Community robustness in discrete-time periodic environments

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Abstract

The influence of seasonal environmental variation on species coexistence is an ecologically important factor. Its two aspects are how seasonal variation contributes to coexistence mechanisms, and, given a seasonally varying coexistence pattern, how sensitive that coexistence is to nonstationary external influences (such as climate change). Here we develop a formula for calculating the robustness of discrete-time periodic dynamics. Robustness is defined as the sensitivity of the position of the cycle in phase space to varying model parameters. Though the results are different, the main biological conclusions are in line with those from a similar study concerning continuous-time cycles (Barabás et al. 2012a): species segregation in the timing of resource use or predator avoidance increases community robustness in a way that is analogous to the effects of resource partitioning. We also connect this formalism with the widely used and successful framework of Peter Chesson (1994), demonstrating that the merging of these two perspectives yields simplified expressions for robustness more amenable to analytical treatment. As an example, we apply our results to a two-cycle in a model of two competing annual plants with seed banks, using our formulas to calculate the range of parameters that allow for the coexistence of the competitors. This helps us understand which components of the environmental variation the coexistence is sensitive to; in our case, the model is fairly robust against changing seed survival, moderately so against changing the variance in seed germination, and quite sensitive to changing the mean seed germination rates.

Keywords: coexistence; cycle; fluctuations; limiting similarity

1 The importance of robustness analysis for the coexistence problem

There are three standard criteria for a given set of species to be considered coexisting in model communities. First, the system should eventually settle down to some stationary behavior, be it a fixed point, a limit cycle, or something more exotic such as a chaotic orbit. We may collectively refer to such stationary states as “equilibria”. Second, these equilibria must lie in the positive region of phase space: as negative population densities are impossible, such a solution would mean the inevitable extinction of at least some of the species. Third, since nature is a noisy place, one cannot expect the system to be right at the equilibrium at all or even most of the time. Therefore, not only does there need to be an all-positive equilibrium: it also needs to be attracting.

Recently, there has been a growing appreciation of the fact that fulfilling these three criteria is not enough (Meszéna et al. 2006, Szilágyi and Meszéna 2009, Gross et al. 2009, Cordoleani et al. 2011, Barabás et al. 2012a,b, Adamson and Morozov 2012, Barabás et al. 2013). We live in a noisy world – not just in terms of dynamical variables (the population densities), but also for the environmental parameters influencing population growth. Since these density-independent parameters inevitably fluctuate, coexistence that is confined to an extremely narrow region in parameter space is not to be taken seriously. Imagine standard Lotka–Volterra competition between two species with equal intrinsic growth rates and carrying capacities, and with interspecific competition coefficients equal to 0.99. Technically speaking, we have stable coexistence. However, if an external influence increased the interspecific competition coefficients above 1 or changed the ratio of the carrying capacities by more than one percent, the stable equilibrium will be destabilized and coexistence lost. This points to the fact that yet another criterion needs to be fulfilled if we want to consider a coexistence analysis complete: existence, positivity, and stability of the equilibrium has to hold for a range of parameter values, not just for special combinations of them. The volume in parameter space allowing for stable coexistence is what is referred to as the robustness of the system (Meszéna et al. 2006).

In practice, the way robustness is often determined is not by explicitly calculating the volume of parameter space in which stable coexistence happens, but by determining the sensitivity of the position of the equilibrium with respect to parameter changes (Meszéna et al. 2006, Szilágyi and Meszéna 2009, 2010, Barabás et al. 2012a). If the equilibrium hardly moves even after substantial changes in parameters, coexistence is robust. If, on the other hand, even tiny changes in parameters lead to sudden shifts of the equilibrium, it will not be able to remain all-positive for long. Robustness is then lost.

Positivity, stability, and robustness are related but separate properties. Indeed, it is possible to have stable equilibria that are not all-positive, or all-positive equilibria that are not stable, or unstable equilibria whose position is relatively insensitive to parameter changes. Of course, the lack of any of these ingredients will make coexistence impossible – i.e., lack of robustness (or lack of positivity or stability) is sufficient for the breakdown of coexistence. One important thing to bear in mind though is that a system that is either stable or unstable must necessarily possess some degree of robustness in the mathematical sense – after all, we can always imagine a perturbation so small that stability is uninfluenced (in our Lotka–Volterra example, the system still remains stable if the change in the competition coefficient is less than 0.01). Needless to say, the system could in principle be so close to the boundary of stability and instability that, from a biological perspective, the system is as good as completely unrobust. The point is that positivity, stability, and robustness of an equilibrium all have to be checked independently to solve the coexistence problem.

This article develops a general robustness analysis of discrete-time limit cycles of fixed period length. We deal with robustness exclusively: existence, stability, and positivity of the cycle are therefore all assumed. First, in section 2, we discuss some preliminaries on the robustness of fixed points, its connection to deeper concepts in ecology such as the ecological niche, and the extension of these results to continuous-time limit cycles (Barabás et al. 2012a). Next, we derive the robustness formulas for discrete-time cycles in section 3. We then go on in section 4 to present a general approximation scheme, based on the celebrated framework of Peter Chesson (1994), which allows for simplified robustness calculations. Finally, we apply our results in section 5 to a two-cycle in a model of annual plant competition with seed banks.

2 Preliminaries

2.1 Robustness of fixed points

When dealing with fixed points, the robustness formulas do not depend on whether the dynamical equations are formulated in discrete or continuous time. As the continuous-time case has often been emphasized before (Meszéna et al. 2006, Szilágyi and Meszéna 2009, 2010, Barabás et al. 2012a), here we focus on the discrete-time formulation. The general set of model equations describing the dynamics of the community can be written as

$$x_i(t+1) = x_i(t) + r_i(\mathbf{R}(x_1(t),\ldots,x_L(t)),\mathbb{E},t) \qquad (i=1,\ldots,L), \tag{1}$$

where x_i is the log-density and r_i is the log of the geometric rate of growth of species i, L is the total number of species in the system, $\mathbb{E}$ is the collection of all density-independent (external) parameters, and $\mathbf{R}$ is the vector function of all density-dependent quantities, which we will call regulating factors (Levin 1970, Case 2000, p. 146, Krebs 2001, p. 288, Meszéna et al. 2006). By definition, the regulating factors mediate all interactions within the community; artificially keeping $\mathbf{R}$ constant would lead to the independent exponential growth or decline of all the species. Regulating factors can be many and varied: they may include resources, predators, pathogens, refuge availability, or any other thing which is involved in the feedback loop between population density and growth rate.

Assuming that the dynamics possesses a fixed point with log-densities x_i^*, the

$$r_i(\mathbf{R}(x_1^*,\ldots,x_L^*),\mathbb{E}) = 0 \tag{2}$$

equilibrium conditions will hold. These are L algebraic equations for the equilibrium log-densities x_i^*. What we are interested in is how much the position of this fixed point is expected to shift after perturbing the external parameters $\mathbb{E}$. Since the equilibrium densities are functions of $\mathbb{E}$, differentiating Eq. (2) with respect to the parameters yields

$$\frac{\partial r_i}{\partial \mathbb{E}} + \sum_{j=1}^{L} \frac{\partial r_i}{\partial x_j} \frac{\mathrm{d}x_j^*}{\mathrm{d}\mathbb{E}} = 0. \tag{3}$$

Rearranging this equation yields the responses of the equilibrium densities to perturbations of $\mathbb{E}$:

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}\mathbb{E}} = -\sum_{j=1}^{L} \left(\frac{\partial r_i}{\partial x_j}\right)^{-1} \frac{\partial r_j}{\partial \mathbb{E}}, \tag{4}$$

where matrix, not element-by-element, inversion is performed. Notice that the inverted matrix is the classical community matrix, giving the competition coefficients in a Lotka–Volterra model (with some scaling involved due to the fact that we differentiate with respect to the log-densities). The fundamental observation is that, since the inverse of a matrix is proportional to the inverse of its determinant, the closer the determinant of the inverted matrix is to zero, the less robust the system will be. Therefore, a necessary condition for robust coexistence is for the matrix to have a determinant that is safely bounded away from zero, so that fluctuations in the parameters do not cause the collapse of the system.

We would also like to emphasize the generality of our approach. Recently, it has been stressed that model robustness should be checked not just against parameter perturbations, but also against changes in the functional forms of the model's ingredient functions (Gross et al. 2009, Cordoleani et al. 2011, Adamson and Morozov 2012, Barabás et al. 2012b, 2013). An example of such a structural perturbation would be changing the functional response curve of a predator from a Michaelis-Menten (Holling 1959) to an exponential (Ivlev 1961) function (which look very similar to the naked eye). We emphasize that, as long as a family of functions can be parametrized in a smooth manner (and this assumption is already there e.g. in the work of Cordoleani et al. 2011 and Adamson and Morozov 2012), there is nothing to stop one from assigning that parameter to be part of $\mathbb{E}$ and analyzing the robustness of the model with respect to it, using Eq. (4). Or, to go even further: Eq. (4) remains formally valid even if $\mathbb{E}$ contains functions and not just numbers – the only thing to modify is to replace differentiation with respect to $\mathbb{E}$ by functional differentiation. Note that this extension to infinitely many parameters comes at a price though: since the concept of a volume is not well defined in function spaces, one can no longer talk about the set of parameters supporting coexistence being "large" or "small". We therefore lose the intuitive notion of the "volume in parameter space allowing for coexistence" when $\mathbb{E}$ is a continuum of parameters.

2.2 Ecological implications

Eq. (4) can be made more useful and biologically interpretable by further expanding the partial derivative of r_i with respect to x_j via the chain rule:

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}\mathbb{E}} = -\sum_{j=1}^{L} \left(\frac{\partial r_i}{\partial \mathbf{R}} \frac{\partial \mathbf{R}}{\partial x_j} \right)^{-1} \frac{\partial r_j}{\partial \mathbb{E}}, \tag{5}$$

where it is understood that all discrete (continuous) indices of the vector $\mathbf{R}$ are summed (integrated) over. The derivative $\partial r_i / \partial \mathbf{R}$ is the response of the ith growth rate to a change in the regulating factors. It is also referred to as the sensitivity niche vector of species i. Similarly, $\partial \mathbf{R} / \partial x_j$, the change in regulation due to an increase in the abundance of the jth species, is called the impact niche vector of species j (Meszéna et al. 2006). Our notation will be $\mathbf{S}_i$ and $\mathbf{I}_j$ for these two quantities, respectively. Since the indices of $\mathbf{R}$ are summed/integrated over, the inverted matrix can be thought of as the overlap of $\mathbf{S}_i$ and $\mathbf{I}_j$.

Let us assume for the moment that the number of regulating factors is actually equal to the number of species in the system, L. In that case, indexing the regulating factors with the symbol m, we have $\mathbf{S}_i = S_{im}$ and $\mathbf{I}_j = I_{mj}$, which are now both square matrices, and

$$\frac{\partial r_i}{\partial x_j} = \sum_{m=1}^{L} S_{im} I_{mj}. \tag{6}$$

Since for any two square matrices the determinant of the product is the product of the determinants, we have

$$\det\left(\frac{\partial r_i}{\partial x_j}\right) = \det(S_{ij})\det(I_{ij}). \tag{7}$$

The well-known geometrical interpretation of the determinant is that its absolute value measures the L-dimensional volume spanned by its rows as vectors (or by the columns – it does not matter). Denoting the volume spanned by the sensitivity vector of each species as $\mathscr{V}_{\mathbf{S}}$ and the volume spanned by the impacts as $\mathscr{V}_{\mathbf{I}}$, we therefore get

$$\left|\det\left(\frac{\partial r_i}{\partial x_j}\right)\right| = \mathscr{V}_{\mathbf{S}}\mathscr{V}_{\mathbf{I}}. \tag{8}$$

A small but important result, found in Meszéna et al. (2006), is the extension of this formula to cases where the number of regulating factors is not equal to the number of species, turning the equation into an inequality, or upper bound:

$$\left|\det\left(\frac{\partial r_i}{\partial x_j}\right)\right| \leq \mathscr{V}_{\mathbf{S}}\mathscr{V}_{\mathbf{I}} \tag{9}$$

(to see this result, consider the two facts that 1) if the number of regulating factors is larger than L, then only the projection onto a lower-dimensional subspace matters, which will have a smaller volume than the original; and 2) if the number of regulating factors is less than L, then there must be some linear dependence between the sensitivities and the impacts, and therefore both the determinant and the two volumes will be zero).

As discussed before, a small determinant signals that the system is close to being structurally unstable. The above result shows that small volumes spanned by the sensitivity and the impact vectors will lead to an even smaller determinant and thus the loss of robustness in the system. Small volumes result when the vectors are either of short length, or are nearly collinear. The first happens when regulation is weak; the second when two or more species are regulated in an overly similar manner. Avoiding such overly similar regulation is therefore a necessary condition for robust coexistence.

This observation connects back to classical ideas of functional niche segregation (Elton 1927, Christiansen and Fenchel 1977, Hutchinson 1978, Chesson 2000, Meszéna et al. 2006). To take an example, if there are two distinct noninteracting resources and two consumers competing for them, then robust coexistence is impossible if, let us say, both consumers eat one of the resources but not the other. Indeed, in this case the second component of the sensitivity vector of both species (the one corresponding to the uneaten resource) is zero, since the growth rates do not depend on that resource at all. This forces the two sensitivity vectors to be parallel. The area (or two-dimensional volume) spanned by two collinear vectors is zero, therefore robustness is lost: only the species with the lower R^* for the consumed resource will persist (Tilman 1982). On the other hand, by consuming both resources and in different proportions from the other consumer, robustness can be ensured and competitive exclusion avoided.

The classical niche concept thus finds a natural implementation via the modern theory of community robustness. The Hutchinsonian "niche space" is then identified with the set of all regulating factors because, as we have seen, these are the variables species have to be different in to coexist robustly. This is true regardless of whether this space is discrete (e.g., two noninteracting resources) or continuous (as in the case of a resource gradient). Classically, the niche of a species within niche space was assumed to be given by a resource utilization function (MacArthur and Levins 1967, Hutchinson 1978). The overlap of these functions measured the strength of competition (the derivative $\partial r_i/\partial x_j$) between two species. Unfortunately, being a phenomenological construct, the resource utilization function lacks a mechanistic underpinning which would allow it to be generalized beyond the confines of the simplest competition models. However, looking at Eq. (5), we see that the strength of competition, $\partial r_i/\partial x_j$, is always necessarily given by the overlap of $\mathbf{S}_i$ and $\mathbf{I}_j$. Therefore, the resource utilization function needs to be replaced by *two* functions: the sensitivity and the impact. Together, they fully characterize the niche of any species within niche space, and they also inherit the fundamental property ascribed to resource utilization functions: too much similarity (i.e., overlap) of the sensitivities and/or the impacts makes coexistence unlikely by rendering it unrobust. And this is not an intuitive, phenomenological statement, but a powerful, general conclusion that will hold regardless of any model details.

2.3 Robustness of continuous-time limit cycles

The above results for the robustness of fixed points have been extended to continuous-time limit cycles by Barabás et al. (2012a). The formulas are not really important for us per se, but we summarize the main conclusions. In brief, it turns out that all results from the fixed point case, in particular Eq. (9), carry over, provided that we treat each regulating factor at each moment in time as a *separate* regulating factor. Putting it another way, time becomes another quantity indexing the vector of regulating factors. Robust coexistence may therefore be achieved, not just through resource partitioning or species-specific natural enemies, but by the proper timing of resource use or predator-avoidance. Moreover, the mathematical structure of time-partitioning is equivalent to that of resource-partitioning. In this way, the extension of robustness analysis to continuous-time limit cycles formalizes the concept of temporal niche segregation (Christiansen and Fenchel 1977, Levins 1979, Chesson 1994, 2000, Szilágyi and Meszéna 2010).

3 Robustness of discrete-time limit cycles

Unfortunately, the continuous-time results on limit cycles do not immediately generalize to discrete-time ones. Mathematically, this is because the derivation of the former rely on the smoothness of the flow generated by continuous-time differential equations (see Barabás et al. 2012a, Appendix 1 for the technical details). As discrete-time systems may jump around in phase space, the derivation has to be done from scratch. Of course, from a biological perspective, one does not expect there to be any essential difference between the two cases, so the extension to discrete time looks to be a mere formality. Still, to be able to actually calculate the robustness of cycles in discrete-time models, one cannot simply apply the continuous-time formulas; hence the derivation in this section.

Let us start with Eq. (1) as our community model and assume it induces a T-cycle with initial conditions $x_i^* = x_i(0)$. We convert this periodic dynamics into an equivalent fixed point dynamics by recording the state of the system stroboscopically at every time T. The cumulative growth rates $\bar{r}_i$ over one cycle read

$$\bar{r}_i = \sum_{\tau=0}^{T-1} r_i(\tau) = 0, \tag{10}$$

where $r_i(\tau) = r_i(\mathbf{R}(x_1(\tau), \ldots, x_L(\tau)), \mathbb{E}, \tau)$. This induces the fixed-point dynamics

$$x_i(t+T) = x_i(t) + \bar{r}_i, \tag{11}$$

whose fixed point is the set of initial conditions x_i^*. Implicit differentiation of the $\bar{r}_i = 0$ condition with respect to $\mathbb{E}$ leads to

$$\frac{\partial \bar{r}_i}{\partial \mathbb{E}} + \sum_{j=1}^{L} \frac{\partial \bar{r}_i}{\partial x_j^*} \frac{\mathrm{d}x_j^*}{\mathrm{d}\mathbb{E}} = 0, \tag{12}$$

and rearranging the result yields the analogue of Eq. (4):

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}\mathbb{E}} = -\sum_{j=1}^{L} \left(\frac{\partial \bar{r}_i}{\partial x_j^*} \right)^{-1} \frac{\partial \bar{r}_j}{\partial \mathbb{E}}. \tag{13}$$

To make this formula useful, $\partial \bar{r}_i / \partial x_j^*$ has to be evaluated. We introduce some simplifying notation:

$$\Phi_{ij}(\tau) = \frac{\partial x_i(\tau)}{\partial x_j^*}, \tag{14}$$

and

$$a_{ij}(\tau) = \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)}. \tag{15}$$

In $a_{ij}(\tau)$, summation/integration for all discrete/continuous indices of the vector $\mathbf{R}(\tau)$ is understood, as before. Note how the two factors of $a_{ij}(\tau)$ are like the sensitivity ($\partial r_i / \partial \mathbf{R}$) and impact ($\partial \mathbf{R} / \partial x_j$) vectors, evaluated at a given moment τ. To keep the nomenclature straight, we will call the niche vectors $\mathbf{S}_i(\tau)$, $\mathbf{I}_j(\tau)$ at any given moment the *momentary* niche vectors, and the collection of all momentary vectors $\mathbf{S}_i(\cdot)$, $\mathbf{I}_j(\cdot)$ the *temporal* niche vectors. Note that this effectively endows the vector of regulating factors by an extra index, τ, on top of the original ones.

We now evaluate the matrix $\partial \bar{r}_i / \partial x_j^*$ (the matrix whose inverse governs robustness):

$$\frac{\partial \bar{r}_i}{\partial x_j^*} = \frac{\partial}{\partial x_j^*} \sum_{\tau=0}^{T-1} r_i(\tau) = \sum_{\tau=0}^{T-1} \sum_{k=1}^{L} \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_k(\tau)} \frac{\partial x_k(\tau)}{\partial x_j^*} = \sum_{\tau=0}^{T-1} \sum_{k=1}^{L} a_{ik}(\tau) \Phi_{kj}(\tau). \tag{16}$$

Using this, $\Phi_{ij}(\tau)$ can be written as

$$\Phi_{ij}(\tau) = \frac{\partial x_i(\tau)}{\partial x_j^*} = \frac{\partial}{\partial x_j^*} \left(x_i^* + \sum_{t=0}^{\tau-1} r_i(t) \right) = \delta_{ij} + \sum_{t=0}^{\tau-1} \sum_{k=1}^{L} a_{ik}(t) \Phi_{kj}(t), \tag{17}$$

where δ_{ij} is the Kronecker symbol, equal to 1 if $i = j$ and to 0 otherwise. From this relationship,

$$\Phi_{ij}(\tau+1) - \Phi_{ij}(\tau) = \sum_{k=1}^{L} a_{ik}(\tau) \Phi_{kj}(\tau) \tag{18}$$

immediately follows. Now Eq. (16) can be simplified:

$$\frac{\partial \bar{r}_i}{\partial x_j^*} = \sum_{\tau=0}^{T-1} \sum_{k=1}^{L} a_{ik}(\tau) \Phi_{kj}(\tau) = \sum_{\tau=0}^{T-1} \Big(\Phi_{ij}(\tau+1) - \Phi_{ij}(\tau) \Big) = \Phi_{ij}(T) - \Phi_{ij}(0). \tag{19}$$

Note that $\Phi_{ij}(0) = \delta_{ij}$ from Eq. (14). To make use of this expression, we need to solve for $\Phi_{ij}(T)$ explicitly. Switching to matrix notation for better readability, Eq. (17) with $\tau \to T$ reads

$$\Phi(T) = 1 + \sum_{\tau=0}^{T-1} a(\tau) \Phi(\tau), \tag{20}$$

with $\Phi(0) = 1$. The solution to this recursion equation is conjectured to be

$$\Phi(T) = \prod_{\tau=T-1}^{0} \Big(1 + a(\tau) \Big) \tag{21}$$

for all $T \geq 1$. Since $\Phi(0) = 1$, for $T = 1$ Eq. (20) gives $\Phi(1) = 1 + a(0)\Phi(0) = 1 + a(0)$, which is the same as the result from Eq. (21). Therefore, the conjecture holds for $T = 1$. We now show it holds for $T + 1$ if it holds for T. Substituting the conjectured solution into Eq. (20), we get

$$\prod_{\tau=T-1}^{0} \Big(1 + a(\tau) \Big) = 1 + \sum_{\tau=0}^{T-1} a(\tau) \prod_{\tau'=\tau-1}^{0} \Big(1 + a(\tau') \Big). \tag{22}$$

Let us call the terms on either side of the equality sign in Eq. (22) D. For $T + 1$ we have

$$\prod_{\tau=T}^{0} \Big(1 + a(\tau) \Big) = 1 + \sum_{\tau=0}^{T} a(\tau) \prod_{\tau'=\tau-1}^{0} \Big(1 + a(\tau') \Big). \tag{23}$$

Factoring out the $\tau = T$ terms, we get

$$\big(1+a(T)\big) \underbrace{\prod_{\tau=T-1}^{0} \Big(1+a(\tau)\Big)}_{D} = a(T) \underbrace{\prod_{\tau=T-1}^{0} \Big(1+a(\tau)\Big)}_{D} + \underbrace{1+\sum_{\tau=0}^{T-1} a(\tau) \prod_{\tau'=\tau-1}^{0} \Big(1+a(\tau')\Big)}_{D}, \tag{24}$$

or

$$\big(1+a(T)\big)D = a(T)D + D, \tag{25}$$

the two sides clearly being equal. This proves by induction that Eq. (21) is indeed the solution giving $\Phi(T)$ for all $T \geq 1$. Now Eq. (19) can be written as

$$\frac{\partial \bar{r}_i}{\partial x_j^*} = \prod_{\tau=T-1}^{0} \Big(\delta_{ij} + a_{ij}(\tau)\Big) - \delta_{ij}. \tag{26}$$

This expression is the discrete-time analogue of Eq. (18) in Barabás et al. (2012a); notice that in the limiting case of infinitely many infinitesimal time steps, this formula becomes identical to the continuous-time one. The full formula for the robustness of the periodic orbit is then obtained by substituting this expression into Eq. (13):

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}\mathbb{E}} = -\sum_{j=1}^{L} \left(\prod_{\tau=T-1}^{0} \Big(\delta_{ij} + \mathbf{S}_i(\tau)\mathbf{I}_j(\tau)\Big) - \delta_{ij} \right)^{-1} \sum_{t=0}^{T-1} \frac{\partial r_j(t)}{\partial \mathbb{E}} \tag{27}$$

(where, again, the inverse refers to inverting the matrix as a whole, not element-by-element inversion).

We now show that linear dependence of the temporal sensitivity vectors $\mathbf{S}_i(\cdot)$ or the temporal impact vectors $\mathbf{I}_j(\cdot)$ leads to the inverted matrix having an eigenvalue of zero. Let us consider linear dependence in the impact vectors first. Linear dependence means there exists a τ-independent vector $\alpha = (\alpha_1, \ldots, \alpha_L)$ such that $\sum_{j=1}^{L} \alpha_j \mathbf{I}_j(\tau) = 0$ for each $\tau = 0, \ldots, T-1$. Then α is a right eigenvector of $a_{ij}(\tau) = \mathbf{S}_i(\tau)\mathbf{I}_j(\tau)$ for each τ, with eigenvalue 0. If it is the sensitivities that are linearly dependent, then the same argument leads to α being a left eigenvector of each $a_{ij}(\tau)$ with eigenvalue 0.

If $a_{ij}(\tau)$ has an eigenvalue of zero for each τ corresponding to the same eigenvector α, $(\delta_{ij} + a_{ij}(\tau))$ will have an eigenvalue of 1 for each τ, and the product of these matrices will also have an eigenvalue of 1 (because the matrices share the eigendirection α). Then, subtracting off the identity matrix from this product as in Eq. (26), the expression as a whole has an eigenvalue of zero. Then, as seen from Eq. (27), the equilibrium densities become infinitely sensitive to perturbations in $\mathbb{E}$: the system is structurally unstable. Also, since eigenvalues are continuous functions of matrix elements, near-linear dependence of sensitivities or impacts will result in $\partial \bar{r}_i / \partial x_j^*$ having an eigenvalue that is nearly zero, which means the system is nearly structurally unstable, i.e., it lacks sufficient robustness.

Linear dependence of the sensitivities and impacts of course means that the volume they span is zero. Similarly, near-linear dependence means the volume they span is small. Thus, we come around full circle: robustness is still measured by the volumes spanned by the niche vectors – the *temporal* niche vectors, that is. Robustness increases with the species having more different sensitivity and/or impact vectors at corresponding points within the T-cycle, i.e., by having species-specific responses to the environment. Just as in the continuous-time case, this can be viewed as segregation with respect to time as a resource axis (now with only finitely many elements), or temporal niche segregation for short (Christiansen and Fenchel 1977, Levins 1979, Chesson 1994, 2000, Barabás et al. 2012a). The basic conclusions of the earlier framework therefore still hold: robustness of a periodically fluctuating community is like that of an equilibrium community, provided that we list all regulating factors at different points in the cycle as separate factors.

4 A method for the analytical estimation of the sensitivity vectors

In general, the temporal sensitivities $\mathbf{S}_i(\cdot)$ and impacts $\mathbf{I}_j(\cdot)$ will depend both on model parameters and on population densities at various moments within the cycle. Moreover, especially in the case of the sensitivities, this dependence may be more intricate and difficult to interpret than in continuous-time models. The reason is that to handle the discrete-time case, we had to employ a log-transformation of the geometric growth rates. Therefore, when taking the derivatives of these log-growth rates to obtain the sensitivities, the result is multiplied by the reciprocal of the original geometric rates. This artifact has no analogue in continuous time.

The difficulty here is that, in order to evaluate these quantities, the densities at various points in the cycle will need to be known. These might be possible to estimate from e.g. field data, but when analyzing theoretical models, we usually would like to say something general about the behavior of the model without actually having to solve it first.

One possible way of doing this is to connect our robustness analysis with the general framework of Chesson (1994) for multispecies competition in variable environments. In that framework we start out from Eq. (1) and take the growth rates r_i to be functions of density-independent (environmental) parameters E_i and density-dependent (competitive) factors C_i, so $r_i = r_i(E_i, C_i)$. We define "equilibrium" values for the environmental and competitive parameters, E_i^* and C_i^*, such that $r_i(E_i^*, C_i^*) = 0$. They are usually not unique, but fixing one will fix the other (also, there are often natural, biologically motivated choices for their values). Next, the r_i are approximated. Since the growth rates are allowed to fluctuate (if E_i and C_i depend on time), a linear approximation will not suffice. Instead, Chesson tells us to perform a quadratic expansion:

$$r_i \approx \alpha_i(E_i - E_i^*) - \beta_i(C_i - C_i^*) + \zeta_i(E_i - E_i^*)(C_i - C_i^*), \tag{28}$$

where $\alpha_i = \partial r_i / \partial E_i$, $\beta_i = -\partial r_i / \partial C_i$, $\zeta_i = \partial^2 r_i / (\partial E_i \partial C_i)$, all evaluated at $E_i = E_i^*$, $C_i = C_i^*$. The $(E_i - E_i^*)^2$ and $(C_i - C_i^*)^2$ terms are not included, because it turns out that, after averaging the growth rates over time, these terms are both small with the assumptions of Chesson (1994) and so can be neglected. To bring this approximation to an even simpler form, Chesson defines $\mathscr{E}_i = \alpha_i(E_i - E_i^*)$, $\mathscr{C}_i = \beta_i(C_i - C_i^*)$, and $\gamma_i = -\zeta_i / (\alpha_i \beta_i)$ to get

$$r_i(t) \approx \mathscr{E}_i(t) - \mathscr{C}_i(t) + \gamma_i \mathscr{E}_i(t) \mathscr{C}_i(t). \tag{29}$$

This model is generally much simpler than the original one while still retaining much of its interesting nonlinearity.

Now consider an arbitrary model with a periodic T-cycle solution and write it in the above form. The total growth over one cycle is

$$\sum_{t=0}^{T-1} r_i(t) \approx \sum_{t=0}^{T-1} \mathscr{E}_i(t) - \sum_{t=0}^{T-1} \mathscr{C}_i(t) + \gamma_i \sum_{t=0}^{T-1} \mathscr{E}_i(t)\mathscr{C}_i(t) = 0. \tag{30}$$

By definition, the competitive factors $\mathscr{C}_i(t)$ are affected by the population densities, while the environmental parameters $\mathscr{E}_i(t)$ are not. Therefore, nothing prevents us from choosing the $\mathscr{C}_i(t)$s as the (time-dependent) regulating variables. Then the sensitivities can be calculated using this approximation:

$$\mathbf{S}_i(t) = S_{ik}(t) = \frac{\partial r_i(t)}{\partial \mathscr{C}_k(t)} = \delta_{ik}\left(\gamma_i \mathscr{E}_i(t) - 1\right), \tag{31}$$

while the impacts will depend on the particular form of the $\mathscr{C}_i(t)$ and their dependence on the log-densities:

$$\mathbf{I}_j(t) = I_{kj}(t) = \frac{\partial \mathscr{C}_k(t)}{\partial x_j(t)}. \tag{32}$$

Alternatively, there is no reason one could not choose the $C_i(t)$ instead of the $\mathscr{C}_i(t)$ as the regulating factors. Then, since by definition $\mathscr{C}_i(t) = \beta_i(C_i(t) - C_i^*)$, it follows that $\mathrm{d}\mathscr{C}_i(t) = \beta_i \mathrm{d}C_i(t)$, and so the sensitivities will read

$$\mathbf{S}_i(t) = S_{ik}(t) = \frac{\partial r_i(t)}{\partial C_k(t)} = \delta_{ik}\beta_k\left(\gamma_i \mathscr{E}_i(t) - 1\right). \tag{33}$$

The impacts will then correspondingly obtain a factor of β_k^{-1}, as they should.

This derivation did not depend on whether we have a continuous or discrete time model. In continuous time, the sums are replaced by integrals in Eq. (30) and the partial derivative by a functional derivative in the sensitivities, but the final forms of the sensitivities and impacts will be unchanged.

How does this help? Notice that the sensitivities derived from the approximated model have a very important feature: they do not depend on the $\mathscr{C}_i(t)$ and so are composed entirely of density-independent parameters. One can therefore evaluate them without having to solve the model. This makes them much more amenable to analytical treatment than the original, unapproximated sensitivities.

Of course, the robustness of the system is not determined by the sensitivities alone – the impacts are also needed. Unfortunately, there does not seem to exist an analogous scheme for approximating the impacts in a density-independent way. However, having a simpler formula just for the sensitivities is already a good crutch. First, regardless of the impacts, if the volume spanned by the temporal sensitivity vectors shrinks to zero, then robustness is lost – this can be used to estimate where in parameter space a critical transition, such as an extinction event, is expected to happen. Second, it will usually be possible to give an upper bound for the impacts, and using this upper bound alongside the approximate sensitivities, the robustness of the system may be estimated even at points where the sensitivity volume is nonzero. Third, the approximated sensitivities may inform us about trends in the response of robustness to varying the parameters: by changing a given parameter in a given direction, we can see whether robustness is expected to increase or decrease.

In summary, the merging of our temporal robustness analysis with the framework of Peter Chesson (1994) offers a potentially useful approximation which allows for the analytical treatment of temporal robustness calculations.

5 Application: the seedbank model

Let us apply our framework to the two-species seedbank model (Ellner 1984, Chesson 1990, 1994, Levine and Rees 2004). In this model the two species compete for a common limiting resource (which we can assume to be space) in a variable environment, which in our model will alternate between "good" and "bad" years. The governing equations read

$$N_i(t+1) = N_i(t)\left(s_i(1-E_i(t)) + \frac{Y_i E_i(t)}{E_1(t)N_1(t)+E_2(t)N_2(t)}\right), \tag{34}$$

where $N_i(t)$ is the density of seeds of species i in the soil seed bank at time t, $E_i(t)$ is the fraction of seeds of species i germinating between time t and $t+1$, s_i is the rate of survival of those seeds that do not germinate, and Y_i is the maximum number of germinating seeds when the species experience one "unit" of competition (to see this, we set both the E_i and the denominator in the above expression to one).

One possible choice for the regulating factors is the single variable $E_1(t)N_1(t)+E_2(t)N_2(t)$, though for reasons to become apparent soon, we take instead the logarithm of this quantity to be our regulating factor: $R(t) = \log\left(E_1(t)N_1(t)+E_2(t)N_2(t)\right)$. The growth rates of the model then read

$$r_i(t) = \log\left(s_i(1-E_i(t)) + \frac{Y_i E_i(t)}{\exp(R(t))}\right). \tag{35}$$

This choice for $R(t)$ immediately reveals an important property of the system: if the environment is constant and the densities settle down to a fixed point equilibrium, coexistence is impossible. This is because in that case there is a single regulating factor $R = \log\left(E_1N_1+E_2N_2\right)$ for both species, and so the sensitivities and the impacts are confined to a one-dimensional space. Since two vectors on the same line necessarily span an area (i.e., 2D volume) of zero, by Eq. (9) the robustness of the system is lost. The conclusion is that fluctuations are strictly necessary for the two species to coexist, a known result for this model (Chesson 1994).

We shall assume that the $E_i(t)$ oscillate between "good" and "bad" years and rely on these fluctuations to generate coexistence that would otherwise be impossible in a constant world. What counts as a good year for species 1 will be considered a bad year for species 2, and vice versa. Let

$P(t)$ be a parity function, equal to -1 if t is odd and to 1 if t is even. Then our choices for the $E_i(t)$ are

$$E_1(t) = \varepsilon_{10}\left(1 - \varepsilon_{1a} P(t)\right) \tag{36}$$

and

$$E_2(t) = \varepsilon_{20}\left(1 + \varepsilon_{2a} P(t)\right), \tag{37}$$

where ε_{i0} and ε_{ia} are the mean and the amplitude of the oscillations (their values have to be chosen so that $E_i(t)$ is confined between 0 and 1 for all t). These functions – predictably – induce a stationary two-cycle in the system.

To obtain the robustness of the stationary cycle against parameter perturbations, we first choose numerical values for all eight model parameters (Table 1). Next, we obtain the stationary two-cycle of the system by iterating the model twice and solving for the densities. The resulting algebraic equations yield $N_1(0) = 0.56$, $N_2(0) = 0.9$ for the initial, and $N_1(1) = 0.41$, $N_2(1) = 0.95$ for the final point in the two-cycle. Finally, we calculate the linear responses of these equilibrium densities to perturbations of each model parameter using Eq. (27); the results are shown in Table 1.

Parameter ($\mathbb{E}$)	Value of $\mathbb{E}$	$\frac{\mathrm{d}N_1(0)}{\mathrm{d}\mathbb{E}}$	$\frac{\mathrm{d}N_2(0)}{\mathrm{d}\mathbb{E}}$	$\frac{\mathrm{d}N_1(1)}{\mathrm{d}\mathbb{E}}$	$\frac{\mathrm{d}N_2(1)}{\mathrm{d}\mathbb{E}}$
ε_{10}	0.5	4.13	−5.31	3.93	−3.72
ε_{20}	0.5	−4.94	4.97	−4.35	2.97
ε_{1a}	0.2	−1.33	1.55	−1.42	1.51
ε_{2a}	0.2	4.26	−4.43	3.27	−3.15
s_1	0.5	2.50	−2.73	2.51	−1.74
s_2	0.6	−1.89	3.12	−1.80	1.97
Y_1	1	3.47	−3.46	3.09	−2.29
Y_2	1	−2.90	4.36	−2.68	3.24

Table 1: The parameters of the two-species seedbank model (column 1), their numerical values (column 2), and the sensitivities of the species' densities to each parameter at both points within the two-cycle, calculated from Eq. (27) (last four columns). Since $N_i = \log(x_i)$, we have converted back to the linear scale by using $\mathrm{d}x_i/\mathrm{d}\mathbb{E} = (1/N_i)(\mathrm{d}N_i/\mathrm{d}\mathbb{E})$. The sensitivity values are to be thought of as multipliers: if the parameter gets perturbed away from its original value by a small $\Delta\mathbb{E}$, the population density of species i at time t within the cycle will be modified by $\Delta N_i(t) = (\mathrm{d}N_i(t)/\mathrm{d}\mathbb{E})\Delta\mathbb{E}$.

From these values it is possible to estimate the amount of parameter change that would cause the extinction of at least one of the species. Of course, this is based on our local approximation; when extrapolating the effects for non-infinitesimal parameter perturbations, this might not give very accurate results. To explore the accuracy of our predictions, we compared them to explicit simulation results, where we numerically solved the model for a wide range of parameter values, recording those where one of the species went extinct (the extinction threshold was $N_{\mathrm{ex}} = \mathrm{e}^{-10}$). A graphical depiction of the parameter ranges that support coexistence can be seen on Figure 1. On this plot, we shaded the domain for each parameter in which both populations oscillate with all-positive densities. The gray shading represents the "true" coexistence range, obtained via simulations, while the white shading is the estimated coexistence range based on Eq. (27). Outside the gray-shaded regions, at least one species will have gone extinct. Note that we vary one parameter at a time, not multiple ones simultaneously.

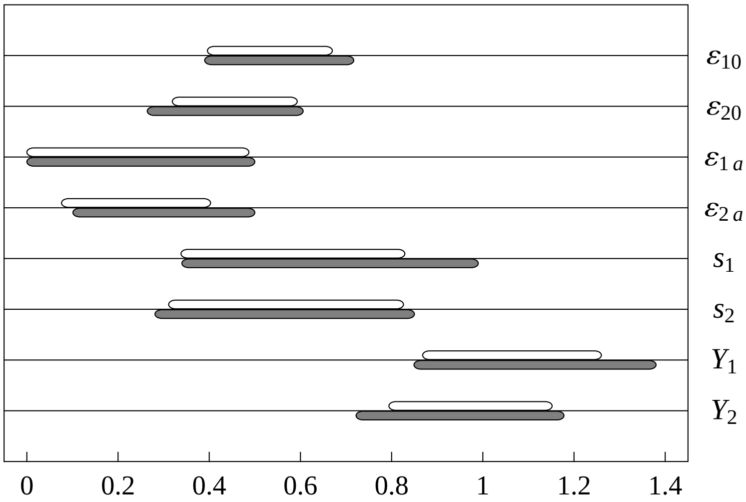

Figure 1: The range of each parameter allowing for the coexistence of the two competitors in the seedbank model. Since the parameters all have comparable magnitudes, they have been put on the same scale. The gray bars represent the "true" ranges, obtained via simulation, while the white bars are obtained by applying Eq. (27) and extrapolating the effects of this linear approximation to see where extinction is predicted to happen. Note the strong correspondence between the simulated and calculated results.

Based on the correspondence between the gray and white regions, the approximation of Eq. (27) clearly does a very good job of predicting where coexistence can happen. It does, however, seem to yield conservative estimates, slightly underestimating the endpoints of the coexistence-yielding parameter range in all cases except for the lower bound on ε_{2a}. As the local approximation measures the slope of the cycle's position in phase space as a function of the parameters, the implication is that this function must have been concave-down for every parameter except ε_{2a}. One possible way to explore the curvature of this function would be to consider the second-order perturbations – i.e., the derivative $\mathrm{d}^2 x_i^* / \mathrm{d}\mathbb{E}^2$. The sign of this second derivative will inform us about the local convexity of the function, and so will give information about whether and how much the linear approximation is expected to under- or overestimate the true parameter range where coexistence can happen. Developing the quadratic perturbation formula is, however, beyond the scope of this article; for now, we will have to be content with the (already good) approximation our linear formula provides.

One may easily calculate the sensitivity and impact vectors for this model. The sensitivities read

$$S_i(t) = \frac{\partial r_i(t)}{\partial R(t)} = \frac{Y_i}{s_i\left(E_1(t)N_1(t) + E_2(t)N_2(t)\right)\left(1 - 1/E_i(t)\right) - Y_i}, \tag{38}$$

and the impacts are, remembering that $x_i = \log(N_i)$,

$$I_j(t) = \frac{\partial R(t)}{\partial x_j(t)} = \frac{\partial R(t)}{\partial N_j(t)} N_j(t) = \frac{E_j(t)N_j(t)}{E_1(t)N_1(t) + E_2(t)N_2(t)}. \tag{39}$$

Notice that the impact vectors are bounded from above: the magnitude of each component cannot exceed one. Therefore, the volume these vectors can span also has an upper bound. That is why we chose to put the regulating factor on the log scale: without this, the form of the impacts would have been simpler, but they would not have been bounded. This means that whenever the volume spanned by the sensitivities is small, the system is guaranteed to be unrobust: it is impossible for the impact volume to offset the effect of a small sensitivity volume, as it cannot grow larger than some specific value (in this case, one).

One final thing to do is to see how well the approximation scheme of the previous section for the sensitivity vectors works in practice. First we calculate the analytical approximation to the sensitivities. We choose $C(t) = R(t)$ for the competitive factor. A natural choice for C^* is $C^* = 0$; substituting this into Eq. (35) with $R(t) \to C^*$ and requiring the growth rates to be zero yields $E_i^* = (1 - s_i)/(Y_i - s_i)$. We use the definitions for α_i, β_i, γ_i, and $\mathscr{E}_i(t)$ given in the previous section to obtain

$$\alpha_i = \left.\frac{\partial r_i(t)}{\partial E_i(t)}\right|_{E_i^*, C^*} = Y_i - s_i, \tag{40}$$

$$\beta_i = -\left.\frac{\partial r_i(t)}{\partial C(t)}\right|_{E_i^*, C^*} = Y_i \frac{1 - s_i}{Y_i - s_i}, \tag{41}$$

$$\gamma_i = -\frac{1}{\alpha_i \beta_i} \left.\frac{\partial^2 r_i(t)}{\partial E_i(t) \partial C(t)}\right|_{E_i^*, C^*} = \frac{s_i}{1 - s_i}, \tag{42}$$

$$\mathscr{E}_i(t) = \alpha_i \left(E_i(t) - E_i^*\right) = (Y_i - s_i)\left(E_i(t) - \frac{1 - s_i}{Y_i - s_i}\right). \tag{43}$$

The approximated sensitivity vectors then read, from Eq. (33), as

$$S_i(t) = \beta_i \left(\gamma_i \mathscr{E}_i(t) - 1\right) = s_i Y_i E_i(t) - Y_i \frac{1 - s_i^2}{Y_i - s_i}. \tag{44}$$

Figure 2 compares the volumes spanned by the true and the approximated sensitivity vectors as functions of the parameters. To obtain the true sensitivities given by Eq. (38), the model has to be simulated numerically for the stationary densities (the main advantage of the approximation is precisely that it obviates the need for this step). The volumes are calculated as the absolute value of the determinant of the 2×2 matrix obtained by stacking the sensitivity vectors of the two species on top of one another in two rows. On each plot, the abscissa represents about one third of the total range of one of the parameters, while the ordinate measures the volume spanned by the sensitivity vectors. The solid lines are the volumes spanned by the true sensitivity vectors, the dashed lines are the volumes spanned by the approximated ones from Eq. (44). We see that the approximation is fair for a reasonably wide range of all the parameters.

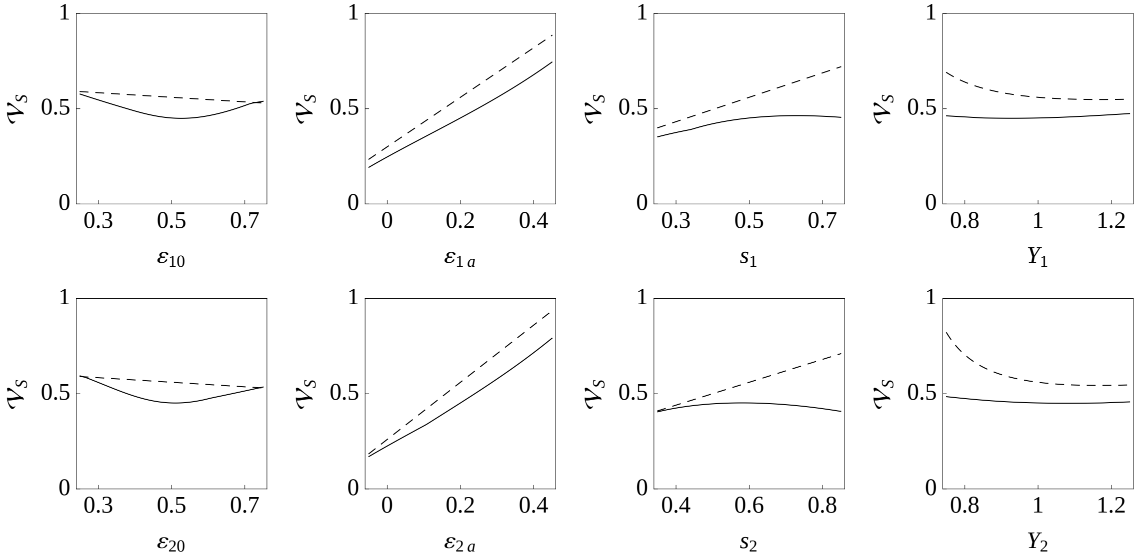

Figure 2: Volumes spanned by the temporal sensitivity vectors of the two species as a function of the parameters. The volumes are calculated as the absolute value of the determinant of the 2×2 matrix obtained by stacking the sensitivity vectors of the two species on top of one another in two rows. On each plot a different parameter is varied in a ± 0.25 range of its original value (Table 1, column 1). The solid lines are the actual sensitivity volumes obtained via simulation; the dashed lines are the approximated sensitivities from Eq. (44).

6 Discussion

In this article we have developed the machinery to evaluate the robustness of discrete-time limit cycles to parameter perturbations. The result, in line with earlier findings (Barabás et al. 2012a), is that every regulating factor at each point in time within the cycle is effectively a separate regulating factor, independent utilization of which will enhance the robustness of the system. Each species' sensitivity and impact vectors have to be considered at every point in time within the T-cycle; small volumes spanned by these vectors will lead to unrobust coexistence that cannot be expected to hold over an appreciable range of parameter space. These volumes will always be small if the vectors are nearly collinear – therefore, sufficient segregation of the niche vectors is a necessary condition for coexistence. We also developed, based on the formalism of Chesson (1994), an approximation scheme that allows for the analytical treatment of the sensitivity vectors. Finally, we demonstrated how our machinery works by applying it to the two-species seedbank model.

Just how much segregation of the niche vectors (sensitivities and impacts) is "sufficient" for robust coexistence will depend on the specific model and the probability distribution of the environmental parameters. In principle, coexistence can be ensured even with a very narrow coexistence bandwidth if one is able to restrict the parameters to that region, for instance in controlled laboratory experiments. The actual model a community obeys, as well as the statistical properties of the environment, are empirical properties that need to be assessed before determining how much niche segregation is needed to confer sufficient robustness to the system. These system-specific questions notwithstanding, no community will be able to sustain itself with zero robustness, therefore in nature some level of segregation in both the sensitivities and the impacts is strictly necessary for coexistence. A lack of such segregation is of course possible, but then the co-occurrence (Leibold and McPeek 2006) of the species will not be stable – instead, it might be sustained by source-sink dynamics, or one of the species might be on its way to extinction. Robustness analysis does not say anything about the speed with which exclusion happens; in principle, such processes could take a long time.

Species' relationships to the regulating factors dictate community robustness, but there is no unambiguous way of picking the regulating variables. For instance, in our seedbank model, we could have chosen the two population densities as regulating factors (this would have made the impact vectors trivial: $I_{mj} = \delta_{mj}$), or the two growth rates themselves (which makes the sensitivities trivial: $S_{im} = \delta_{im}$). Needless to say, we could have chosen any function of the weighted sum of densities as well, not just their logarithm – the number of choices is infinite. Importantly however, robustness itself is invariant to the choice of regulating factors: as is seen from Eq. (5), the matrix whose inverse determines robustness does not ultimately depend on this choice. Whatever differences there would be in the sensitivities due to choosing the regulating factors in a certain way, they will be compensated by corresponding differences in the impacts. Therefore, choosing the set of regulating factors is as much an art as a science: one should strive to make a choice that makes the niche vectors as simple and as biologically informative as possible. In the seedbank model for instance, the fact that there is a single regulating factor immediately reveals that coexistence is impossible – unless fluctuations increase this number. Since in the fluctuating framework every regulating factor at every moment in time counts as a different factor, the two-cycle increases the number of factors to two. Two-species coexistence therefore becomes possible, but not the coexistence of three or more species. Also, by making the seemingly arbitrary decision of putting the regulating factors on the log scale, it turned out that the impact volumes become bounded this way, making the volumes spanned by the sensitivities (which can be analytically approximated) more meaningful.

The present state of the theory of community robustness is rather incomplete. On the practical side, applications to real-world communities and data will be necessary to assess just how useful the theory is in practice. On the theoretical side, here is how we stand. Fixed-point robustness analysis of unstructured populations is available (Meszéna et al. 2006, summarized earlier in this article). An extension to structured populations at fixed points is found in Szilágyi and Meszéna (2009), but the types of perturbations this framework can analyze is rather restricted, so a generalization of those results will be needed. The theory for periodically fluctuating unstructured populations is covered in Barabás et al. (2012a) and in the present paper. The framework for arbitrary stationary fluctuations with unstructured populations and (the most complicated case) with structured ones is still lacking. Working these cases out is the next step in developing the robustness framework further.

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