

# Fixed point sensitivity analysis of interacting structured populations



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## HIGHLIGHTS

- We give a fully general sensitivity formula for interacting structured populations.
- We apply the formula to a model of ontogenetic niche shift.
- The formula works reasonably even for large perturbations and far from equilibrium.

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## ABSTRACT

Sensitivity analysis of structured populations is a useful tool in population ecology. Historically, methodological development of sensitivity analysis has focused on the sensitivity of eigenvalues in linear matrix models, and on single populations. More recently there have been extensions to the sensitivity of nonlinear models, and to communities of interacting populations. Here we derive a fully general mathematical expression for the sensitivity of equilibrium abundances in communities of interacting structured populations. Our method yields the response of an arbitrary function of the stage class abundances to perturbations of any model parameters. As a demonstration, we apply this sensitivity analysis to a two-species model of ontogenetic niche shift where each species has two stage classes, juveniles and adults. In the context of this model, we demonstrate that our theory is quite robust to violating two of its technical assumptions: the assumption that the community is at a point equilibrium and the assumption of infinitesimally small parameter perturbations. Our results on the sensitivity of a community are also interpreted in a niche theoretical context: we determine how the niche of a structured population is composed of the niches of the individual states, and how the sensitivity of the community depends on niche segregation.

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## 1. Introduction

Sensitivity analysis has been a long-standing and distinguished tool in population ecology. It asks the question what is the linear response of some variable of interest to a change in some parameter. Though the concept is very general, arguably the most successful branch of applications came from linear structured population models (Caswell, 2001, chapter 9). Sensitivity analysis of this deceptively simple class of models has led to deep ecological and evolutionary insights into the theory of senescence (Hamilton, 1966; Gleason, 1984; Caswell, 2011), life history tradeoffs (Templeton, 1980; Caswell, 1982, 1984), classification of plant strategies (Silvertown et al., 1992; Franco and Silvertown, 1996), the analysis of transient population dynamics (Caswell, 2007), and the assessment of extinction risk and suggestion of viable conservation

measures (Crouse et al., 1987; Silvertown et al., 1993; Noon and McKelvey, 1996; Forsman et al., 1996; Seamans et al., 1999; Fujiwara and Caswell, 2001; Hunter et al., 2010).

Indeed, sensitivity analysis of linear structured population models has been generating so many interesting results that, ironically, extensions of this methodology to other types of models have been somewhat lagging behind. Nevertheless, sensitivity analysis of density-dependent structured population models with fixed point equilibria is now available (Takada and Nakajima, 1992, 1998; Grant and Benton, 2000, 2003; Caswell, 2008). Behind this extension lies an important insight. Although calculating the sensitivity of any quantity to any parameter is straightforward in linear models, it has usually been the leading eigenvalue's sensitivity that has received most attention. The leading eigenvalue is a measure of the long-term growth rate of the population. However, in density-dependent models, populations eventually reach a stationary state where there is no long-term growth. Therefore, eigenvalue sensitivities are not very informative (but see Caswell et al., 2004). Instead, it is the sensitivity of the stationary state itself that is of great interest: when perturbing a parameter, how much is the

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fixed point expected to shift? Caswell (2008) provides a completely general sensitivity formula for fixed points in density-dependent structured population models. Moreover, by extension, this result may also be applied to periodic dynamics as well, since a discrete-time periodic model can be converted into one with a fixed point by repeated composition.

As we can see, sensitivity analysis for a fairly general class of population models is now available. A natural next step is to extend the methodology to communities of interacting populations, which has the potential to address problems in diverse areas of ecology, such as food web theory, coevolutionary processes, or questions related to coexistence. As any community model with dynamic feedbacks between the species will necessarily be density and/or frequency dependent, once again the variable of interest is the sensitivity of the stationary state to parameter perturbations. The main motivation behind such an extension is that we want to consider the response of a species to changes in its environment in a way that takes into account its interactions with other species; also, we want to know how the species interactions themselves change as the environment changes. Potential questions that might be answered using community-level sensitivity analysis range from fundamental to more applied: what changes in the environment, and what types of interaction webs, are conducive to a trophic cascade? How sensitive can we expect the abundance of a particular species of interest to be when the environment changes in a way that is critical to one of its mutualists? Is the coexistence of a particular set of competitors found in the field robust, i.e., is it viable over a wide range of parameters, or is it overly sensitive to the vagaries of the weather, leading to the inevitable loss of at least some of the species?

For the simplest case of fixed points with unstructured populations, the extension of sensitivity analysis to communities has been done by Levins (1974) and MeszÉna et al. (2006). This has subsequently been generalized to (unstructured) community dynamics in random (SzilÁgyi and MeszÉna, 2010) and periodic (Barabás et al., 2012; Barabás and Ostling, 2013) environments, and – partially – to structured community dynamics with fixed point attractors (SzilÁgyi and MeszÉna, 2009a,b). Potential practical applications aside, these studies revealed that the sensitivity analysis of coexistence maintains a surprisingly deep connection with some fundamental concepts in ecology, such as that of the ecological niche (Grinnell, 1914; Elton, 1927; MacArthur and Levins, 1967; Hutchinson, 1978; Leibold, 1995; Chesson, 2000b; Chase and Leibold, 2003; MeszÉna et al., 2006). Indeed, based on their results, MeszÉna et al. (2006); SzilÁgyi and MeszÉna (2009a), and Barabás et al. (2012) have proposed a niche concept that unifies functional, temporal, and spatial modes of niche segregation (Christiansen and Fenchel, 1977), keeping in the spirit of but generalizing the classical Hutchinsonian notion of the niche.

Here we wish to address the method for calculating sensitivities in communities of interacting structured populations at fixed point equilibria. As stated before, an important step in this direction has already been made by SzilÁgyi and MeszÉna (2009a). They considered the sensitivity of the total population densities to perturbing the projection matrix of each species by a scalar times the identity matrix. This particular form of the perturbation was sufficient to establish the general claim that limited similarity of structured populations is necessary for their coexistence. Our goal in this paper is to generalize their approach to arbitrary perturbations, and to be able to calculate the sensitivity of not just the total population densities, but that of an arbitrary function of the stage class abundances.

In this article, after fixing notational conventions in Section 2, we derive a general formula for the sensitivity of a fixed point describing coexistence of interacting structured populations in Section 3. The formula can handle generic perturbations of any

lower-level parameter  $\mathbb{E}$ , assuming the projection matrices depend on  $\mathbb{E}$  differentially. It also allows for the sensitivity analysis of any function of the abundance vectors. Finally, in Section 4, we apply our findings to a two-species model of competing structured populations, where both species are assumed to undergo an ontogenetic niche shift. After obtaining the sensitivities of the equilibrium densities to all model parameters, we check what happens when relaxing the assumptions that the system is at its equilibrium, and that the parameter perturbations are infinitesimal. As our results prove sensitive to neither of these assumptions, we have good indication that our framework is applicable even to systems not close to their equilibria, and to perturbations that are not very small.

## 2. Model framework, notation, and normalization conventions

A general model of interacting structured populations reads, in discrete time, as

$$\mathbf{n}_i(t+1) = \mathbf{A}_i(\mathcal{R}_\mu(\mathbf{n}_1, \dots, \mathbf{n}_S), \mathbb{E}) \mathbf{n}_i(t) \quad (i = 1 \dots S). \quad (1)$$

Here  $S$  is the total number of species in the community,  $\mathbf{n}_i(t)$  is the population structure vector of the  $i$ th species at time  $t$ ,  $\mathbb{E}$  represents the model's parameters,  $\mathbf{A}_i$  is the projection matrix of the  $i$ th species as a function of both density-dependent and density-independent factors, and  $\mathcal{R}_\mu$  is the vector of regulating variables (Levin, 1970; MeszÉna et al., 2006). By definition, these regulating factors mediate all interactions between individuals, so that artificially keeping their values fixed would lead to the density-independent increase or decrease of each population. They may include resources, predators, pathogens, refuge availability, or any other thing which provides a feedback between a population's growth rate and density. Also, though  $\mathbb{E}$  may represent an arbitrary number of model parameters, we will assume (unless noted otherwise) that it stands for a single parameter of interest, while all other parameters are kept constant. This will not lead to any loss of generality, and will make the derivation simpler in Section 3.

As quantities may bear three distinct types of indices (namely: species, structure, and regulation indices), we will use matrix notation only for the population structure. For species and regulating factors, we adopt index notation, where inner products and matrix multiplication are indicated by summation over appropriate indices. We reserve lowercase Latin subscripts ( $i, j, \dots$ ) for species indices and lowercase Greek subscripts ( $\mu, \nu, \dots$ ) for the regulating factors. Also, quantities bearing any regulation indices will be denoted in calligraphic face ( $\mathcal{R}, \mathcal{G}, \dots$ ) to further distinguish them from other quantities. Function notations like  $\mathbf{A}_i(\mathcal{R}_\mu(\mathbf{n}_1, \dots, \mathbf{n}_S))$  mean that the matrix  $\mathbf{A}_i$  depends on all components of the regulation vector with the generic component  $\mathcal{R}_\mu$ , and  $\mathcal{R}_\mu$  in turn depends on all the population structure vectors. As the regulating factors may have discrete and continuous indices at the same time (the former might represent specialist predators or distinct resources, while an example for the latter would be a resource continuum), the single index  $\mu$  is used to symbolically refer to all of them at once. Correspondingly, the symbolic summation  $\sum_\mu$  will refer to summation (integration) for all discrete (continuous) indices of the regulating factors.

The identity matrix is denoted by the Kronecker symbol  $\delta_{ij}$ , equal to 1 if  $i = j$  and to 0 otherwise. When inverting matrices,  $(M_{ij})^{-1}$  will refer to the  $(i, j)$ th element of the inverse matrix (and not to the reciprocal of the  $(i, j)$ th element):  $\sum_k (M_{ik})^{-1} M_{kj} = \delta_{ij}$ .

For the population structure we employ matrix notation, where vectors and matrices are denoted in boldface by lowercase and uppercase letters, respectively. The number of distinct stage classes for species  $i$  is  $s_i$ . The inner product of two vectors  $\mathbf{a}$  and  $\mathbf{b}$  is written simply as  $\mathbf{a}\mathbf{b}$ . Their outer product  $\mathbf{a} \otimes \mathbf{b}$  is by definition

the matrix such that  $(\mathbf{a} \otimes \mathbf{b})\mathbf{c} = \mathbf{a}(\mathbf{b}\mathbf{c})$  for any vector  $\mathbf{c}$ . The  $s_i$ -dimensional identity matrix is  $\mathbf{I}_i$ . The one-norm (absolute sum of the components) of a vector  $\mathbf{a}$  is denoted  $|\mathbf{a}|$ .

Each matrix  $\mathbf{A}_i$  is assumed to be primitive. Note that primitive matrices are also necessarily irreducible (Caswell, 2001, chapter 4). Irreducibility means that each stage class is reachable from any other: this assumption excludes cases like postreproductive age classes or spatial locations which cannot be reached from any other location. Primitivity means that the greatest common divisor of all loop lengths in the life cycle graph is one: this excludes models which create persistent generation-cycles (Turchin, 2003), such as an age-structured population with three age classes in which only the eldest class can reproduce.

The assumption of primitivity guarantees that each matrix  $\mathbf{A}_i$  possesses a unique eigenvalue that is real, positive, larger in modulus than all the other eigenvalues, its corresponding left and right eigenvectors are unique, and these eigenvectors are real and have positive components (Perron–Frobenius theorem; Caswell, 2001, chapter 4). This special eigenvalue is the “leading” eigenvalue, corresponding to the long-term geometric growth rate of the population, while its right eigenvector is the stable stage distribution, and its left eigenvector is the reproductive value vector.

The  $k$ th eigenvalue of the  $i$ th population projection matrix  $\mathbf{A}_i$  is denoted  $\lambda_i^k$ . For  $k = 1$  we simply write  $\lambda_i$ , and it is understood that this is the leading eigenvalue of  $\mathbf{A}_i$ . The  $k$ th right and left eigenvectors of species  $i$  are denoted  $\mathbf{w}_i^k$  and  $\mathbf{v}_i^k$ , respectively. Again, for  $k = 1$  we simply write  $\mathbf{w}_i$  and  $\mathbf{v}_i$  and it is understood that these are the vectors corresponding to the leading eigenvalue, i.e., are the stable stage distribution and the reproductive value of species  $i$ .

The normalization of the eigenvectors is such that

$$\mathbf{w}_i^k \mathbf{v}_i^l = \delta_{kl} \quad (k, l = 1 \dots s_i) \quad (2)$$

for every species  $i$  (where  $\mathbf{w}_i^1 = \mathbf{w}_i$ ,  $\mathbf{v}_i^1 = \mathbf{v}_i$ ). Moreover, the stable stage distribution of each species is normalized to give the proportions living in each stage class:

$$|\mathbf{w}_i| = 1. \quad (3)$$

We will make use of weighted population sizes. Let  $\mathbf{q}_i$  be an arbitrary nonzero vector with nonnegative components. Then

$$n_i = \mathbf{q}_i \mathbf{n}_i \quad (4)$$

is the weighted population size of species  $i$ . For instance,  $n_i$  is the total population size when  $\mathbf{q}_i$  is a vector of ones, and it is the abundance in the first stage class if the first component of  $\mathbf{q}_i$  is one and the rest are zero. We also introduce the reduced population structure vectors

$$\mathbf{p}_i = \frac{\mathbf{n}_i}{n_i}. \quad (5)$$

Obviously,  $\mathbf{q}_i \mathbf{p}_i = 1$ . At a point equilibrium the population abundance vector  $\mathbf{n}_i$  is by definition an eigenvector of  $\mathbf{A}_i$ . Moreover, it will point in the direction of the leading eigenvector  $\mathbf{w}_i$  due to the Perron–Frobenius theorem. Therefore one may write

$$\mathbf{p}_i = \frac{\mathbf{n}_i}{n_i} = \frac{\mathbf{n}_i}{\mathbf{q}_i \mathbf{n}_i} = \frac{\mathbf{w}_i}{\mathbf{q}_i \mathbf{w}_i}, \quad (6)$$

as  $\mathbf{w}_i$  is just the normalized version of  $\mathbf{n}_i$  (note that we used the strict positivity of the stable stage distribution here). This expression only holds at equilibrium, however.

### 3. Deriving the sensitivity formula

Here we derive the sensitivity of the equilibrium densities to perturbations of the model parameters. There are two possible

strategies to obtain the result. One can write down the dynamical equations at equilibrium, apply implicit differentiation with respect to our parameter of interest  $\mathbb{E}$ , and rearrange to solve for the response of the equilibrium population structure vectors to perturbations of  $\mathbb{E}$ . This approach (followed by Caswell, 2007, 2008, albeit for single populations only), yields a formula that is difficult to interpret biologically. The other strategy, the one we will follow here, is to perturb not the dynamical equations but the eigenvalues and eigenvectors. While this makes the derivation more involved, the result lends itself better to biological interpretation.

The outline of the derivation below is as follows. We start from the condition that all leading eigenvalues at equilibrium must be equal to one. We then perturb this condition by slightly changing  $\mathbb{E}$ , and write this perturbed equation as a function of  $d\mathbf{p}_j$  and  $dn_j$ . After expressing  $d\mathbf{p}_j$ , we solve for  $dn_j$ , and differentiate by  $\mathbb{E}$  to obtain the final result.

When the community described by Eq. (1) is at a fixed point, none of the populations are growing or declining, which imposes the condition

$$\lambda_i(\mathcal{R}_\mu(\mathbf{n}_1, \dots, \mathbf{n}_S), \mathbb{E}) = 1 \quad (7)$$

on each of the leading eigenvalues  $\lambda_i$ . Here the population structure vectors  $\mathbf{n}_i$  all assume their equilibrium values, and the dependence of the leading eigenvalues on the regulating factors  $\mathcal{R}_\mu$  and the model parameter  $\mathbb{E}$  is explicitly noted.

Expanding the equations in their arguments leads to

$$\sum_\mu \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} d\mathcal{R}_\mu + \frac{\partial \lambda_i}{\partial \mathbb{E}} d\mathbb{E} = 0. \quad (8)$$

Here and in every formula after this point, all quantities are evaluated at the original equilibrium point except when noted otherwise, and “d” will denote the (total) difference from the value at the original equilibrium.

We now expand the differential  $d\mathcal{R}_\mu$  in terms of  $\mathbf{n}_j$ , but then use  $\mathbf{n}_j = \mathbf{p}_j n_j$  to write it in terms of  $\mathbf{p}_j$  and  $n_j$  instead:

$$d\mathcal{R}_\mu = \sum_{j=1}^S \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} d\mathbf{n}_j = \sum_{j=1}^S \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} (\mathbf{p}_j dn_j + n_j d\mathbf{p}_j). \quad (9)$$

At this point, we could substitute this expression back into Eq. (8), solve for  $dn_i$ , and differentiate by  $\mathbb{E}$  to obtain  $dn_i/d\mathbb{E}$ , the sensitivities we are looking for. However, for this to work, we first need to express the unknown  $d\mathbf{p}_j$ . So we now turn to deriving this quantity.

If we needed to express  $d\mathbf{w}_j$  instead of  $d\mathbf{p}_j$ , we would have a ready-to-use result because, according to Caswell (2001, pp. 247–251) and Szilágyi and MeszÉna (2009a, Appendix B),

$$d\mathbf{w}_j = \mathbf{Q}_j d\mathbf{A}_j \mathbf{w}_j, \quad (10)$$

where  $\mathbf{Q}_j$  is given by

$$\mathbf{Q}_j = \sum_{k=2}^{s_j} \left( \frac{\mathbf{w}_j^k - |\mathbf{w}_j^k| \mathbf{w}_j}{\lambda_j - \lambda_j^k} \right) \otimes \mathbf{v}_j^k. \quad (11)$$

However, we want  $d\mathbf{p}_j$ , not  $d\mathbf{w}_j$ . We therefore need to connect these two quantities. This can easily be done by taking differentials in Eq. (6):

$$d\mathbf{p}_j = \frac{d\mathbf{w}_j}{\mathbf{q}_j \mathbf{w}_j} - \frac{\mathbf{w}_j (\mathbf{q}_j d\mathbf{w}_j)}{(\mathbf{q}_j \mathbf{w}_j)^2} = \frac{1}{\mathbf{q}_j \mathbf{w}_j} \left( \mathbf{I}_j - \frac{\mathbf{w}_j \otimes \mathbf{q}_j}{\mathbf{q}_j \mathbf{w}_j} \right) d\mathbf{w}_j. \quad (12)$$

Using the notation

$$\mathbf{P}_j = \frac{1}{\mathbf{q}_j \mathbf{w}_j} \left( \mathbf{I}_j - \frac{\mathbf{w}_j \otimes \mathbf{q}_j}{\mathbf{q}_j \mathbf{w}_j} \right), \quad (13)$$

this is written as

$$d\mathbf{p}_j = \mathbf{P}_j d\mathbf{w}_j. \tag{14}$$

Then, using Eq. (10), we get

$$d\mathbf{p}_j = \mathbf{P}_j \mathbf{Q}_j d\mathbf{A}_j \mathbf{w}_j \tag{15}$$

(note that  $\mathbf{P}_j$ ,  $\mathbf{Q}_j$  and  $\mathbf{w}_j$  are evaluated using the original  $\mathbf{A}_j$ ). The product  $\mathbf{P}_j \mathbf{Q}_j$  can be rewritten using the simple relation  $(\mathbf{a} \otimes \mathbf{b})(\mathbf{c} \otimes \mathbf{d}) = (\mathbf{bc})(\mathbf{a} \otimes \mathbf{d})$ :

$$\begin{aligned} \mathbf{T}_j &= \mathbf{P}_j \mathbf{Q}_j = \frac{1}{\mathbf{q}_j \mathbf{w}_j} \left( \mathbf{I}_j - \frac{\mathbf{w}_j \otimes \mathbf{q}_j}{\mathbf{q}_j \mathbf{w}_j} \right) \left( \sum_{k=2}^{s_j} \frac{(\mathbf{w}_j^k - |\mathbf{w}_j^k| \mathbf{w}_j) \otimes \mathbf{v}_j^k}{\lambda_j - \lambda_j^k} \right) \\ &= \frac{1}{\mathbf{q}_j \mathbf{w}_j} \sum_{k=2}^{s_j} \frac{1}{\lambda_j - \lambda_j^k} \left( \mathbf{w}_j^k - \frac{\mathbf{q}_j \mathbf{w}_j^k}{\mathbf{q}_j \mathbf{w}_j} \mathbf{w}_j \right) \otimes \mathbf{v}_j^k. \end{aligned} \tag{16}$$

Then, Eq. (15) can be written as

$$\begin{aligned} d\mathbf{p}_j &= \mathbf{T}_j d\mathbf{A}_j \mathbf{w}_j = \left( \frac{1}{\mathbf{q}_j \mathbf{w}_j} \sum_{k=2}^{s_j} \frac{1}{\lambda_j - \lambda_j^k} \right. \\ &\quad \left. \times \left( \mathbf{w}_j^k - \frac{\mathbf{q}_j \mathbf{w}_j^k}{\mathbf{q}_j \mathbf{w}_j} \mathbf{w}_j \right) \otimes \mathbf{v}_j^k \right) d\mathbf{A}_j \mathbf{w}_j. \end{aligned} \tag{17}$$

The first term of the inner parentheses corresponds to regular eigenvector perturbation calculus (Caswell, 2001, chapter 9), which preserves the Euclidean norm and yields no change in the direction of the leading eigenvector. The second term adds the proper correction into the leading direction to preserve the one-norm instead of the Euclidean norm.

We are still not quite finished with finding  $d\mathbf{p}_j$  because of the unknown  $d\mathbf{A}_j$  in Eq. (17). We therefore expand  $d\mathbf{A}_j$  as

$$d\mathbf{A}_j = \sum_v \frac{\partial \mathbf{A}_j}{\partial \mathcal{R}_v} d\mathcal{R}_v + \frac{\partial \mathbf{A}_j}{\partial \mathbb{E}} d\mathbb{E}. \tag{18}$$

Substituting this into Eq. (17) yields the final expression for  $d\mathbf{p}_j$ :

$$d\mathbf{p}_j = \mathbf{T}_j \left( \sum_v \frac{\partial \mathbf{A}_j}{\partial \mathcal{R}_v} d\mathcal{R}_v + \frac{\partial \mathbf{A}_j}{\partial \mathbb{E}} d\mathbb{E} \right) \mathbf{w}_j. \tag{19}$$

Substituting this result into Eq. (9) yields

$$\begin{aligned} d\mathcal{R}_\mu &= \sum_{j=1}^s \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \mathbf{p}_j dn_j \\ &\quad + \sum_{j=1}^s n_j \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \mathbf{T}_j \left( \sum_v \frac{\partial \mathbf{A}_j}{\partial \mathcal{R}_v} d\mathcal{R}_v + \frac{\partial \mathbf{A}_j}{\partial \mathbb{E}} d\mathbb{E} \right) \mathbf{w}_j, \end{aligned} \tag{20}$$

where we run into a problem:  $d\mathcal{R}_\mu$  appears on both sides of the equation. We therefore rearrange to solve for  $d\mathcal{R}_\mu$  explicitly. But first, just to simplify notation, we introduce the function

$$\mathcal{G}_\mu(\mathcal{R}_v, \mathbb{E}) = \sum_{j=1}^s n_j \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \mathbf{T}_j \mathbf{A}_j(\mathcal{R}_v, \mathbb{E}) \mathbf{w}_j, \tag{21}$$

where we emphasize that the dependence of  $\mathcal{G}_\mu$  on  $\mathcal{R}_v$  and  $\mathbb{E}$  comes exclusively from the dependence of the matrix  $\mathbf{A}_j$  on these variables, as denoted; all other factors are evaluated at the unperturbed equilibrium. This function is summed over all species and so is the property of the community as a whole. Using this notation, Eq. (20) becomes

$$d\mathcal{R}_\mu = \sum_{j=1}^s \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \mathbf{p}_j dn_j + \sum_v \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_v} d\mathcal{R}_v + \frac{\partial \mathcal{G}_\mu}{\partial \mathbb{E}} d\mathbb{E}. \tag{22}$$

We now rearrange and solve for  $d\mathcal{R}_\mu$  to get

$$d\mathcal{R}_\mu = \sum_v \left( \delta_{\mu v} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_v} \right)^{-1} \left( \sum_{j=1}^s \frac{\partial \mathcal{R}_v}{\partial \mathbf{n}_j} \mathbf{p}_j dn_j + \frac{\partial \mathcal{G}_v}{\partial \mathbb{E}} d\mathbb{E} \right). \tag{23}$$

And now, we can finally go ahead with our original plan of substituting this expression back into Eq. (8), differentiating by  $\mathbb{E}$ , and solving for  $dn_i/d\mathbb{E}$  to complete the derivation. Substitution into Eq. (8) yields

$$\begin{aligned} \sum_\mu \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \sum_v \left( \delta_{\mu v} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_v} \right)^{-1} \left( \sum_{j=1}^s \frac{\partial \mathcal{R}_v}{\partial \mathbf{n}_j} \mathbf{p}_j dn_j \right. \\ \left. + \frac{\partial \mathcal{G}_v}{\partial \mathbb{E}} d\mathbb{E} \right) + \frac{\partial \lambda_i}{\partial \mathbb{E}} d\mathbb{E} = 0. \end{aligned} \tag{24}$$

Differentiation by  $\mathbb{E}$  gives

$$\begin{aligned} \sum_\mu \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \sum_v \left( \delta_{\mu v} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_v} \right)^{-1} \left( \sum_{j=1}^s \frac{\partial \mathcal{R}_v}{\partial \mathbf{n}_j} \mathbf{p}_j \frac{dn_j}{d\mathbb{E}} \right. \\ \left. + \frac{\partial \mathcal{G}_v}{\partial \mathbb{E}} \right) + \frac{\partial \lambda_i}{\partial \mathbb{E}} = 0, \end{aligned} \tag{25}$$

or

$$\begin{aligned} \sum_{j=1}^s \sum_{\mu, v} \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \left( \delta_{\mu v} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_v} \right)^{-1} \frac{\partial \mathcal{R}_v}{\partial \mathbf{n}_j} \mathbf{p}_j \frac{dn_j}{d\mathbb{E}} \\ + \sum_{\mu, v} \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \left( \delta_{\mu v} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_v} \right)^{-1} \frac{\partial \mathcal{G}_v}{\partial \mathbb{E}} + \frac{\partial \lambda_i}{\partial \mathbb{E}} = 0. \end{aligned} \tag{26}$$

Solving for  $dn_i/d\mathbb{E}$ , we obtain

$$\begin{aligned} \frac{dn_i}{d\mathbb{E}} = - \sum_{j=1}^s \left( \sum_{\mu, v} \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \left( \delta_{\mu v} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_v} \right)^{-1} \frac{\partial \mathcal{R}_v}{\partial \mathbf{n}_j} \mathbf{p}_j \right)^{-1} \\ \times \left( \frac{\partial \lambda_j}{\partial \mathbb{E}} + \sum_{\sigma, \varrho} \frac{\partial \lambda_j}{\partial \mathcal{R}_\sigma} \left( \delta_{\sigma \varrho} - \frac{\partial \mathcal{G}_\sigma}{\partial \mathcal{R}_\varrho} \right)^{-1} \frac{\partial \mathcal{G}_\varrho}{\partial \mathbb{E}} \right). \end{aligned} \tag{27}$$

The quantities  $\partial \lambda_i / \partial \mathcal{R}_\mu$  and  $\partial \lambda_i / \partial \mathbb{E}$  would be difficult to evaluate directly, but fortunately, using the chain rule, one can write

$$\frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} = \frac{\partial \lambda_i}{\partial \mathbf{A}_i} \frac{\partial \mathbf{A}_i}{\partial \mathcal{R}_\mu} = \mathbf{v}_i \frac{\partial \mathbf{A}_i}{\partial \mathcal{R}_\mu} \mathbf{w}_i \tag{28}$$

(and analogously for  $\partial \lambda_i / \partial \mathbb{E}$ ), where we used the fact that the derivative of the leading eigenvalue with respect to the matrix elements  $d\lambda_i/d\mathbf{A}_i$  is equal to  $\mathbf{v}_i \otimes \mathbf{w}_i$ , the outer product of the reproductive value vector and the stable stage distribution (Caswell, 2001, chapter 9). The derivative of  $\mathbf{A}_i$  with respect to the regulating factors  $\mathcal{R}_\mu$  or the parameter  $\mathbb{E}$  is of course directly calculable from the model definition. Substitution of these expressions into Eq. (27) yields our final result:

$$\begin{aligned} \frac{dn_i}{d\mathbb{E}} = - \sum_{j=1}^s \left( \sum_{\mu, v} \left( \mathbf{v}_i \frac{\partial \mathbf{A}_i}{\partial \mathcal{R}_\mu} \mathbf{w}_i \right) \left( \delta_{\mu v} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_v} \right)^{-1} \frac{\partial \mathcal{R}_v}{\partial \mathbf{n}_j} \mathbf{p}_j \right)^{-1} \\ \times \left( \mathbf{v}_j \frac{\partial \mathbf{A}_j}{\partial \mathbb{E}} \mathbf{w}_j + \sum_{\sigma, \varrho} \left( \mathbf{v}_j \frac{\partial \mathbf{A}_j}{\partial \mathcal{R}_\sigma} \mathbf{w}_j \right) \left( \delta_{\sigma \varrho} - \frac{\partial \mathcal{G}_\sigma}{\partial \mathcal{R}_\varrho} \right)^{-1} \frac{\partial \mathcal{G}_\varrho}{\partial \mathbb{E}} \right), \end{aligned} \tag{29}$$

where

$$\begin{aligned} \mathcal{G}_\mu(\mathcal{R}_v, \mathbb{E}) &= \sum_{j=1}^s \left( \frac{n_j}{\mathbf{q}_j \mathbf{w}_j} \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \sum_{k=2}^{s_j} \frac{1}{\lambda_j - \lambda_j^k} \right. \\ &\quad \left. \times \left( \mathbf{w}_j^k - \frac{\mathbf{q}_j \mathbf{w}_j^k}{\mathbf{q}_j \mathbf{w}_j} \mathbf{w}_j \right) \otimes \mathbf{v}_j^k \right) \mathbf{A}_j(\mathcal{R}_v, \mathbb{E}) \mathbf{w}_j. \end{aligned} \tag{30}$$

To interpret Eq. (29), let us first write it in a form that captures its general structure:

$$\frac{dn_i}{d\mathbb{E}} = \sum_{j=1}^S (M_{ij})^{-1} g_j, \quad (31)$$

where the matrix  $M_{ij}$  is given by

$$M_{ij} = \sum_{\mu, \nu} \left( \mathbf{v}_i \frac{\partial \mathbf{A}_i}{\partial \mathcal{R}_\mu} \mathbf{w}_i \right) \left( \delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \frac{\partial \mathcal{R}_\nu}{\partial \mathbf{n}_j} \mathbf{p}_j, \quad (32)$$

and the vector  $g_j$  by

$$g_j = \mathbf{v}_j \frac{\partial \mathbf{A}_j}{\partial \mathbb{E}} \mathbf{w}_j + \sum_{\sigma, \varrho} \left( \mathbf{v}_j \frac{\partial \mathbf{A}_j}{\partial \mathcal{R}_\sigma} \mathbf{w}_j \right) \left( \delta_{\sigma\varrho} - \frac{\partial \mathcal{G}_\sigma}{\partial \mathcal{R}_\varrho} \right)^{-1} \frac{\partial \mathcal{G}_\varrho}{\partial \mathbb{E}}. \quad (33)$$

Note that neither  $M_{ij}$  nor  $g_j$  depend on regulation or population structure indices, since these are all summed over. Therefore, these quantities really only depend on the species indices  $i$  and  $j$ .

This means that the rows and columns of  $M_{ij}$  express properties of the species: the  $i$ th row is a property of species  $i$ , and the  $j$ th column is a property of species  $j$ . In Eq. (31) we take the inverse of  $M_{ij}$ . The inverse of a matrix is proportional to the inverse of its determinant, and the determinant will be close to zero if any two rows or columns of the matrix are nearly linearly dependent. Therefore, it is immediately seen that the fixed point will become overly sensitive if any two species become very similar, as that will lead to similar rows/columns in the matrix to be inverted. This property can be used to give a more biological interpretation to the formula (see the Discussion).

A simple corollary of Eq. (29) is that the sensitivity of any function of the population structure vectors  $\mathbf{n}_i$  may now be calculated. If we are interested in the sensitivity of some nonlinear function  $f(\mathbf{n}_1, \dots, \mathbf{n}_S)$  of the stage classes (e.g., the sensitivity of the ratio of adults to juveniles), we simply use the chain rule:

$$\frac{df}{d\mathbb{E}} = \sum_{i=1}^S \frac{df}{d\mathbf{n}_i} \frac{d\mathbf{n}_i}{d\mathbb{E}}, \quad (34)$$

where the  $k$ th component of  $d\mathbf{n}_i/d\mathbb{E}$  is obtained via Eq. (29) by choosing the  $k$ th component of  $\mathbf{q}_i$  to be equal to 1 and all its other components to be 0.

The sensitivity  $dn_i/d\mathbb{E}$  is the amplification factor by which a perturbation in  $\mathbb{E}$  is translated into a perturbation of the weighted equilibrium density:

$$\Delta n_i = \left( \frac{dn_i}{d\mathbb{E}} \right) \Delta \mathbb{E}, \quad (35)$$

where the derivative is calculated from Eq. (29). As this is a local approximation, two consequences follow. First, the formula will be more accurate with  $\Delta \mathbb{E}$  being smaller. Whether it yields acceptable results for non-infinitesimal parameter perturbations is a question we will examine in the next section. Second, if multiple parameters are perturbed simultaneously, the total effect of these perturbations will be the sum of the individual effects:

$$\Delta n_i = \sum_k \left( \frac{dn_i}{d\mathbb{E}_k} \right) \Delta \mathbb{E}_k, \quad (36)$$

where  $\mathbb{E}_k$  is the  $k$ th parameter. This additivity of the individual effects of each parameter is a consequence of the linearization in Eq. (8).

Eq. (29) is a rather complicated object, partly because of its generality. It is therefore instructive to see what this formula reduces to in certain simple special cases. First, we can ask what happens when the interacting populations are unstructured. In this

case, it is seen from Eq. (30) that  $\mathcal{G}_\mu$  will be identically equal to zero: the summation over  $k$  does not go anywhere because for unstructured populations the number of distinct stage classes  $s_j$  is equal to one. Also, due to the lack of population structure, using Eq. (27) instead of Eq. (29) actually simplifies the equation, leading to

$$\frac{dn_i}{d\mathbb{E}} = - \sum_{j=1}^S \left( \sum_{\mu, \nu} \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \delta_{\mu\nu} \frac{\partial \mathcal{R}_\nu}{\partial \mathbf{n}_j} \mathbf{p}_j \right)^{-1} \frac{\partial \lambda_j}{\partial \mathbb{E}}, \quad (37)$$

where  $\lambda_i$  is simply the discrete geometric rate of growth of species  $i$ . For unstructured populations,  $\mathbf{n}_i = n_i$  and so  $\mathbf{p}_i = 1$  due to Eq. (5). Therefore the above expression simplifies to

$$\frac{dn_i}{d\mathbb{E}} = - \sum_{j=1}^S \left( \sum_{\mu} \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \frac{\partial \mathcal{R}_\mu}{\partial n_j} \right)^{-1} \frac{\partial \lambda_j}{\partial \mathbb{E}}, \quad (38)$$

which is the standard fixed point sensitivity formula for communities of unstructured populations (Meszóna et al., 2006).

Second, we can ask what the sensitivity formula reduces to for just a single structured population. In that case the species indices  $i$  and  $j$  can only take on the value 1. This means that the expression for  $\mathcal{G}_\mu$  is unchanged except that we can forget about the summation over  $j$ , and Eq. (29) simplifies to

$$\frac{dn}{d\mathbb{E}} = - \frac{\mathbf{v} \frac{\partial \mathbf{A}}{\partial \mathbb{E}} \mathbf{w} + \sum_{\sigma, \varrho} \left( \mathbf{v} \frac{\partial \mathbf{A}}{\partial \mathcal{R}_\sigma} \mathbf{w} \right) \left( \delta_{\sigma\varrho} - \frac{\partial \mathcal{G}_\sigma}{\partial \mathcal{R}_\varrho} \right)^{-1} \frac{\partial \mathcal{G}_\varrho}{\partial \mathbb{E}}}{\sum_{\mu, \nu} \left( \mathbf{v} \frac{\partial \mathbf{A}}{\partial \mathcal{R}_\mu} \mathbf{w} \right) \left( \delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \frac{\partial \mathcal{R}_\nu}{\partial \mathbf{n}} \mathbf{p}}. \quad (39)$$

As a final remark, we note that while here and throughout the main text we work in a discrete-time framework, all our results readily generalize to continuous-time models of interacting structured populations. See the Appendix for this generalization.

## 4. Application: a model of ontogenetic niche shift

### 4.1. The model

As a demonstration, we now apply our results to a simple model of two interacting structured populations. The model is similar in spirit to the ones by Moll and Brown (2008) and Fujiwara et al. (2011). Within each species there are two stage classes, juveniles and adults. Competition occurs between members of the same stage class, but there is no juvenile–adult interaction. This represents an ontogenetic niche shift (Werner and Gilliam, 1984), wherein adults consume completely different resources from juveniles. We also assume that adults consume a single resource (and are thus complete competitors *sensu* Hardin, 1960), while juveniles partition two independent resources.

Moll and Brown (2008) have demonstrated that stable coexistence of such species is possible, even though observing only the adults would lead to the erroneous conclusion that the species are complete competitors and thus are either in the process of excluding each other, or else are coexisting neutrally. Here we ask the question: how robust would such a coexistence be to changes in model parameters? Is excessive fine-tuning of parameters required for this coexistence to happen, or is niche differentiation within the juvenile class sufficient to offset the destabilizing effects of adult competition? As we shall see, coexistence can be quite robust in this model.

There are three resources the populations consume: one for the adults and two for the juveniles. Consumption is assumed to be linear, therefore we may write down direct formulas for the

**Table 1**

Parameter values and their sensitivities in our model of ontogenetic niche shift. The first column lists all the parameters of the model; the second shows their numerical values. The third and fourth columns are the respective sensitivities of the total population sizes of species 1 and 2 to perturbations of each model parameter, calculated from Eq. (29).

Parameter ( $\mathbb{E}$ )	Value of $\mathbb{E}$	$dn_1/d\mathbb{E}$	$dn_2/d\mathbb{E}$
$F_1$	8	0.83	-0.69
$F_2$	8	-0.69	0.83
$p_1$	0.36	16.23	-13.89
$p_2$	0.36	-13.89	16.23
$s_1$	0.3	7.12	-6.07
$s_2$	0.3	-6.07	7.12
$z_1$	0.7	11.40	-9.68
$z_2$	0.7	-9.68	11.40
$\beta_{12}$	0.8	-2.74	2.31
$\beta_{21}$	0.8	2.31	-2.74

exploitation of the resources:

$$\mathcal{R}_0 = n_{1,2} + n_{2,2}, \quad (40a)$$

$$\mathcal{R}_1 = \beta_{11}n_{1,1} + \beta_{12}n_{2,1}, \quad (40b)$$

$$\mathcal{R}_2 = \beta_{21}n_{1,1} + \beta_{22}n_{2,1}. \quad (40c)$$

Here  $\mathcal{R}_\mu$  ( $\mu = 0, 1, 2$ ) represents the amount of resource  $\mu$  locked up in the biomass of the two species,  $n_{i,a}$  is the  $a$ th stage class of species  $i$  with  $a = 1$  meaning juveniles and  $a = 2$  adults, and the  $\beta_{\mu i}$  express the per capita load of species  $i$ 's juveniles on resource  $\mu$ . We assume  $\beta_{11} = \beta_{22} = 1$ .

Using these three regulating factors, the projection matrices of the species read

$$\mathbf{A}_i = \begin{pmatrix} (1-p_i)\frac{z_i}{1+\mathcal{R}_i} & \frac{F_i}{1+\mathcal{R}_0} \\ p_i\frac{z_i}{1+\mathcal{R}_i} & \frac{s_i}{1+\mathcal{R}_0} \end{pmatrix}, \quad (41)$$

where  $z_i$  is the probability of juvenile survival,  $p_i$  the probability of morphing into an adult,  $F_i$  is adult fertility, and  $s_i$  is the adult survival probability (all probabilities are per capita per time step). As seen from Eq. (41), the fertility, juvenile survival, and adult survival are density-dependent through the regulating factors with a Beverton–Holt-style density dependence. Notice that while the juveniles of the two species are affected by two different regulating factors,  $\mathcal{R}_1$  and  $\mathcal{R}_2$ , the adults are affected by the same factor  $\mathcal{R}_0$ . With the projection matrices thus specified, the dynamics evolves according to Eq. (1).

This model is similar to the one by Fujiwara et al. (2011) in the form of the density dependence, but is closer to the model of Moll and Brown (2008) in the assumption of a strict ontogenetic niche shift (they employed Ricker-style density dependence). The advantage of the Beverton–Holt density dependence is that it generates fixed points, while Ricker and other overcompensating curves may lead to fixed points, cycles, or chaos, depending on parameters. As our framework is as yet only applicable to fixed points, we chose Beverton–Holt density regulation.

## 4.2. Results

The first step is to choose values for all model parameters (see Table 1). These parameter values lead to the equilibrium population vector  $\mathbf{n}_i = (0.899, 0.114)$  for both species. The fact that  $\mathbf{n}_1 = \mathbf{n}_2$  should not be surprising, as the species are symmetric with respect to their assigned parameters (but they are not equivalent due to  $\beta_{12} = \beta_{21} = 0.8$ ; therefore the fixed point is stable, not neutrally stable). Then, after obtaining the eigenvalues and eigenvectors of the two projection matrices, calculation of the sensitivities via Eq. (29) is a straightforward exercise – see Table 1 for the

results. We will use the total population density as the weighted population size, i.e.,  $\mathbf{q}_i = (1, 1)$  for both species. The total equilibrium population densities are then  $n_i = \mathbf{q}_i \mathbf{n}_i = 1.013$ .

When interpreting the sensitivity values in Table 1, the same considerations apply as in standard eigenvalue sensitivity analyses of single populations. Namely, the numbers alone will not tell us whether the model is “sensitive” to a given parameter or not: the biologically realistic variation of that parameter also needs to be known. The sensitivity values are merely amplifiers: perturbations of the parameters are multiplied by those numbers to yield the change in equilibrium densities via Eq. (36). For instance, our model shows great sensitivity to changes in the probability of morphing into adults (the  $p_i$ ), but if this probability is a parameter that is evolutionarily set and the environment has little or no effect on it, then the model can be quite robust even with those large sensitivity values, as long as selection is negligible. Conversely, small sensitivities may be lethal to a species if the natural variation of the parameter is too large.

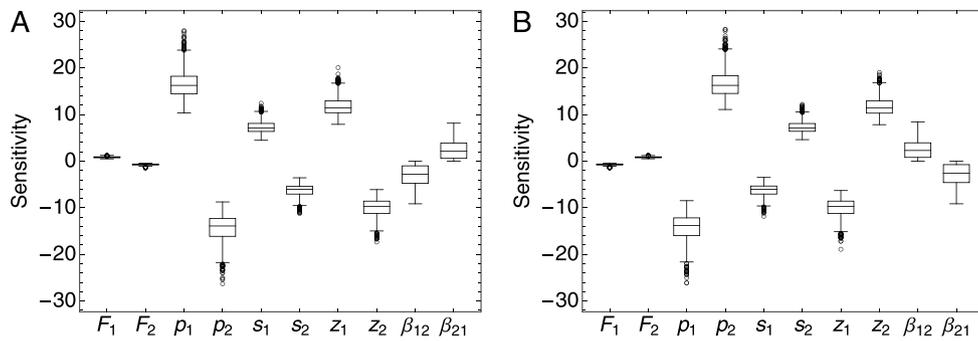
There are some natural questions arising from our results:

1. How much do the sensitivity values in Table 1 depend on our particular choice of parameters?
2. Sensitivity analysis is of course a locally valid approximation. As stated before, Eq. (36) is in principle only accurate for small  $\Delta\mathbb{E}$  values. How much is this accuracy compromised when the parameter perturbations are not infinitesimally small?
3. To use Eq. (29), the equilibrium stage distribution needs to be known, but this cannot usually be analytically obtained except in the simplest of models. Instead, field data may be used to estimate this distribution – which may be difficult to do, not to mention the problem that the system might not be at or even near its equilibrium point at the time of measurement. Assuming that the stage distribution is off of its true equilibrium value (which we have the benefit of knowing due to our *in silico* approach), how much are the sensitivity values of Table 1 altered?

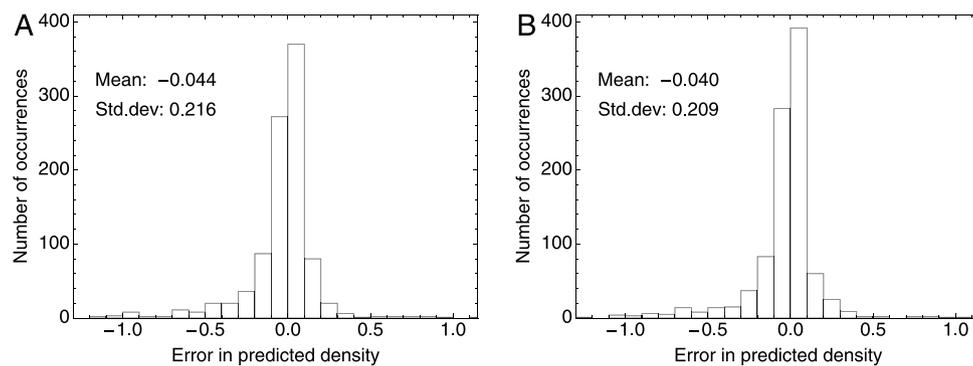
To answer the first question, we randomized the parameters by simultaneously changing them within a  $\pm 10\%$  band of their original values with a uniform probability distribution. Then the model was simulated with these new parameters until equilibrium was reached. The equilibrium condition was that the leading eigenvalues of the two species cannot differ from 1 by more than  $10^{-5}$ . Then, Eq. (29) was used to obtain the sensitivities to each parameter. This procedure was then repeated 1000 times. The results are seen on Fig. 1. While there certainly is variation around the original sensitivities, it is immediately seen that they still give a good general idea of how much sensitivity there is to be expected.

For the second question we performed the same randomization of parameters, ran the model on the computer until equilibrium, and then calculated the difference between the densities predicted by the local sensitivity analysis and the actual densities obtained via simulation. By “predicted” change we mean the following. We determined  $\Delta\mathbb{E}$  for each parameter (the difference between the randomly generated value and the original one in Table 1). Then, using the already determined sensitivity values (also in Table 1), the contribution of all parameters to  $\Delta n$  was calculated using Eq. (36). One thousand such comparisons of simulated and predicted densities are seen on Fig. 2. The implications are clear: in the majority of cases, local sensitivity analysis did a good job predicting densities for the  $\pm 10\%$  parameter variation we introduced in each parameter.

One manual correction was used in making Fig. 2. If predicted densities turned out negative, we tested to see whether the species in question indeed went extinct. If so, we took the predicted density to have precisely matched the simulated one, i.e., registered such a case as a perfect prediction. This procedure might in principle be sensitive to the extinction threshold, but we found that the



**Fig. 1.** Distribution of sensitivity values in parameter space for the ontogenetic niche shift model. First all the parameters are randomly changed within a  $\pm 10\%$  range of their original values in Table 1. Then the sensitivity to each parameter is calculated using Eq. (29). Repeating this process a thousand times, we get a distribution of sensitivities for each parameter, depicted here using box plots. Panel (A) shows the sensitivities for species 1, panel (B) for species 2. The interpretation of the box plots: median (lines), 25% to 75% quartiles (boxes), ranges (whiskers), outliers (circles, defined as falling outside 1.5 times the interquartile range of the box). The median lines may also be interpreted as the sensitivities with the original set of parameters in Table 1 – the difference between the two is invisibly slight in all cases.



**Fig. 2.** Histograms of the difference between predicted and actual changes to equilibrium densities in the ontogenetic niche shift model. First, all the parameters are randomly changed within a  $\pm 10\%$  range of their original values in Table 1. The difference between the random values and the original ones is  $\Delta \mathbb{E}$ . We used these  $\Delta \mathbb{E}$  along with the sensitivity values in Table 1 to calculate the predicted change in the equilibrium densities from Eq. (36). We then simulated our model with the randomized parameter values, recording the equilibrium densities. The difference between the simulated and calculated densities is a measure of how well the sensitivity formula captures the actual change in equilibrium abundances. The histograms summarize a thousand such comparisons; panel (A) is the difference for species 1, panel (B) for species 2. Note that with the original parameter values the total population size is  $n_i = 1.013 \approx 1$  for both species, so the abscissas of the histograms can be interpreted as proportional errors relative to that size.

results were essentially unchanged for extinction threshold values between  $10^{-3}$  and  $10^{-14}$ . Incidentally, the fraction of simulations in which at least one species went extinct also showed the same insensitivity to the extinction threshold: it was always about 15% of all cases.

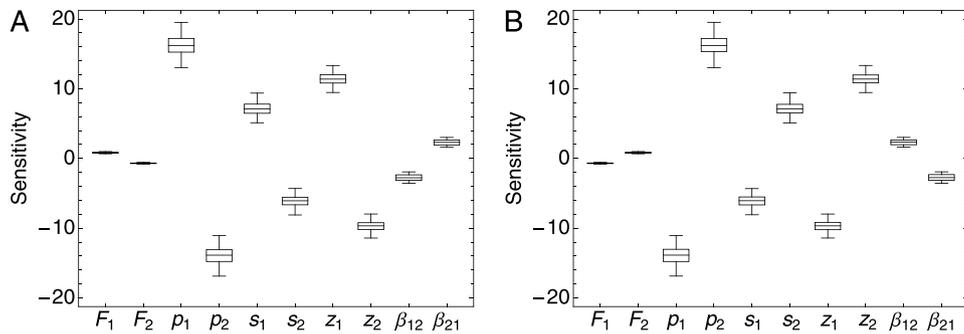
Finally, to answer the third question we kept the original parameter values fixed but randomized the stable stage distribution in a  $\pm 30\%$  band of their original values. Applying Eq. (29) to the randomized values as if they were the true equilibria of the model, we calculated the (modified) sensitivities to each parameter. Repeating the process 1000 times, we ended up with the variation depicted on Fig. 3. The error due to an incorrect assessment of the equilibrium is slight even for very large errors in the densities. This suggests that in field studies, it is acceptable to use measured data as a proxy for the actual equilibrium distributions, as the error due to the fact that the measured values are not the actual equilibrium densities will be small – at least for the model in question.

## 5. Discussion

In this article we derived a general perturbation formula for the equilibrium densities of interacting structured populations to changes in model parameters. Each population may be age- or stage-structured with arbitrarily many stage classes, and species' projection matrices may depend on those stage classes in arbitrarily complicated ways. Our formula yields the response of any function of the stage class abundances to perturbations of any model

parameter. We applied our results to a model of two competing species undergoing ontogenetic niche shifts. After obtaining the sensitivity of each species' density to each model parameter, we investigated the fragility of these results to relaxing some of the key assumptions of our theory, such as the system being right at its equilibrium, or that the perturbations of the parameters are infinitesimally small. We found that the model was surprisingly robust to violating the equilibrium assumption, and that the locally approximated sensitivities gave good results even for relatively large perturbations of the parameters. Thus, the technical limitations of our framework seem not to be very important, which is in line with similar findings for sensitivity analyses within population ecology (de Kroon et al., 2000).

Elasticities (Caswell et al., 1984) also enjoy considerable popularity as measures of how sensitive models are to parameter perturbations. The difference is that sensitivities describe the effects of additive perturbations, while elasticities describe the effects of multiplicative ones. Our sensitivities are easily converted into elasticities. By definition, the derivative of  $\log n_i$  with respect to  $\log \mathbb{E}$  is the elasticity, therefore  $(\mathbb{E}/n_i)(dn_i/d\mathbb{E})$  will yield the elasticities. Or, if we are interested in the elasticity of  $f(n_i)$  with  $f$  being an arbitrary function, we get  $(\mathbb{E}/f(n_i))(df(n_i)/d\mathbb{E})$ , where the derivative of  $f$  with respect to  $\mathbb{E}$  is given by Eq. (34). As in conventional eigenvalue elasticity analysis of linear models, the elasticity to a parameter whose value is zero will be 0. However, elasticities of equilibrium densities cannot be thought of as contributions of matrix elements to the  $n_i$ , as that property hinges on Euler's homogeneous function theorem (Mesterton-Gibbons, 1993), and



**Fig. 3.** Distribution of sensitivity values in the ontogenetic niche shift model when randomizing the equilibrium abundance vectors  $\mathbf{n}_i$ . We fix the parameters at the values in Table 1, which lead to  $\mathbf{n}_i = (0.899, 0.114)$  at equilibrium for both species. Now, as a first step, we randomize each stage class of each species within a  $\pm 30\%$  band of these values. We then use Eq. (29) to calculate the sensitivities as if the randomized abundance vectors represented the true equilibrium point. Repeating this process a thousand times, we get the distribution of sensitivities shown by the box plots. Panel (A) is for species 1, panel (B) is for species 2. As in Fig. 1, the median markers may stand for either the median or the original sensitivities of Table 1.

the  $n_i$  are not homogeneous functions of matrix elements in general (and, even in the realm of eigenvalue elasticities, thinking of the elements as “contributions” to  $\lambda_i$  requires considerable care of interpretation). Even though this property is lacking, there is no obstacle to using our formulas to get at the effects of proportional as opposed to additive perturbations.

We can give a more biological interpretation to Eq. (29), the formula for the perturbation of the weighted population densities. We start out from the already stated fact that the rows and columns of the inverted matrix express properties of the species themselves, and that therefore too much similarity in the species leads to similar rows or columns in the matrix to be inverted, making the fixed point overly sensitive to parameter perturbations. The rows and columns are not just some complicated summary of the species’ properties; they have straightforward biological interpretations. The row index  $i$  appears in the derivative of the projection matrix with respect to the regulating factors, weighted by the reproductive value and the stable stage distribution: it is therefore a measure of how sensitive species  $i$  is to the regulating factors (not to be confused with “sensitivity” as a measure of the robustness of the fixed point). The column index  $j$  appears in the derivative of the regulating factors with respect to the population structure vector, averaged over the reduced population structure vector: this is a measure of the impact of species  $j$  on the regulating factors (Szilágyi and Meszéna, 2009a). Our earlier statement that near-linear dependence of the rows or columns leads to an overly sensitive fixed point thus translates into the following: species that are too similar in either their sensitivities to or their impacts on the regulating factors will make the fixed point unrobust to parameter perturbations. In the limiting case where two species share exactly the same sensitivities and/or impacts, the system becomes infinitely sensitive, signaling the destabilization of the system.

The biological interpretation arising from our expression for the fixed point sensitivity of interacting populations is consistent with interpretations arising in existing formulas for the sensitivity of interacting populations, both for equilibrium (Meszéna et al., 2006; Szilágyi and Meszéna, 2009a,b) and fluctuating (Szilágyi and Meszéna, 2010; Barabás et al., 2012; Barabás and Ostling, 2013) community dynamics. No two species that are too similar in their way of regulation can realistically coexist in the long run because, even if stability can be ensured (a necessary condition for coexistence), the smallest change in  $\mathbb{E}$  may result in an erratic swing of the equilibrium population densities, leading to the elimination of at least one of the species. This recasting of the familiar competitive exclusion principle (Hardin, 1960; Levin, 1970) therefore shifts the emphasis from the stability of coexistence to its sensitivity: coexistence of similar species is not

impossible (stability can be forced by careful choice of model parameters), just extremely unlikely, precisely because of the required fine-tuning.

This property connects sensitivity analysis with niche theory. Modern reinterpretations of the niche concept, based on the expectation of stable coexistence (Leibold, 1995; Chesson, 2000b; Chase and Leibold, 2003) have essentially two components. The first, inspired by Levin (1970), is that the niche of a species is to be identified, in some way or another, with the factors it is regulated by. The second is the realization of the importance of the two-way interaction between species and the factors that regulate them. Leibold (1995) and Chase and Leibold (2003) emphasize that resources, predators/pathogens, or the two combined may serve as the niche. They also distinguish requirements (effect of regulator on species) and impacts (effect of species on regulator), and show that only a proper consideration of both can give a full account of the niche. In Chesson’s (2000b) terminology, niche space has four “main” axes (each of which may in turn be constituted of multiple axes): resources, predators/pathogens, space, and time. Space and time as niche dimensions mean that each regulating factor at each spatial location and/or point in time serves as a separate factor (spatial and temporal storage effect, Chesson and Warner, 1981; Chesson, 1991, 1994, 2000a, 2009; Chesson and Huntly, 1997; Snyder and Chesson, 2004). Indeed, the fixed point theory of coexistence and the niche can be extended to fluctuating environments via considering this time-dependence of regulating factors – these studies have revealed that, in a periodically fluctuating environment, time behaves mathematically analogously to a resource continuum (Barabás et al., 2012; Barabás and Ostling, 2013). And the main goal of Szilágyi and Meszéna (2009a), whose work we extended here, was to establish the role of space as a niche axis. Chesson stresses that the niche of a species is not a Hutchinsonian hypervolume, but is given by both the effect of a species on each point in niche space, and the response of the species to each point (again, the two-way paradigm). This is of course entirely correct, but it may be added that this replacement of terminology could also be seen as part of a progression of more and more formal niche descriptions. The hypervolume (crudest level) has been made more realistic with the introduction of resource utilization functions (MacArthur and Levins, 1967). These in turn have been superseded by the sensitivity/impact picture, one that is both formal and generally applicable in any ecological scenario.

In our framework the two-way nature of regulation is apparent: species have sensitivities to and impacts on the regulating factors. Therefore, one can identify niche space with the set of all regulating factors, and the sensitivities and impacts describe the two-way relationship between species and points in this niche space,

in complete agreement with the picture suggested by Chesson (2000b). With the shift in focus from the stability (the fundamental basis for Leibold, 1995 and Chesson, 2000b) to the sensitivity of coexistence, the original intuition behind niche theory is retained: too much niche overlap – i.e., too much similarity in either the sensitivities or the impacts – confines any coexistence to a very limited range of parameter space, making it unrealistic. Note that this niche interpretation is carried over from Szilágyi and Meszéna (2009a): the reason is that the niche theoretical conclusions hinge on the properties of the inverted matrix in Eq. (29), and this matrix has the same general form here as it did in the original study. This is why the impact-sensitivity conclusions have not been changed. However, the whole perturbation story has changed significantly: perturbations can have a direct effect on the population structure, and this direct effect induces further, indirect effects through population interactions. The perturbations of different species' population structures are therefore not independent: instead, they are intrinsically correlated.

In terms of future directions, there are several ways in which sensitivity analyses of interacting populations still have to be developed. One open avenue is the sensitivity analysis of transient community dynamics where, instead of concentrating on the stationary state, the focus is on the parameter dependence of short-term dynamics (Caswell, 2007 has followed this approach but only for single populations). But even in the realm of the analysis of stationary states, there is work to do. Although fixed point (Meszéna et al., 2006) and limit cycle (Barabás et al., 2012; Barabás and Ostling, 2013) analysis of unstructured models is available, and here, by extending the results of Szilágyi and Meszéna (2009a), we have obtained a general formula for fixed point analysis of structured community models, sensitivity calculations for communities in general aperiodic environments are still lacking, both for the unstructured and the structured case. Developing the formalism to deal with these extra complexities will be the next step in the theory of community-wide sensitivities.

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## Appendix. Sensitivities for continuous-time models

In the main text we have been sticking to a discrete-time framework. However, our results are easily generalized to continuous-time models. The general model equations now read

$$\frac{d\mathbf{n}_i(t)}{dt} = \mathbf{A}_i(\mathcal{R}_\mu(\mathbf{n}_1, \dots, \mathbf{n}_S), \mathbb{E}) \mathbf{n}_i(t) \quad (i = 1 \dots S), \quad (42)$$

where the basic definitions are the same as they were for Eq. (1). Importantly though, the matrices  $\mathbf{A}_i$  do not have the same general structure as in discrete-time models: the diagonal entries express survival rates of the corresponding stage classes, and therefore may be positive or negative (the off-diagonal entries are still strictly nonnegative, otherwise they could generate negative stage class abundances).

In continuous time, the following generalization of the Perron–Frobenius theorem applies (Szilágyi and Meszéna, 2009a, Appendix A). Suppose a nonzero matrix is irreducible, real, and nonnegative except possibly for entries along its main diagonal. Then it possesses a unique eigenvalue that is real and larger than the real part of all the other eigenvalues, its corresponding left and right eigenvectors are unique, and these eigenvectors are real and

have positive components. This is what we refer to as the leading eigenvalue in continuous time.

There are three differences from the discrete-time case. First, the matrix does not need to be primitive, only irreducible. Second, the leading eigenvalue is the one with the largest real part as opposed to the largest modulus. Third, though the leading eigenvalue is real, it can be negative, corresponding to a declining population in continuous time.

We therefore assume that the  $\mathbf{A}_i$  are irreducible. This means that their leading eigenvalues exist. At equilibrium, we then have

$$\lambda_i(\mathcal{R}_\mu(\mathbf{n}_1, \dots, \mathbf{n}_S), \mathbb{E}) = 0, \quad (43)$$

the continuous-time analogue of Eq. (7). At this point, we can expand these equations in their arguments, which will lead to Eq. (8), and so from this point on the whole derivation of Section 3 carries over. The main result, Eq. (29), therefore still holds.

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