Fixed point sensitivity analysis of interacting structured populations

György Barabás [a,*], Géza Meszéna [b], Annette Ostling [a]

[a] Department of Ecology and Evolutionary Biology, University of Michigan, 830 North University, Ann Arbor, MI 48109-1048, United States
[b] Department of Biological Physics, Eötvös Loránd University, Pázmány Péter sétány 1A, H-1117, Budapest, Hungary

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.

ARTICLE INFO

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.

© 2013 Elsevier Inc. All rights reserved.

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; Gleeson, 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

* Corresponding author.
E-mail addresses: dysordys@umich.edu (G. Barabás), geza.meszena@elte.hu (G. Meszéna), aostling@umich.edu (A. Ostling).

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 $\mathbb{E}$ differentiably. 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

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

Here S is the total number of species in the community, $\mathbf{n}_i(t)$ is the population structure vector of the ith species at time t, $\mathbb{E}$ represents the model's parameters, $\mathbf{A}_i$ is the projection matrix of the ith 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 $(i, j, \ldots)$ for species indices and lowercase Greek subscripts $(\mu, \nu, \ldots)$ for the regulating factors. Also, quantities bearing any regulation indices will be denoted in calligraphic face $(\mathcal{R}, \mathcal{G}, \ldots)$ to further distinguish them from other quantities. Function notations like $\mathbf{A}_i(\mathcal{R}_\mu(\mathbf{n}_1, \ldots, \mathbf{n}_S))$ 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 μ 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 δ_{ij}, equal to 1 if $i = j$ and to 0 otherwise. When inverting matrices, $\left(M_{ij}\right)^{-1}$ 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 $\mathbf{ab}$. Their outer product $\mathbf{a} \otimes \mathbf{b}$ is by definition