth rates are determined by the vector $\boldsymbol{I}$, the equilibrium equation for species i can be written as

$$r^{(i)}\left(\boldsymbol{I}(n^{(1)}, n^{(2)}, \ldots, n^{(L)})\right) - \Delta^{(i)} = 0 \qquad (i = 1, 2, \ldots, L), \tag{1}$$

where $r^{(i)}$ and $n^{(i)}$ are the growth rate and the density of species i, respectively. The term $\Delta^{(i)}$ represents the "extra" mortality acts on species i, their negative values correspond to decreased mortalities. (For sake of simplicity we take into account only fix point dynamics.) The coexistence is considered robust if a fixed point exists and remains in the positive range for a wide range of $\Delta^{(i)}$s. Therefore "robustness" is proportional to the volume of $\Delta^{(i)}$s that allows coexistence (cf. "coexistence bandwidth", Armstrong (1976); Abrams and Holt (2002)).

The system (1) consists of L equations for D unknowns. Generically, it can be solved only if $L \leq D$. This "discrete" version of the competitive exclusion principle (MacArthur and Levins, 1964; Rescigno and Richardson, 1965; Levin, 1970; Armstrong and McGehee, 1980; Heino et al., 1997) shows the connection between coexistence and regulation. Below we demonstrate that robustness of coexistence requires sufficient difference between the populations in their relationship to the regulating variables.

Differentially, the interaction between the ith species and the regulating variables is characterized by two vectors, $\boldsymbol{C}^{(i)}$ and $\boldsymbol{S}^{(i)}$ that will be referred to as *impact* and *sensitivity* niche vectors of that species:

$$C_k^{(i)} = \frac{\partial I_k}{\partial n^{(i)}}, \qquad S_k^{(i)} = -\frac{\partial r^{(i)}}{\partial I_k}, \qquad (i = 1, 2, \ldots, L; \;\; k = 1, 2, \ldots, D). \tag{2}$$

The quantities $C_k^{(i)}$ and $S_k^{(i)}$ measure the population's impact on and sensitivity towards the kth regulating factor, respectively. The sign convention for the sensitivity corresponds to the case when the regulating variables describe the *deterioration* of the environment, e.g. the exploitation of the resources.

One can determine the sensitivity of the equilibrium population sizes toward the additional mortalities by implicit differentiation:

$$\frac{\partial n^{(i)}}{\partial \Delta^{(j)}} = -\sum_{j=1}^{L} (a^{-1})_{ij} \Delta^{(j)} = -\frac{1}{J} \sum_{j=1}^{L} \mathrm{adj}(a)_{ij} \Delta^{(j)}, \tag{3}$$

where

$$a_{ij} = -\frac{\partial r^{(i)}}{\partial n^{(j)}} = \sum_{k=1}^{D} S_k^{(i)} C_k^{(j)} = \boldsymbol{S}^{(i)} \cdot \boldsymbol{C}^{(j)} \tag{4}$$

is the community/competition matrix, $\mathrm{adj}(a)$ denotes its adjunct matrix. The determinant

$$J = \det(a_{ij}) \tag{5}$$

measures the strength of the community-level regulation.

If $|J|$ is small, i.e. if the community is weakly regulated, Eq. (3) predicts strong dependence of the population sizes on the extra mortalities. In this case a small additional mortality could drive some of the populations into extinction. Therefore, the coexistence is not robust (see Meszéna et al., 2006, for the precise, probabilistic treatment). As one can see from Eq. (4), if the sensitivity niche vectors of two different species are the same, then the corresponding two rows of the community matrix are the same and $J = 0$. This situation is approached when the sensitivity niche vectors are similar, leading to small $|J|$ and weak regulation. Analogous argument holds for the impact niches and for the columns of the matrix.

More quantitatively, Meszéna et al. (2006) proves that

$$|J| \leq \mathcal{V}_{\boldsymbol{S}} \cdot \mathcal{V}_{\boldsymbol{C}}, \tag{6}$$

where $\mathcal{V}_S$ and $\mathcal{V}_C$ denote the L dimensional volume of the parallelepiped spanned by the $\boldsymbol{C}^{(i)}$ and $\boldsymbol{S}^{(i)}$ vectors, respectively. These volumes are the measures of the dissimilarity (in the linear sense) of the sensitivity/impact niche vectors.

To sum it up, robust coexistence requires sufficient difference between the impact, as well as between the sensitivity niche vectors of the species. Diminishing difference between the niche vectors leads diminishing likelihood of coexistence.

2.2 Continuous time matrix dynamics

We extend the ideas presented in the previous subsection for structured populations. To simplify the formalism, we restrict our attention to a finite number of individual states. It is assumed that individuals belongs to one of the s different individual states (i-state, Metz and Diekmann, 1986). Then the s-dimensional vector $\boldsymbol{n}$ specifies the state of the population (p-state). Its generic element n_l is the number of individuals belonging to the i-state l. One can also write

$$\boldsymbol{n} = \tilde{n}\boldsymbol{p}, \tag{7}$$

where $\tilde{n} = \sum_{l=1}^{s} n_l$ is the total population size and vector $\boldsymbol{p} = \boldsymbol{n}/\tilde{n}$ describes the population structure; $\sum_{l=1}^{s} p_l = 1$.

While such models often formulized in discrete time, we will apply a continuous time description because of its simpler-smoother behavior. The continuous-time population dynamics is described by the matrix differential equation

$$\frac{\mathrm{d}\boldsymbol{n}}{\mathrm{d}t} = \boldsymbol{M}\boldsymbol{n}, \tag{8}$$

where the $s \times s$ matrix $\boldsymbol{M}$ is the dynamical matrix. The eigenvalues will be denoted by ϱ_j $(j = 1, 2, \ldots, s)$; the corresponding right and left eigenvectors by $\boldsymbol{w}_j$ and $\boldsymbol{v}_j$, respectively. Analogously to the discrete-time theory (Caswell, 2001; Hastings and Botsford, 2006a,b; Smith et al., 2004), the long-term growth rate of the population is the dominant eigenvalue of the dynamical matrix.

In discrete time all elements of the dynamical matrix are nonnegative. Together with the usual assumption of irreducibility, the Perron-Frobenius theorem guaranties the necessary properties for biological interpretation: The leading eigenvalue is simple and positive; the leading eigenvectors are positive. In the continuous case both death and state transitions contribute negative terms to a diagonal element. Therefore, only the off-diagonal elements must be non-negative. From the assumed irreducibility again, the growth rate ϱ_1 simple and real, but not necessarily positive; the eigenvectors $\boldsymbol{w_1}$ and $\boldsymbol{v_1}$ remain positive (see Appendix A for the proof).

Positivity of $\boldsymbol{w}_1$ allows us to normalize it as $\sum_{l=1}^{s} w_{1l} = 1$. From that,

$$\boldsymbol{p} = \boldsymbol{w}_1. \tag{9}$$

The left eigenvectors are normalized to satify the orthogonality relation

$$\boldsymbol{w}_i \boldsymbol{v}_j = \delta_{jk}. \tag{10}$$

We will use the notation $\boldsymbol{v} = \boldsymbol{v}_1$, its generic element is $v_l = v_{1l}$.

2.3 Limiting similarity for structured populations

The overall growth rate of the population can be calculated from the matrix elements, i.e. from the demographic parameters of the i-states. In the same spirit, we intend to determine the overall impact and sensitivity niche vectors of structured populations based on the impact and sensitivity parameters of the i-states. We demonstrate that this overall niche description does provide the limiting similarity conclusion in line with the unstructured case.

Instead of Eq. (1), the equilibrium equation can be written as

$$\frac{\mathrm{d}\boldsymbol{n}^{(i)}}{\mathrm{d}t} = \left[\boldsymbol{M}^{(i)}\left(\boldsymbol{I}\left(\boldsymbol{n}^{(1)}, \boldsymbol{n}^{(2)}, \ldots, \boldsymbol{n}^{(L)}\right)\right) - \Delta^{(i)}\mathbf{1}\right]\boldsymbol{n}^{(i)} = \mathbf{0}, \tag{11}$$

where $\mathbf{1}$ denotes the identity matrix.

Note the analogy to the chemostat. The rate of excess mortality $\Delta^{(i)}$ can also be seen as a (species-dependent!) removal, or dilution, rate. This way our equilibrium population can be seen as an exponentially growing one with the tunable growth rate $\Delta^{(i)}$. Accordingly, the equilibrium p-state vector of species i is an eigenvector of its dynamical matrix $\boldsymbol{M}^{(i)}$ with the (leading) eigenvalue $\Delta^{(i)}$. As the equilibrium is affected by the dilution rates, changing $\Delta^{(i)}$s result in perturbation of the population structures. Importantly, the dynamical matrix

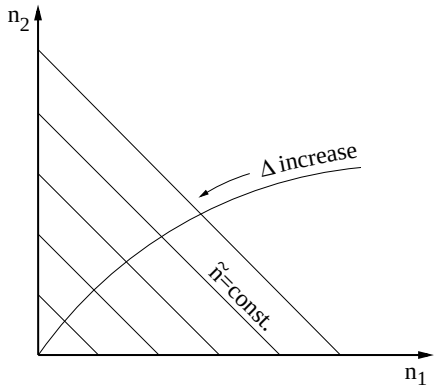

Figure 1: *Dimension reduction. The two axes represents* $n_1^{(i)}$ *and* $n_2^{(i)}$*, i.e. the number of individuals in two i-states of one of the species. Under changing one of the excess mortalities the equilibrium point moves on a curve. (In the figure the species' own mortality is tuned, so the curve follows the fate of that population until extinction.) The curve can be parameterized also by the total population size* $\tilde{n}^{(i)}$*. The* $\tilde{n}^{(i)} =$ constant *points lie on a straight line of* -45^0 *direction.*

should be evaluated at the equilibrium values of the regulating variables affected by the dilution rate.

Our first job is to build the connection between this $L \times s$ dimensional dynamical system and the L dimensional case of unstructured populations. We are interested in olny whether the populations can survive the extra mortalities. From this point of view $\tilde{n}^{(i)}$s are the only relevant parameters. When the L dilution rates are tuned, the equilibrium point of dynamics (11) moves on an L dimensional submanifold of the $L \times s$ dimensional state space (Fig. 1). This manifold can be parameterized also by the L equilibrium values of the total population sizes $\tilde{n}^{(1)}, \tilde{n}^{(2)}, \ldots, \tilde{n}^{(L)}$.

With this change of the variables, one can consider the equilibrium $\boldsymbol{I}$ as a function of the $\tilde{n}^{(i)}$s:

$$\boldsymbol{I} = \hat{\boldsymbol{I}}\left(\tilde{n}^{(1)}, \tilde{n}^{(2)}, \ldots, \tilde{n}^{(L)}\right). \tag{12}$$

Moreover, the growth rate (the dominant eigenvalue of the dynamical matrix) can be written as a function of the regulating variables:

$$r^{(i)} = r^{(i)}(\boldsymbol{I}). \tag{13}$$

Eqs. (12-13) establishes a description that is isomorphic to Eq. (1).

A note of precision is needed here. The equilibrium point of dynamics (11) at a given dilution rate is not necessarily unique. However as we consider a stable fixed point, implicit function theorem guaranties that the equilibrium point is *locally* unique and a smooth function of $\Delta^{(i)}$s. We assume that the local map $(\Delta^{(1)}, \ldots, \Delta^{(L)}) \to (\tilde{n}^{(1)}, \ldots, \tilde{n}^{(L)})$ is invertible. (Recall from Section 2.1, that the non-invertibility would mean structural instability of coexistence.) This inversion allows us to locally parameterize the manifold by the total population sizes, leading also to the locally unique mapping (12).

Based on this reduction of the number of variables, now we build the quantitative connection between the robustness analysis of structured and unstructured descriptions.

We begin the work with the sensitivity side: How does the population growth rate depend on the regulating variables? On the i-state level our starting point is the sensitivity of the elementary demographic rates which is considered to be known from the model definition. It can be described by the linear operator $T^{(i)}_{jkm}$

$$\mathrm{d}M^{(i)}_{jk} = -\sum_{m=1}^{D} T^{(i)}_{jkm}\mathrm{d}I_m \qquad (j,k=1,2,\ldots,s). \tag{14}$$

where $\mathrm{d}M^{(i)}_{jk}$ is the change of the population matrix of species ith under the perturbation $\mathrm{d}I_m$ of the regulating variables. The operator can be determined via differentiating the map $\boldsymbol{M}^{(i)}(\boldsymbol{I})$, which is given by the model definition. Like in Eq. (2), the minus sign corresponds to the depletive interpretation of the regulating variables.

The change of the population growth rate is determined by the perturbation of the dynamical matrix as (Caswell, 2001, Appendix B)

$$\mathrm{d}r^{(i)} = \sum_{j,k=1}^{s} v^{(i)}_j \mathrm{d}M^{(i)}_{jk} p^{(i)}_k. \tag{15}$$

Obviously, the perturbation of the $k \to j$ rate contributes to the change of the population growth rate proportional to the frequency p_k of initial state k and to the reproductive value v_j of the final state j.

Comparison of Eq. (15) with the definition (2) leads to the identification

$$\sum_{m=1}^{D} S^{(i)}_m \mathrm{d}I_m = \sum_{j,k=1}^{s}\sum_{m=1}^{D} v^{(i)}_j T^{(i)}_{jkm}\mathrm{d}I_m . p^{(i)}_k \tag{16}$$

Then, the sensitivity vector can be written as

$$S^{(i)}_m = \sum_{j,k=1}^{s} v^{(i)}_j T^{(i)}_{jkm} p^{(i)}_k \qquad (m=1,2,\ldots,D). \tag{17}$$

Interpretation is inherited from the perturbation result (15). Sensitivity of a population towards the regulating variables is composed of the sensitivities of its elementary rates. Each rate is weighted by the frequency of the initial state as well as by the reproductive value of the final state.

Now we turn our attention to determine the impact niche vectors. Here the starting point is: How does the change of the regulating variables receive contribution from the perturbation of the number of individuals in a given i-state of a given population? It is described by the $D \times s$ matrix $\boldsymbol{F}$ via the relation

$$\mathrm{d}I_m = \sum_{i=1}^{L}\sum_{j=1}^{s} F^{(i)}_{mj}\mathrm{d}n^{(i)}_j \qquad (m=1,2,\ldots,D). \tag{18}$$

Matrix $\boldsymbol{F}$ is considered to be directly calculable from the specific model.

In line with the definition of the impact niche vector, we want to express the perturbation $\mathrm{d}\boldsymbol{I}$ solely by the total population sizes $\mathrm{d}\tilde{n}^{(i)}$, as

$$\mathrm{d}I_m = \sum_{i=1}^{L} C_m^{(i)} \mathrm{d}\tilde{n}^{(i)} \qquad (m = 1, 2, \ldots, D). \tag{19}$$

Naively, one could expect that the vector

$$\tilde{C}_m^{(i)} = \sum_{j=1}^{s} F_{mj}^{(i)} p_j^{(i)} \qquad (m = 1, 2, \ldots, D) \tag{20}$$

plays the role of $\boldsymbol{C}^{(i)}$ (cf. Eq. (7)). Impacts of each state contribute to the impact of the population proportional to the frequency of that state. This would be the case if the population structures $\boldsymbol{p}^{(i)}$ were unperturbed. We will refer to $\tilde{\boldsymbol{C}}^{(i)}$ as the *uncorrected* impact vector of species i.

However the equilibrium population structures receive perturbation also under the change of the dilution rates $\Delta^{(i)}$. As Appendix B demonstrates, the change of the equilibrium population structure $\boldsymbol{p}$ is

$$\mathrm{d}p_j^{(i)} = \sum_{k,l=1}^{s} A_{jk}^{(i)} \mathrm{d}M_{kl}^{(i)} p_l^{(i)} \qquad (j = 1, 2, \ldots, s), \tag{21}$$

where

$$\boldsymbol{A}^{(i)} = \sum_{j \neq 1}^{s} \frac{(\boldsymbol{w}_j^{(i)} - U_j{}^{(i)} \boldsymbol{p}^{(i)}) \circ \boldsymbol{v}_j^{(i)}}{\varrho_1^{(i)} - \varrho_j^{(i)}} \tag{22}$$

is an $s \times s$ matrix describing the dependence of the population structure on the perturbations of the dynamical matrix. Matrix $\mathbf{A}$ is finite provided that the dynamical matrix is primitive. The sum runs over the non-dominant eigenvalues/vectors, $\circ$ denotes dyadic product and

$$U_j^{(i)} = \sum_{k=1}^{s} w_{jk}^{(i)} \qquad (j = 2, \ldots, s). \tag{23}$$

(Note that $U_1^{(i)} = 1$ by the normalization of w_1. Similar normalization for $U_j^{(i)}$, $j \neq 1$ might not be possible, as these quantities are allowed to be zero.) Existence of $\boldsymbol{A}^{(i)}$ relies on the fact that the dominance of eigenvalue ϱ_1 (cf. Appendix A) implies $\varrho_1^{(i)} > \varrho_j^{(i)}$ for all $j > 1$.

Combination of Eqs. (14) and (21) leads to

$$\mathrm{d}p_j^{(i)} = -\sum_{k,l=1}^{s} \sum_{m=1}^{D} A_{jk}^{(i)} T_{klm}^{(i)} \mathrm{d}I_m p_l^{(i)} \qquad (j = 1, 2, \ldots, s). \tag{24}$$

The perturbation of the population structure comes from the change of the total population size and from the change of the distribution. The total derivative of $n_j^{(i)} = \tilde{n}^{(i)} p_j^{(i)}$ gives

$$\mathrm{d}n_j^{(i)} = \mathrm{d}\tilde{n}^{(i)} p_j^{(i)} + \tilde{n}^{(i)} \mathrm{d}p_j^{(i)} \qquad (j = 1, 2, \ldots, s). \tag{25}$$

From Eqs. (18), (24) and (25) we get

$$\left(\delta_{mn} + H_{mn}\right)\mathrm{d}I_n = \sum_{i=1}^{L}\sum_{j=1}^{s}\mathrm{d}\tilde{n}^{(i)}F_{mj}^{(i)}p_j^{(i)} \qquad (m = 1, 2, \ldots, D), \tag{26}$$

where the $D \times D$ matrix $\boldsymbol{H}$ has the form

$$H_{mn} = \sum_{i=1}^{L}\sum_{j,k,l=1}^{s}\tilde{n}^{(i)}F_{mj}^{(i)}A_{jk}^{(i)}T_{kln}^{(i)}p_l^{(i)} \quad (m, n = 1, 2, \ldots, D). \tag{27}$$

It characterizes the consequences of the perturbed population structure on the regulation of the community. Note that matrix $\boldsymbol{H}$ is a property of the whole ecosystem. Therefore, it is the same for all species involved.

The impact niche vector is an immediate consequence of Eq. (26):

$$\boldsymbol{C}^{(i)} = \frac{\partial \boldsymbol{I}}{\partial n^{(i)}} = (\mathbf{1} + \boldsymbol{H})^{-1}\,\boldsymbol{F}^{(i)}\boldsymbol{p}^{(i)} = (\mathbf{1} + \boldsymbol{H})^{-1}\,\tilde{\boldsymbol{C}}^{(i)}. \tag{28}$$

Note that

$$\mathcal{V}_{\boldsymbol{C}} = \frac{1}{\det(\mathbf{1} + \boldsymbol{H})}\mathcal{V}_{\tilde{\boldsymbol{C}}}. \tag{29}$$

Recall that matrix $\mathbf{A}$ and therefore matrix $\mathbf{H}$ is finite for primitive dynamical matrices. That is, the linear dissimilarity of the impact niche vectors is proportional to the dissimilarity of the uncorrected impact vectors, with a nonzero constant of proportionality. The two impact niche vectors became linearly dependent under the same circumstances. Therefore, the empirically more accessible uncorrected vectors could be a good proxy for the corrected ones.

Formulae (17) and (28) establish the connection between the population-level niche vectors and the detailed (i-state-level) description of the structured population. With the exception of the correction represented by matrix $\boldsymbol{H}$, this relationships are intuitively transparent. The dimension reduction procedure depicted in Fig. 1 ensures that the calculated impact and sensitivity niche vectors obey the coexistence theory described in Section 2.1. Therefore we succeeded in establishing the theory of limiting similarity and niche sensu Meszéna et al. (2006).

3 Spatial structure: the minimal model

3.1 Analytic results

The theory of Section 2.3 applies for any kind of structured populations with finite i-states. However, because of the ecological importance of spatial distribution, it is worth to consider the minimal model of spatiality as a special case, when the different locations are the only source of population structure as well as of species diversity. In this subsection we concentrate on the analytic consequences of these simplifications.

We assume that the investigated populations live in a metapopulation environment of s habitats, or patches, in which the environmental conditions may

differ. The individuals are equivalent except their locations. Moreover, we assume that population regulation operates locally. In this case, the regulating variables (i.e., the resource exploitations) in the different patches must be considered as different variables (Levin, 1974), each of them has a contribution to the metapopulation-level regulation. There is a single regulating variable in each patch. As the total number of them is $D = s$, at most s species can coexist in a stable fixed point of the population dynamics.

The state transitions correspond to migration between habitats. These can be specified by a migration matrix for each population. Its generic element $\mu_{jk}^{(i)}$ $(j, k = 1, 2, \ldots, s)$ represents the rate of migration of species i from patch k to patch j. Then the elements of the dynamical matrix are

$$m_{jk}^{(i)} = \begin{cases} r_j^{(i)} - \sum_{l=1}^{s} \mu_{lj}^{(i)} & \text{if } j = k \\ \mu_{jk}^{(i)} & \text{if } j \neq k \end{cases}. \tag{30}$$

It is assumed that any patch is reachable from any other via consecutive migration steps. Irreducibility of the population matrix is ensured in this case.

For simplicity we further assume that resource exploitation is proportional to the total number of individuals in the respective patch. Without losing generality, we choose the constant of proportionality to be 1. From that the regulating variable in habitat j is

$$I_j = \sum_i n_j^{(i)}, \tag{31}$$

where $n_j^{(i)}$ denotes the population size of species i in patch j.

The ecological tolerance of species i towards the environmental conditions of habitat j is described by the local intrinsic growth rate $r_{0j}^{(i)}$ in the respective patch. The actual local growth rate $r_j^{(i)}$ is assumed to be negatively affected by the resource exploitation I_j in patch j:

$$r_j^{(i)} = r_{0j}^{(i)} - \alpha I_j \tag{32}$$

where α characterizes the strength of regulation.

The reduction of generality allows us to simplify considerably the formulae developed in the previous section. The matrix $F^{(i)}$ (cf. Eq. (18)) becomes the identity matrix

$$F_{jk}^{(i)} = \delta_{jk}, \tag{33}$$

as a consequence of Eq. (31). Comparison of Eq. (30) with Eq. (32) shows that only the element M_{mm} of the dynamical matrix depends on the regulating variable I_m. Therefore (see Eq. (14)),

$$T_{mnk}^{(i)} = -\alpha \delta_{mn} \delta_{nk}. \tag{34}$$

Then, Eq. (17) reduces to a simplified expression for the sensitivity niche vector:

$$\boldsymbol{S}^{(i)} = \alpha \begin{pmatrix} v_1^{(i)} p_1^{(i)} \\ v_2^{(i)} p_2^{(i)} \\ \vdots \\ v_s^{(i)} p_s^{(i)} \end{pmatrix}. \tag{35}$$

The sensitivity towards the regulating factor in a given patch is the product of the local density and the reproductive value of the individuals in that locality. The growth rate of the population is more sensitive to the exploitation of that patches where a larger fraction of the population lives as well as to the ones where the possibilities to contribute to the next generations is better.

By Eq. (33), the uncorrected impact vector is simply

$$\tilde{\boldsymbol{C}}^{(i)} = \boldsymbol{p}^{(i)}, \tag{36}$$

while the corrected one, from Eq. (28) is

$$\boldsymbol{C}^{(i)} = (\boldsymbol{1} + \boldsymbol{H})^{-1} \boldsymbol{p}^{(i)}. \tag{37}$$

That is, apart from the correction related to the perturbation of the population structure, the local impact of a population is proportional to ration of the population living in the given location.

More detailed analysis together with numerical studies are presented in Szilágyi and Meszéna (in press) for the special case of two patches (see also Meszéna et al., 1997).

3.2 Numerical studies

We perform numerical analysis for a linearly ordered chain of patches. Migration is possible between the neighboring habitats. The migration rate from patch j to patch $j \pm 1$ is $\mu_{j\pm1,j}$ uniformly for all species. The dynamical matrix reads as

$$\boldsymbol{M}^{(i)} = \begin{pmatrix} r_1^{(i)} - \mu_{21} & \mu_{12} & \dots & 0 \\ \mu_{21} & r_2^{(i)} - \mu_{12} - \mu_{32} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \mu_{s;s-1} & r_s^{(i)} - \mu_{s-1;s} \end{pmatrix}. \tag{38}$$

If all the μ's are nonzero, the matrix $\boldsymbol{M}^{(i)}$ is irreducible, as required.

We assume monotonically changing environmental conditions along the chain of s habitats. Coexistence of $L = s$ species will be investigated. Species i is optimized to the conditions in patch i. We specify the intrinsic local growth rate of species i in patch j as a Gaussian function

$$r_{0j}^{(i)} = \frac{A}{\sqrt{2\pi}\sigma} e^{-\frac{(i-j)^2}{2\sigma^2}}, \tag{39}$$

where A is a scale-factor.

An asymmetry to migration is introduced. Imagine, for instance, migration of flying insects in an environment with a dominant wind direction from the

left to the right. While all migration rates to the right are higher, the ones to the left are lower that a reference rate μ by a factor of c ($\mu_{j;j+1} = c\mu$ and $\mu_{j+1;j} = \mu/c$ for $j = 1, \ldots, s-1$).

The 4th order Runge-Kutta method was used to study the dynamics (11). The equilibrium densities were determined by numerical integration until convergence. We have never found an internal attractor other than the unique fixed point. As a consequence, at most so many populations can coexist, as many patches are present.

At the equilibrium point, each eigenvalue and the corresponding left and right eigenvectors of the dynamical matrix for all populations were determined numerically. Then, the theory of Section 3.1 provided the impact and sensitivity niche vectors of the coexisting species. Finally, the regulation strength J of the community was calculated via Eqs. (4-5).

The theoretical prediction about the robustness of coexistence provided by the regulation strength was compared to the numerically determined robustness. To this end, the equilibrium was studied as a function of the extra mortalities with the constraint

$$\sum_{i=1}^{L} \Delta^{(i)} = 0. \tag{40}$$

That is, the perturbations affecting all populations identically (i.e., not introducing advantage/disadvantage) were disregarded. The combination of the $\Delta^{(1)}, \Delta^{(2)}, \ldots, \Delta^{(L)}$ values, that allows coexistence fills an $L-1$ dimensional volume (the coexistence volume), which is the subset of the simplex defined by Eq. (40). The volume of the simplex is proportional to the robustness of coexistence.

Fig. 2 depicts the population and niche vectors for $s = 3$. According to (39) Species 1, 2 and 3 have the highest fitness in Patch 1, 2 and 3, respectively. The migration difference between the two directions redistribute the *density* compared to the symmetric migration. This asymmetry in migration makes density differences between the patches smaller for Species 1 and larger for Species 3 than in the symmetric migration case.

The *reproductive value* of Species 1 decreases monotonically and rapidly in the direction of large migration. For Species 3, it changes in the opposite way, but this change is less pronounced. The reason is that an individual of Species 3 in Patch 2, or in Patch 1 has a high chance to move into a better patch. Therefore an individual in a suboptimal patch has a higher reproductive value than in the case of symmetric migration. For Species 2, there is only a small difference between the reproductive values in patch 1 (from where the migration take individuals to the optimal patch) and in patch 2 (which is the optimal patch).

As one expects, a species is most sensitive and has the highest *sensitivity* in its own optimal patch. Recall, that sensitivity is the product of the frequency and the reproductive value. For Species 1 and 3 both of these quantities have a clear maximum in their respective optimal patch. For Species 2 the two quantities changes from patch to patch in the opposite way. Consequently, the sensitivity values of Species 2 are more even across the metapopulation, a kind of more 'generalist' behavior.

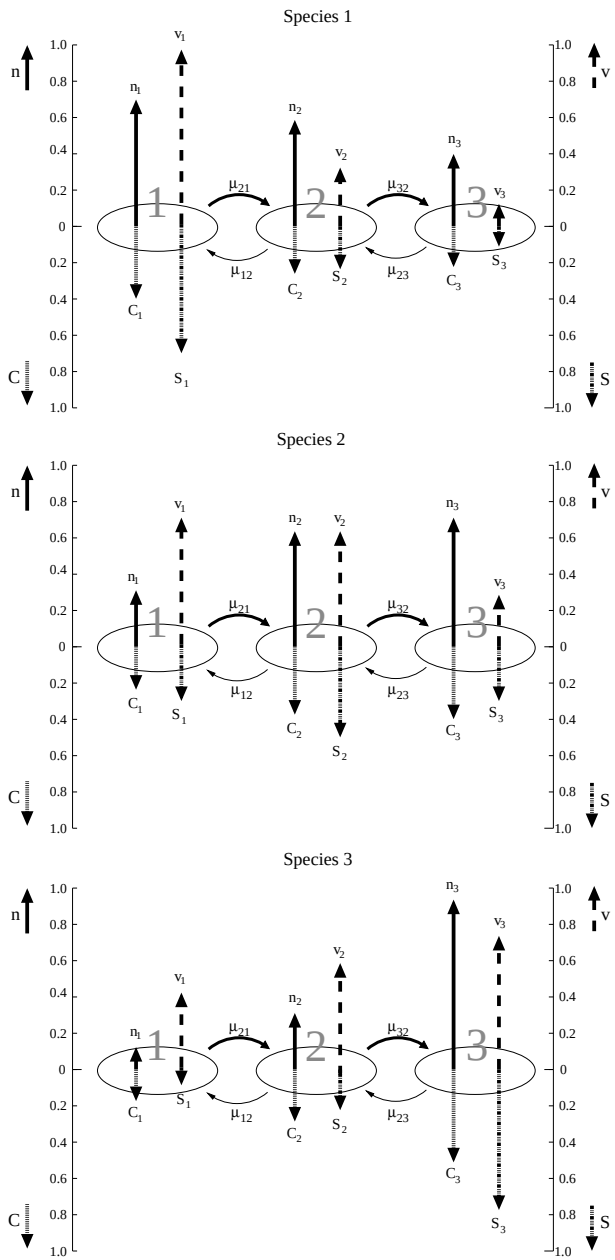

Figure 2: *Coexistence of three species in three patches with asymmetric migration. Each pane represents one of the species. In each patch the lengths of the two upward-pointing arrows represent the population size and the reproductive value of the species in the given patch. Similarly, downward-pointing arrows represent the impact and sensitivity of the population towards the specific patch. Parameters:* $A = 1/40$; $\sigma = 1$; $\alpha = 10^{-3}$; $\mu = 0.05$; $c = 1.5$.

Fig. 3 presents the result of robustness analysis for $s = 3$ and for $s = 5$. The coexistence volume is plotted as a function of the migration rate. The volume spanned by the impact vectors as the volume of the sensitivity vectors and the regulation strength $J = det(a)$ are plotted also as a function of the migration rate. In our simple case $L = s$ then the regulation strength is simply the product of the two volumes $J = \mathcal{V}_C \cdot \mathcal{V}_S$. (Both of the *average* and the *maximum* of J over the coexistence volume were determined and plotted, where different.)

For $s = 3$, the coexistence volume was determined via systematic screening of the simplex. In case of more patches and species this procedure would require immense computation. Instead, the more efficient Monte-Carlo integration was applied for $s = 5$. That is, we tested coexistence at a large number of randomly chosen points of the simplex. Measuring the probability of coexistence under uniform distribution of the extra mortalities provided the coexistence volume.

Increased migration tends to equalize the distribution of each population along the chain. This, in turn, makes the impact, as well as the sensitivity niches of the species more similar, resulting in a decreasing strength of regulation (see also Szilágyi and Meszéna, in press). This tendency predicts less robust coexistence for increasing migration rate. It is confirmed by the also decreasing coexistence volume.

Note the quite parallel decrease of the two (independently calculated) quantities by more than two orders of magnitude during a ten-fold increase of the migration rate. While not plotted, the coexistence volume shrinks roughly isotropically. That is, we found no direction of perturbation for which the coexistence is extremely sensitive, as compared to the other directions.

4 Discussion

Competitive exclusion and limiting similarity are unavoidable concepts of evolutionary ecology. Here we contributed to their theory by extending the analysis of Meszéna et al. (2006) for structured populations. By studying coexistence of spatially structured populations we established the minimal model of spatial niche segregation. Instead of using the phenomenological concept of resource utilization, the background theory of Meszéna et al. (2006) describes the niche of a species by the population's impact on, and sensitivity towards the regulating variables. We developed the connection between the population-level niche-description and the impact/sensitivity of the individual states.

We stress the generality of our approach. Limiting similarity was proposed in the context of the competitive Lotka-Volterra model (MacArthur and Levins, 1967). Being a "strategic" model, it maintains little connection with the complicacies of most of the ecological situations. However, expecting and not finding a strict limit of similarity in other model studies caused disillusionment towards limiting similarity (Maynard Smidth and Szathmáry, 1995; Rosenzweig, 1995). Only a model-independent analysis can provide a firm answer to the question whether limiting similarity and niche theory are proper guides of biological though.

Early enthusiasm towards niche theory faded away partially because the false expectation for easily reachable quantitative predictions did not materialize. We are developing a longer, but more realistic route from first principles (cf. Vandermeer and Goldberg, 2003) to results of practical relevance. In some sense,

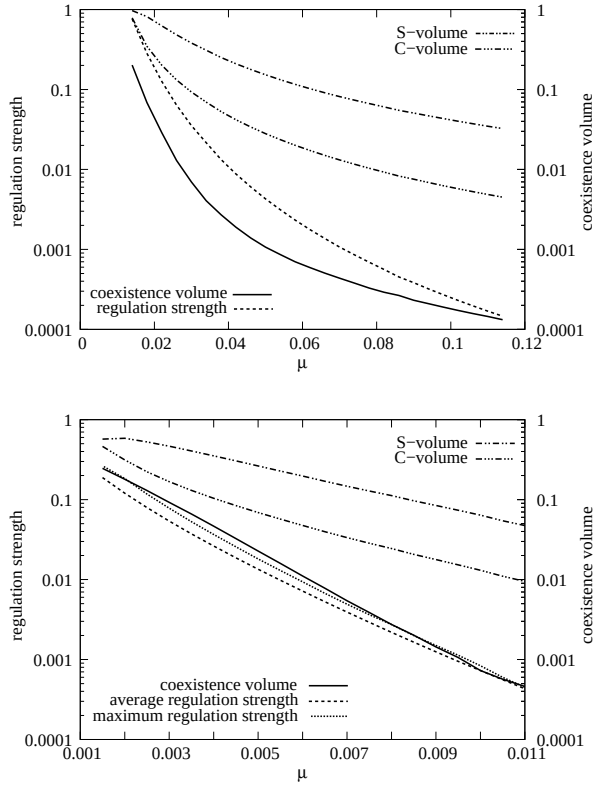

Figure 3: *The volume of coexistence, the strength of the regulation (determinant J) and the volumes spanned by the* $\mathbf{C}$ *and* $\mathbf{S}$ *vectors as a function of the migration rate μ for three patches (upper pane) and for five patches (lower pane). The parameters are the same, as in Fig. 2 expect $\sigma = 1/2$ for the five patches case. An arbitrary scaling was applied on the volume curves. On the left pane the average and the maximal volumes are the same with the precision of line thickness. On the lower pane the C- and S-volumes ($\mathcal{V}_C$ and $\mathcal{V}_S$) correspond to the maximal regulation strength.*

Meszéna et al. (2006) already provided the prediction by quantitatively connecting robustness of coexistence to decrease of interspecific competition. Here we described the recipe to specify this relationship for an arbitrary structured population. Still, even the specific model we discussed was a demonstration of the concept than a model aiming for quantitative fidelity. As a next step, one can apply our methodology for a tactical model of a specific ecological situation and arrive to specific numerical results on the robustness of coexistence.

One source of our generality is the perturbation approach. Instead of searching for a strict limit of similarity, we studied the gradual loss of robustness with increasing similarity. This change of attitude was suggested first by Abrams (1983) ("similarity-coexistence relationship", see also May, 1973, p. 158); a model-independent analysis was provided by Meszéna et al. (2006). We tested robustness of coexistence via varying the extra mortalities $\Delta^{(i)}$ (cf. coexistence bandwidth, Armstrong (1976)).

Note that it was a nontrivial choice to apply the same mortality rate for each i-state of a species. We wanted to concentrate on the single issue whether ecological interactions through the regulating variables stabilize coexistence against competitive exclusion. This ecological stabilizing feedback is distinguished from the purely demographic stabilization of population structure. Because of the interaction between the two types of stabilization, the distinction between them is a matter of definition by some extent. The state-independent mortality does not affect the population structures directly, only through the ecological feedback. On the other hand, it directly influences the fitnesses of the populations. Therefore, this kind of perturbation tests whether the ecological feedback eliminates fitness differences robustly.

Obviously, robustness against the chosen type of perturbation does not guarantee robustness against other types of perturbations. In principle it is possible that a strange interaction between ecology and demography could destabilize a coexistence that our theory would allow to exist. (We are not aware of a biologically realistic example.) The present analysis provides only a necessary condition for robust coexistence when state that sufficient niche segregation is required.

Another source of generality is the notion of regulating variables. Levin (1970) demonstrated already that the (discrete) principle of competitive exclusion (MacArthur and Levins, 1964; Rescigno and Richardson, 1965) can be generalized beyond resource competition by counting all quantities that behaves like resource concentrations (see also Heino et al., 1997). Unfortunately, the unifying nature of this idea did not receive the proper attention in community ecology. Instead, a multitude of reasons, which invalidates the resource competition theory, was investigated. In particular, interference competition was considered in this vein (e.g. Schoener, 1976). Following Krebs (2001), we prefer to use the term "regulating variables" for all variables involved in the regulating feedback loop, because "limiting factors" often means external ecological conditions, like temperatures, that are not density-dependent and, therefore, not regulating. Note that the term "environmental feedback variable" is used with the same meaning in a part of the literature (Metz and Diekmann, 1986; Diekmann et al., 1998, 2001, 2003). The prize for generality is that *all* interactions between the individuals must be considered as mediated by the regulating variables. In case of interference competition, one has to introduce variables like the experienced attack intensity. In case of apparent competition, mediated by

a common predator, the predation pressure is the proper variable (see Leibold, 1995 for the comparable role of resources and predators in niche theory).

As competitive exclusion is avoided by diversification with respect to the regulating variables, the *set* of theses variables is the proper generalization of Hutchinson's "niche space" (Meszéna et al., 2006). This "space" is either a discrete set, when we are dealing with a finite number of regulating variables, or a continuous entity, spanned by the "niche axes". The canonical example for the latter case is the seed-size continuum, partitioned by consumer populations. Importantly, the niche axis is the seed-size and *not* the seed densities. The latter ones are the (infinitely many) regulating variables.

In a heterogeneous environment, concentrations of the same resources at different locations may behave as different regulating variables, allowing coexistence through spatial segregation (Levin, 1974, see Szabó and Meszéna, 2007 for the consequences of local vs. non-local operation of population regulation). This way, the notion of regulating variables plays the role of the unifying concept in the case a functional and habitat type niche segregation. As pointed out by Levin (1974), the concentrations of a given kind of resource in different habitats are different variables in the feedback loop. Therefore they should be counted as different regulating variables. This way, both kinds of niche-segregation can be considered as a segregation with respect to the regulating variables. Still, the description of habitat-segregation is more complicated than the functional one because it must involve handling the spatial structure of the populations. This problem was solved here together with any other kinds of population structure.

When the nature of the niche space is understood, the next issue is the specification of the niche of a given species within that space. Originally, species' niche was conceived as a subset (Hutchinson, 1957) of the niche space. Later, it was made more precise by introducing the resource utilization function (MacArthur and Levins, 1967), describing the "fuzzy" nature of the subset. Unfortunately, this function is entirely a phenomenological concept, for which no unequivocal measuring instruction exists. Operationally, one has to study two questions, instead of one (cf. Abrams, 1988; Goldberg, 1990): How does resource availability depend on the population density? How does population growth rate depend on resource availability? The niche theoretical relevance of the two-way interaction was recognized by Leibold (1995). Meszéna et al. (2006) introduced the differential measures of these relations, the impact and the sensitivity vectors, as the proper representation that connects niche segregation and coexistence in a precise and general way.

It is quite common, but not necessary, that individuals in different i-states consume different resources. Therefore, the i-states, like the larva and the imago of an insect, may have very different niches. Our theory provides a clear prescription for constructing the niche description of the whole population from the ones for the i-states. In particular, we developed the exact connection between the population-level sensitivity niche vector and the sensitivity of the elementary demographic rates. Let us phrase it for age structure and discrete time! The sensitivity of the survival rate from age 4 to age 5 contributes to the population-level sensitivity proportional to the fraction of individuals in the age-class 4 in the equilibrium age-distribution *and* by the reproductive value of an individual of age 5. The reproductive rate in age 4 contributes according to the frequency of the 4-years-olds and to the reproductive value of a newborn. The very same intuitive idea applies for any other types of population structure. In our spa-

tial examples the i-state sensitivity was the same in each habitat. Then the population sensitivity towards the regulating factor in a given patch was just determined by the local density and reproductive value. (In case of symmetric migration this dependence reduces to square local density, see Szilágyi and Meszéna, in press.) The impact case is more involved. One must not consider the state distribution as a fixed property of the population. As the different states may be regulated differently, the population structure may become perturbed under a change of the population size. Moreover, the structures of the coexisting populations mutually influence each other through competition. An extra mortality of one of the species may perturb the state-distribution of all of them. To be precise, one must take into account all of these interrelated structure-perturbations when the environmental impact of a change in a population size is calculated. This is the role of matrix $\boldsymbol{H}$ in Eq. (28). Note that calculation of the sensitivity niche vectors was a direct application of the sensitivity analysis by Caswell (2001). In contrast, determining the impact niche vector required a fully different analysis, because we had to take care of the effect of perturbation on the population structure. The procedure we applied is a derivative of the perturbation theory widely used in quantum mechanics.

Empirical determination of the matrix $\boldsymbol{H}$ would be an immense task. Fortunately, for the qualitative limiting similarity conclusion it is sufficient to consider only the uncorrected version of the impact niche vectors (cf. Eq. (29)). It is just the sum of the impacts of all states, weighted by the frequencies of the states (Eq. (20)). No precision is lost this way. The true impact niche vectors, corrected by using matrix $\boldsymbol{H}$, were needed only to calculate the community matrix (4). Fortunately, it is possible to determine in a more direct way through Eq. (3) via experimentally applied extra mortality. Still, the consistency of niche theory requires us to state clearly that the corrected impact vector plays the prescribed role for structured populations.

In general, the number of regulating factors and the number of the i-states are unrelated. However, in Section 3 we concentrated on the minimal model of the situation when spatial heterogeneity was the sole source of species diversity. Therefore we assumed a single regulating factor for each patches. Moreover, we assumed no differences between the individuals other than spatial location. Consequently, both the number of i-states and the number of the regulating factors equaled to the number of patches, in this case.

Leibold (1995); Shugart (1998); Soberon (2007) distinguish between "Eltonian" and "Grinnelian" niche. The first one corresponds to the functional niche in our terminology, or to the bionomic niche in Hutchinson's parlance. The second one is something like the habitat/scenopoetic niche, but usually discussed outside the context of competitive exclusion principle, as an alternative name for the tolerance range. Here we provided an integrated notion that firmly roots both kinds of niche in competition/coexistence theory.

The model by Abrams and Wilson (2004) demonstrates clearly that habitat niche cannot be equated with the environmental tolerance of the species for the purpose of coexistence theory. In this two-patch model both species have the higher fitness (i.e., lower R^* value) at the same patch. Still, they may be able to coexist if their mobility is different. If the locally inferior species has a lower migration rate, then its better localization on the better patch may compensate for its local inferiority. Then, the different spatial distribution of the two species establishes a kind of niche segregation. It would be overlooked, if the ecological

tolerance vector $\boldsymbol{r}_i^0$ was considered as a descriptor of niche.

The environmental gradient (therefore, the scenopoetic niche axis of Hutchinson) can be considered as a limiting case of the linear chain of habitats. Technically, our analysis does not apply because of the infinitely many locations. Still, we expect our conclusions to remain valid provided, that a *finite* spatial interval is considered. The dynamical matrix would be replaced by a reaction-diffusion operator with discrete spectrum (Shigesada and Kawasaki, 1997). Instead of the right and left eigenvectors we would have eigenfunctions specifying population distribution and the location-dependent reproductive value. The isolatedness of the dominant eigenvalue guarantees the validity of the perturbation expansion. See Durrett and Levin (1998) for a study of interspecific competition in such context. Mizera et al. (in prep.) studies the possibilities of niche-segregation along the gradient. Mizera and Meszéna (2003) analyses the possibility of evolutionary branching in this ecology; see Doebeli and Dieckmann (2003) for the corresponding speciation simulation.

Note that Diekmann et al. (1998, 2001) provided a measure theoretical formulation for the theory of structured population that allows infinitely many i-states. While not discussed here, we expect our theory to extend for their more general formalism.

Modeling of coexistence maintained by spatial heterogeneity was initiated by the seminal paper of Levene (1953), using population genetics context. Kisdi and Geritz (1999); Geritz and Kisdi (2000) continued the evolutionary study of Levene's model by discussing emergence of reproductive isolation in this context. Meszéna et al. (1997) investigated adaptive dynamics and evolutionary branching in a continuous-time two-pach model. Szilágyi and Meszéna (in press) complemented this model by the impact/sensitivity niche description. They argued that the symmetry between habitat and functional niche segregation translates to a conceptual symmetry between allopatric and parapatric niche segregation. The purely ecological study of heterogeneity-maintained coexistence was initiated by Levin (1974); see Amarasekare (2003) for a recent review.

Chesson's theory (Chesson, 2000b) suggests a deeper, unifying understanding of coexistence. Necessarily, any kinds of species coexistence are based on stabilizing effects. Resource partitioning is the simplest example for such mechanism. Fluctuations may result in two additional mechanisms, the "storage effect" and the "effect of relative nonlinearity" (Chesson, 1994). Both of them are related to the nontriviality of averaging. Therefore they are vanishing in a fully additive linear model, that behaves like its averaged counterpart (Chesson and Huntly, 1997). Chesson (2000a) extended the theory for spatially varying environment. The effects of storage and relative nonlinearity work identically to the previous case. However, spatial averaging results in an additional diversity-stabilizing effect, which is related to the spatial covariance between the local density and local growth rate.

Instead of the spatial averaging, we used the theory of structured populations. Still, the approach presented here is entirely consistent with Chesson's one. The first and the second terms of our Eq. (32) correspond to his standardized environmental ($\mathcal{E}$) and competitive ($\mathcal{C}$) parameters, respectively. The additive linear construction of our model ensures, that both the storage effect and the effect of relative nonlinearity is vanishing. (The first one would correspond to non-additivity of the environmental and the competition parameter; the second one would mean a difference between the invader and the resident

in the spatially averaged competition parameter.) Consequently, the type of coexistence, which was studied in Section 3, is completely explained by the density-growth rate covariance. This conclusion is in line with the intuitive picture: The essential point is that a species maintains a higher density in the patch, in which its growth rate is higher. This covariance is diminishing at high migration rates. Small modifications of the current model would lead to reappearance of the other two effects. Still, the covariance effect seems to be the main issue in the investigated type of coexistence.

While Levene (1953) used the term "niche" for the two patches of his model, later fragmentation of the theory disconnected the specific studies of (spatial, or not) species coexistence from the verbal "niche theory", mostly referring to Hutchinson's niche axes. Still, development of coexistence theory has remained consistent with the original concept of competitive exclusion and niche segregation. Both Levins's understanding on the role of regulating variables (Levin, 1970, 1974) and Chesson's one on the need to be averaged differently point to the necessity for ecological differentiation. The expectation that space-time heterogeneity can weaken competition and de-emphasize the importance of segregation for coexistence was falsified (Chesson, 1991; Chesson and Huntly, 1997). The explicit interest towards niche theory, as the "central organizing aspect of modern ecology", was rejuvenated by Leibold (1995). The investigation presented here closed the circle by mathematically connecting the spatial/structured coexistence problem to a formalized concept of competitive niche.

Acknowledgement

We thank Mats Gyllenberg, Kolos Kőszeghy, Hans Metz, Liz Pásztor and for the late Pál Juhász-Nagy for discussions. This work was financed by the OTKA grant T049689.

A Perron-Frobenius for continuous dynamics

Perron-Frobenius theorem plays an important role in the discrete-time matrix population theory (Caswell, 2001, p. 79). We use in a slightly different for continuous time, as discussed bellow.

All off-diagonal elements of the continuous-time dynamical matrix must be non-negative. It is a consequence of the requirement that abundance of the i-states must remain non-negative under all circumstances. (Assume, that $M_{ij} < 0$ for any $i \neq j$ and only n_j is different from zero. Then, the resulting $\mathrm{d}n_i/\mathrm{d}t < 0$ would be absurd.) Moreover, irreducibility of the dynamical matrix is assumed. Then we prove the following statements:

- The dominant eigenvalue (defined as the eigenvalue with the greatest real part) is real, unique and simple, i.e. the corresponding left and right eigenvectors are unique.
- The left and right eigenvectors, corresponding to the dominant eigenvalue, are real and strictly positive.

Proof One can chose a real positive constant Λ such that the matrix

$$\boldsymbol{M}^+ = \boldsymbol{M} + \Lambda \mathbf{1} \tag{41}$$

is nonnegative. Matrix $\boldsymbol{M}^+$ inherits irreducibility from matrix $\boldsymbol{M}$. Perron-Frobenius theorem applies for $\boldsymbol{M}^+$ and guaranties the existence of a real positive eigenvalue ϱ_1^+, that has the greatest magnitude and is simple; the corresponding left and right eigenvectors are real and strictly positive. Obviously ϱ_1^+ can be characterized as the eigenvalue of matrix $\boldsymbol{M}^+$ with the greatest real part (Fig. 4). Matrix $\boldsymbol{M}$ has the very same eigenvectors as of $\boldsymbol{M}^+$ but its eigenvalues are shifted by the real constant $-\Lambda$. Obviously, the eigenvalue of matrix $\boldsymbol{M}$ with the greatest real part is

$$\varrho_1 = \varrho_1^+ - \Lambda, \tag{42}$$

which proves the statements.

Note that ϱ_1 is not necessarily the eigenvalue of the greatest magnitude of matrix $\boldsymbol{M}$. As the matrix $\boldsymbol{M}^+$ is allowed to be imprimitive, it may have additional eigenvalues with the same magnitude as ϱ_1^+. Still, ϱ_1^+ and ϱ_1 are unique in their capacity of being the eigenvalue (of the corresponding matrix) with the greatest real part. In discrete time, imprimitivity with imprimitivity index d would result in periodic behavior with period d. No such issue exists in real time. Therefore, while primitivity is a usual assumption in discrete time, it is not needed for the continuous case.

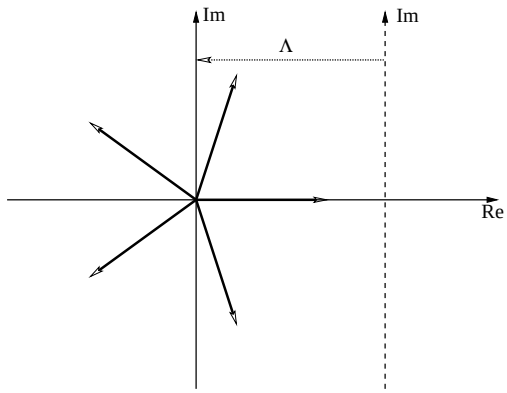

Figure 4: *Eigenvalues with the greatest magnitude in an imprimitive matrices with $d = 5$.*

B Perturbation of growth rate and population structure

Here we derive Eqs. (21-22) by determining the perturbation of the growth rate r and population structure $\boldsymbol{p}$ of any population under a small change $\mathrm{d}\boldsymbol{M}$ of the dynamical matrix $\boldsymbol{M}$.

The perturbed quantities will be denoted by prime. The perturbed eigenvalue equation is

$$\boldsymbol{M}'\boldsymbol{p}' = \varrho_1'\boldsymbol{p}', \tag{43}$$

where

$$\boldsymbol{M}' = \boldsymbol{M} + \mathrm{d}\boldsymbol{M} \tag{44}$$

is the perturbed dynamical matrix.

We want to express the perturbed population structure $\boldsymbol{p}'$ in terms of the unperturbed right eigenvectors of the matrix $\boldsymbol{M}$, as

$$\boldsymbol{p}' = \sum_{j=1}^{D} c_j \boldsymbol{w}_j, \tag{45}$$

where c_j are coefficients to determine.[1] Substitution into Eq. (43) leads to

$$(\boldsymbol{M} + \mathrm{d}\boldsymbol{M}) \sum_j c_j \boldsymbol{w}_j = \varrho_1' \sum_j c_j \boldsymbol{w}_j. \tag{46}$$

We multiply this equality with the dominant left eigenvector $\boldsymbol{v}_1$ from the left and use the orthogonality relation (10).

[1] It is always possible, if the matrix has D different eigenvectors, i.e. if it is of simple structure.

$$\sum_j c_j \boldsymbol{v}_1 \mathrm{d}\boldsymbol{M}\boldsymbol{w}_j = (\varrho_1' - \varrho_1)c_1. \tag{47}$$

By Eq. (9), vanishing perturbation corresponds to $c_1 = 1$. Then, one can write

$$c_1 = 1 + \mathrm{d}c_1 + \text{h.o.t.}, \tag{48}$$

where $\mathrm{d}c_1$ is proportional to the perturbation; the higher order terms are omitted. The rest of the coefficients vanish without the perturbation, so

$$c_j = \mathrm{d}c_j + \text{h.o.t} \qquad j \neq 1. \tag{49}$$

With substitution of these forms into Eq. (47) and omission of the higher order terms one arrives to the change of the growth rate

$$\mathrm{d}r = \mathrm{d}\varrho_1 = \varrho_1' - \varrho_1 = \boldsymbol{v}_1 \mathrm{d}\boldsymbol{M}\boldsymbol{w_1} = \boldsymbol{v}\mathrm{d}\boldsymbol{M}\boldsymbol{p}, \tag{50}$$

where the notations $\boldsymbol{v} = \boldsymbol{v}_1$, $\boldsymbol{p} = \boldsymbol{w}_1$ were used (cf. Caswell, 2001, p. 209).

Now we turn to determine the perturbation of the population structure. Eq. (46) is multiplied with $\boldsymbol{v}_i$ ($i \neq 1$) from the left, leading to

$$\sum_j c_j \boldsymbol{v}_i \mathrm{d}\boldsymbol{M}\boldsymbol{w}_j = (\varrho_1' - \varrho_i)c_i. \tag{51}$$

Using Eq. (49) results in

$$\mathrm{d}c_i = \frac{\boldsymbol{v}_i \mathrm{d}\boldsymbol{M}\boldsymbol{p}}{\varrho_1 - \varrho_i} \qquad i \neq 1. \tag{52}$$

Then the perturbed population structure is

$$\boldsymbol{p}' = (1 + \mathrm{d}c_1)\boldsymbol{p} + \sum_{i \neq 1} \frac{\boldsymbol{v}_i \mathrm{d}\boldsymbol{M}\boldsymbol{p}}{\varrho_1 - \varrho_i}\boldsymbol{w}_i. \tag{53}$$

The value of $\mathrm{d}c_1$ is determined by the requirement of preserving the summation the elements of $\boldsymbol{p}$:

$$1 = \sum_{l=1}^{s} p_l' = 1 + \mathrm{d}c_1 + \sum_{i \neq 1} \mathrm{d}c_i U_i, \tag{54}$$

where U_i was defined by Eq. (23). This leads to

$$\mathrm{d}c_1 = -\sum_{i \neq 1} \mathrm{d}c_i U_i. \tag{55}$$

Then, from Eq. (45),

$$\mathrm{d}\boldsymbol{p} = \boldsymbol{p}' - \boldsymbol{p} = \mathrm{d}c_1 \boldsymbol{p} + \sum_{i \neq 1} \mathrm{d}c_i \boldsymbol{w}_i. \tag{56}$$

Substituting this into Eq. (53) leads to

$$\mathrm{d}\boldsymbol{p} = \sum_{i \neq 1} \frac{(\boldsymbol{w}_i - U_i \boldsymbol{p}) \circ \boldsymbol{v}_i}{\varrho_1 - \varrho_i}\, \mathrm{d}\boldsymbol{M}\boldsymbol{p}, \tag{57}$$

which can be written into the form (21) by introducing the matrix $\boldsymbol{A}$ with (22).

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