Two-patch model of spatial niche segregation

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Abstract

Spatial niche segregation between two habitats and the related adaptive dynamics are investigated. Independent population regulations operate in the two patches by a single resource in each. The populations migrate between the habitats with a constant rate. In line with a general mathematical concept published elsewhere, the niche of a species is described by the measures of the two-way interactions between the species and the resources. Increasing migration rate tends to equalize the population sizes between the habitats and diminish the dependence of the niches on the environmental tolerances of the species. In line with the expectations, when two species coexist, their realized niches are more segregated than their fundamental ones. We demonstrate that robust coexistence requires sufficient niche segregation. That is, the parameter range that allows coexistence of the two species shrinks to nil when the niche-differences between the species disappear. In turn, niche segregation requires separation of tolerances and sufficiently low migration rate. For the evolutionary study we assume a continuous, clonally inherited character that has different optima at the two patches. Evolution of this trait may end up in an intermediate "generalist" optimum, or it can branch and leads to a dimorphic population. The condition of the latter outcome is in line with the conditions that allow niche segregation: The patches have to be sufficiently different and the migration has to be sufficiently low.

1 Introduction

Hutchinson's (1959) famous question, "Why are there so many kinds of animals?", was an evolutionary one and an ecological one at the same time. His essential answer originates from Darwin (1859): each species is a unique adaptation to something. That "something" was later considered as the "niche" of the species (Grinnel, 1914; Elton, 1927). It was established that coexistence requires niche segregation (Gause, 1934). The concept of "niche" deserves a central place in evolutionary ecology, analogously to the role of "fitness" in evolution. However, the first one is often considered too vague and too tautologic to be useful; a status similar to that of the latter several decades ago.

As a more recent development, theory of adaptive dynamics (Metz et al. 1996; Dieckmann & Law, 1996; Geritz et al., 1997, 1998; Meszéna et al., 2005; Durinx et al., 2007) establishes a clear connection between the ecological and the evolutionary aspects of species diversity on the principal level. On the ecological side, the "basic tenet" of niche theory (Case, 2000, p. 368) states that increasing niche segregation weakens competition between the involved species. Lowered interspecies competition provides an advantage to the rare species as compared to the abundant one, stabilizing their coexistence (Chesson, 2000a). From an evolutionary point of view, a rare advantage corresponds to negative frequency dependence (Christiansen, 1988; Bulmer, 1994, p. 124). In turn, frequency dependence may lead to evolution towards a fitness minimum (Eshel, 1983). Then the emerging disruptive selection leads to evolutionary branching in asexual models (Geritz et al., 1997, 1998). For sexual organisms, it was proposed, that the very same selection regime may select also for reproductive isolation between the branches, leading to adaptive (or competitive) speciation

(Rosenzweig, 1978; Seger, 1985; Dieckmann & Doebeli, 1999; Dieckmann et al., 2004). Easiness and importance of this mode of origin of a new species are ongoing debates; see Gavrilets (2005) for a skeptical opinion.

The intuitive notion of niche was profoundly shaped by Hutchinson (1978) when he introduced the "niche space of niche variables" picture. His distinction between the "fundamental" and the "realized" niches found its invariant place in ecology textbooks. Following Grinnel (1904), Hutchinson recognized two kinds of niche segregation: Species may adapt to different environmental conditions ("scenopoetic" niche axis) or to different kinds of food ("bionomic" axis). We will refer to these two cases as "habitat" and "functional" segregation, respectively. One should also recognize that continuity is not an essential feature of the niche "space". If the environment consists of a continuum of seed-sizes to consume, then seed-size can be considered as a continuous niche axis to be partitioned by the consumer species. However, if there are only two distinct types of food, then the consumers can partition only this two-element set. Thus, logically, this finite set of different resources must be considered as the niche space (Rescigno & Richardson, 1965; Petraitis, 1989). Analogously, if two different habitats are available, then we have two different niches (Levene, 1953). On the other hand, one should consider an environmental gradient as a continuum of habitat-niches.

Terminology varies: In many contexts, the meaning of niche is restricted either to the functional, or to the habitat sense (see the historical analysis of Leibold, 1995; Chase & Leibold, 2003). On the evolutionary side, in most cases, adaptive/competitive speciation is considered in connection with local, functional niche segregation. This is due to the fact that the traditional "allopatric" theory of speciation (Mayr, 1942; Gavrilets, 2004) postulates the necessity of spatial segregation between old and new species. Therefore, the empirical evidences (Schileven et al, 1994; Via, 2001) for sympatric speciation necessitate a new theory of speciation. Adaptive speciation is regarded as an explanation for this "surprising" way of emergence of a new kind of creature.

If the functional and the habitat segregations are comparable ways of decreasing interspecies competition, one may wonder if the latter one can also be the basis of competitive speciation. To explore this possibility, Meszéna et al. (1997) provided the analysis of adaptive dynamics in a two-patch environment (see also Day, 2000). The main conclusion was that evolutionary branching can be initiated either by increasing the difference between the environmental conditions in the two patches, or by decreasing the migration between them. Mizera & Meszéna (2003) investigated the adaptive dynamics of the corresponding continuous niche space, the environmental gradient; Doebeli & Dieckmann (2003) studied emergence of reproductive isolation in the same context.

The underlying problem is, that – while adaptive dynamics provides a fairly general connection between ecology and evolution – the many different ways of competitive coexistence are often studied via unrelated models at the ecological level (see Amarasekare, 2003 for a recent review). Traditionally, the Lotka-Volterra competition model (MacArthur & Levins, 1967) is used to demonstrate the principle of niche partitioning. It is a phenomenological model, that *postulates* the connection between competition and niche overlap. In some simple cases of resource competition the mechanistic modeling of the resource-consumer interaction faithfully reproduces the Lotka-Volterra assumptions (MacArthur, 1969; Yodzis, 1989, p.119; Tilman, 1982). However, for the general case, the Lotka-Volterra model is no more than a mathematical illustration of the principle.

Prevalence of limiting similarity is a quite common conclusion of investigations (Abrams, 1983). However, no model-independent minimum of allowed similarity could be found to find (May & MacArthur, 1972; Rosenzweig, 1995, p. 127). To remedy this situation, Meszéna et al. (2006) introduced a model-independent theory of limiting similarity and niche segregation (see also Szabó & Meszéna, 2006a). They demonstrated that large overlap of the – properly defined – niches results in a decreasing and, eventually, disappearing likelihood of coexistence. This conclusion establishes a firm mathematical basis for the connection between Gause's principle and the notion of niche.

Application of this theory for functional niche segregation is straightforward. Here we are concerned with the next step: the analysis of spatial niche segregation as an ecological underpinning of the possibility of geographical adaptive speciation. We use the two-patch model of Meszéna et al. (1997) as the context of our investigation. Section 2 summarizes the reference theory of Meszéna et al. (2006). Section 3 introduces the specific model. We also provide the niche-analysis first for a single species and for two coexisting ones. Finally, we compare our findings with the adaptive dynamics of the model.

2 Background: coexistence and niche segregation

Here we summarize the theory of limiting similarity by Meszéna et al. (2006). The goal is to remedy the "phenomenological" status of the Lotka-Volterra competition model, and to replace it with a theory of potential quantitative fidelity without sacrificing generality. In particular, we ought to substitute the notion of resource utilization function with something that is clearly defined in any ecological situation.

The classical concept of limiting similarity (MacArthur & Levins, 1967) postulates that interspecies (resource) competition is proportional to the overlap of the resource utilizations of the two species. If species 1 consumes a given kind of resource, then the decreasing concentration of that resource affects the growth rate of species 2 provided, that species 2 utilizes the same food. This intuition becomes precise when we consider the *impact* of species 1 on the resource concentration and the *sensitivity* of species 2 towards this concentration.

We will need a generalization of the notion of resource. An environmental factor/variable will be considered as a "regulating" one, if it is involved in the feedback loop of population regulation. (See Krebs, 2001 for the distinction between limiting and regulating factors.) While, in case of resource competition, the number of coexisting species is limited by the number of resources (MacArthur & Levins, 1964; Armstrong & McGehee, 1980), a similar statement holds for the number of regulating factors in the general situation (Levin, 1970; Heino et al., 1997). We shall consider the species' impact on, and sensitivity towards the regulating factors. Competition between two species is reduced if they differ with respect to their impact and sensitivity towards the regulating factors.

The *set* of regulating factors constitutes the – either discrete, or continuous – niche space to be partitioned between the species. A "niche axis" of Hutchinson corresponds to a *continuum* of the regulating factors. Along a bionomic axis (functional niche segregation) one has to consider all seed-sizes as different factors. Along a scenopoetic axis (habitat segregation) the resource concentrations at the different locations (under different environmental conditions) are to be considered as different regulating variables.

In quantitative terms, write the dependence of the growth rate of the *i*th species (i = 1, 2, ..., L) on the densities $n_1, ..., n_L$, as

$$r_i = r_i \left(I(n_1, n_2, \dots, n_L) \right) \qquad (i = 1, 2, \dots, L),$$
 (1)

where the vector $I = (I_1, I_2, ..., I_D)$ collects the *D* number of regulating variables. Then, the elements of the competition (or community) matrix are

$$a_{ij} = -\frac{\partial r_i}{\partial n_j} = \sum_{k=1}^{D} S_{ik} C_{jk} = \mathbf{S}_i \cdot \mathbf{C}_j, \qquad (2)$$

where the partials

$$C_{ik} = \frac{\partial I_k}{\partial n_i} , \qquad S_{ik} = -\frac{\partial r_i}{\partial I_k}$$
(3)

measure the *i*th species' impact on, and sensitivity towards, the *k*th regulating factor, respectively (the chain rule was used). The vectors $C_i = \{C_{i1}, C_{i2}, \ldots, C_{iD}\}$ and $S_i = \{S_{i1}, S_{i2}, \ldots, S_{iD}\}$ will be referred to as the *impact* and *sensitivity* niches of the *i*th species. The negative sign in eq. (2) corresponds to the choice that the competition coefficients are positive for negative interaction between the species. Negative a_{ij} represents a positive influence. The sign convention in eq. (3) means that (in case of resource competition) we will consider the exploitations as the regulating variables.

As the equilibrium conditions $r_i(I) = 0$ represent L equations for the D variables, generically $L \leq D$ must be satisfied for the existence of the community. Coexistence of L populations requires L different regulating mechanisms to adjust all population sizes for equilibrium when all growth rates are zero. Accidentally, it is possible to have equal birth and death rates without regulation. However, such unregulated equilibrium disappears suddenly if, by whatever reasons, an arbitrarily small additional mortality starts to affect some, but not all, populations. That is, the essential issue of coexistence is the robustness against an extra mortality.

Imagine that a sufficient number of regulating factors are present, but some of them are very similar to each other from the point of view of the species (see Abrams, 1988 for an analysis of this problem). This is an intermediary situation between having, or not having L independent regulating mechanisms. Alternatively, assume that the regulating factors themselves are different enough, but the species are not, again leading to the situation in which the existence of L different regulations is in doubt. Then the community is regulated, but weakly. It has some tolerance towards additional mortalities, but only a weak one. While an infinitesimal additional mortality does not destroy coexistence, a small one does.

More quantitatively, assume that an environmental change imposes additional mortalities, denoted by Δ_i for the *i*th species. Then the new equilibrium equations read as

$$r_i \left(I(n_1, n_2, \dots, n_L) \right) - \Delta_i = 0 \qquad (i = 1, 2, \dots, L).$$
(4)

 $\Delta_i = 0$ corresponds to the original situation; negative Δ_i s mean newly acquired advantages. The sensitivity of the equilibrium population sizes towards the additional mortalities can be determined by implicit differentiation:

$$\frac{\partial n_i}{\partial \Delta_j} = -\sum_{j=1}^L (a^{-1})_{ij} \Delta_j = -\frac{1}{J} \sum_{j=1}^L \operatorname{adj}(a)_{ij} \Delta_j,$$
(5)

where $\operatorname{adj}(a)$ denotes the adjunct of the community matrix. The determinant $J = \det(a_{ij})$ measures the strength of regulation on the community level. As it appears in the denominator, a weakly regulated community is sensitive towards the extra mortalities. If the sensitivity niches of two different species coincide, the corresponding two rows of matrix a are the same and J = 0. This situation is approached when two of the S_i vectors are similar. That is, similarity of the sensitivity niches results in small J and weak regulation. A similar argument holds for the impact niches and for the columns of the matrix. Whilst a weakly regulated community reacts to any change of the external parameters with a large change in its population size, a small perturbation can drive some of the populations into extinction. Therefore the existence of the community is restricted to a narrow region of the Δ parameter space. Robust coexistence requires strong regulation and, consequently, sufficient difference between the impact, as well as between the sensitivity niches of the species forming the community, (see Meszéna et al., 2006 for the more precise analysis).

Our interest here is to apply these concepts for spatially distributed populations. If the environment consists of different patches with *local* resource limitation (e.g., the resources do not diffuse freely between the habitats, see also Szabó & Meszéna, 2007), the same resource in the different patches behaves as different regulating factors. Is this way, the notion of the regulating variables unifies the cases of "single patch, two resources" and "two patches, one resource". In both situations, at most two species can coexist.

We are interested in the regulation of the populations as a whole, because the possibility of coexistence is determined at a global level. Accordingly, we have to consider the *total number* of individuals on the whole territory as n_i , while r_i should be the overall growth rate of the *i*th population, as determined by the theory of structured populations (Metz & Diekmann, 1986; Metz et al., 1992; Caswell, 2001). If population regulation operates locally, the regulating variables of the different localities must be considered as separate variables, each of them having a contribution to the overall regulation. We have to assess the derivatives (3) while the spatial distribution remains

in equilibrium. As we will see, this can be different from having a fixed spatial distribution, as changing the total population size may change the equilibrium distribution also.

In a *thought experiment*, one can apply any combination of extra mortalities (the Δ_i s) to the populations and observe the correlated change of the equilibrium population sizes of the species and the regulating variables. (The additional mortalities can also be interpreted as removal rates, that maintain a chemostat-like constant growth rate $r_i = \Delta_i$.) From this data set one can reconstruct the functions $r(\mathbf{I})$ and $\mathbf{I}(n_1, n_2, \ldots, n_L)$ together with their derivatives, the niche vectors. This is the unique correct definition as long as the robustness analysis is the intended use of the niche vectors.

3 Model definition

Following Meszéna et al. (1997), we consider an environment consisting of two habitats of equal size, A and B, with different environmental conditions. We assume independent population regulation in the patches (Levene, 1953; "soft selection" regime, Christiansen, 1975). As the number of regulating factors is D = 2, at most two species can coexist in equilibrium.

The regulating variables (e.g. the local resource exploitations) are denoted by $I_{\rm A}$ and $I_{\rm B}$ in the two habitats. Resource exploitation is proportional to the total number of individuals in the respective patch. Without losing generality, we chose the constant of proportionality to be 1, i.e.,

$$I_X = \sum_i n_{iX} \tag{6}$$

for the patch X = A, B; n_{iX} is the density of the *i*th species in patch X.

The tolerance of species *i* towards the environmental condition in patch X is specified by the local intrinsic growth rate r_{iX}^0 . The actual growth rate is negatively affected by the resource exploitation I_X in the patch:

$$r_{iX} = r_{iX}^0 - \alpha I_X$$
 (*i* = 1, 2; *X* = A, B), (7)

where α characterizes the strength of regulation. In the evolutionary study in Section 4.3 (but only there) we assume that a species' tolerances are determined by an evolvable trait, or strategy, x. The trait has different optima, denoted by x_A^{opt} and x_B^{opt} in the two patches. Then, the local intrinsic growth rate of strategy x in patch X is specified, as

$$r_X^0(x) = \frac{1}{\sqrt{2\pi\sigma}} \exp\left[-\frac{(x - x_X^{\text{opt}})^2}{2\sigma^2}\right].$$
 (8)

We assume a constant migration rate μ for all species. The population dynamics is defined as

$$\frac{d}{dt} \begin{pmatrix} n_{iA} \\ n_{iB} \end{pmatrix} = \begin{pmatrix} r_{iA} - \mu & \mu \\ \mu & r_{iB} - \mu \end{pmatrix} \begin{pmatrix} n_{iA} \\ n_{iB} \end{pmatrix}$$
(9)

for all *i*. Note that the dynamics of the different species are coupled through the regulating variables. The matrix on the r.h.s. of the equation will be referred to as the "dynamical matrix". The overall growth rate of the population and the dynamics of spatial relaxation at fixed values of the regulating variables can be calculated from the eigenvalues of this matrix (Box 1).

We found no other internal attractor than a unique fixed point. The equilibrium distribution was determined by fourth-order Runge-Kutta numerical integration of the dynamics until convergence.

The niche vectors were calculated in two ways with coinciding results. First, they were determined via numerically reproducing the thought experiment described at the end of Section 2. Second, they were calculated from the equilibrium distribution by the analytic formulas of Box 2 (see the Appendix in Supplementary Material for derivations).

Box 1: Population growth and relaxation in the model

Following the lead of Metz & Diekmann (1986), Diekmann et al. (1998, 2001, 2003) consider first the dynamics of a population at fixed I. This condition means that the loop of population regulation is cut open, the populations become independent and grow exponentially after an initial spatial relaxation.

The relevant quantities are the two eigenvalues of the dynamical matrix:

$$\varrho_i^{\pm} = \frac{r_{iA} + r_{iB}}{2} - \mu \pm \sqrt{\left(\frac{r_{iA} - r_{iB}}{2}\right)^2 + \mu^2}.$$

The exponential growth rate that plays the role of overall growth rate r_i in the general setup of Section 2, is the leading eigenvalue, i.e., $r_i = \rho_i^+$ (see Metz & Diekmann, 1986; Caswell, 2001 for the general idea and Meszéna et al., 1997 for the specific calculations). It is instructive to calculate two limiting cases:

$$r_i \approx \begin{cases} (r_{iA} + r_{iB})/2 & \text{if } \mu \gg |r_{iA} - r_{iB}|/2, \\ \max(r_{iA}, r_{iB}) - \mu & \text{if } \mu \ll |r_{iA} - r_{iB}|/2. \end{cases}$$

While the overall growth rate is the average of the local growth rates when the migration is high, it roughly equates to the higher local growth rate when the migration is low.

The equilibrium distribution is given by the eigenvector of the dynamical matrix. It is easy to see, that an additional mortality, which is the same in the two patches, does not alter this distribution. The rate of relaxation to the equilibrium distribution is determined by the difference between the two eigenvalues:

$$\Delta \varrho_i = \varrho_i^+ - \varrho_i^- = \sqrt{(r_{iA} - r_{iB})^2 + 4\mu^2}.$$

Observe that there are two processes contributing to this relaxation. The first one is the difference between the local growth rates. It tends to redistribute the population into the patch that is better for the species. Another one is the migration that tends to equalize the distribution between the patches. When $r_{iA} - r_{iB} = \mu = 0$, there is no relaxation, i.e., the initial distribution is retained.

Consider now the realistic case when the regulation loop is closed. Then, the regulating variables are adjusted until the equilibrium condition $r_i = \varrho_i^+ = 0$ is met. An additional mortality may change the equilibrium distribution through modifying the equilibrium I. This effect becomes stronger, when the I-independent relaxation is weak, i.e., when $\Delta \varrho_i$ is small.

4 Results

Behavior of any population is characterized by four two-dimensional vectors; the two dimensions correspond to the two habitats:

- The vector $\boldsymbol{r}_i^0 = (r_{iA}^0, r_{iB}^0)$ of tolerances.
- The vector $\boldsymbol{n}_i = (n_{iA}, n_{iB})$ of abundances.
- The impact niche vector $\boldsymbol{C}_i = (C_{iA}, C_{iB}).$
- The sensitivity niche vector $\mathbf{S}_i = (S_{iA}, S_{iB})$.

 \mathbf{r}_i^0 is a fixed property of the species. Its *direction* represents the *relative* tolerance with respect to the patches. A change of the *length* of \mathbf{r}_i^0 would correspond to an increase/decrease of the fitness of the species. We will chose all tolerance vectors to have the same length, because the fitness differences will be scaled via the (possibly negative) extra mortality Δ_i . Note, that it is a matter of definition, which mortality is considered as "extra". Accordingly, $\Delta_i = 0$ means nothing else here, than correspondence to the arbitrary choice of having tolerance vectors of equal lengths.

The vectors n_i , C_i and S_i of a species are determined together by its tolerance vector, the migration rate and the possible competition between the species. Fig. 1 shows the behavior of the four vectors for a single species at different migration rates. Fig. 2 demonstrates the effect of competition, i.e., the comparison between the behavior of two species, when alone, and when together. Fig. 3 depicts the detailed dependence on the migration rate in a different representation: the angle between the respective vector and the A axis is plotted. Figs. 4 and 5 present the results on the robustness of coexistence. Figs. 6 and 7 are about the evolutionary results.



Figure 1: The four two-dimensional vectors, describing a lone population, at different values of the migration rate μ . The tolerance vector $\mathbf{r}_1^0 = (0.04, 0.01)$ is a fixed property of the species, independent of μ . The angle between this vector and the 45⁰ direction is a measure of specialization. The vector $\mathbf{n} = (n_A, n_B)$ of abundances approaches the 45⁰ direction – representing the even distribution – with increasing migration. The impact niche \mathbf{C} and the sensitivity niche \mathbf{S} behaves similarly. ($\alpha = 0.008$ is used here and for the other figures.)

4.1 Fundamental niche of a single species

Hutchinson's (1978) distinction between the fundamental and the realized niches is implemented by calculating the niche of a species in absence, and in presence, of its competitors, respectively (Meszéna et al., 2006). Here we study the (fundamental) niche of a lone species; the (realized) niches of coexisting species will be considered in the next section.

The abundance vector n of our species behaves as it is expected intuitively. At very low

Box 2: Niche vectors of the model

We provide analytic formulas for the niche vectors; see the Appendix in Supplementary Material for the derivations. For the *i*th species, the sensitivity niche is determined by the distribution of the species between the patches:

$$\mathbf{S}_i = \frac{\alpha}{(n_{i\mathrm{A}}^2 + n_{i\mathrm{B}}^2)} \left(\begin{array}{c} n_{i\mathrm{A}}^2 \\ n_{i\mathrm{B}}^2 \end{array} \right).$$

The sensitivities are proportional to the square of the local densities due to the following reasons. *First*, the larger the fraction of the population living in one of the patches is, the more sensitive its overall growth rate is to the resource exploitation in that patch. This effect alone would lead to a simple proportionality. *Second*, the individuals themselves have different possibilities to contribute to the future generations depending on the quality of their patch. The latter effect is described by the notion of the "reproductive value" of the individual in the given patch. The reproductive values are elements of the left eigenvector of the dynamical matrix, while the equilibrium distribution corresponds to the right eigenvector (Caswell, 2001). As our dynamical matrix happens to be symmetric, the left and the right eigenvectors are the same. That is, the reproductive value in a patch is proportional to the population density in that patch, leading to the quadratic dependence of the sensitivity.

The impact niche is

$$\boldsymbol{C}_{i} = \frac{1}{2G+1} \left[\left(\begin{array}{c} n_{i\mathrm{A}}/n_{i} \\ n_{i\mathrm{B}}/n_{i} \end{array} \right) + G \left(\begin{array}{c} 1 \\ 1 \end{array} \right) \right],$$

where

$$G = \sum_{i} \frac{\alpha}{\Delta \varrho_{i}} \frac{n_{i\mathrm{A}} n_{i\mathrm{B}}}{n_{i\mathrm{A}} + n_{i\mathrm{B}}}.$$

 $(n_i = n_{iA} + n_{iB}$ is the total population size of species *i*.)

The first term is easy to interpret: the impact of a population on one of the patches is proportional to its relative abundance in that patch. The second term is a consequence of the fact that the population distribution changes with perturbation. The second term is large, when the small $\Delta \varrho_i$ s make the change of the distribution significant (Box 1). In case of $\mu = 0$, the local growth rates are regulated to zero independently (i.e., $r_{iA} = r_{iB} = 0$), implying $\Delta \varrho_i = 0$. Then the second terms dominates C_i , that has direction 45^0 .

migration rates, the population lives predominantly, but not exclusively, in the patch which is better for it. Increasing the migration rate tends to equalize the local abundances. That is, the angle of vector \boldsymbol{n} converges to 45^0 with increasing migration rate (Fig. 1; Fig. 3 top row, continuous curve).

The sensitivity niche vector S behaves similarly. The population, as a whole, is more sensitive to the patch which is more suitable for it. This is a double effect. The inferior patch contains a smaller fraction of the population *and* any specific individual in that patch has a disadvantage in contributing to the future generations (Box 2). Therefore, the difference between the sensitivities in the two patches is more pronounced than between the densities. As plotted in Fig. 3 (top row, dotted curve), the sensitivity niche vector lies further apart from the 45⁰ direction, than the abundance vector. Still, the two vectors share the property of converging to the 45⁰ direction for large migration rate. The impact niche vector C is a sum of two vectors. One of them is proportional to the abundance vector, while the other one has a 45⁰ direction (Box 2). (The latter component is the consequence of the fact that the equilibrium population distribution also changes as a consequence of the perturbation of the total population size.) Therefore, vector C lies in between vector n and the 45⁰ direction (Fig. 1; Fig. 3, top row, dash-dotted curve). Direction of vector C changes non-monotonously with migration rate (Fig. 3).

At $\mu = 0$, C lies exactly in the 45⁰ direction. In this case the subpopulations in the two patches are regulated separately. An additional mortality decreases the two local densities by the same *amount*, instead of by the same *ratio*. With slightly increased migration rate, the direction of C approaches the direction of n. Then, at a high migration rate, n and C converge to the 45⁰ direction together.



Figure 2: Effect of competition on two coexisting species, which are characterized by the tolerance vectors $\mathbf{r}_1^0 = (0.04, \ 0.01)$ (the same as in Fig. 1) and $\mathbf{r}_2^0 = (0.02, \ 0.036)$). In the \mathbf{n} , \mathbf{C} and \mathbf{S} plots, the dashed and solid arrows represents the populations, when alone, and while they coexist, respectively. Competition makes the population distributions and the niches more segregated. ($\mu = 0.01$ is used.)

4.2 Niche segregation between two species

Consider now the coexistence of two species. Fig. 2 demonstrates the effect of competition on the vectors n, C and S. One can observe that the spatial distributions of the coexisting species are more segregated than their distributions, when alone. The same applies to the C_i s and the S_i s, as the niche vectors are related to the abundance vector (Box 2). Using the Hutchinson's term (1978), the realized niches are more segregated than the fundamental ones.

Fig. 3 depicts the same comparison as the function of the migration rate. Without migration, the "coexisting" Species 1 and 2 are completely segregated into patches A and B, respectively. Their impact and sensitivity niches behave accordingly. This remains true even if one considers a competition of the specialist Species 2 with a generalist one denoted by G.



Figure 3: The angle of vectors \mathbf{n} , \mathbf{C} and \mathbf{S} with respect to axis A, as a function of the migration rate. The two specialist species (denoted by "1" and "2") are characterized by the tolerance vectors that were used already in Fig. 2. The generalist Species "G" has the uniform tolerance $r_{\rm G}^0 =$ (0.029, 0.029). The two upper plots represent the specialists, when alone. The lower plots depict coexistence of Species 2 with Species 1 (bottom left) and with Species G (bottom right). Again, coexistence makes the populations more segregated. At extremely low migration they are separated completely.

While the two patches are equally appropriate for the generalist without competition, it is restricted to patch A when patch B is occupied by the specialist.

In particular, note that the angle of the impact vectors of the two coexisting species are 0^0 and 90^0 (i.e., the segregation of the impact niches are complete) for $\mu = 0$, despite the fact that both of the fundamental impact niches have the angle 45^0 .

Complete segregation at zero migration rate implies that weak enough migration results in wide segregation of the realized niches even if the difference in the tolerance vectors (consequently: the difference in the fundamental niches) is not so large. That is, a relatively low physiological difference may be sufficient for robust coexistence provided that the migration is weak.

Similarly to the one-species case, the increasing migration makes the distributions more even, i.e., the angle of the vectors n_i , as well as the niche vectors, approach the 45⁰. That is, the segregation of the fundamental as well as of the realized niche diminishes with increasing migration even if the difference in the tolerance vectors is significant.

These results indicate that the dissimilarity of the tolerance vectors and the migration rate are the two relevant variables that determine the segregation of the realized niches. We demonstrate the connection between the robustness of coexistence and the niche dissimilarity in both respects.

Fig. 4 presents dependence on the angle between the two tolerance vectors at a given value of the migration rate. The unsurprising observation is, that the dissimilarity of the abundance vectors, as well as the dissimilarity of both kinds of niche vectors go to zero together with the dissimilarity of the tolerance vectors. The significant point is that the region of the extra mortality, that allows coexistence, also shrinks to nil.

If the tolerance vectors of the two species coincide, the (neutral) coexistence requires exact equality of the fitness'; an arbitrarily small extra mortality is detrimental for the coalition. At a small difference between the tolerances, a small difference in the fitness is allowed. Robust coexistence, that is not very sensitive to external perturbations, requires significant difference in the tolerances.

Fig. 5 depicts the dependence on the migration rate. In this specific example, at $\Delta_1 = 0$, the first species dies out when the migration rate becomes larger than a given value. However, this threshold is not a strict upper bound on migration, or on niche similarity, that constrains coexistence. Species 1 dies out because it is more specialized, than Species 2, so it is affected adversely by increased migration. If this negative effect is compensated by a fitness advantage represented by a negative Δ_1 , coexistence is still possible, and remains possible even at high migration rates.

Nevertheless, this additional gain in fitness should not be too large, because Species 2 will be outcompeted then. At a large migration rate, only a small range of Δ_1 allows coexistence. Just like increasing similarity of the tolerances, increasing migration decreases niche-segregation, therefore it is detrimental to coexistence. Note that our Figs. 4 and 5 are in complete analogy with Fig. 6.4 of May (1973, p. 158).



Figure 4: Robustness of coexistence of two species against an extra mortality. Δ_1 of the first species is plotted as a function of the angle between the two tolerance vectors. Species 1 is characterized again by the tolerance vector $\mathbf{r}_1^0 = (0.04, 0.01)$. The tolerance vector of Species 2 is specified via the angle between the two vectors. The grey region represents the interval of the extra mortality, which allows coexistence, as a function of the migration rate. The curves depict the angle difference between the two \mathbf{n} vectors, the two $\mathbf{C}s$ and the two $\mathbf{S}s$. Observe the correlated changes: As the direction of the tolerance vectors become more similar, so do the niches of the two species. Consequently, the region of coexistence shrinks.($\mu = 0.01$ is used.)

4.3 Evolving tolerances

Now we turn our attention to the adaptive dynamics of the model following Meszéna et al. (1997). The relevant evolutionary question is whether a single strategy, a "generalist", or a pair of specialists will exploit the two patches.

The tolerance vector of a species is now determined by its strategy x through eq. (8). In line with the methodology of adaptive dynamics (Metz et al., 1996; Meszéna et al., 1997; Geritz et



Figure 5: Robustness of coexistence of the two species of Fig. 2 against an extra mortality Δ_1 of the first species is plotted as a function of migration rate. Notations are the same as in Fig. 4. Robustness decreases with increasing migration, as the niches become similar. Increasing migration is more advantageous to the more generalist type, so the more specialized Species 1 dies out at $\mu = 0.041$. At a larger migration rate, coexistence is possible only for negative Δ_1 . The allowed Δ_1 interval is getting narrower with the increase of μ . (The curves are calculated for $\Delta_1 = 0$, so they are not continued after $\mu = 0.041$.)

al., 1997, 1998), the strategy is clonally inherited. Populations of the existing strategies follow the dynamics (9). Occasionally, a mutant strategy that is similar to an already existing one appears with a low population size. Strategies reaching an extremely low population size are considered extinct.

We choose $\sigma = 1$ in eq. (8) as a fixation of the scale and specify that

$$x_{\rm A} = \frac{d}{2}$$
 and $x_{\rm B} = -\frac{d}{2}$, (10)

where $d = x_A - x_B$ is the difference between the two optima. Note that x = 0 is the "central" strategy that implement the compromise between the two patches. We have two free parameters to specify the evolutionary problem: the patch difference d and the migration rate μ . The fitness of a strategy can be defined by its exponential growth rate r, as calculated in Box 1 (Metz et al., 1992).

It is instructive to consider first the symmetric situation, when the two patches are equally exploited: $I_A = I_B$ (Fig. 6). This happens if either the central strategy is present alone, or two symmetrically located strategies exist in equal size. According to Box 1, in the case of a large migration rate the fitness function is the *sum* of two Gaussian functions, with distance *d* between their peaks. This sum is unimodal for a small *d*, but bimodal for a large one. On the other hand, if μ is small, the fitness is the *maximum* of the two exponentials. Such a function is always bimodal. That is, in the symmetric case, the fitness function is unimodal with a fitness maximum at the central strategy for large μ and small *d*. Either decreasing migration or increasing patch difference lead to bimodal fitness function with a minimum at the central strategy.

This analysis specifies the evolutionary stability of the central strategy. It is an ESS if and only if the patch difference is small enough and the migration rate is large enough. This result is in agreement with common sense as well as with the niche analysis of the previous sections: significant patch difference and low migration make specialization to one of the patches possible. Asymmetric loading of the patches by a specialized strategy introduces negative frequency dependence as adaptation to the overloaded patch becomes less favoured. The possible consequence is that evolution may converge first to the central strategy, even if it is not an ESS. Then, evolutionary branching happens, and two specialist strategies appear. The phase portrait in the leftmost pane of Fig. 7 depicts the stability of the central strategy as a function of the parameters. First, decreasing migration and/or increasing patch difference changes this strategy from an ESS to a branching point. Further parameter change, however, makes the central strategy so disadvantageous, that it becomes an evolutionary repellor.

The more complete evolutionary behavior of the model is represented on the remaining two panes of Fig. 7. When the generalist strategy is a repellor, evolution converges to a more specialized strategy and may or may not branch there. Evolutionarily stable coexistence of two specialist may be possible even if it is evolutionarily unreachable from a monomorphic case. See Meszéna et al. (1997) for further details.



Figure 6: Invasion fitness function for four combination of the patch difference d and migration rate μ in the evolutionary version of the model. Horizontal axes: strategy; vertical axes: fitness. It is assumed that the two patches are loaded symmetrically. This happens, for instance, if the central strategy is the only one present. The central strategy is a local maximum (an ESS) if the patch difference d is sufficiently small and the migration rate μ is sufficiently large. In the rest of the cases, when either the migration rate decreases sufficiently, or the patch difference increases sufficiently, the central strategy becomes a pessimum between two – more specialized – optima.

5 Discussion

Our investigation was motivated by the possible evolutionary consequences of the symmetry between the habitat and the functional types of niche segregation. Does the corresponding symmetry exist in the speciation modes also? The main stumbling block to study this issue is the lack of conceptual clarity of the notion of niche (Leibold, 1995). Here we made a step forward to rectify the situation by modeling the spatial niche segregation in a precise theoretical context of Meszéna et al. (2006). We learnt that the conditions of a significant niche segregation and of the possibility of evolutionary branching are analogous: Both of them require a sufficiently high difference between the habitats and sufficiently slow migration between them.



Figure 7: Behavior of the evolutionary model. (a) Phase portrait of the stability of the central strategy as a function of parameters: the patch difference d and the inverse migration rate $1/\mu$. The other two panes depict the complete behavior as a function of the inverse migration rate at fixed d = 1.5 (b) and as a function of the patch difference with fixed $\mu = 0.1$ (c). In (b) and (c), vertical axis is the strategy. The dotted-dashed lines at $x = \pm d/2$ represent the local optima in the patches. All other lines represent singular strategies. Thin lines: monomorphic singular strategies; the thick line: dimorphic singular strategy. Continuous lines: ESS; dashed: branching strategy; dotted: repellor.

Meszéna et al. (2006) identifies the niche "space" to the set of regulating factors, which is either a discrete or a continuous set. This picture is in line with the classical, intuitive one: The species partition the kinds of regulating factors between themselves. Resources in different habitats should be counted as different regulating factors. Here we studied the minimal model of the discrete habitat segregation. Our analysis of the two-patch situation complements Tilman's (1982) study of coexistence on two resources. The third way of niche segregation, the temporal one (Christiansen & Fenchel, 1977, Chesson, 2000b), is not discussed here.

The niche of a species is usually specified by its "resource utilization". Unfortunately, resource utilization is a phenomenological term; there is no unequivocal prescription to measure it. Operationally, one can study two questions (cf. Fig. 2 in Goldberg, 1990). How does resource availability depend on the population density? And how does population growth rate depend on resource availability? The differential measures of these relations, the impact and sensitivity vectors together constitute the proper representation of the niche of a species (Meszéna et al., 2006). The essential issue that makes the habitat segregation more complicated than the functional one is the role of the spatial distribution of the population. In this case, one should define/measure impact and sensitivity with extra care: The spatial distribution should remain in equilibrium during their determination.

Note that the niche theoretical relevance of the two-way interaction between a population and its environment was first emphasized by Leibold (1995). He distinguished between "requirement" and "impact" niches and analyzed the history of the niche concepts in these terms.

The abundance vector is a reasonable proxy to the niche vectors, because in general they behave qualitatively similarly to the function of the parameters; the niche vectors are actually calculable from the abundance vector. In contrast, the tolerance vector fails to take into account the migration and the resulting source-sink structure of the population, so it is an appropriate proxy for niche only if the effect of migration is negligible. The relevance of this issue is clearly demonstrated by the two-patch model of Abrams & Wilson (2004). See Szabó & Meszéna (2006b) for a different study, which emphasizes the role of localised vs. non-localised resource uptake in coexistence.

As the spatial distribution, and hence the utilization of the resources in the different patches, is determined jointly by the tolerances and the migration behavior of the species, both the decreasing difference between species tolerances and increasing migration result in decreased niche segregation. This, in turn, leads to a shrinking region of the external parameters that allow coexistence. Large migration diminishes niche-segregation even in the case of large differences between the tolerances of the species. On the other hand, the difference between the realized niches can be significant even if the tolerance vectors are similar, provided, that the migration rate is small enough.

Such joint determination of the niche by physiological and ecological factors can be expected in the case of functional niche segregation as well. For example, the preferred diet of a species is likely to depend on what is available, instead of being determined by a fixed resource utilization function. Therefore, the difference between the fundamental and the realized niches should be present in the non-spatial situations as well.

It is straightforward to make a connection to the continuous case by considering an arbitrary number of patches in a similar way (Szilágyi & Meszéna, in prep.). One can also consider the continuous limit of a linear series of patches along an environmental gradient where the impact and sensitivity niche vectors are functions of the continuous "niche variable" along the gradient (see Mizera & Meszéna (2003)).

Chesson (2000a) provided a general theory of coexistence in spatially varying environments. The type of coexistence that is studied here is explained by the effect of covariance between the density and the growth rate. The two other effects in his theory, the "storage effect" and the "effect of relative nonlinearity", vanish in our case because of the simple linear-additive way of population regulation.

The early predecessor of our study was Levene's (1953) seminal paper about the population genetical consequences of environmental heterogeneity. He demonstrated that spatial heterogeneity can maintain genetic polymorphism. The way of regulation was the essential issue: Polimorphysm can be maintained only in case of separate regulation in the various habitats (Christiansen 1975). The analogous problem with functional niche segregation was studied by Christiansen & Loeschcke (1980, 1987). These investigations assumed random mating, which precluded emergence of species diversity.

Adaptive dynamics introduced a significant simplification by separating the study of frequency dependence from the complications of diploid genetics. In clonal models it is clear that the diversitymaintaining effect of niche segregation may lead to evolutionary branching, if the negative frequencydependence is strong enough. Branching evolution in the Lotka-Volterra model was demonstrated already in Metz et al. (1996). Following Meszéna et al. (1997), here we showed that in a two patch environment evolutionary branching can be initiated either by decreasing the migration rate between patches or by increasing the difference between them. The first one is reminiscent of allopatric speciation, initiated by a newly emerging migration barrier. The second one is a clonal equivalent of parapatric speciation, when no migration barrier emerges. In genetic modeling, Dieckmann & Doebeli (1999) demonstrated the possibility of adaptive speciation; Doebeli & Dieckmann (2003) dealt with the case of environmental gradient. While a similar analysis is still to be done for the two-patch case, based on the already existing results, we expect the adaptive dynamical results to be indicative for the possibility of the adaptive parapatric and allopatric speciation.

If arrested gene flow were a prerequisite of speciation, parapatric speciation would be just as impossible as the sympatric one. In the context of adaptive speciation, however, the sympatric (based on functional niche segregation), the parapatric and the allopatric modes of speciation are on equal footing: all of them are adaptations to different ways of niche segregations. This way we hope to find a biologically plausibile unifying concept for all speciation modes.

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Appendix

Derivation of the analytic formulas for the niche vectors

Supplementary material for Szilágyi & Meszéna: Two-patch model of spatial niche segregation

The dynamics of species i in our model is described by the equation

$$\frac{\mathrm{d}}{\mathrm{d}t}\boldsymbol{n}_i = \boldsymbol{M}_i \boldsymbol{n}_i,\tag{A1}$$

where $\mathbf{n}_i = (n_{iA}, n_{iB})$ is the abundance vector of species *i* and

$$\boldsymbol{M}_{i} = \begin{pmatrix} r_{iA}^{0} - \alpha I_{A} - \mu & \mu \\ \mu & r_{iB}^{0} - \alpha I_{B} - \mu \end{pmatrix}$$
(A2)

is the dynamical matrix;

$$I_X = \sum_i n_{iX} \tag{A3}$$

for X = A, B are the regulating variables collected into the vector I.

The 2 × 2 symmetrical dynamical matrix¹ M_i has two real eigenvalues, the leading/larger one (ϱ_i^+) , which is the growth rate of species *i*, and the smaller one (ϱ_i^-) . The corresponding eigenvectors $(\boldsymbol{w}_i^+ \text{ and } \boldsymbol{w}_i^-)$ satisfy

$$\boldsymbol{M}_{i}\boldsymbol{w}_{i}^{+}=\varrho_{i}^{+}\boldsymbol{w}_{i}^{+}$$
 and $\boldsymbol{M}_{i}\boldsymbol{w}_{i}^{-}=\varrho_{i}^{-}\boldsymbol{w}_{i}^{-}.$ (A4)

Symmetry of the dynamical matrix implies that the two eigenvectors are orthogonal:

$$\boldsymbol{w}_i^+ \cdot \boldsymbol{w}_i^- = 0. \tag{A5}$$

We assume normalization:

$$\boldsymbol{w}_i^+ \cdot \boldsymbol{w}_i^+ = 1$$

$$\boldsymbol{w}_i^- \cdot \boldsymbol{w}_i^- = 1.$$
(A6)

One can express the abundance vector n_i with the distribution vector p_i :

$$\boldsymbol{n}_i = n_i \boldsymbol{p}_i,\tag{A7}$$

where n_i is the total number of individuals of species *i* and $p_{i1} + p_{i2} = 1$. In equilibrium the abundance vector is proportional to \boldsymbol{w}_i^+ (Caswell, 2001), so

$$\boldsymbol{p}_i = Q \boldsymbol{w}_i^+, \tag{A8}$$

where Q is a factor of proportionality. We can express the eigenvectors and distribution vectors of species i with the number of individuals in the patches:

$$\boldsymbol{w}_{i}^{+} = \begin{pmatrix} \frac{n_{iA}}{\sqrt{n_{iA}^{2} + n_{iB}^{2}}} \\ \frac{n_{iB}}{\sqrt{n_{iA}^{2} + n_{iB}^{2}}} \end{pmatrix} \qquad \boldsymbol{w}_{i}^{-} = \begin{pmatrix} \frac{-n_{iB}}{\sqrt{n_{iA}^{2} + n_{iB}^{2}}} \\ \frac{n_{iA}}{\sqrt{n_{iA}^{2} + n_{iB}^{2}}} \end{pmatrix} \qquad \boldsymbol{p}_{i} = \begin{pmatrix} \frac{n_{iA}}{n_{iA} + n_{iB}} \\ \frac{n_{iB}}{n_{iA} + n_{iB}} \end{pmatrix}.$$
(A9)

¹In this section we denote the vectors with boldface lowercase letters, the matrices boldface block letters (expected the impact and sensitivity niche vectors, what we denote with C and S, respectively).

In line with the perturbation approach in defining the niche vectors (Section 2 of the main text), one has to determine how the growth rate and the population distribution of the *i*th species vary with a small variation dM_i of the dynamical matrix M_i . This derivation is performed in the next section of the current Appendix with the following result. The change of the growth rate is

$$\mathrm{d}r_i = \mathrm{d}\varrho_i^+ = \boldsymbol{w}_i^+ \mathrm{d}\boldsymbol{M}_i \boldsymbol{w}_i^+ \tag{A10}$$

(see also Caswell, 2001), while the change of the distribution vector p_i is

$$\mathrm{d}\boldsymbol{p}_i = \boldsymbol{A}_i \; \mathrm{d}\boldsymbol{M}_i \; \boldsymbol{p}_i, \tag{A11}$$

where

$$\boldsymbol{A}_{i} = \frac{(\boldsymbol{w}_{i}^{-} - \frac{U^{-}}{U^{+}} \boldsymbol{w}_{i}^{+}) \circ \boldsymbol{w}_{i}^{-}}{\Delta \varrho_{i}}.$$
(A12)

 $\Delta \varrho_i = \varrho_i^+ - \varrho_i^-$ is the difference between the eigenvalues. 'o' denotes the diadic product. The notations $U^+ = w_{i1}^+ + w_{i2}^+$ and $U^- = w_{i1}^- + w_{i2}^-$ were used. After some computation, with use of eq. (A9), one gets

$$\boldsymbol{A}_{i} = \frac{1}{\Delta \varrho_{i}} \frac{1}{n_{iA} + n_{iB}} \begin{pmatrix} n_{iB} & -n_{iA} \\ -n_{iB} & n_{iA} \end{pmatrix}.$$
(A13)

We express the variation of the dynamical matrix with the variation of the regulating variables, as

$$\mathrm{d}\boldsymbol{M}_i = -\underline{\boldsymbol{T}}_i \mathrm{d}\boldsymbol{I}.\tag{A14}$$

The linear operator \underline{T}_i makes a 2×2 matrix from a 2-vector, so this is a 2×2×2 matrix ("tensor"). Instead of complicating the notation by attempting full precision, we will rely on the common sense of the Reader not to confuse the three indexes. The '-' sign is introduced for consistence of the definition of the impact niche vector.

To derive the sensitivity-niche vectors we start from the definition:

$$\mathrm{d}r_i = \mathrm{d}\varrho_i^+ = -\boldsymbol{S}_i \mathrm{d}\boldsymbol{I}.\tag{A15}$$

Substituting eq. (A14) into eq. (A10) leads to

$$\mathrm{d}r_i = -\boldsymbol{w}_i^+ \underline{\boldsymbol{T}}_i \boldsymbol{w}_i^+ \mathrm{d}\boldsymbol{I}. \tag{A16}$$

Comparison of eqs. (A15) and (A16) implies, that

$$\boldsymbol{S}_i = \boldsymbol{w}_i^+ \boldsymbol{\underline{T}}_i \boldsymbol{w}_i^+. \tag{A17}$$

To compute the sensitivity vector of species i, keep in mind, that only the M_{11} component of the dynamical matrix depends in I_1 , and only the M_{22} depends on I_2 (see eq. (A2))². Then:

$$\underline{\boldsymbol{T}}_{i}\boldsymbol{w}_{i}^{+} = \alpha \begin{pmatrix} w_{i1} & 0\\ 0 & w_{i2} \end{pmatrix} = \frac{\alpha}{\sqrt{n_{iA}^{2} + n_{iB}^{2}}} \begin{pmatrix} n_{iA} & 0\\ 0 & n_{iB} \end{pmatrix}.$$
(A18)

Consequently:

$$\mathbf{S}_{i} = \frac{\alpha}{n_{iA}^{2} + n_{iB}^{2}} \begin{pmatrix} n_{iA}^{2} \\ n_{iB}^{2} \end{pmatrix}.$$
(A19)

The perturbation of the impact vector comes from differentiating eq. (A7):

$$d\boldsymbol{I} = \sum_{i} d\boldsymbol{n}_{i} = \sum_{i} dn_{i} \boldsymbol{p}_{i} + \sum_{i} n_{i} d\boldsymbol{p}_{i}$$
(A20)

²In the parlance of indices, \underline{T}_i is not zero if all there indices are the same, in which case the value is α . $(T_{i,111} = T_{i,222} = \alpha$, in other cases is zero.)

(eq. (A3) was used). Substituting eqs. (A11) and (A14) into the last term, leads to

$$\overbrace{\left[1+\sum_{i}^{B}n_{i}\boldsymbol{A}_{i}\boldsymbol{\underline{T}}_{i}\boldsymbol{p}_{i}\right]}^{B}\mathrm{d}\boldsymbol{I}=\sum_{i}^{B}\boldsymbol{p}_{i}\mathrm{d}n_{i}.$$
(A21)

where **1** is the unite matrix; the 2×2 matrix in the square bracket is denoted by **B**.

Then, the impact vector can be expressed, as

$$\boldsymbol{C}_i = \frac{\mathrm{d}\boldsymbol{I}}{\mathrm{d}n_i} = \boldsymbol{B}^{-1}\boldsymbol{p}_i. \tag{A22}$$

Similarly to eq. (A18),

$$\underline{\boldsymbol{T}}_{i}\boldsymbol{p}_{i} = \alpha \begin{pmatrix} p_{i1} & 0\\ 0 & p_{i2} \end{pmatrix} = \frac{\alpha}{n_{iA} + n_{iB}} \begin{pmatrix} n_{iA} & 0\\ 0 & n_{iB} \end{pmatrix}.$$
(A23)

From here and from eq. (A13), one can arrive to

$$\boldsymbol{B} = \begin{pmatrix} G+1 & -G\\ -G & G+1 \end{pmatrix},\tag{A24}$$

where

$$G = \sum_{i} \frac{\alpha}{\Delta \varrho_i} \frac{n_{iA} n_{iB}}{n_{iA} + n_{iB}}.$$
 (A25)

To compute the impact niche vector, we has to determine the inverse of B:

$$\boldsymbol{B}^{-1} = \frac{1}{2G+1} \begin{pmatrix} G+1 & G\\ G & G+1 \end{pmatrix}.$$
 (A26)

Eqs. (A9), (A22)) and (A26) lead to

$$\boldsymbol{C}_{i} = \boldsymbol{B}^{-1} \boldsymbol{p}_{i} = \frac{1}{2G+1} \begin{pmatrix} G + \frac{n_{iA}}{n_{iA}+n_{iB}} \\ G + \frac{n_{iB}}{n_{iA}+n_{iB}} \end{pmatrix}.$$
(A27)

Derivation of the perturbation equations (A10) and (A11)

Here we investigate how the growth rate (i.e., the larger eigenvalue) and the equilibrium distribution p (the corresponding eigenvector normalized such, that its elements sum to 1) change under a perturbation of matrix M.³

dM denotes the perturbation of the matrix, M'=M+dM is the perturbed one. Similar notation applies to the other quantities.

The eigenvalue equations for the unperturbed and the perturbed matrices are

$$Mp = \varrho^+ p,$$

$$M'p' = \varrho'^+ p'.$$
(A28)

To compute the correction of the leading eigenvalue and distribution vector at first, we express the distribution vector of the perturbed system in the terms of the normed eigenvectors of unperturbed system with the coefficients⁴ c^+ , c^- :

$$p' = c^+ w^+ + c^- w^-.$$
 (A29)

So, eigenvector equation of the perturbed system is

$$(\boldsymbol{M} + \mathrm{d}\boldsymbol{M})(c^+\boldsymbol{w}^+ + c^-\boldsymbol{w}^-) = \varrho'^+(c^+\boldsymbol{w}^+ + c^-\boldsymbol{w}^-).$$
(A30)

³In this subsection we omit the species' index i.

 $^{^4\}mathrm{It}\ensuremath{^\mathrm{s}}$ always possible when \pmb{w}^+ and \pmb{w}^- are not parallel.

Perturbation of the leading eigenvalue

Multiplying equation (A30) with w^+ from left, using the orthogonality relation (A5) and the norm relations (A6), after some rearrangement we get

$$c^{+}(\varrho'^{+}-\varrho^{+}) = c^{+}\boldsymbol{w}^{+}\mathrm{d}\boldsymbol{M}\boldsymbol{w}^{+} + c^{-}\boldsymbol{w}^{+}\mathrm{d}\boldsymbol{M}\boldsymbol{w}^{-}.$$
(A31)

Using that the unperturbed quantities are ρ^+ and w^+ , write ρ'^+ , c^+ and c^- in an expansion series as:

$$\varrho'^+ = \varrho^+ + d\varrho^+ + \dots; \qquad c^+ = Q + dc^+ + \dots; \qquad c^- = 0 + dc^- + \dots$$
(A32)

The first terms represent the unperturbed system. The second terms are the changes coming from the perturbation; there are in the order of $w^+ dMw^+$. The higher terms are smaller and we neglect them.

Putting the first two terms of the series into eq. (A31) and neglecting the higher order terms leads to

$$\mathrm{d}\varrho^+ = \boldsymbol{w}^+ \mathrm{d}\boldsymbol{M}\boldsymbol{w}^+,\tag{A33}$$

as we claimed in eq. (A10).

Perturbation of the distribution vector

Multiplying eq. (A30) with w^- from left, using eqs. (A5) and (A6) after some rearrangement we get:

$$c^{-}(\varrho'^{+} - \varrho^{-}) = c^{+} \boldsymbol{w}^{-} \mathrm{d} \boldsymbol{M} \boldsymbol{w}^{+} + c^{-} \boldsymbol{w}^{-} \mathrm{d} \boldsymbol{M} \boldsymbol{w}^{-}.$$
(A34)

After putting the first two terms of eq. (A32) into the equation above, and neglecting the higher order terms we get

$$\mathrm{d}c^{-} = \frac{\boldsymbol{w}^{-}\mathrm{d}\boldsymbol{M}\boldsymbol{p}}{\Delta\varrho}.\tag{A35}$$

The first order correct form of the perturbed distribution vector is

$$\boldsymbol{p}' = \boldsymbol{p} + \mathrm{d}c^+ \boldsymbol{w}^+ + \mathrm{d}c^- \boldsymbol{w}^-.$$

Combining this with the constraint

$$p_1' + p_2' = p_1 + p_2 = 1$$

$$dc^+ = -\frac{U^-}{U^+} dc^-$$
(A36)

leads to

(recall, that
$$U^+ = w_{i1}^+ + w_{i2}^+$$
 and $U^- = w_{i1}^- + w_{i2}^-$). Then, the correction for the distribution vector is

$$d\boldsymbol{p} = \boldsymbol{p}' - \boldsymbol{p} = dc^+ \boldsymbol{w}^+ + dc^- \boldsymbol{w}^- = \left(\boldsymbol{w}^- - \frac{U^-}{U^+} \boldsymbol{w}^+\right) dc^- = \\ = \left(\boldsymbol{w}^- - \frac{U^-}{U^+} \boldsymbol{w}^+\right) \frac{\boldsymbol{w}^- d\boldsymbol{M} \boldsymbol{p}}{\Delta \varrho} = \frac{\left(\boldsymbol{w}^- - \frac{U^-}{U^+} \boldsymbol{w}^+\right) \circ \boldsymbol{w}^-}{\Delta \varrho} d\boldsymbol{M} \boldsymbol{p}, \quad (A37)$$

as stated in eqs. (A11-A12).