Sensitivity Analysis of Coexistence in Ecological Communities: Theory and Application

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Abstract

Sensitivity analysis, the study of how ecological variables of interest respond to changes in external conditions, is a theoretically well-developed and widely applied approach in population ecology. Though the application of sensitivity analysis to predicting the response of species-rich communities to disturbances also has a long history, derivation of a mathematical framework for understanding the factors leading to robust coexistence has only been a recent undertaking. Here we suggest that this new development opens up a new perspective, providing advances ranging from the applied to the theoretical. First, it yields a framework to be applied in specific cases for assessing the extinction risk of community modules in the face of environmental change. Second, it can be used to determine trait combinations allowing for coexistence that is robust to environmental variation, and limits to diversity in the presence of environmental variation, for specific community types. Third, it offers general insights into the nature of communities that are robust to environmental variation. We apply recent community-level extensions of mathematical sensitivity analysis to example models for illustration. We discuss the advantages and limitations of the method, and some of the empirical questions the theoretical framework could help answer.

Keywords: coexistence; model analysis; niche theory; robustness

1 Introduction

A key approach to understanding the processes shaping communities in nature is to consider them in the context of the conditions needed for long-term species coexistence. Most often considered is when coexistence of a set of species is dynamically stable, meaning that small perturbations of the population densities are damped and the system returns to some attractor (Armstrong & McGehee 1980). Similar, useful dynamical concepts include resilience and reactivity (Neubert & Caswell 1997), which quantify the rate of return to equilibrium and the initial amplification of perturbations, respectively.

Here we focus instead on the property of *robustness* of coexistence (Abrams 2001, Meszéna *et al.* 2006). Robustness refers to the response of a system's equilibrium state to altering model parameters:

if the equilibrium state does not change much even for relatively large parameter perturbations, the system is robust, otherwise it is unrobust. Note that "equilibrium states" may include fixed points, limit cycles, or any other long-term behavior. Robustness takes a different focus than stability and related concepts mentioned above. It considers the response of variables (e.g. population densities) to changes in parameters (intrinsic death rates, predator conversion efficiencies, etc.) governing the system, rather than the response of variables to perturbations of the variables themselves with parameters fixed.

Within population ecology, the study of robustness has had a long and distinguished history, though the approach is better known as sensitivity analysis (Caswell 2001, chapter 9). Sensitivity analysis focuses on how a variable of interest (such as population growth rate or density) is expected to change in response to parameter perturbations. Sensitivity and robustness express the same information, but are inversely related: a population growth rate or density is sensitive to parameter changes if it is not robust to them, and vice versa. Sensitivity analysis in population ecology has led to deep insights both in an applied context, for population viability analyses, conservation, and management (Crouse *et al.* 1987, Hochberg *et al.* 1992, Silvertown *et al.* 1993, Noon & McKelvey 1996, Seamans *et al.* 1999, Fujiwara & Caswell 2001, Hunter *et al.* 2010), and in a theoretical context, especially in life history theory (Hamilton 1966, Charlesworth & Leon 1976, Michod 1979, Caswell 1982, 1984, Gleeson 1984, Pásztor *et al.* 1996, Caswell 2011).

The application of sensitivity analysis to communities also began early, with several different approaches emerging. First, the concept of robust coexistence and coexistence region (bandwidth) was introduced by Armstrong (1976) as the range of parameters allowing for stable coexistence (see also Vandermeer 1975). Abrams and co-workers later followed up with this perspective, using simulations to determine coexistence regions in various resource consumption (Abrams 1984) and predator-prey (Abrams *et al.* 2003) models, including competition and resource fluctuations (Abrams & Holt 2002, Abrams 2004), and mutualistic interactions (Abrams & Nakajima 2007).

In a parallel development, Levins (1974) introduced loop analysis to predict the effects of small perturbations of model parameters on the equilibrium state of large communities characterized only by the sign structure of the interactions between its members. Bender *et al.* (1984) established the use of the inverse community matrix (Levins 1968, May 1973) in calculating the sensitivity of equilibrium population sizes to press perturbations of abundances (corresponding to a constant rate of influx/outflow of individuals in time). Several studies have built on this approach (Yodzis 1988, 2000, Dambacher *et al.* 2002, Novak *et al.* 2011), finding very high sensitivities to press perturbations in large ecological systems, hampering predictability due to imperfect knowledge of parameters. Using the technique of generalized modeling (Yeakel *et al.* 2011), Aufderheide *et al.* (2013) developed a numerical method for estimating the importance of each species in a community and thus identifying parameters the community is especially sensitive to.

Recently, the influence of the presence or absence of species on communities has also been explored (community viability analysis; Ebenman & Jonsson 2005), which specifically considers the sensitivity of community composition to species removal in terms of the number of resulting secondary extinctions (Ebenman *et al.* 2004, Allesina & Pascual 2009). Finally, the study of the sensitivity of model predictions to altering the form of their ingredient functions has also been an important approach—for instance, the effect of replacing the Holling type-II functional response with an Ivlev function in predator-prey models (Gross *et al.* 2009, Cordoleani *et al.* 2011, Adamson & Morozov 2012).

Despite this lively area of research over a number of decades, a mathematical framework for understanding the factors resulting in robust coexistence did not emerge, until recently. In relation to the problem of competitive exclusion and limiting similarity, Meszéna *et al.* (2006) presented a new approach for studying the robustness of coexistence and offered a theoretical framework for the construction of community-wide sensitivity formulas which explicitly quantify the response of population abundances to perturbations of arbitrary model parameters. Recently, a series of such formulas have been worked out for nonequilibrium communities and communities of structured populations within this framework (Szilágyi & Meszéna 2009a,b, 2010, Barabás *et al.* 2012a,b, 2013, Barabás & Ostling 2013, Barabás *et al.* 2014).

Here we suggest that this new mathematical framework opens up a perspective providing both applied and theoretical advances. Our dual purpose is to show how one can use the framework in practice, and to demonstrate these advances and the emerging insights by applying it to model examples. In particular, we suggest the framework provides: 1) a mathematical framework for assessing the extinction risk of interacting populations in the face of environmental perturbations; 2) a tool for determining expected trait distribution in and limits to the diversity of specific community types; and 3) general insights into the nature of robust communities.

This article is structured as follows. First we provide a guide to the mathematical framework of calculating sensitivities of stationary abundances to parameter perturbations, and demonstrate its use on a simple pedagogical example. We then go on to discuss three further examples, each significantly more complicated than the previous toy model. These both demonstrate the power of the framework to handle a variety of complex dynamics (including nonequilibrium behavior and population structure), and illustrate its use for assessing extinction risk and as a tool for determining expected trait diversity and limits to similarity. Next, we point out some of the generalities that emerge from the framework. Irrespective of model details or the particular mechanisms maintaining diversity, a biologically easily interpretable geometric picture emerges for describing community robustness. It can be used to draw general conclusions about the coexistence of similar species: beyond some level of similarity, coexistence gets more sensitive as species get more similar. We close by pointing out limitations of the framework, and outlining some of the empirical questions we believe its use could help answer.

2 Community-wide sensitivity analysis of population abundance: a field guide

We start out from a general model of S interacting species:

$$\frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} = r_i\left(\mathcal{R}_\mu\left(N_j,t\right),\mathbb{E},t\right) \qquad (i = 1\ldots S), \tag{1}$$

where N_i is the density of species i, and r_i is its per capita growth rate—the "species fitness" of Chesson (2000)—which is a function of:

- t, time. Any variability in the external environment (the vagaries of the weather) will result in an explicit time dependence of the r_i.
- $\mathbb{E}$, the collection of model parameters. Parameters are characteristics of the system governing species dynamics: they may include environmental variables (like temperature), heritable traits (bill depth in birds), or phenomenological characteristics possibly containing the effects of both (intrinsic death rates). We use the convention that parameters are never time-dependent. For instance, if the community is subjected to regularly oscillating weather described by $a\cos(\omega t)$, then $\mathbb{E}$ will include the amplitude a and the frequency ω, but the time dependence will be treated as an explicit dependence of the r_i on t.
- $\mathcal{R}$, the collection of variables mediating density-dependent effects—which are therefore functions of the species abundances N_j. $\mathcal{R}_\mu$ refers to the μth component of this vector. We call $\mathcal{R}_\mu$ the *regulating factors* (Levin 1970, Meszéna *et al.* 2006); $\mathcal{R}_\mu$ measures the quantity/concentration of the μth factor. Regulating factors may include resources, predators, pathogens, refuge availability, or any other thing involved in the feedback between population densities and growth rates. The important point is that *all* interactions in the community have to be mediated by the $\mathcal{R}_\mu$. See Box 1 for a more in-depth look at regulating factors.

Let us assume Eq. (1) has a fixed point. Our central question is how the position of this fixed point is expected to change in phase space after perturbing the parameters $\mathbb{E}$. At equilibrium all growth rates are zero: $r_i\left(\mathcal{R}_\mu\left(N_j(\mathbb{E})\right), \mathbb{E}\right) = 0$. Since these equations are inherently nonlinear, there is no general way of solving them for the equilibrium densities $N_i(\mathbb{E})$. It is however possible to determine the response of the fixed point to small perturbations of $\mathbb{E}$ via linearization. This formula reads

$$\sigma_i = -\sum_{j=1}^{S} a_{ij}^{-1} z_j \tag{2}$$

(Meszéna *et al.* 2006). Here σ_i is the sensitivity of the equilibrium abundance of species i to perturbations of the parameter $\mathbb{E}$, the community matrix a_{ij} describes species interactions, a_{ij}^{-1} refers to the (i,j)th entry of the inverse of this matrix (and not to the inverse of the (i,j)th entry), and z_j gives the response of species j's growth rate to $\mathbb{E}$:

$$\sigma_i = \frac{\mathrm{d}N_i}{\mathrm{d}\mathbb{E}}, \qquad a_{ij} = \sum_\mu \frac{\partial r_i}{\partial \mathcal{R}_\mu}\frac{\partial \mathcal{R}_\mu}{\partial N_j}, \qquad z_j = \frac{\partial r_j}{\partial \mathbb{E}}, \tag{3}$$

where all quantities are evaluated at the unperturbed equilibrium. Here $\mathbb{E}$ refers to a single model parameter (it is therefore a scalar); N_i, σ_i, z_j, and r_j are the ith (jth) entries of vectors of length S; $\mathcal{R}_\mu$ is the μth entry of a vector whose length is the number of regulating factors; and a_{ij} is the (i,j)th entry of an $S \times S$ matrix.

Box 1: Regulating factors

In this work we stick to the convention that all interactions between individuals within the community are parametrized via regulating factors. The two major groups of regulating factors are resources and natural enemies, as these not only influence population growth but are also affected by them. Population regulation may arise from direct or indirect interactions between individuals. For instance, if the frequency of density-dependent aggressive interactions depends on the average level of stress hormones in individuals, then its distribution within the population may function as a regulating factor. Also, regulating factors may be spatiotemporally structured. If two bird species are regulated by the number of available nesting sites and use the exact same sites but in alternative seasons, then we have effectively two separate factors. Similarly, the same type of resource in different spatial locations may function to regulate two populations independently, becoming two factors instead of one.

The concept of regulating factors might appear confusing at first because, importantly, there is no unique way of choosing them. As long as all interactions are mediated by some set of regulating factors, the choice is valid. A simple procedure to see if indeed all feedbacks have been considered is this: 1) pretend that all potential regulating factors have fixed values that do not change; 2) check if now each species in the community is undergoing simple density-independent exponential growth/decline. Fixing the quantities of the regulating factors amounts to lifting the burden of the checks and balances of nature from the species: food always gets replenished, predators and parasites are kept at bay. In fact, ever since the influential studies of Birch (1953), such removal of the feedbacks between population densities and growth rates has been the standard practice in experimental studies determining species' tolerance curves to environmental factors (such as temperature or pH).

Importantly, the final sensitivities do not depend on the particular choice of regulating factors. The impact and sensitivity vectors do change, but the generalized community matrix a_{ij} is unaffected, as can be seen from any of the equations in Box 3.

What strategy should one follow in choosing the regulating factors for specific models? There are always two "trivial" choices to go by that always work: 1) choose the population densities themselves; 2) choose the per capita growth rates. The first choice makes the impact vectors trivial, the second makes the sensitivity vectors trivial, putting all the complications in the other vector (see Section 2). In implicit, phenomenological models where the underlying mechanisms are not considered (e.g., Lotka–Volterra models), often this is the only way to go. In this case, nothing is really gained by using regulating factors.

Often however, and especially in more mechanistic, process-based models, it is better to include other regulating variables and consider the impact and sensitivity vectors separately. To take a very simple example, consider piscivorous fish which will consume any species of prey as long as the prey's body size falls within some given range. Let us also assume that none of the prey exhibit any behavioral patterns that would differentiate them in the eyes of the predator. How should we choose the regulating variables? One could go by the obvious choice of assigning all prey population densities as separate regulating factors and end up with a very complicated model. However, if we realize that from the point of view of the predators all prey species are the same, we can make the (weighted) sum of all prey densities a *single* regulating factor, thus reducing the number of variables and simplifying the problem considerably.

In fact, it is a good general principle to try finding the *minimal* set of regulating factors for any problem. Not only does this reduce the number of variables, it also constrains the maximum number of robustly coexisting species, which cannot exceed the number of regulating factors (see Sections 2 and 5.1).

In summary, there is no "right" way of choosing regulating factors, only more or less useful ways of doing so. As long as all feedbacks between growth rates and densities are taken into account, the formalism will work. At worst, nothing is gained; at best, one can analyze models via a good choice of regulating factors that otherwise would be impossible to treat. See Section 4.3 (and the corresponding section in the Supporting Information) for an example where choosing regulating factors well makes the difference in whether the model can be analyzed.

Note that Eq. (2) is interpreted differently from the classic, Lotka–Volterra-based formulation of the Levins school (Levins 1974, Yodzis 1988, Dambacher *et al.* 2002, Novak *et al.* 2011): we use the per capita instead of the total population growth rates to calculate a_{ij}, and since all interactions between individuals are mediated through the regulating factors, we assume an explicit formulation of the model in question. Though using a slightly different approach and notation, this formula was also derived by Verdy & Caswell (2008, Eqs. 29, 30).

The determinant of a_{ij} is the key measure of community robustness against parameter perturbations: small/large values of $\det(a_{ij})$ imply low/high robustness (high/low sensitivity). For a set of species coexisting at a stable fixed point, small $\det(a_{ij})$ implies that the position of the point undergoes large shifts even for small changes in $\mathbb{E}$, possibly moving it out of the all-positive region of phase space, causing extinctions. See Box 2 for more details on the relationship between sensitivity, dynamical stability, and $\det(a_{ij})$.

In contrast to earlier approaches to sensitivity analysis in the community context, Meszéna *et al.* (2006) connected $\det(a_{ij})$ to quantities that are both generally defined and biologically meaningful:

- The effect of species j's density on the μth regulating factor. This is the *impact vector* $\mathcal{I}_{j,\mu}$.
- The effect of the μth regulating factor on species i's growth rate. This is the *sensitivity vector*[1] $\mathcal{S}_{i,\mu}$.

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[1] There is an unfortunate clash of terminology here: the "sensitivity vector" has nothing to do with sensitivities as in the response of variables to parameter perturbations. To avoid confusion, we will consistently refer to $\mathcal{S}_{i,\mu}$ as the "sensitivity vector".

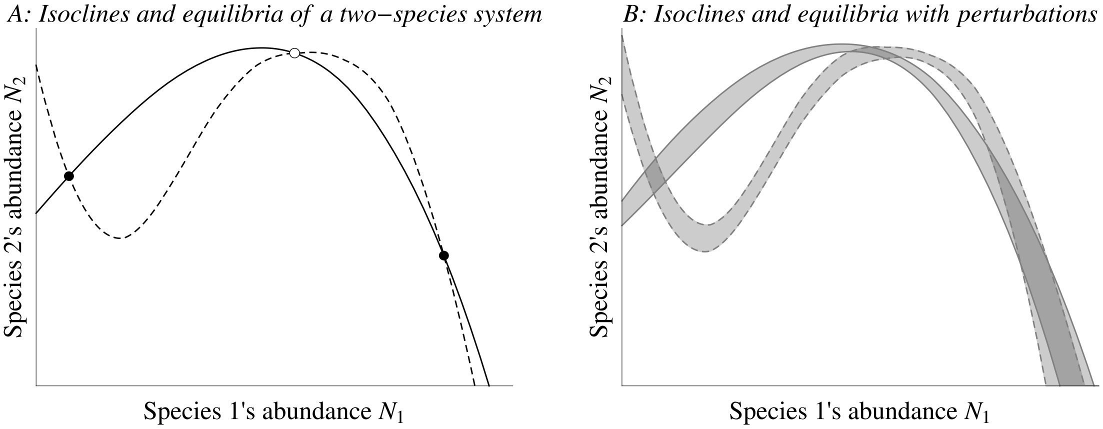

Figure 1: The relationship between stability and sensitivity. Panel A shows the isoclines of a hypothetical two-species community. Stable/unstable fixed points are denoted by black/white circles. Notice that near the rightmost equilibrium the two isoclines are almost parallel, implying weak stability. On panel B some model parameters are allowed to vary slightly, making the isoclines' positions fuzzy. These "isobands" do not cross at a single point, but at a region (darkly shaded areas). The equilibria may be anywhere within these regions. It is apparent that the first two equilibria have reasonably well-defined positions (they are robust), but the rightmost equilibrium's position is highly indeterminate, and is even touching the N_1-axis, where species 2 is extinct (unrobust equilibrium).

At a fixed point, these vectors are given by

$$\mathcal{I}_{j,\mu} = \frac{\partial \mathcal{R}_\mu}{\partial N_j}, \qquad \mathcal{S}_{i,\mu} = \frac{\partial r_i}{\partial \mathcal{R}_\mu}. \tag{4}$$

Let us now consider not these vectors by themselves, but the volumes they span, $\mathcal{V}_\mathcal{I}$ and $\mathcal{V}_\mathcal{S}$. The "impact volume" $\mathcal{V}_\mathcal{I}$ means the following. Take the impact vectors of all S species. Each vector has as many components as the number of regulating factors. Starting from the origin, we draw each impact vector and consider them to be the basal edges of a parallelotope (an "S-dimensional parallelogram"). The volume of this parallelotope in S dimensions is what we mean by $\mathcal{V}_\mathcal{I}$. The definition for $\mathcal{V}_\mathcal{S}$ is completely analogous, but with the sensitivity vectors spanning the parallelotope instead (Fig. 2A). See the Supporting Information (SI) for a simple and general recipe for calculating such volumes.

These volumes provide general measures of ecological similarity. Their generality is a consequence of the fact that the impact and sensitivity vectors are well-defined for arbitrary ecological situations via Eq. (4). Their role in measuring ecological similarity becomes clear when we consider that 1) they characterize the way species relate to their environments; 2) small volumes are a consequence of having species with very similar vectors, i.e., vectors with large overlap. In analogy with classical theory, where the overlap between resource utilization functions determined interaction coefficients (MacArthur & Levins 1967), the volumes are a measure of the aggregate overlap between several species (Fig. 2).

Box 2: Sensitivity and dynamical stability

Fig. 1 illustrates the basic idea behind the community-wide sensitivity analysis of coexistence and its relationship with conventional dynamical stability. Panel A shows the phase space of a two-species community. The isoclines of the two species are shown; stable/unstable equilibria are indicated by black/white circles (we ignore the "trivial" unstable equilibrium at the origin where both species are absent).

Panel B shows what happens when certain model parameters are slightly altered. In response to the perturbations, the isoclines' positions change. The two thick bands represent the possible positions of the isoclines after all possible (small) parameter perturbations, which is relevant because in nature parameters are expected to be continuously perturbed by extrinsic factors. The width of these "isobands" is not uniform: there is no reason to expect model parameters to influence all parts of the isoclines equally. Importantly, the equilibria now cease to have well-defined locations: they may be anywhere within the area where the "isobands" cross (shaded regions of overlap). It is apparent that the positions of the two equilibria to the left are not very sensitive to parameter perturbations. On the other hand, the rightmost equilibrium may be located in a much wider region—and, since this region touches the horizontal axis, certain parameter changes may even result in the extinction of the second species. The size of the shaded area measures the sensitivity (robustness) of the equilibrium to parameter perturbations, with the two terms inversely related: a sensitive equilibrium (large area of overlap) is unrobust, while an insensitive one (small overlap) is robust.

Note that it makes perfect sense to measure the sensitivity of the unstable equilibrium (which in this case is quite robust). Sensitivity and stability are therefore separate properties: stability/instability means that small perturbations of the *densities* will decay/amplify, while sensitivity measures how much the position of the equilibrium changes in phase space after small perturbations of the *parameters*—regardless of whether the equilibrium is stable or not. Though an unstable equilibrium does not describe coexistence *per se*, its sensitivity may still provide useful information about the system. For instance, in classic predator-prey models an unstable equilibrium is often surrounded by a stable limit cycle. If the unstable equilibrium point is sensitive enough that it may actually cross one of the coordinate axes, then so will the cycle, meaning that the species are at risk of extinction.

Observe on Fig. 1 that the isoclines at the rightmost equilibrium point intersect at a very small angle. It is known (Kuznetsov 2004) that the smaller the angle of intersection, the smaller the Jacobian's determinant at the equilibrium; in the limit of tangentially touching isoclines, the determinant is zero. Since the determinant is the product of the eigenvalues, such an equilibrium must have at least one eigenvalue very close to zero, signaling weak stability/instability. These weakly stable/unstable equilibria are also the most sensitive to parameter perturbations, because near-parallel isoclines mean that even a slight thickening of the isoclines into "isobands" will create large areas of overlap, as seen on Fig. 1. Conversely, strongly stable/unstable equilibria are robust to parameter perturbations. Note that this is only a tendency: if the isoclines do not thicken appreciably after perturbation, then even near-parallel isoclines will not translate into high sensitivity. For instance, the angle of intersection for the unstable equilibrium in the middle is not particularly high, and yet it is quite robust because the thickness of the isobands is very small near that point. Eq. (2) formalizes this intuitive relationship between stability and sensitivity, and extends it to an arbitrary number of species: a_{ij} measures the angle between isoclines, and z_j measures the "thickening" of the isoclines into isobands near the equilibrium point.

Finally, note that for simplicity we have considered fixed point equilibria of unstructured populations, but the exact same conclusions turn out to be valid for limit cycles and/or structured populations (Box 3). Though for these more complicated scenarios the matrix a_{ij} in Eq. (2) cannot be interpreted as a simple Jacobian anymore, the result that a small $\det(a_{ij})$ signals an oversensitive system still holds, irrespective of model details.

Armed with these concepts, it turns out the determinant of a_{ij} may always be approximated as

$$\left|\det(a_{ij})\right| \leq \mathcal{V}_I \mathcal{V}_S \tag{5}$$

(Meszéna *et al.* 2006). In words, the product of the volumes spanned by the impact and sensitivity vectors puts an upper bound on the magnitude of a_{ij}'s determinant. This implies that whenever $\mathcal{V}_I \mathcal{V}_S$ is small, all other things being equal, robustness will also be small. Knowing these volumes therefore opens up a possible shortcut to exploring community robustness, a property we will use in Sections 4.2 and 4.3.

So far we have only discussed the sensitivity analysis of fixed point equilibria in continuous time, for communities of unstructured populations. However, the same methodology may be extended to more complex dynamical states, like limit cycles (Barabás *et al.* 2012a, Barabás & Ostling 2013) or aperiodic stationary oscillations (Szilágyi & Meszéna 2010), both in discrete and continuous time. One may also consider communities where the species have complex life cycles, requiring structured population models (Szilágyi & Meszéna 2009a, Barabás *et al.* 2014). All this extra complexity can be incorporated into the framework described above. Importantly, though the particular expressions for σ_i, a_{ij}, and z_j do change, the general form of the sensitivity formulas, Eqs. (2) and (5), remain the same for all these scenarios, revealing a unified structure underneath all such calculations. Importantly, impact and sensitivity vectors can be identified in each. Box 3 summarizes these formulas and gives the proper interpretation of Eq. (2) when various complexities are incorporated. Due to this common structure, we refer to a_{ij} as the "generalized community matrix", which reduces to the classical community matrix for point equilibria of unstructured communities, but may also account for additional complexities such as temporal fluctuations and population structure.

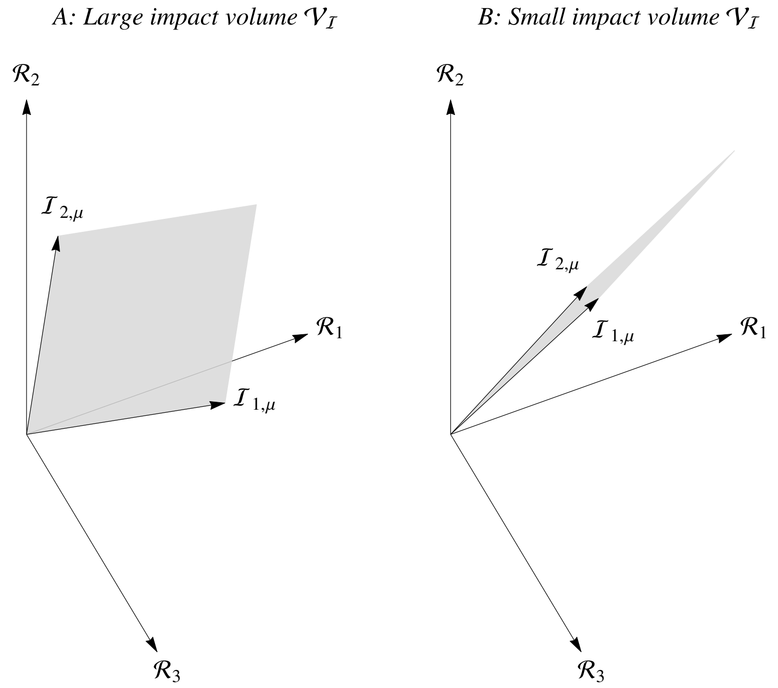

Figure 2: The volume spanned by the impact vectors of two interacting species. Let us assume there are three regulating factors in the system. We draw the two impact vectors $\mathcal{I}_{1,\mu}$ and $\mathcal{I}_{2,\mu}$ in the space whose axes correspond to the regulating factors (but what is actually measured along these axes is the impact on the given regulating factor). Since there are two species, we are interested in the two-dimensional volume (area) these vectors span (gray parallelograms). Panel A: the area spanned by the two impact vectors is large, indicating robust coexistence. Panel B: the angle between the two impact vectors is small, resulting in a much smaller area and thus reduced robustness.

3 A simple example

This section first discusses all necessary steps required to perform the community-wide sensitivity analysis of stationary abundances to parameter perturbations, and then applies this procedure to a very simple pedagogical example. The list of steps are as follows.

- *Step 0:* Determine whether the model is in discrete or continuous time, whether the populations are structured, and what type of equilibrium (fixed point, limit cycle, . . .) is under consideration.
- *Step 1:* Designate the regulating factors.

- *Step 2:* Based on Step 0, look up the necessary formulas in Box 3 and calculate the impact and sensitivity vectors of each species.
- *Step 3:* Calculate the volumes $\mathcal{V}_{\mathcal{I}}$ and $\mathcal{V}_{\mathcal{S}}$. A small product $\mathcal{V}_{\mathcal{I}}\mathcal{V}_{\mathcal{S}}$ signals an oversensitive system. For more precise quantitative estimates, move on to Step 4.
- *Step 4:* Calculate a_{ij} using the appropriate formula.
- *Step 5:* Pick an arbitrary model parameter $\mathbb{E}$ of interest and obtain the vector z_j.
- *Step 6:* Calculate the sensitivities from the general equation Eq. (2).

The toy example we look at here is a simple consumer-resource model with two species and two noninteracting abiotic resources. The dynamics of the consumers is given by

$$r_i = \frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} = b_{i1}G_1 + b_{i2}G_2 - m_i, \tag{6}$$

where r_i, N_i, and m_i are the per capita growth rate, population density, and mortality rate of species i, respectively; G_μ represents the available concentration of resource μ; and $b_{i\mu}$ is the amount of population growth species i can achieve on one unit of resource μ. The resource dynamics is in turn given by

$$\frac{\mathrm{d}G_\mu}{\mathrm{d}t} = k_\mu\left(D_\mu - G_\mu\right) - c_{\mu 1}N_1 - c_{\mu 2}N_2, \tag{7}$$

where D_μ, k_μ, and $c_{\mu i}$ are respectively the saturation concentration, turnover rate, and species i's per capita consumption rate of resource μ. We assume $k_\mu = 1$.

Let us designate specific values for the entries of $b_{i\mu}$ and $c_{\mu i}$:

$$b_{i\mu} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}, \qquad c_{\mu i} = \begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix}. \tag{8}$$

The above choice for $b_{i\mu}$ means each consumer can achieve population growth on only one of the resources. They might still consume the indigestible resource: this cross-consumption is measured by the parameter ρ.

Let us now perform the steps of the analysis outlined above.

Step 0. We know (Tilman 1982) that this type of consumer-resource model has a fixed point equilibrium. We can solve for this equilibrium: due to $\mathrm{d}G_\mu/\mathrm{d}t = 0$ the resources satisfy

$$G_\mu = D_\mu - c_{\mu 1}N_1 - c_{\mu 2}N_2 \tag{9}$$

(we used $k_\mu = 1$), and the equilibrium densities are calculated from Eq. (6) by setting $r_i = 0$ and using Eqs. (8) and (9):

$$N_1 = \frac{\overline{D}_1 - \rho\overline{D}_2}{1-\rho^2}, \qquad N_2 = \frac{\overline{D}_2 - \rho\overline{D}_1}{1-\rho^2}. \tag{10}$$

Here we introduced the quantities $\overline{D}_i = D_i - m_i$. Note that m_i is the threshold value for D_i above which the ith consumer can survive in monoculture; $\overline{D}_i$ denotes the excess above this minimum. These expressions are singular when $\rho = 1$, yielding meaningful equilibrium densities only when $\overline{D}_1$ is exactly equal to $\overline{D}_2$.

For $\rho < 1$ the conditions for $N_1, N_2 > 0$ read

$$\overline{D}_1 > \rho \overline{D}_2, \qquad \overline{D}_2 > \rho \overline{D}_1, \tag{11}$$

or

$$\rho \overline{D}_1 < \overline{D}_2 < \frac{1}{\rho} \overline{D}_1. \tag{12}$$

These can only be simultaneously satisfied for $0 < \rho < 1$. Observe that, for $\overline{D}_1$ fixed, the range of values of $\overline{D}_2$ allowing for coexistence shrinks with increasing ρ (Fig. 3A). One could also derive a similar condition for positive equilibrium densities when $\rho > 1$; however, these solutions are dynamically unstable and therefore of no interest to us.

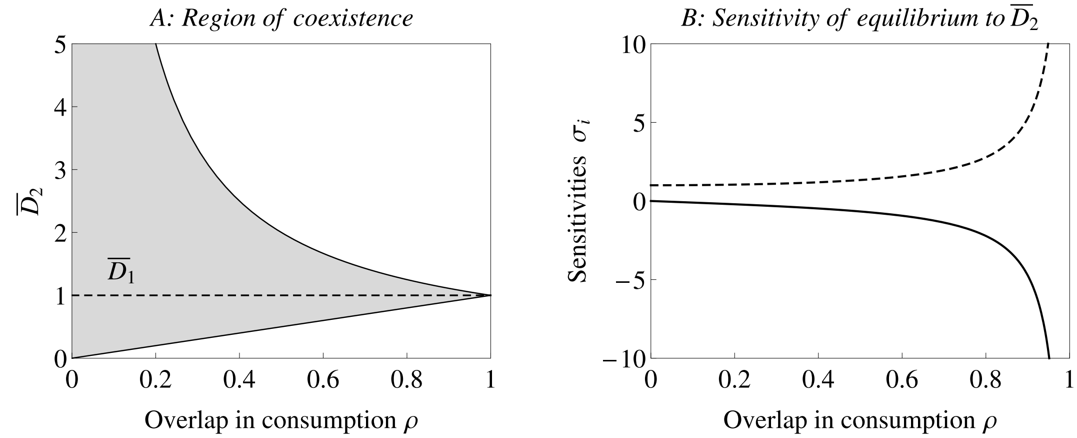

Figure 3: Coexistence regions and sensitivities in the toy model of Section 3. Panel A: coexistence region for the parameter $\overline{D}_2$ as a function of ρ, based on Eq. (12). The value of $\overline{D}_1$ is fixed at 1 (dashed line). The shaded area represents the $\overline{D}_2$ values allowing for coexistence. Notice that this region shrinks to a point at $\rho = 1$: here coexistence is only possible by fine-tuning $\overline{D}_2$ to be exactly equal to $\overline{D}_1$. Panel B: sensitivities of species 1 (solid curve) and 2 (dashed curve) to perturbing $\overline{D}_2$, given by Eq. (23); units are [abundance/resource concentration]. The curves diverge to minus/plus infinity as $\rho \to 1$, signaling that an arbitrarily small perturbation could knock the species to extinction—in line with the result on panel A.

In this model we have the benefit of knowing the precise dependence of the equilibrium densities on the parameters via Eq. (10), therefore sensitivity analysis is, strictly speaking, not even necessary. However, our purpose here is to show how the method works in an example where we can compare the results with the exact solution. The same procedure will then work for problems where we cannot solve for the equilibrium state explicitly—see Section 4 for particular examples.

The model is at a fixed point in continuous time, and the populations are unstructured. Therefore the ingredients needed for the analysis are given by Eq. (33) in Box 3:

$$\sigma_i = \frac{\mathrm{d}N_i}{\mathrm{d}\mathbb{E}}, \qquad a_{ij} = \sum_\mu \underbrace{\frac{\partial r_i}{\partial \mathcal{R}_\mu}}_{\mathcal{S}_{i,\mu}} \underbrace{\frac{\partial \mathcal{R}_\mu}{\partial N_j}}_{\mathcal{I}_{j,\mu}}, \qquad z_j = \frac{\partial r_j}{\partial \mathbb{E}}. \tag{13}$$

Step 1. We choose the regulating factors for Eq. (6). Remember that the only criterion for this choice is that the regulating variables have to mediate all density-dependent interactions (see Box 1). Here we go with $\mathcal{R}_\mu = G_\mu$.

Step 2. Calculate the impact and sensitivity vectors of each species based on the definitions in Eq. (13):

$$\mathcal{I}_{j,\mu} = \frac{\partial \mathcal{R}_\mu}{\partial N_j} = \frac{\partial}{\partial N_j}\Big(D_\mu - c_{\mu 1}N_1 - c_{\mu 2}N_2\Big) = -c_{\mu j}, \tag{14}$$

$$\mathcal{S}_{i,\mu} = \frac{\partial r_i}{\partial \mathcal{R}_\mu} = \frac{\partial}{\partial \mathcal{R}_\mu}\Big(b_{i1}\mathcal{R}_1 + b_{i2}\mathcal{R}_2 - m_i\Big) = b_{i\mu}. \tag{15}$$

Observe, using Eq. (8), that the sensitivity vectors of the two species, $(1,\ 0)$ and $(0,\ 1)$, are markedly different. In contrast, the impact vectors $(-1,\ -\rho)$ and $(-\rho,\ -1)$ are identical for $\rho = 1$ and become increasingly different as ρ departs from the value 1.

We could also calculate these vectors for different choices of the regulating variables. As mentioned in Box 1, different choices of the regulating factors can change the impact and sensitivity vectors, but will leave a_{ij} unchanged. For instance, we could make the resource depletion levels the regulating factors instead of the resources themselves: $\hat{\mathcal{R}}_\mu = \sum_i c_{\mu i}N_i = D_\mu - G_\mu$ (the hat distinguishing this alternative choice from our original one). Expressing the growth rates r_i as functions of these factors:

$$r_i = b_{i1}\left(D_1 - \hat{\mathcal{R}}_1\right) + b_{i2}\left(D_2 - \hat{\mathcal{R}}_2\right) - m_i. \tag{16}$$

We can now calculate the alternative vectors:

$$\hat{\mathcal{I}}_{j,\mu} = \frac{\partial \hat{\mathcal{R}}_\mu}{\partial N_j} = \frac{\partial}{\partial N_j}\Big(c_{\mu 1}N_1 + c_{\mu 2}N_2\Big) = c_{\mu j}, \tag{17}$$

$$\hat{\mathcal{S}}_{i,\mu} = \frac{\partial r_i}{\partial \hat{\mathcal{R}}_\mu} = \frac{\partial}{\partial \hat{\mathcal{R}}_\mu}\Big(b_{i1}\left(D_1 - \hat{\mathcal{R}}_1\right) + b_{i2}\left(D_2 - \hat{\mathcal{R}}_2\right) - m_i\Big) = -b_{i\mu}. \tag{18}$$

This alternative choice reverses the direction of the impact and sensitivity vectors.

Step 3. We calculate the volumes $\mathcal{V}_\mathcal{I}$ and $\mathcal{V}_\mathcal{S}$, which carry valuable information on robustness (Section 2). In our case, as $\mathcal{I}_{j,\mu}$ and $\mathcal{S}_{i,\mu}$ happen to form square matrices, the volume is given by the absolute values of their determinants (see the Supporting Information):

$$\mathcal{V}_\mathcal{I} = \left|\det\left(-c_{\mu j}\right)\right| = \left|\det\begin{pmatrix} -1 & -\rho \\ -\rho & -1 \end{pmatrix}\right| = 1 - \rho^2, \quad \mathcal{V}_\mathcal{S} = \left|\det\left(b_{i\mu}\right)\right| = \left|\det\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}\right| = 1. \tag{19}$$

Using Eq. (5), $\mathcal{V}_{\mathcal{I}}\mathcal{V}_{\mathcal{S}} = 1-\rho^2$, so without any further calculations we know that coexistence will get more and more sensitive to parameter perturbations as ρ approaches 1. At the point where ρ is precisely equal to 1, $\mathcal{V}_{\mathcal{I}}\mathcal{V}_{\mathcal{S}} = 0$ and coexistence has infinite sensitivity (zero robustness). This is consistent with Eq. (12) and Fig. 3A: the parameter region allowing for coexistence shrinks with increasing ρ, and at $\rho = 1$ becomes a single point.

Step 4. We calculate the matrix a_{ij} from Eq. (13):

$$a_{ij} = \sum_{\mu=1}^{2} \frac{\partial r_i}{\partial \mathcal{R}_\mu}\frac{\partial \mathcal{R}_\mu}{\partial N_j} = \sum_{\mu=1}^{2} \mathcal{S}_{i,\mu}\mathcal{I}_{j,\mu} = -\sum_{\mu=1}^{2} b_{i\mu}c_{\mu j} = -\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}\begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix} = \begin{pmatrix} -1 & -\rho \\ -\rho & -1 \end{pmatrix}. \tag{20}$$

We get the exact same result using $\hat{\mathcal{R}}_\mu$, or any other choice of the regulating factors. Since a_{ij} depends on $\mathcal{R}_\mu$ only through the chain rule, this dependence must ultimately cancel from the final expression.

Step 5. We pick a model parameter $\mathbb{E}$. Let us choose $\mathbb{E} = \overline{D}_2$: we are interested in the consequences of increasing the excess resource supply for Species 2 while keeping it constant for Species 1. Since the original equations are expressed in terms of D_i instead of $\overline{D}_i$, we rewrite the growth rates at equilibrium as functions of $\overline{D}_i = D_i - m_i$. Substituting Eq. (9) into Eq. (6):

$$0 = r_j = \sum_{k=1}^{2} b_{jk}D_k - m_j - \sum_{\mu=1}^{2}\sum_{k=1}^{2} b_{j\mu}c_{\mu k}N_k = \sum_{k=1}^{2} b_{jk}\overline{D}_k + \sum_{k=1}^{2} b_{jk}m_k - m_j - \sum_{\mu=1}^{2}\sum_{k=1}^{2} b_{j\mu}c_{\mu k}N_k, \tag{21}$$

and now we can calculate z_j:

$$z_j = \frac{\partial r_j}{\partial \overline{D}_2} = \frac{\partial}{\partial \overline{D}_2}\left(\sum_{k=1}^{2} b_{jk}\overline{D}_k + \sum_{k=1}^{2} b_{jk}m_k - m_j - \sum_{\mu=1}^{2}\sum_{k=1}^{2} b_{j\mu}c_{\mu k}N_k\right) = b_{j2} = \begin{pmatrix} 0 \\ 1 \end{pmatrix}. \tag{22}$$

Step 6. Determine the sensitivities σ_i of the equilibrium abundances to perturbing $\overline{D}_2$ using the general formula Eq. (2):

$$\begin{aligned} \sigma_i =& \frac{\mathrm{d}N_i}{\mathrm{d}\overline{D}_2} = -\sum_{j=1}^{S} a_{ij}^{-1} z_j = -\begin{pmatrix} -1 & -\rho \\ -\rho & -1 \end{pmatrix}^{-1}\begin{pmatrix} 0 \\ 1 \end{pmatrix} \\ =& \frac{1}{1-\rho^2}\begin{pmatrix} 1 & -\rho \\ -\rho & 1 \end{pmatrix}\begin{pmatrix} 0 \\ 1 \end{pmatrix} = \frac{1}{1-\rho^2}\begin{pmatrix} -\rho \\ 1 \end{pmatrix}. \end{aligned} \tag{23}$$

If all went well, we should have gotten the same result as if we had directly taken the derivative of Eq. (10) with respect to $\overline{D}_2$—which is indeed the case. Fig. 3B shows these sensitivities.

As a side note, observe that the σ_i are meaningful even for $-1 < \rho < 0$. A negative ρ means the ith consumer facilitates the resource it cannot digest. A stable equilibrium still ensues in this case, but species 1, instead of responding negatively to an increase in $\overline{D}_2$, will respond positively due to this facilitation. This is not apparent from looking only at $\mathcal{V}_{\mathcal{I}}\mathcal{V}_{\mathcal{S}} = 1-\rho^2$, which is independent of the sign of ρ. The volumes do give general information about robustness, but the numerical details are only given by the full sensitivity formula.

In summary, the key quantity determining the sensitivity of equilibrium abundances to $\overline{D}_2$ in this example is ρ, measuring the segregation between the two impact vectors. As ρ approaches 1 from below, the impact vectors become similar and therefore sensitivity towards parameter perturbations becomes large. Also, the range of $\overline{D}_2$ values allowing for coexistence shrinks to zero gradually as ρ increases, as shown by Eq. (12) and Fig. 3. For $\rho \approx 1$, it becomes very hard to fine-tune $\overline{D}_2$ to support coexistence.

4 Applications

This section applies the community-wide sensitivity framework to three different model studies in order to demonstrate how the machinery outlined above can handle situations that are significantly more complicated than the previous toy example, and to demonstrate uses of the framework for assessing extinction risk and determining species traits predicted by a species interaction model. In particular, there are three complicating factors we consider. The first is temporal fluctuations in the environment (Section 4.1), where we also show how coexistence regions and extinction risk can be estimated from sensitivities. The second is spatial heterogeneity (Section 4.2), where we derive effective limits to species similarity using sensitivities. The third are noncompetitive interactions (Section 4.3) in a model where stability criteria do not put a bound on the number of potentially coexisting species, but sensitivities do.

The details of our calculations are found in the Supporting Information. Importantly, we present each model with regulating factors already assigned. This is not to say other choices are not possible (see Box 1), but the details of how and why we choose them are relegated to the Supporting Information.

4.1 Handling temporal fluctuations: assessing extinction risk in a model of forb-grass competition

Here we perform community-wide sensitivity analysis on a competition model, proposed by Levine & Rees (2004), to describe a mechanism of persistence of rare native forbs with exotic grasses on a California grassland. They proposed that environmental fluctuations are key for generating coexistence, with the otherwise rare forbs benefiting from occasional good years while being buffered against bad years due to their superior seed banks (storage effect; Chesson & Warner 1981, Chesson 1994, 2000). Their annual plant model can be written

$$N_i(t+1) = \left((1-g_i(t))(1-d_i) + \frac{\lambda_i(t) g_i(t)}{1+\alpha_i \mathcal{R}(t)}\right) N_i(t), \tag{24}$$

where i may be 1 (forb) or 2 (grass), $N_i(t)$ is the density of species i's seeds in the seedbank at time t, $\alpha_i = (\alpha,\ 1)$, and the time-dependent regulating factor is a linear function of the densities:

$$\mathcal{R}(t) = \frac{g_1(t) N_1(t)}{\alpha} + g_2(t) N_2(t). \tag{25}$$

See the caption to Fig. 4 for a description of the model's parameters (see also Table S1); we used the field estimates of Levine & Rees (2004) for their values (black tick marks on Fig. 5). As environmental variability is needed to generate coexistence (Levine & Rees 2004), we assume that both the fraction of germinating seeds $g_i(t)$ and the annual fecundities $\lambda_i(t)$ are fluctuating periodically between "good" and "bad" years. Knowing the value of every parameter, we can numerically evaluate the model's sensitivity to each. These sensitivities can then be used to estimate coexistence regions, which in turn may in principle be used to make informed management decisions to help prevent species extinctions.

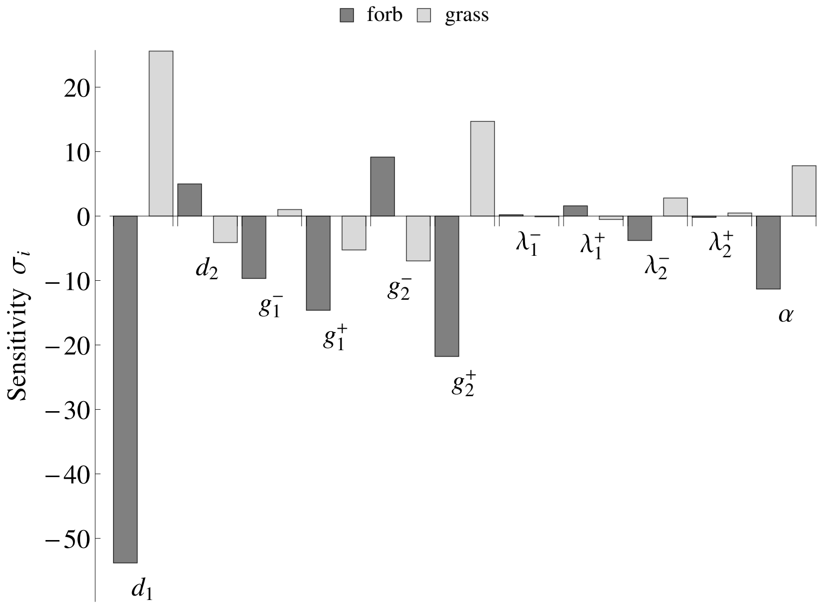

Figure 4: Sensitivities of the Levine–Rees model of forb-grass competition to each model parameter (Section 4.1). The parameters are α: reciprocal competition coefficient; d_i: species i's seed mortality; $g_i^{\pm}$: fraction of species i's seeds germinating in good/bad years; $\lambda_i^{\pm}$: per capita number of seeds produced by species i in good/bad years. The darker bars represent the sensitivity values of the forb; the lighter bars represent the sensitivity values of the grass. These sensitivities are valid in bad years. The sensitivities in good years are qualitatively similar; see Table S3 in the Supporting Information for their values.

This is a discrete-time model where the periodically fluctuating environment generates a limit cycle. We therefore take the appropriate sensitivity formula off the shelf—in our case, Eq. (34)—and use the estimated parameter values to calculate the sensitivity of each species' abundances along the limit cycle to each model parameter. The details of the calculation are in the Supporting Information; the results are shown on Fig. 4.

These sensitivities may be used to estimate the parameter ranges allowing for coexistence. Since $N_i^{(\text{new})} \approx N_i^{(\text{old})} + \sigma_i \Delta\mathbb{E}$, we calculate how much $\Delta\mathbb{E}$ would be needed to make $N_i^{(\text{new})}$ hit zero for at

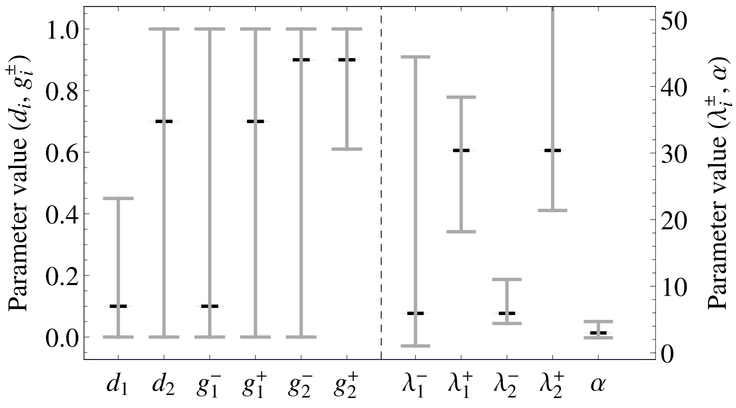

Figure 5: Values (black tick marks) and coexistence regions (gray error bars) for each parameter in the forb-grass competition model (Section 4.1). The dashed line separates parameters measured by the scales on the left/right side. The upper limit for λ_2^+ is cut off due to scale disparity; its value is 128.5. The coexistence regions are calculated, using the stationary densities in Eq. (S5) and the sensitivity values in Table (S3) in the Supporting Information (also shown on Fig. 4 for bad years), as the most extreme parameter values for which both species are still persisting with positive abundances at each point along the limit cycle.

least one of the species. The results are in Fig. 5. It is immediately seen that there are a handful of parameters with relatively narrow coexistence regions. For instance, forb germination in good years and grass fecundity in bad years have restrictive enough ranges that they might warrant attention. As long as the model is an accurate representation of the true dynamics in this system, the implications would be that careful monitoring of these quantities is necessary to prevent the extinction of the species.

4.2 Handling spatial heterogeneity: trait combinations leading to robust coexistence in the tolerance-fecundity tradeoff model

We now turn our attention to a model where the species have population structure. This model, the tolerance-fecundity tradeoff, was originally proposed by Muller-Landau (2010) and later generalized by D'Andrea *et al.* (2013). It is a mechanistic model which enjoys empirical support as a potential driver for maintaining seed size diversity in plant communities (Lonnberg & Eriksson 2013). In this model sessile individuals produce seeds competing for sites of varying environmental stress levels, ranging from s_1 (lowest) to s_M (highest). The tradeoff is realized via the assumption that the more tolerant a species is to stressful conditions, the fewer seeds it produces. The stress tolerance of species i's seeds is given by the function $T_i(s)$, measuring the probability of an individual seed of species i surviving on a site of stress level s. We assume $T_i(s)$ is a sigmoid function: each species is really good at tolerating a given range of stress levels, after which the tolerance quickly falls to low values. One particular functional form implementing this property is

$$T_i(s) = \frac{\tanh\big(\tau(s_M - f_i - s)\big) + 1}{2}, \tag{26}$$

where the parameter τ controls the abruptness of the transition between the tolerant and intolerant regimes (Fig. 6A).

The governing equation for this model reads

$$\frac{\mathrm{d}N_{i,a}}{\mathrm{d}t} = \sum_{b=1}^{M} \Big(f_i T_i(s_a) \mathcal{R}(s_a) - m_i \delta_{ab} \Big) N_{i,b}, \tag{27}$$

where $N_{i,a}$ is the abundance of species i across sites of stress level s_a, f_i and m_i are the adult fecundity and mortality rates of species i, δ_{ab} is the identity matrix (equal to 1 if $a = b$ and to 0 otherwise), and the regulating variables are given by

$$\mathcal{R}(s_a) = \frac{c(s_a) - \sum_{i=1}^{S} N_{i,a}}{\sum_{k=1}^{S} f_k N_k T_k(s_a)}. \tag{28}$$

Here $c(s_a)$ is the number of sites of stress level s_a, and N_k is the total abundance of species k across all sites. $\mathcal{R}(s_a)$ measures the effect of crowding in sites of stress level s_a, with larger values corresponding to less crowding (see the Supporting Information).

This model is a continuous-time structured model. Previous studies show it converges to a fixed point (D'Andrea *et al.* 2013). We therefore take Eq. (36) off the shelf for the analysis. In the Supporting Information we show that the sensitivity vectors are given by

$$\mathcal{S}_{i,\sigma} = f_i T_i(s_\sigma). \tag{29}$$

This expression has a very important property: *it is independent of the equilibrium population distributions $N_{i,a}$*. Therefore, it can be evaluated without having to solve for the equilibrium state.

By Eq. (5), a small $\mathcal{V}_\mathcal{S}$ will lead to small robustness. Let us consider just two competing species. We can then plot the volume spanned by $\mathcal{S}_{1,\sigma}$ and $\mathcal{S}_{2,\sigma}$ as a function of the two fecundities f_1 and f_2 (Fig. 6B; see the Supporting Information for the calculations). We can see from Fig. 6B that coexistence is most likely when one species has high fecundity and the other an intermediate one: that is the portion of the plot where the volume $\mathcal{V}_\mathcal{S}$ is the largest. Notice also that robustness is always low near the $f_1 = f_2$ line. This property imposes an effective limit to the similarity of coexisting species: though stable coexistence of very similar fecundity values is possible, it is unlikely because of the low associated robustness.

Note that we used $\mathcal{V}_\mathcal{S}$ as a proxy for robustness, when in fact the relevant quantity is $\mathcal{V}_\mathcal{I}\mathcal{V}_\mathcal{S}$ (Eq. 5). We show in the Supporting Information however that $\mathcal{V}_\mathcal{I}$ is correlated with $\mathcal{V}_\mathcal{S}$, therefore whenever the latter is small, so is the former. Also, the result in Fig. 6B is easily generalized to S species by considering the S-dimensional volume spanned by the vectors $\mathcal{S}_{i,\mu} = f_i T_i(s_\mu)$—though visualizing the results might prove challenging for $S \geq 3$.

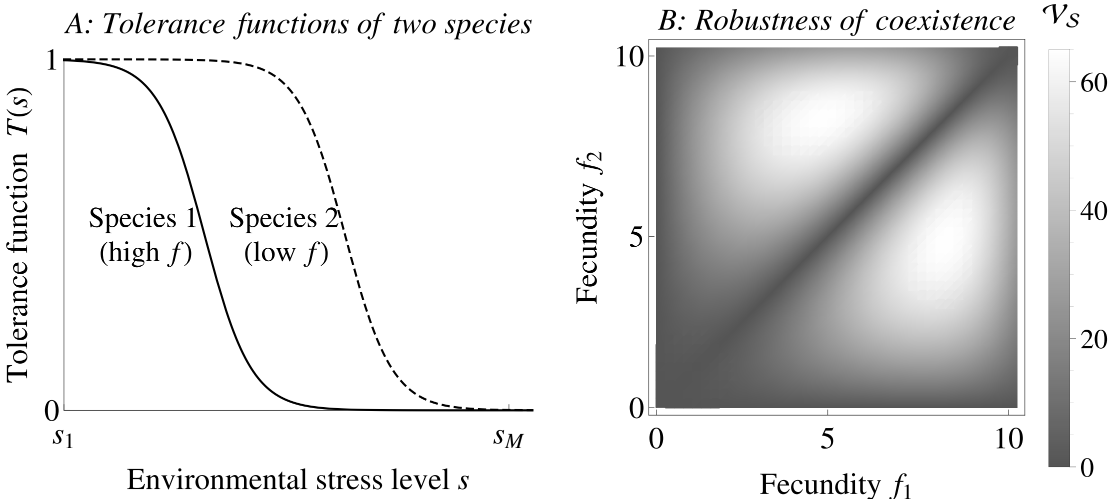

Figure 6: The tolerance-fecundity tradeoff model (Section 4.2). Panel A: tolerance functions of two species (solid and dashed curves). The abscissa represents stress, ranging from s_1 to s_M. The ordinate is the probability that a seed survives the given stress level. The tolerance functions are sigmoid curves with a relatively abrupt transition from the tolerant to the intolerant regime. The tradeoff is implemented by making the species with the higher fecundity f less tolerant. Panel B: The volume $\mathcal{V}_S$ spanned by the sensitivity vectors of two species, as a function of their fecundities; units are $[1/\text{time}^2]$. The volume is largest where one species has high fecundity and the other an intermediate one. Both species possessing similar fecundities leads to small volumes. We know from Eq. (5) that a small volume is sufficient for making coexistence oversensitive and therefore unrealistic; only in the high-volume regions is coexistence even a possibility.

4.3 Handling noncompetitive interactions: stability vs. robustness of coexistence in the Gross model of interspecific facilitation

For our final example we analyze a model of interspecific facilitation proposed by Gross (2008). There have been ongoing efforts to incorporate facilitation into ecological theory in a general way for more than a decade now (Bruno *et al.* 2003), and the model of Gross (2008) is an important step in this direction. This example demonstrates how large a difference it makes to shift the emphasis from the stability of coexistence to its robustness against varying parameters. If one only considers stability, expected diversity is in fact unlimited. Taking sensitivities into account, the maximum number of species turns out to be strongly limited.

The Gross model is one of intraguild mutualism (Crowley & Cox 2011), where several consumer species compete for a single resource. Facilitation is included via the assumption that an increase in the abundance of one competitor reduces the death rate of another. Empirical examples include plant species providing cushion for others (Cerfonteyn *et al.* 2011, McIntire & Fajardo 2013), and Müllerian mimicry rings in butterflies (Elias *et al.* 2008) or catfish (Alexandrou *et al.* 2011), where joining the ring confers an advantage to otherwise competing species by reducing nonregulatory predation pressure.

In the simplest version of the model only two species compete: in this case, the coexistence condition is that the mutualistic effects must confer enough advantage on the species to turn their invasion growth rates positive when the other species is resident. When generalizing the model to several species, the facilitation network may in principle be arbitrarily complicated, but Gross (2008) made a simplifying assumption to keep the model tractable: facilitation was assumed to be hierarchical. This means species 1 is not facilitated by anyone, species 2 is facilitated only by species 1, species 3 is facilitated by species 1 and 2, and so on. This assumption actually allows for more coexistence on average than random facilitation networks (Gross 2008). The equations for this model read

$$\frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} = f_i(R) - m_i^0 + d_i\left(1 - \exp\left(-\theta\sum_{k<i} N_k\right)\right) \qquad (i = 1 \ldots S) \tag{30}$$

for the consumers, and

$$\frac{\mathrm{d}R}{\mathrm{d}t} = g(R) - \sum_{i=1}^{S} c_i f_i(R) N_i \tag{31}$$

for the resource (SI). Here S is the total number of consumer species, N_i is the density of species i, $f_i(R)$ is its per capita resource-dependent growth rate, m_i^0 its baseline mortality, d_i the maximum advantage it can gain from facilitation (we assume $d_i \leq m_i^0$), θ measures the facilitative advantage conferred by a single species, R is the resource, $g(R)$ the resource supply rate, and c_i the species' consumption rates.

The consequences of this facilitation on coexistence are drastic: Gross (2008) has proven that an arbitrary number of species may coexist on the single resource. His proof relies on demonstrating that, given a community of S species, one can always choose parameters such that an $(S+1)$th species can be added without causing any extinctions. In dynamical terms: if there was a stable equilibrium point for S species, there will also be one for $S+1$ species as well.

Stable coexistence of an arbitrary number of species is therefore possible. However, one can also ask how sensitive this nontrivial stable fixed point is to altering parameters. As proven in the Supporting Information, increasing the number of species will make the community ever more sensitive to parameter changes. The asymptotic robustness of the community, for large S, is shown to be

$$\sqrt[S]{\mathcal{V}_{\mathcal{I}}\mathcal{V}_{\mathcal{S}}} \sim N\theta \exp\left(-N\theta S/2\right), \tag{32}$$

where N is the smallest of the equilibrium densities of the consumer species. Taking the Sth root of $\mathcal{V}_{\mathcal{I}}\mathcal{V}_{\mathcal{S}}$ makes robustness comparable across different values of S; see the Supporting Information for details.

This demonstrates that robustness decays exponentially with the number of species: any S substantially larger than $S_{\max} \approx 1/(N\theta)$ will make this expression exponentially small. Fig. 7 shows robustness as a function of S and $N\theta$: clearly, we cannot realistically expect more than a handful of species. Robustness considerations therefore significantly alter the level of expected diversity compared with estimates based on stability criteria, which do not put a limit on the number of species at all.

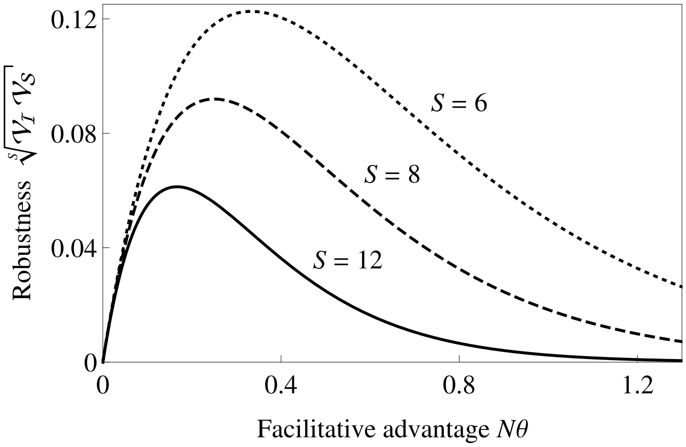

Figure 7: Robustness in the Gross model (Section 4.3). Robustness is measured by $\sqrt[S]{\mathcal{V}_I \mathcal{V}_S}$ as a function of the (scaled) facilitative advantage $N\theta$ for various values of the species richness S, based on Eq. (32). Overall, robustness decreases with increasing S. For a fixed number of species, the most robust scenario always happens at an intermediate $N\theta$ value. The figure underlines the result that coexistence of more than a handful of species through the cascade of facilitation in the Gross model is a highly unrobust, and therefore unlikely, outcome.

The theory is thus in line with the empirical observation that facilitation leads to the evolutionary convergence of traits acting to reduce nonregulatory predation (Elias *et al.* 2008), and also with the fact that robustness of coexistence is enhanced by divergence along other trait dimensions. Since we have seen that the maintenance of very many species via pure facilitation with a single limiting resource is not possible, one should expect segregation along other regulating factors as well in species-rich communities—as was aptly demonstrated by Alexandrou *et al.* (2011).

5 Discussion

5.1 General insights regarding robust coexistence

In this work we have attempted to demonstrate through a handful of examples the kinds of benefits a new way of analyzing the sensitivity of coexistence might hold for ecology. The examples were aimed at covering a diverse range of different situations: fluctuation-mediated coexistence, spatially structured communities, and noncompetitive interactions. Yet behind the diversity of applications underlies a fundamental unity in how the problems are approached and what methods are employed. This unified perspective is achieved through the consideration of regulating factors, and through the introduction of impact and sensitivity vectors describing species' interactions with these factors. Just as in the context of population-level sensitivity analyses (Caswell 2008), having explicit sensitivity formulas means one can gain general insights not accessible via purely simulation-based approaches.

The generality and flexibility of the concept of regulating factors allows for the common treatment of seemingly very different types of interactions. Traditional resource competition, predator-mediated effects (such as apparent competition), facilitation, spatial effects, and temporal segregation are all handled on the same footing: the details do change (Box 3), but both their underlying mathematical structure and their basic biological interpretation remains the same.

The mathematical framework presented here further shows that species' impact and sensitivity vectors characterize the system's sensitivity to environmental perturbations, regardless of whether the system is at equilibrium or not, or whether there is spatial structure, or noncompetitive interactions. Specifically, the volumes spanned by these vectors are key in determining sensitivity via Eq. (5): large volumes imply low sensitivity, while small volumes imply high sensitivity. Hence, high environmental variability coupled with small volumes is expected to lead to extinctions, making it less likely that such communities would be observed. This provides a general understanding of the distribution of species traits expected in robust communities, and reveals constraints that robustness requirements may put on communities, beyond those imposed by stability.

What causes impact and sensitivity vectors to span small volumes? There are two options. First, volumes will be small if the vectors are short, i.e., the regulating interactions of the populations are weak. Second, volumes will be small if the vectors spanning them are nearly collinear or, more generally, linearly dependent (Fig. 2): that is, when the regulating interactions of the different species are not differentiated sufficiently.

This second possibility is nothing else than the classical idea of limiting similarity, formulated in a precise way. Sensitivity analysis adds precision in three ways. First, it clarifies that coexistence of similar species it is not impossible, just unlikely, requiring a narrow set of environmental parameters. Second, it yields a quantitative estimate of this parameter range. Third, it clarifies that the property in which species must differ for robust coexistence is their way of being regulated, described by the impact and sensitivity vectors.

When the number of regulating factors is smaller than the number of species, the framework shows that not only is it impossible for all of the species to coexist stably (Levin 1970), it is also impossible for them to coexist robustly, since $\mathcal{V}_{\mathcal{I}}$ (or $\mathcal{V}_{\mathcal{S}}$) will be zero. Moreover, even when the number of regulating factors is infinite (Section 4.2) or unbounded (Section 4.3), in which case consideration of stability alone would suggest that coexistence of infinitely many species is at least possible, sensitivity analysis shows infinite diversity is not expected, because too much coexistence leads to overly similar impact and sensitivity vectors. We saw this explicitly in the results of our analysis of the tolerance-fecundity tradeoff model (Fig. 6B): robustness is zero along the line of identical fecundities $f_1 = f_2$. This is because the sensitivity vectors of identical species are the same, so they point in the same direction, leading to $\mathcal{V}_{\mathcal{S}} = 0$. Robustness is still very small if the two fecundities are nearly equal. Importantly, what we see on Fig. 6B reflects a property we will observe in *all* cases, because $\mathcal{V}_{\mathcal{I}}$ and $\mathcal{V}_{\mathcal{S}}$ are continuous functions of the impact and sensitivity vectors. Therefore, near-identical species will always have near-zero robustness.

In this way, the community-wide sensitivity analysis of coexistence essentially recreates what usually goes under the umbrella of "niche theory" (Case 2000, p. 368): avoiding competitive exclusion requires limited niche overlap as measured by impact and sensitivity vectors. Though the expectation of strict limits to similarity is mathematically and biologically naive, sensitivity analysis leads to the conclusion that *effective* limits to similarity are still the expected rule of thumb (Section 4.2, Szabó & Meszéna 2006, Barabás & Meszéna 2009, Barabás *et al.* 2012b).

The robustness perspective naturally leads to the empirical question of how robust natural communities tend to be. As we have seen, sensitivities, coupled with a knowledge of the size of typical environmental perturbations, yield viable parameter regions. How wide do these regions tend to be in natural communities compared to what is strictly required for the community's persistence? Put another way, does the regime of environmental variation have a big influence on community structure, or do other forces governing community structure (e.g., selection for trait differences among species) act to generate communities even more robust than required? One study by Adler *et al.* (2010) in a perennial plant community suggests the stabilization of coexistence is quite strong (much stronger than strictly necessary to compensate for fitness differences between the species), suggesting it should also be quite robust. However, the parameter region allowing for coexistence must be compared with the range of environmental fluctuations in this system if we are to get a definitive answer.

In fact, one may wonder whether community robustness tends to vary systematically along environmental gradients. Certain environments are relatively constant; some are more variable, which in general means more perturbed. More perturbed communities require, *ceteris paribus*, a wider coexistence region. Does this actually play out in nature? And if so, what consequences does it have for expected community and diversity patterns? We believe that the community-wide sensitivity framework will help answer these and similar empirical questions.

5.2 Limitations of the framework

Though the presented method does provide the applied and theoretical advantages outlined above, it also comes with its inevitable drawbacks and caveats. The most important drawback is that the method is based on linearization: sensitivity values are accurate only for *small* parameter perturbations. Therefore, extrapolations to large parameter changes should be treated with care, which will only be accurate if the sensitivities themselves are not very sensitive. If they are heavily convex/concave functions, or if the analyzed equilibria undergo saddle-node bifurcations between their current locations and zero (signaling a potential catastrophic shift), the linear extrapolations will be unreliable. Then, the method's safest domain of application is looking at the response of systems strictly to small parameter changes. This is an important point in the context of the Levine–Rees model (Section 4.1), where the coexistence regions of Fig. 5 are all derived using linear extrapolation.

Fortunately, a common experience in performing sensitivity analyses is that extrapolations based on sensitivities yield surprisingly accurate results even for large perturbations, both in a population (de Kroon *et al.* 2000) and a community-wide (Barabás & Ostling 2013, Barabás *et al.* 2014) context.

Under what circumstances we may expect such accuracy is an open question. However, use of the linear approximation means our methods are ill-suited for studying the effects of species removal on communities (Ebenman *et al.* 2004, Ebenman & Jonsson 2005, Allesina & Pascual 2009), because such perturbations involve very large changes in the system.

Another issue is that all parameter estimates possess a level of uncertainty. How can we know the degree to which measurement errors affect sensitivity results? There are two aspects to this problem. First, as mentioned above, if the linear approximation is not very good, sensitivity values might themselves sensitively depend on measured parameter values. Second, even if sensitivities are accurate for a wide range of parameters, predictive power may be hampered if their values are very large: then, even a small error in measurement would mean a large error in prediction.

How can one deal with this problem in practice? First, it can be approached in the same way as any other kind of uncertainty: by considering the confidence intervals of parameter estimates, and repeating the sensitivity calculations for various randomly chosen parameter values within the parameters' confidence intervals. This way, one obtains a distribution of sensitivities instead of a single sensitivity value. See Barabás & Ostling (2013) and Barabás *et al.* (2014) for how this is done in practice. The same procedure could then be applied, for instance, to the Levine–Rees model if we had data on parameter error estimates.

Second, note that, in contrast to experience with smaller communities (Barabás & Ostling 2013, Barabás *et al.* 2014), several studies (Yodzis 1988, Dambacher *et al.* 2002, Novak *et al.* 2011) have found very high sensitivities of equilibrium abundances to press perturbations when analyzing large ensembles of species. Systematic application of our methods to large systems is work in progress, but if we believe these results to be general (i.e., large communities are more sensitive), then one possibility for avoiding the problem of overly high sensitivities is to concentrate on smaller community compartments which can be thought of as independent mesocosms consisting of just a handful of species (Krause *et al.* 2003, Guimerà *et al.* 2010, Stouffer & Bascompte 2011).

Yet another caveat comes with using the volumetric approach, based on $\mathcal{V}_\mathcal{I}$ and $\mathcal{V}_\mathcal{S}$, to gain insight into the robustness of coexistence. As we have seen, these volumes can provide a shortcut to robustness calculations. They are, however, only part of the story because in Eq. (2) the vector z_j also plays a role. Though the volumes may be small, the vector z_j may also be small and therefore robustness may not be as weak as it appears based on the volumes alone (or vice versa). In an extreme case, imagine that the growth rates are at a local maximum or minimum with respect to $\mathbb{E}$; then $z_j = \partial r_j / \partial \mathbb{E} = 0$, so sensitivity is zero regardless of $\mathcal{V}_\mathcal{I}\mathcal{V}_\mathcal{S}$. In Section 3 for instance, $\mathcal{V}_\mathcal{I}\mathcal{V}_\mathcal{S}$ was insensitive to the sign of ρ, but the sensitivities were not. The volumes do reveal general information, but not the numerical details.

Moreover, though the presented framework can already treat a variety of dynamics, the list is far from complete. We do not yet have formulas for the sensitivity of general, aperiodic stationary oscillations (with or without population structure), or formulas for the sensitivity of transients instead of stationary states. Transient sensitivities would enable us to assess the short-term consequences of parameter changes, an endeavor just as important as being able to calculate long-term consequences.

Finally, a note about the procedure outlined in Section 3 for performing sensitivity analyses (which we consistently follow in the main text and the Supporting Information as well). Although it looks straightforward, this does not mean all case studies will look the same. To take an analogy, consider conventional sensitivity analysis of structured populations. One could say it is very simple: 1) construct the life cycle graph; 2) estimate the transition probabilities and fecundities; 3) calculate the leading eigenvalue; 4) calculate the corresponding left and right eigenvectors; 5) create their tensor product to obtain the sensitivity matrix. But, as Caswell himself pointed out: “Every population analysis that I have been involved with has required some unique methodological twists and turns” (Caswell 2001, p. 107). What we provided is merely an outline, which does not imply that particular models can have no “special needs” in their analyses.

6 Conclusions

The recently developed mathematical framework for the sensitivity analysis of stationary abundances of interacting species to parameter perturbations provides an important new perspective in community ecology. It opens up the possibility of an analytical approach to estimating extinction risk. It provides a tool for understanding how diversity and community patterns may be influenced by environmental variation, in addition to stability constraints. Finally, it yields insight into the nature of the interaction between robustly coexisting species, in terms of species’ interactions with regulating factors. These insights apply fairly generally, even to models with complex dynamics, and provide a new perspective on the concept of niche differentiation in ecology. Here we have guided the reader on the use of this new mathematical framework and illustrated its potential through application to a variety of models. Although the framework has limitations—most notably in that it is based on a linear approximation—its application could help answer a set of empirical questions in community ecology regarding the degree to which environmental fluctuations and robustness constraints determine the structure of communities.

Box 3: Community-wide sensitivity formulas

Below we give a catalog list of the sensitivity formulas for various dynamical scenarios. The general structure of each equation is given by Eq. (2):

$$\sigma_i = -\sum_{j=1}^{S} a_{ij}^{-1} z_j,$$

where a_{ij}^{-1} is the (i,j)th entry of the inverse matrix, not the inverse of the (i,j)th entry. For each case we state the applicability of the given formula, reference where it was originally derived, give the interpretation of σ_i along with the formulas for a_{ij} and z_j, and indicate the impact and sensitivity vectors $\mathcal{I}_{j,\mu}$ and $\mathcal{S}_{i,\mu}$.

1. Fixed point dynamics, in either discrete or continuous time, for communities of unstructured populations (Meszéna *et al.* 2006):

$$\sigma_i = \frac{\mathrm{d}N_i}{\mathrm{d}\mathbb{E}}, \qquad a_{ij} = \sum_{\mu} \underbrace{\frac{\partial r_i}{\partial \mathcal{R}_\mu}}_{\mathcal{S}_{i,\mu}} \underbrace{\frac{\partial \mathcal{R}_\mu}{\partial N_j}}_{\mathcal{I}_{j,\mu}}, \qquad z_j = \frac{\partial r_j}{\partial \mathbb{E}}. \tag{33}$$

In discrete time, r_i is the natural log of species i's discrete geometric rate of growth from time t to $t+1$: $r_i = \log(N_i(t+1)/N_i(t))$. In continuous time, r_i is the per capita growth rate of species i: $r_i = \mathrm{d}N_i/(N_i \mathrm{d}t)$.

2. Limit cycle of fixed period length T in discrete time, for communities of unstructured populations (Barabás & Ostling 2013):

$$\sigma_i = \frac{1}{N_i(0)} \frac{\mathrm{d}N_i(0)}{\mathrm{d}\mathbb{E}}, \quad a_{ij} = -\delta_{ij} + \prod_{t=T-1}^{0} \left(\delta_{ij} + \sum_{\mu} \underbrace{\frac{\partial r_i(t)}{\partial \mathcal{R}_\mu(t)}}_{\mathcal{S}_{i,\mu}(t)} \underbrace{\frac{\partial \mathcal{R}_\mu(t)}{\partial N_j(t)} N_j(t)}_{\mathcal{I}_{j,\mu}(t)} \right), \quad z_j = \sum_{t=0}^{T-1} \frac{\partial r_j(t)}{\partial \mathbb{E}}, \tag{34}$$

where $r_i(t) = \log(N_i(t+1)/N_i(t))$, and δ_{ij} is the identity matrix (equal to 1 if $i = j$ and to 0 otherwise). The product from $t = T-1$ to 0 above refers to the (i,j)th entry of a product of matrices (taken in decreasing order in time), not to the product of the (i,j)th entries—see Eqs. (S12) and (S13) in the Supporting Information for the special case of $T = 2$. Note that the regulating factors are functions of t within the cycle, so each regulating variable at each moment in time can potentially serve as a separate regulating factor.

3. Limit cycle of fixed period length T in continuous time, for communities of unstructured populations (Barabás *et al.* 2012a): this is obtained simply from Eq. (34) in the limit of infinitely many infinitesimally small discrete time steps Δt (Barabás & Ostling 2013):

$$\sigma_i = \frac{1}{N_i(0)} \frac{\mathrm{d}N_i(0)}{\mathrm{d}\mathbb{E}}, \; a_{ij} = -\delta_{ij} + \mathcal{T}\mathrm{Exp}\left(\int_0^T \sum_{\mu} \underbrace{\frac{\partial r_i(t)}{\partial \mathcal{R}_\mu(t)}}_{\mathcal{S}_{i,\mu}(t)} \underbrace{\frac{\partial \mathcal{R}_\mu(t)}{\partial N_j(t)} N_j(t)}_{\mathcal{I}_{j,\mu}(t)} \,\mathrm{d}t \right), \; z_j = \int_0^T \frac{\partial r_j(t)}{\partial \mathbb{E}} \,\mathrm{d}t, \tag{35}$$

where Exp means matrix exponential (obtained by substituting the matrix in the argument into the usual Taylor series of the exponential function), and $\mathcal{T}$ is the time-ordering operator that rearranges a product of matrices to decreasing order in time (Barabás *et al.* 2012a).

4. Fixed point dynamics in either discrete or continuous time, for communities of structured populations (Szilágyi & Meszéna 2009a, Barabás *et al.* 2014):

$$\sigma_i = \frac{\mathrm{d}N_i}{\mathrm{d}\mathbb{E}}, \quad a_{ij} = \sum_{\mu} \underbrace{\left(\sum_{a,b} v_{i,a} \frac{\partial A_{i,ab}}{\partial \mathcal{R}_\mu} w_{i,b} \right)}_{\mathcal{S}_{i,\mu}} \underbrace{\sum_{\nu} \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \left(\sum_{c} \frac{\partial \mathcal{R}_\nu}{\partial N_{j,c}} w_{j,c} \right)}_{\mathcal{I}_{j,\mu}},$$

$$z_j = \sum_{a,b} v_{j,a} \frac{\partial A_{j,ab}}{\partial \mathbb{E}} w_{j,b} + \sum_{\mu,\nu} \left(\sum_{a,b} v_{i,a} \frac{\partial A_{i,ab}}{\partial \mathcal{R}_\mu} w_{i,b} \right) \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \frac{\partial \mathcal{G}_\nu}{\partial \mathbb{E}}, \tag{36}$$

where $A_{i,ab}$ is the (a,b)th entry of species i's projection matrix evaluated at equilibrium; N_i is the weighted total abundance of species i; $\delta_{\mu\nu}$ is the identity matrix; $v_{i,a}$, $w_{i,a}$, and $N_{i,a}$ are the ath component of species i's leading left and right eigenvectors and population abundance vector, respectively; the inverses always refer to the (μ,ν)th entries of the inverse matrix as opposed to the inverse of the (μ,ν)th entries; and

$$\mathcal{G}_\mu(\mathcal{R}_\nu, \mathbb{E}) = \sum_{j} \sum_{a,b,c} \left(\frac{n_j}{\sum_d q_{j,d} w_{j,d}} \frac{\partial \mathcal{R}_\mu}{\partial n_{j,a}} \sum_{k=2}^{s_j} \frac{1}{\lambda_j - \lambda_j^k} \left(w_{j,a}^k - \frac{\sum_e q_{j,e} w_{j,e}^k}{\sum_f q_{j,f} w_{j,f}} w_{j,a} \right) v_{j,b}^k \right) \\ \times A_{j,bc}(\mathcal{R}_\nu, \mathbb{E}) \, w_{j,c} \tag{37}$$

describes the effect of perturbing the species' population structures on the regulation of the community (the dependence of $\mathcal{G}_\mu$ on $\mathcal{R}_\nu$ and $\mathbb{E}$ comes strictly from $A_{j,bc}$; all other quantities are evaluated at the unperturbed equilibrium). Here $q_{j,a}$ is a positive vector giving the weight of the ath stage class in the weighted total abundance of species j, λ_j is species j's leading eigenvalue, s_j is the number of stage classes of species j, and the superscript k means we are considering the kth (non-leading) eigenvalue/eigenvector. The eigenvectors are normalized so that $\sum_a w_{i,a} = 1$ and $\sum_a v_{i,a}^k w_{i,a}^l = \delta_{kl}$ for every species i. Though the nature of the population structure can be arbitrary (age, stage, physiological, spatial,...), in the special case of spatial structure a single regulating factor $\mathcal{R}$ can be thought of as splitting up into as many different factors as the number of distinct spatial locations.

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Sensitivity Analysis of Coexistence in Ecological Communities: Theory and Application

Supporting Information

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Sensitivity analysis of forb-grass competition

Model description

The model of Levine & Rees (2004) is a discrete-time annual plant model. The equations read

$$N_i(t+1) = \left((1-g_i(t))(1-d_i) + \frac{\lambda_i(t) g_i(t)}{1+\alpha_i\left(g_1(t)N_1(t)/\alpha + g_2(t)N_2(t)\right)} \right) N_i(t), \qquad \text{(S1)}$$

where the species index i may be 1 (forb) or 2 (grass), and $N_i(t)$ is the number of seeds of species i in the seed bank in year t prior to germination. The vector $\alpha_i = (\alpha,\ 1)$ is shorthand for α when $i = 1$ and 1 when $i = 2$. The description and numerical value of each parameter are given in Table S1. In this model we assume that the fecundities and germination rates fluctuate periodically between "good" and "bad" years.

$\mathbb{E}$	Description	Value
d_1	Forb death rate in the seed bank	0.1
d_2	Grass death rate in the seed bank	0.7
g_1^-	Fraction of forb seeds germinating in a bad year	0.1
g_1^+	Fraction of forb seeds germinating in a good year	0.7
g_2^-	Fraction of grass seeds germinating in a bad year	0.9
g_2^+	Fraction of grass seeds germinating in a good year	0.9
λ_1^-	Number of forb seeds/individual in a bad year	5
λ_1^+	Number of forb seeds/individual in a good year	30
λ_2^-	Number of grass seeds/individual in a bad year	5
λ_2^+	Number of grass seeds/individual in a good year	30
α	Reciprocal interspecific competition coefficient	2

Table S1: Numerical value and description of each parameter in the Levine–Rees model. The environment is assumed to oscillate between good $(+)$ and bad $(-)$ years, as shown by the variation in the fecundities and germination probabilities. The symbol $\mathbb{E}$ stands for any one model parameter.

The expression in parentheses in Eq. (S1) is the annual geometric growth rate of species i; its natural log is the growth rate $r_i(t)$:

$$r_i(t) = \log\left((1-g_i(t))(1-d_i) + \frac{\lambda_i(t) g_i(t)}{1+\alpha_i\left(g_1(t)N_1(t)/\alpha + g_2(t)N_2(t)\right)} \right). \qquad \text{(S2)}$$

Sensitivity analysis

Here we go through all the steps of calculating the sensitivity of the stationary state to each model parameter. The steps required for the analysis are outlined in the Box.

Box: The steps of community-wide sensitivity analysis

- *Step 0:* Determine whether the model is in discrete or continuous time, whether the populations are structured, and what type of equilibrium (fixed point, limit cycle, ...) is under consideration.
- *Step 1:* Designate the regulating factors.
- *Step 2:* Based on Step 0, look up the necessary formulas for the impact and sensitivity vectors, and calculate them for each species.
- *Step 3:* Calculate the volumes $\mathcal{V}_{\mathcal{I}}$ and $\mathcal{V}_{\mathcal{S}}$. A small product $\mathcal{V}_{\mathcal{I}}\mathcal{V}_{\mathcal{S}}$ signals an oversensitive system. For more precise quantitative estimates, move on to Step 4.
- *Step 4:* Calculate a_{ij} using the formula appropriate for the particular dynamical scenario under consideration.
- *Step 5:* Pick an arbitrary model parameter $\mathbb{E}$ of interest and obtain the vector z_j from the appropriate formula.
- *Step 6:* Calculate the sensitivities σ_i from the general equation

$$\sigma_i = -\sum_{j=1}^{S} a_{ij}^{-1} z_j,$$

where a_{ij}^{-1} refers to the (i,j)th entry of the inverse matrix, as opposed to the inverse of its (i,j)th entry.

Step 0. As mentioned before, we assume the environment alternates regularly between good and bad years. This will generate a stationary two-cycle. If the model has a two-cycle, the twice-compounded model has a fixed point. Solving for the fixed point yields two possible solutions, corresponding to the two distinct points within the cycle. Using Eq. (S2), the total population growth over two time steps is zero:

$$\begin{aligned}&\log\left((1-g_i(0))(1-d_i)+\frac{\lambda_i(0)g_i(0)}{1+\alpha_i\left(g_1(0)N_1(0)/\alpha+g_2(0)N_2(0)\right)}\right)\\&+\log\left((1-g_i(1))(1-d_i)+\frac{\lambda_i(1)g_i(1)}{1+\alpha_i\left(g_1(1)N_1(1)/\alpha+g_2(1)N_2(1)\right)}\right)=0.\end{aligned} \tag{S3}$$

Expressing $N_i(1)$ through $N_i(0)$ by setting $t = 0$ in Eq. (S1), and substituting the result into Eq. (S3), we get

$$
\begin{aligned}
&\log\left((1-g_i(0))(1-d_i)+\frac{\lambda_i(0)g_i(0)}{1+\alpha_i\left(g_1(0)N_1(0)/\alpha+g_2(0)N_2(0)\right)}\right)\\
&+\log\Bigg((1-g_i(1))(1-d_i)+\lambda_i(1)g_i(1)\\
&\times\Bigg[1+\frac{\alpha_i g_1(1)}{\alpha}\left((1-g_1(0))(1-d_1)+\frac{\lambda_1(0)g_1(0)}{1+g_1(0)N_1(0)+\alpha g_2(0)N_2(0)}\right)\\
&+\alpha_i g_2(1)\left((1-g_2(0))(1-d_2)+\frac{\lambda_2(0)g_2(0)}{1+g_1(0)N_1(0)/\alpha+g_2(0)N_2(0)}\right)\Bigg]^{-1}\Bigg)=0.
\end{aligned}
\tag{S4}
$$

This constitutes one equation for $N_1(0)$ and $N_2(0)$ each, giving the fixed point of the twice-compounded model (i.e., the limit cycle of the original one). With the parameters given in Table S1, the solution can be obtained numerically via any reputable algorithm for solving systems of nonlinear algebraic equations. The two pairs of solutions are

$$
\begin{aligned}
&\left(N_1^- = 23.636;\quad N_2^- = 10.044\right),\\
&\left(N_1^+ = 19.697;\quad N_2^+ = 4.329\right),
\end{aligned}
\tag{S5}
$$

as is easily verified by substituting these values back into Eq. (S4) along with the parameter values in Table S1 (naturally, there will be some rounding error involved). The N_i^- and N_i^+ are the population densities along the two-cycle. Though the literal calculation we performed was for obtaining the densities in year $t = 0$, we got two different results because it is completely arbitrary whether we designate $t = 0$ to be a bad or a good year. This means that we can interpret N_i^- as the densities in a bad year, and N_i^+ as the densities in a good year.

As this is a discrete-time model with unstructured populations, and since the attractor under consideration is a limit cycle, the formulas needed for the analysis are

$$
\sigma_i=\frac{1}{N_i(0)}\frac{\mathrm{d}N_i(0)}{\mathrm{d}\mathbb{E}},\quad a_{ij}=-\delta_{ij}+\prod_{t=T-1}^{0}\left(\delta_{ij}+\sum_{\mu}\underbrace{\frac{\partial r_i(t)}{\partial\mathcal{R}_\mu(t)}}_{\mathcal{S}_{i,\mu}}\underbrace{\frac{\partial\mathcal{R}_\mu(t)}{\partial N_j(t)}N_j(t)}_{\mathcal{I}_{j,\mu}}\right),\quad z_j=\frac{\partial}{\partial\mathbb{E}}\sum_{t=0}^{T-1}r_j(t)
\tag{S6}
$$

(Barabás & Ostling 2013), where δ_{ij} is the identity matrix, equal to 1 if $i = j$ and to 0 otherwise. These quantities are connected through the general sensitivity formula

$$
\sigma_i=-\sum_{j=1}^{S}a_{ij}^{-1}z_j,
\tag{S7}
$$

where a_{ij}^{-1} is the (i, j)th entry of the inverse matrix, not the inverse of its (i, j)th entry.

Step 1. We choose the regulating factors. It is actually possible to designate a single time-dependent regulating factor for this model:

$$\mathcal{R}(t) = \frac{g_1(t)N_1(t)}{\alpha} + g_2(t)N_2(t). \tag{S8}$$

The growth rates in Eq. (S2) read, as a function of this regulating factor, as

$$r_i(t) = \log\left((1-g_i(t))(1-d_i) + \frac{\lambda_i(t)g_i(t)}{1+\alpha_i\mathcal{R}(t)}\right). \tag{S9}$$

Keeping $\mathcal{R}(t)$ constant, we see that these growth rates would become density-independent, therefore our choice for the regulating factors is valid.

Step 2. We calculate the impact and sensitivity vectors. From their definitions in Eq. (S6):

$$\mathcal{I}_j(t) = \frac{\partial\mathcal{R}(t)}{\partial N_j(t)} = \frac{g_j(t)}{\alpha_j}, \tag{S10}$$

$$\mathcal{S}_i(t) = \frac{\partial r_i(t)}{\partial\mathcal{R}(t)} = \left((1-g_i(t))(1-d_i) + \frac{\lambda_i(t)g_i(t)}{1+\alpha_i\mathcal{R}(t)}\right)^{-1} \frac{\alpha_i\lambda_i(t)g_i(t)}{(1+\alpha_i\mathcal{R}(t))^2}. \tag{S11}$$

Step 3. The volumes spanned by the impact and sensitivity vectors may now be calculated using Eq. (S69) (see the Appendix). We do not perform this step here (we will do so for our other two model examples); instead, we go straight to the detailed sensitivity analysis.

Step 4. The matrix a_{ij} in Eq. (S6) is written for our model as

$$a_{ij} = -\delta_{ij} + \prod_{t=1}^{0}\left(\delta_{ij} + \frac{\partial r_i(t)}{\partial\mathcal{R}(t)}\frac{\partial\mathcal{R}(t)}{\partial N_j(t)}N_j(t)\right), \tag{S12}$$

or, writing out the matrix product, as

$$a_{ij} = -\delta_{ij} + \sum_{k=1}^{2}\left(\delta_{ik} + \frac{\partial r_i(1)}{\partial\mathcal{R}(1)}\frac{\partial\mathcal{R}(1)}{\partial N_k(1)}N_k(1)\right)\left(\delta_{kj} + \frac{\partial r_k(0)}{\partial\mathcal{R}(0)}\frac{\partial\mathcal{R}(0)}{\partial N_j(0)}N_j(0)\right). \tag{S13}$$

We substitute into this expression the equations for the impact and sensitivity vectors, the parameter values in Table S1, and the stationary densities in Eq. (S5). We get two different results depending on whether the initial moment $t = 0$ of the cycle is a bad or a good year. If it is a bad year, we get

$$a_{ij}^{-} = -\begin{pmatrix} 0.449 & 0.079 \\ 0.641 & 0.818 \end{pmatrix}. \tag{S14}$$

Alternatively, if $t = 0$ is a good year, we get

$$a_{ij}^{+} = -\begin{pmatrix} 0.461 & 0.283 \\ 0.196 & 0.805 \end{pmatrix}. \tag{S15}$$

$\mathbb{E}$	z_1^-	z_2^-	z_1^+	z_2^+
d_1	-0.819	0.623	-1.329	0.024
d_2	0.062	-0.199	0.001	-0.243
g_1^-	-0.176	-0.181	-0.831	-0.980
g_1^+	-0.319	-0.825	-0.298	-0.175
g_2^-	0.119	-0.318	-0.026	-0.495
g_2^+	-0.297	0.605	-0.311	0.181
λ_1^-	0.003	-0.003	0.006	0
λ_1^+	0.026	0	0.026	-0.003
λ_2^-	-0.050	0.125	0	0.186
λ_2^+	0	0.033	-0.001	0.008
α	-0.153	0.328	-0.152	-0.134

Table S2: The two components of the vector z_j for each parameter. The superscript of z_j is "$-$" if the initial moment of the cycle is a bad year, and "$+$" if it is a good year.

$\mathbb{E}$	$\mathrm{d}N_1^-/\mathrm{d}\mathbb{E}$	$\mathrm{d}N_2^-/\mathrm{d}\mathbb{E}$	$\mathrm{d}N_1^+/\mathrm{d}\mathbb{E}$	$\mathrm{d}N_2^+/\mathrm{d}\mathbb{E}$
d_1	-53.81	25.59	-67.16	3.73
d_2	4.98	-4.11	4.33	-1.54
g_1^-	-9.68	1.01	-24.45	-3.96
g_1^+	-14.61	-5.26	-11.89	-0.31
g_2^-	9.15	-6.96	7.41	-3.06
g_2^+	-21.78	14.69	-18.77	1.98
λ_1^-	0.20	-0.11	0.28	-0.02
λ_1^+	1.58	-0.53	1.34	-0.09
λ_2^-	-3.79	2.80	-3.28	1.18
λ_2^+	-0.20	0.47	-0.18	0.05
α	-11.32	7.81	-9.99	1.26

Table S3: Sensitivity of forb and grass densities at the initial moment of the cycle to parameter perturbations. The superscript of N_i is "$-$" if the initial moment of the cycle is a bad year, and "$+$" if it is a good year.

Step 5. To obtain the z_j from Eq. (S6), we need the sum of the growth rates for the two points of the cycle. This is given by the left hand side of Eq. (S4). We then take the derivative of this expression with respect to each parameter in turn and substitute numerical values from Table S1 and Eq. (S5) into the results to get the z_j. Again, two different sets of results emerge depending on whether we designate $t = 0$ to be a bad or a good year. Table S2 contains the results.

Step 6. The cycle's sensitivity to each parameter can now be obtained via Eq. (S7). That is, if $t = 0$ is a bad year, we multiply the vector z_j^- (given in Table S2) by the inverse of the matrix a_{ij}^-

times minus one. Since the sensitivity σ_i is given by the derivative of the densities divided by the densities (Eq. S6), we multiply the result by N_i^- (given in Eq. S5) to obtain $\mathrm{d}N_i(0)/\mathrm{d}\mathbb{E}$. If $t = 0$ is a good year, then we multiply z_j^+ by the inverse of a_{ij}^+ and then multiply by minus one times N_i^+. See Table S3 for all sensitivity values.

As a final remark, we emphasize again that coexistence in this model is maintained purely by environmental fluctuations. Using the framework and terminology of Chesson, coexistence is maintained by pure storage effect (Chesson & Warner 1981, Chesson 1994, 2000). Relative nonlinearity is not operating because $\mathcal{R}(t)$ is a linear function of the population densities (Eq. S8), and fluctuation-independent mechanisms are also not operating because in the absence of fluctuations there is just a single regulating factor and therefore no coexistence.[*] Therefore the only stabilizing mechanism is the temporal storage effect. We highlight that our sensitivity approach to understanding coexistence differs from Chesson's in that Chesson uses the invader's long-term growth rate to see whether coexistence is possible via mutual invasibility, while the sensitivity approach quantifies coexistence via the range of parameters that will allow for it. See Barabás *et al.* (2012, Appendix 3) and Barabás & Ostling (2013, Section 4) for the precise mathematical relationship between the two frameworks.

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[*] A single regulating factor means the impact and sensitivity vectors are confined to a one-dimensional space. The volume spanned by the vectors of more than one species is therefore necessarily zero, leading to loss of robustness and the breakdown of coexistence.

The tolerance-fecundity tradeoff model

Model description

Consider a set of sites, each of which may be occupied by a single sessile individual. The sites vary in the local stress level s_a, where a runs from 1 to M: s_1 is the stress level of the least stressful site and s_M is that of the most stressful, with various gradations in between (by choosing a sufficiently large M, the classification of stress levels can be made arbitrarily fine-grained). Individuals produce seeds that disperse into all sites with a uniform probability distribution. Their fecundities are high enough that no site remains empty after reproduction. Once a seed reaches a vacant site, it has to survive the local stress conditions. Among the seeds that do survive, a lottery draw decides who wins the site. Regardless of stress level, once an individual wins a site, it cannot be displaced except by natural death happening at a species-specific mortality rate.

Assuming that the community consists of S species, this model may be written as

$$\frac{\mathrm{d}N_{i,a}}{\mathrm{d}t} = f_i N_i Q_i(s_a) - m_i N_{i,a} \qquad (i = 1 \ldots S), \tag{S16}$$

where $N_{i,a}$ is the number of sites of stress level s_a occupied by species i, f_i is species i's per capita rate of seed production, m_i is the adult mortality rate of species i, $Q_i(s_a)$ is the probability that one of species i's seeds fall on a site of stress level s_a and recruits there, and N_i is the total number of sites species i occupies, i.e.

$$N_i = \sum_{a=1}^{M} N_{i,a}. \tag{S17}$$

The per-seed probability of successful recruitment $Q_i(s_a)$ is the product of three independent probabilities. First, we need to calculate the probability $G(s_a)$ that a seed arrives at an empty site of stress level s_a. This is given by

$$G(s_a) = \frac{c(s_a) - \sum_{i=1}^{S} N_{i,a}}{\sum_{b=1}^{M} c(s_b)}, \tag{S18}$$

where $c(s_a)$ is the number of sites of stress level s_a, so the numerator expresses the number of sites of stress s_a that are not yet occupied, and the denominator is simply the total number of sites altogether. Second, once a seed arrives at a site, it has to survive the local stress level. Let us denote the probability that species i's seed survives stress level s by $T_i(s)$ and call it the tolerance function (Figure S1A). It is assumed to be a decreasing function of stress level, and it is also assumed that species with higher fecundities f_i are less tolerant of stress, which is the essence of the tolerance-fecundity tradeoff (Muller-Landau 2010, D'Andrea *et al.* 2013). Third, from the pool of seeds that arrived at a site of stress level s_a and survived, one is chosen via lottery draw to win the site. Let $F(s_a)$ be the total number of seeds that survive on a site of stress level s_a. Then $1/F(s_a)$ is the probability of winning the lottery draw. But $F(s_a)$ is simply given by

$$F(s_a) = \frac{\sum_{k=1}^{S} f_k N_k T_k(s_a)}{\sum_{b=1}^{M} c(s_b)}, \tag{S19}$$

the total number of surviving seeds divided by the total number of sites. Therefore, $Q_i(s_a)$ may be written

$$Q_i(s_a) = G(s_a)T_i(s_a)\frac{1}{F(s_a)} = T_i(s_a)\frac{c(s_a) - \sum_{i=1}^{S} N_{i,a}}{\sum_{k=1}^{S} f_k N_k T_k(s_a)}. \tag{S20}$$

Substituting this expression into Eq. (S16) yields

$$\frac{\mathrm{d}N_{i,a}}{\mathrm{d}t} = f_i N_i T_i(s_a)\frac{c(s_a) - \sum_{i=1}^{S} N_{i,a}}{\sum_{k=1}^{S} f_k N_k T_k(s_a)} - m_i N_{i,a}. \tag{S21}$$

Let us cast this model equation in the form of traditional structured population models:

$$\frac{\mathrm{d}N_{i,a}}{\mathrm{d}t} = \sum_{b=1}^{M}\left(f_i T_i(s_a)\frac{c(s_a) - \sum_{i=1}^{S} N_{i,a}}{\sum_{k=1}^{S} f_k N_k T_k(s_a)} - m_i \delta_{ab}\right) N_{i,b}, \tag{S22}$$

where we used Eq. (S17) in the first term on the right hand side, and the δ_{ab} in the second term is the identity matrix, equal to 1 if $a = b$ and to 0 otherwise. The expression in parentheses is the projection matrix $A_{i,ab}$ of species i, multiplying the stage distribution vector $N_{i,b}$:

$$A_{i,ab} = f_i T_i(s_a)\frac{c(s_a) - \sum_{i=1}^{S} N_{i,a}}{\sum_{k=1}^{S} f_k N_k T_k(s_a)} - m_i \delta_{ab}. \tag{S23}$$

The model therefore describes a community of interacting structured populations in continuous time, where the ath stage class of species i measures the number of sites of stress level s_a that species i occupies.

Sensitivity analysis

For the tolerance-fecundity tradeoff model we are only performing qualitative sensitivity analysis, i.e., we calculate the impact and sensitivity vectors and the volumes they span but do not evaluate the full sensitivity formula.

Step 0. As demonstrated elsewhere numerically (D'Andrea *et al.* 2013), this model converges to a stable equilibrium state. We therefore wish to analyze the sensitivity of this fixed point, generated by the model which is in continuous time and involves population structure. The appropriate sensitivity formulas are therefore given by

$$\sigma_i = \frac{\mathrm{d}N_i}{\mathrm{d}\mathbb{E}}, \quad a_{ij} = \sum_{\mu} \underbrace{\left(\sum_{a,b} v_{i,a}\frac{\partial A_{i,ab}}{\partial \mathcal{R}_\mu} w_{i,b}\right)}_{\mathcal{S}_{i,\mu}} \underbrace{\left(\sum_{c} \frac{\partial \mathcal{R}_\mu}{\partial N_{j,c}} w_{j,c}\right)}_{\mathcal{I}_{j,\mu}}, \quad z_j = \sum_{a,b} v_{j,a}\frac{\partial A_{j,ab}}{\partial \mathbb{E}} w_{j,b} \tag{S24}$$

(Szilágyi & Meszéna 2009, Barabás *et al.* 2014), where $v_{i,a}$ and $w_{i,a}$ are the ath component of the left and right leading eigenvectors of $A_{i,ab}$, respectively. Note that these are simplified expressions;

the fully general form (which we do not need here) is found in Box 3 of the main text or in Barabás *et al.* (2014, Eq. 29). For these formulas to hold, the normalization conditions

$$\sum_{a=1}^{M} w_{i,a} = 1, \qquad \sum_{a=1}^{M} v_{i,a} w_{i,a} = 1 \tag{S25}$$

have to be observed for all i. Biologically, since Eq. (S24) is evaluated at equilibrium, the left leading eigenvector is the reproductive value vector while the right leading eigenvector is the stable stage distribution.

In general we would need to solve the model for the equilibrium state. This model is complicated enough that this would only be possible using numerical simulations. However, as we will see, explicit knowledge of the equilibrium state is not needed to draw useful qualitative conclusions about the behavior of this system.

Step 1. We choose the regulating factors. Notice that the $A_{i,ab}$ depend on the densities only through the fraction in the first term of Eq. (S23). Therefore a natural choice for the regulating factors is

$$\mathcal{R}(s_a) = \frac{c(s_a) - \sum_{i=1}^{S} N_{i,a}}{\sum_{k=1}^{S} f_k N_k T_k(s_a)} = \frac{G(s_a)}{F(s_a)}, \tag{S26}$$

which is the density-dependent factor in $Q_i(s_a)$. The projection matrices then read

$$A_{i,ab} = f_i T_i(s_a) \mathcal{R}(s_a) - m_i \delta_{ab}, \tag{S27}$$

which is density-independent if we keep $\mathcal{R}(s_a)$ artificially fixed for all a, i.e., this is indeed a proper choice for the regulating factors.

In this model, space is the only limiting resource. However, space is not homogeneous, as sites differ in stress level. One therefore has to measure crowding for each stress level separately, resulting in M different regulating factors, the $\mathcal{R}(s_a)$ for every a. If the gradation of various stress levels is infinitely fine-grained (i.e., we have a smooth stress gradient), $M \to \infty$ and we have infinitely many regulating factors, in perfect analogy with a resource continuum.

Step 2a. We first calculate the sensitivity vectors, and then the impact vectors (Step 2b). From Eq. (S24), the sensitivity of the ith species to the μth regulating factor reads

$$\mathcal{S}_{i,\mu} = \sum_{a=1}^{M} \sum_{b=1}^{M} v_{i,a} \frac{\partial A_{i,ab}}{\partial \mathcal{R}(s_\mu)} w_{i,b}. \tag{S28}$$

The derivative can be calculated directly using Eq. (S27):

$$\frac{\partial A_{i,ab}}{\partial \mathcal{R}(s_\mu)} = \frac{\partial}{\partial \mathcal{R}(s_\mu)} \Big(f_i T_i(s_a) \mathcal{R}(s_a) - m_i \delta_{ab} \Big) = f_i T_i(s_a) \delta_{a\mu}. \tag{S29}$$

To evaluate the eigenvectors of $A_{i,ab}$, notice first that the second term on the right hand side of Eq. (S27) is proportional to the identity matrix and does not influence the eigenvectors. Therefore, only the first term (let us denote it by U_{ab}) needs to be considered for calculating eigenvectors. This first term can also be written $U_{ab} = g_a h_b$, where $g_a = f_i T_i(s_a)\mathcal{R}(s_a)$ and $h_b = 1$ (each component of h_b is equal to 1). Such a matrix has only one right and corresponding left eigenvector (given by g_a and h_b themselves) such that their corresponding eigenvalue is nonzero. Indeed, for any vector x_a,

$$\sum_{b=1}^{M} U_{ab} x_b = \sum_{b=1}^{M} g_a h_b x_b = g_a \left(\sum_{b=1}^{M} h_b x_b \right), \tag{S30}$$

therefore $x_a = g_a$ is the only right eigenvector with a nonzero eigenvalue. Similarly, h_a is the only left eigenvector with a nonzero eigenvalue, because for any vector x_a,

$$\sum_{b=1}^{M} x_b U_{ba} = \sum_{b=1}^{M} x_b g_b h_a = h_a \left(\sum_{b=1}^{M} g_b x_b \right). \tag{S31}$$

From this it is also clear that the nonzero eigenvalue itself is given by $\sum_{a=1}^{M} g_a h_a$. As both g_a and h_a are, in our case, vectors with positive components, this eigenvalue must be some positive number. This means that, since all the other eigenvalues are zero, this eigenvalue is the leading one. Therefore, its left and right eigenvectors must correspond to the reproductive value and the stable stage distribution, respectively.

The stable stage distribution is then proportional to $g_a = f_i T_i(s_a)\mathcal{R}(s_a)$:

$$w_{i,a} = q_i f_i T_i(s_a)\mathcal{R}(s_a), \tag{S32}$$

where

$$q_i = \left(\sum_{a=1}^{M} f_i T_i(s_a)\mathcal{R}(s_a) \right)^{-1} \tag{S33}$$

ensures proper normalization. Similarly, since $h_a = 1$, the properly normalized left eigenvector is

$$v_{i,a} = 1 \tag{S34}$$

for all species. Using Eqs. (S29), (S32), and (S34), the sensitivity vectors can now be calculated from the definition Eq. (S28):

$$\begin{aligned} \mathcal{S}_{i,\mu} &= \sum_{a=1}^{M} \sum_{b=1}^{M} v_{i,a} \frac{\partial A_{i,ab}}{\partial \mathcal{R}(s_\mu)} w_{i,b} = \sum_{a=1}^{M} \sum_{b=1}^{M} f_i T_i(s_a) \delta_{a\mu} q_i f_i T_i(s_b) \mathcal{R}(s_b) \\ &= \sum_{a=1}^{M} f_i T_i(s_a) \delta_{a\mu} q_i \underbrace{\left(\sum_{b=1}^{M} f_i T_i(s_b) \mathcal{R}(s_b) \right)}_{1/q_i} = \sum_{a=1}^{M} f_i T_i(s_a) \delta_{a\mu} = f_i T_i(s_\mu). \end{aligned} \tag{S35}$$

In words, the sensitivity vector of species i is its tolerance function weighted by its fecundity. This can be evaluated without any knowledge of the system's dynamics or current state.

Step 2b. The formula for the impact vector of the jth species on the μth regulating factor in structured community models is given in Eq. (S24) as

$$\mathcal{I}_{j,\mu} = \sum_{a=1}^{M} \frac{\partial \mathcal{R}(s_\mu)}{\partial N_{j,a}} w_{j,a}. \tag{S36}$$

Using Eq. (S32), this becomes

$$\mathcal{I}_{j,\mu} = \sum_{a=1}^{M} \frac{\partial \mathcal{R}(s_\mu)}{\partial N_{j,a}} q_j f_j T_j(s_a) \mathcal{R}(s_a). \tag{S37}$$

We calculate the partial derivative:

$$\begin{aligned}\frac{\partial \mathcal{R}(s_\mu)}{\partial N_{j,a}} &= -\frac{\delta_{a\mu}}{\sum_{k=1}^{S} f_k N_k T_k(s_\mu)} - \frac{c(s_\mu) - \sum_{i=1}^{S} N_{i,\mu}}{\left(\sum_{k=1}^{S} f_k N_k T_k(s_\mu)\right)^2} \underbrace{\frac{\partial}{\partial N_{j,a}} \left(\sum_{k=1}^{S} f_k \left(\sum_{b=1}^{M} N_{k,b} \right) T_k(s_\mu) \right)}_{f_j T_j(s_\mu)} \\ &= -\frac{\delta_{a\mu}}{\sum_{k=1}^{S} f_k N_k T_k(s_\mu)} - \frac{c(s_\mu) - \sum_{i=1}^{S} N_{i,\mu}}{\left(\sum_{k=1}^{S} f_k N_k T_k(s_\mu)\right)^2} f_j T_j(s_\mu),\end{aligned} \tag{S38}$$

or, using Eq. (S26) in the second term,

$$\frac{\partial \mathcal{R}(s_\mu)}{\partial N_{j,a}} = -\left(\frac{\delta_{a\mu}}{\sum_{k=1}^{S} f_k N_k T_k(s_\mu)} + \frac{f_j T_j(s_\mu) \mathcal{R}(s_\mu)}{\sum_{k=1}^{S} f_k N_k T_k(s_\mu)} \right). \tag{S39}$$

The impact vectors then read

$$\mathcal{I}_{j,\mu} = -\sum_{a=1}^{M} \left(\frac{\delta_{a\mu}}{\sum_{k=1}^{S} f_k N_k T_k(s_\mu)} + \frac{f_j T_j(s_\mu) \mathcal{R}(s_\mu)}{\sum_{k=1}^{S} f_k N_k T_k(s_\mu)} \right) q_j f_j T_j(s_a) \mathcal{R}(s_a), \tag{S40}$$

which can be written as

$$\mathcal{I}_{j,\mu} = -\frac{q_j f_j T_j(s_\mu) \mathcal{R}(s_\mu)}{\sum_{k=1}^{S} f_k N_k T_k(s_\mu)} - \frac{f_j T_j(s_\mu) \mathcal{R}(s_\mu)}{\sum_{k=1}^{S} f_k N_k T_k(s_\mu)} q_j \sum_{a=1}^{M} f_j T_j(s_a) \mathcal{R}(s_a). \tag{S41}$$

Since the last sum is simply equal to $1/q_j$ due to Eq. (S33), the impact vectors are given by

$$\mathcal{I}_{j,\mu} = -\frac{(q_j + 1) f_j T_j(s_\mu) \mathcal{R}(s_\mu)}{\sum_{k=1}^{S} f_k N_k T_k(s_\mu)}. \tag{S42}$$

Step 3a. Here we calculate the volume spanned by the sensitivity vectors. In doing so, it is cleanest to assume there is an arbitrarily fine gradation of stress levels, therefore the sensitivity vector $\mathcal{S}_{i,\mu} = f_i T_i(s_\mu)$ becomes a smooth sensitivity function $\mathcal{S}_i(\mu) = f_i T_i(\mu)$. The volume $\mathcal{V}_\mathcal{S}$

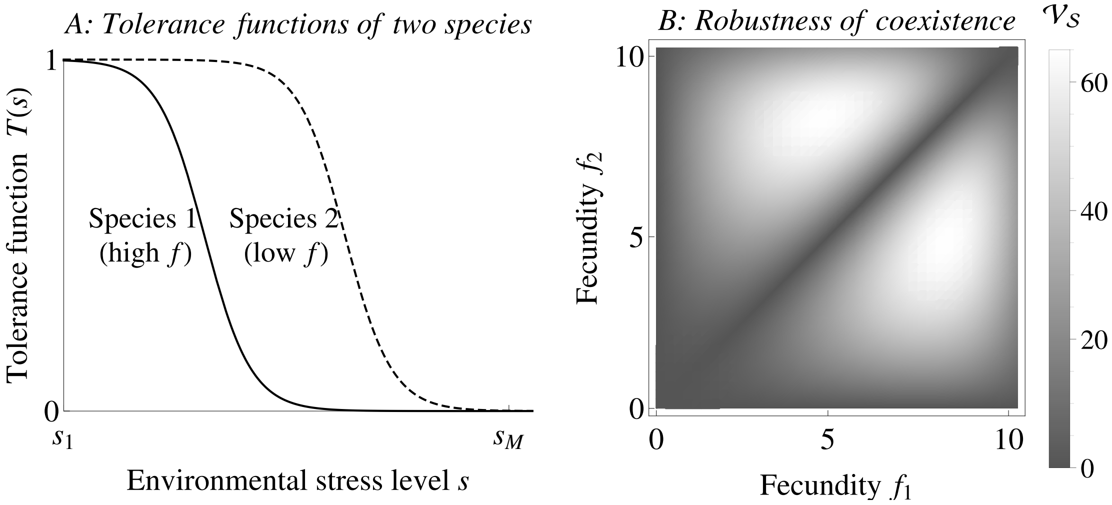

Figure S1: Panel A shows the tolerance functions of two species (solid and dashed curves). The abscissa represents stress, ranging from s_1 (minimum level) to s_M (maximum level). The ordinate is the probability that a seed survives the given stress level. The tolerance functions are sigmoid curves with a relatively abrupt transition from the tolerant to the intolerant regime. The tolerance-fecundity tradeoff is implemented by making the species with the higher fecundity f less tolerant. Panel B shows the volume $\mathcal{V}_S$ spanned by the sensitivity vectors of two species, as a function of their fecundities. The volume is largest where one species has a high fecundity and the other an intermediate one. Both species possessing similar fecundities leads to small volumes. Since a small volume is sufficient for making coexistence oversensitive and therefore unrealistic, it is only in the high-volume regions where coexistence is even a possibility.

(which is an area in our case because we consider $S = 2$) spanned by two sensitivity functions $\mathcal{S}_1(\mu)$ and $\mathcal{S}_2(\mu)$ is given by Eq. (S69) as the determinant of the matrix of scalar products, taking its absolute value and square root (see the Appendix):

$$\mathcal{V}_S = \sqrt{\left| \left(\int_{s_1}^{s_M} \mathcal{S}_1^2(\mu)\,\mathrm{d}\mu \right) \left(\int_{s_1}^{s_M} \mathcal{S}_2^2(\mu)\,\mathrm{d}\mu \right) - \left(\int_{s_1}^{s_M} \mathcal{S}_1(\mu)\mathcal{S}_2(\mu)\,\mathrm{d}\mu \right)^2 \right|}. \tag{S43}$$

The particular form we use for the tolerance function is

$$T_i(s) = \frac{\tanh\left(\tau(s_M - f_i - s)\right) + 1}{2}, \tag{S44}$$

shown on Figure S1A.

We can evaluate the integrals. The indefinite integral of $\mathcal{S}_i^2(\mu)$ is

$$\begin{aligned}\int \mathcal{S}_i^2(\mu)\,\mathrm{d}\mu = f_i^2 \int T_i^2(\mu)\,\mathrm{d}\mu = \frac{f_i^2}{4}\int \bigl(\tanh\bigl(\tau(s_M - f_i - \mu)\bigr)+1\bigr)^2\,\mathrm{d}\mu \\ = -\frac{f_i^2}{4\tau}\left(\tanh\left(\tau\left(f_i+\mu-s_M\right)\right)+2\log\left(\cosh\left(\tau\left(f_i+\mu-s_M\right)\right)\right)-2a\mu\right)+\text{const},\end{aligned} \tag{S45}$$

as is easily verified by taking the expression's derivative with respect to μ. The definite integral then reads

$$\begin{aligned}\int_{s_1}^{s_M}\mathcal{S}_i^2(\mu)\,\mathrm{d}\mu = \frac{f_i^2}{4\tau}\bigl(-\tanh\left(\tau\left(f_i\right)\right)-2\log\left(\cosh\left(\tau\left(f_i\right)\right)\right) \\ +\tanh\left(\tau\left(f_i+s_1-s_M\right)\right)+2\log\left(\cosh\left(\tau\left(f_i+s_1-s_M\right)\right)\right)+2\tau s_M-2s_1\tau\bigr).\end{aligned} \tag{S46}$$

The other integral is

$$\begin{aligned}&\int \mathcal{S}_1(\mu)\mathcal{S}_2(\mu)\,\mathrm{d}\mu = \frac{f_1f_2}{4\tau}\bigl(-\log\left(\cosh\left(\tau\left(f_1+\mu-s_M\right)\right)\right)-\log\left(\cosh\left(\tau\left(f_2+\mu-s_M\right)\right)\right) \\ &+\coth\left(\left(f_1-f_2\right)\tau\right)\left(\log\left(\cosh\left(\tau\left(f_2+\mu-s_M\right)\right)\right)-\log\left(\cosh\left(\tau\left(f_1+\mu-s_M\right)\right)\right)\right)+2\mu\tau\bigr) \\ &+\text{const}.\end{aligned} \tag{S47}$$

Its definite integral is then

$$\begin{aligned}\int_{s_1}^{s_M}\mathcal{S}_1(\mu)\mathcal{S}_2(\mu)\,\mathrm{d}\mu = \frac{f_1f_2}{4\tau}\bigl(-\log\left(\cosh\left(\tau\left(f_1+s_M-s_M\right)\right)\right)-\log\left(\cosh\left(\tau\left(f_2\right)\right)\right) \\ -\coth\left(\left(f_1-f_2\right)\tau\right)\log\left(\cosh\left(\tau\left(f_1\right)\right)\right)+\coth\left(\left(f_1-f_2\right)\tau\right)\log\left(\cosh\left(\tau\left(f_2\right)\right)\right) \\ +\log\left(\cosh\left(\tau\left(f_1+s_1-s_M\right)\right)\right)+\log\left(\cosh\left(\tau\left(f_2+s_1-s_M\right)\right)\right) \\ +\coth\left(\left(f_1-f_2\right)\tau\right)\log\left(\cosh\left(\tau\left(f_1+s_1-s_M\right)\right)\right) \\ -\coth\left(\left(f_1-f_2\right)\tau\right)\log\left(\cosh\left(\tau\left(f_2+s_1-s_M\right)\right)\right) \\ +2\tau s_M-2s_1\tau\bigr).\end{aligned} \tag{S48}$$

Substituting Eqs. (S46) and (S48) into Eq. (S43), we get an explicit expression for $\mathcal{V}_{\mathcal{S}}$ as a function of the two fecundities f_1 and f_2:

$$\begin{aligned}\mathcal{V}_{\mathcal{S}} =& \frac{f_1f_2}{4\tau}\Bigl|\bigl(-\tanh(\tau(f_1+s_1-s_M))+2(-\log(\cosh(\tau(f_1+s_1-s_M))) \\ &+\log(\cosh(f_1\tau))+s_1\tau-s_M\tau)+\tanh(f_1\tau)\bigr)\bigl(-\tanh(\tau(f_2+s_1-s_M)) \\ &+2(-\log(\cosh(\tau(f_2+s_1-s_M)))+\log(\cosh(f_2\tau))+s_1\tau-s_M\tau)+\tanh(f_2\tau)) \\ &-\bigl(-\log(\cosh(\tau(f_1+s_1-s_M)))-\log(\cosh(\tau(f_2+s_1-s_M))) \\ &+\coth((f_1-f_2)\tau)\bigl(-\log(\cosh(\tau(f_1+s_1-s_M)))+\log(\cosh(\tau(f_2+s_1-s_M))) \\ &+\log(\cosh(f_1\tau))-\log(\cosh(f_2\tau))\bigr)+\log(\cosh(f_1\tau))+\log(\cosh(f_2\tau)) \\ &+2s_1\tau-2s_M\tau\bigr)^2\Bigr|^{1/2}.\end{aligned} \tag{S49}$$

This is the function plotted on Figure S1B, with $s_1 = 0$, $s_M = 10$, and $\tau = 1$.

Step 3b. The volume spanned by the impact vectors. As Eq. (S42) depends on the stationary densities N_k, the volume $\mathcal{V}_\mathcal{I}$ cannot be evaluated without knowing these quantities. However, this volume is not needed for drawing qualitative conclusions based on the sensitivity vectors only, for the following reason.

In Eq. (S42), $T_j(s_\mu)$ and $\mathcal{R}(s_\mu)$ in the numerator are are quantities whose values fall between 0 and 1. The denominator expresses the seed rain, and since we have made the assumption at the outset that the seed rain contains at least one seed per empty site, the denominator cannot be smaller than 1. The magnitude of any one component of the jth sensitivity vector therefore cannot exceed $(q_j + 1) f_j$. There is no reason why this factor should be very large: f_j is a rate and so proportional to the log of the annual seed production, while q_j is simply a normalizing constant. This means that every component of each impact vector is bounded in magnitude. Therefore, the volume spanned by these vectors will also be bounded.

Since robustness is determined by $\mathcal{V}_\mathcal{I}\mathcal{V}_\mathcal{S}$, this observation means that whenever the volume spanned by the sensitivity vectors is small, robustness will also necessarily be small, because $\mathcal{V}_\mathcal{I}$ is bounded from above and so cannot compensate for a small $\mathcal{V}_\mathcal{S}$.

Moreover, we can see from Eq. (S42) that $\mathcal{I}_{j,\mu}$ is actually proportional to $\mathcal{S}_{j,\mu} = f_j T_j(s_\mu)$, therefore $\mathcal{V}_\mathcal{I}$ will be large/small wherever $\mathcal{V}_\mathcal{S}$ is large/small.

This means that the volumes spanned by the sensitivity vectors are sufficient to determine the robustness of coexistence in the sense that wherever the sensitivity volume is small, coexistence cannot be expected to hold.

The Gross model

Model description

In the model of Gross (2008), there is a single resource and several consumer species. The consumers have facilitative effects on one another: an increase in the abundance of one species reduces the death rate of another. The general form of these death rates is chosen to be

$$m_i = m_i^0 - d_i \left(1 - \exp\left(- \sum_{k=1}^{S} \theta_{ik} N_k \right) \right), \tag{S50}$$

where S is the total number of consumer species, m_i^0 is the baseline mortality of species i, d_i is the maximum advantage it can gain from facilitation (we assume $d_i \leq m_i^0$), N_k is the density of species k, and θ_{ik} is a matrix of scaling factors, measuring the benefit species k confers to species i. Since there is no self-facilitation, the diagonal elements are all zero: $\theta_{ii} = 0$ for all $i = 1 \ldots S$. Using these mortalities, the model equations are written

$$r_i = \frac{1}{N_i} \frac{\mathrm{d}N_i}{\mathrm{d}t} = f_i(R) - m_i \qquad (i = 1 \ldots S) \tag{S51}$$

for the species (r_i is the per capita growth rate of species i as always), and

$$\frac{\mathrm{d}R}{\mathrm{d}t} = g(R) - \sum_{i=1}^{S} c_i f_i(R) N_i \tag{S52}$$

for the resource. Here $f_i(R)$ is the per capita resource-dependent growth rate of species i, the m_i are given by Eq. (S50), R is the amount of resource in the system, $g(R)$ is the resource supply rate, and the c_i measure the amount of resource species i has to consume to produce one unit of biomass.

The form of the mortalities in Eq. (S50) is fairly general. Gross (2008) made the assumption of hierarchical facilitation to narrow it further down. This is implemented by choosing θ_{ik} to be zero for $k \geq i$ and a positive constant otherwise:

$$m_i = m_i^0 - d_i \left(1 - \exp\left(-\theta \sum_{k<i} N_k \right) \right). \tag{S53}$$

Notice that, since the sum only runs through species $k < i$, species i is facilitated only by those who have a lower species index: species 1 is not facilitated by anyone, species 2 is facilitated by species 1, species 3 is facilitated by species 1 and 2, and so on. Also, the advantage a species receives (if any) from a single other species is always the same, θ.

Sensitivity analysis

Here we perform qualitative sensitivity analysis again, calculating the product of the volumes spanned by the impact and sensitivity vectors, and showing that this product converges to zero for large S.

Step 0. It was already proved by Gross (2008) that this system has a stable all-positive fixed point. In the two-species case, limit cycles were also observed. While they cannot be ruled out for $S > 2$, they have not been observed in numerical simulations. Even if there happen to be alternative attractors in phase space, we will concentrate on the sensitivity of the nontrivial fixed point only. Fortunately, as we will see, an explicit knowledge of this equilibrium state will not be needed for our analysis.

Since the model is unstructured, continuous time, and we are analyzing the sensitivity of a fixed point, the appropriate sensitivity formulas are given by

$$\sigma_i = \frac{\mathrm{d}N_i}{\mathrm{d}\mathbb{E}}, \qquad a_{ij} = \sum_{\mu} \underbrace{\frac{\partial r_i}{\partial \mathcal{R}_\mu}}_{\mathcal{S}_{i,\mu}} \underbrace{\frac{\partial \mathcal{R}_\mu}{\partial N_j}}_{\mathcal{I}_{j,\mu}}, \qquad z_j = \frac{\partial r_j}{\partial \mathbb{E}} \tag{S54}$$

(Meszéna *et al.* 2006).

Step 1. We need to designate the regulating factors. We make the following choice:

$$\begin{aligned} \mathcal{R}_1 &= R, \\ \mathcal{R}_\mu &= \exp\left(-\theta \sum_{k<\mu} N_k\right) \qquad (\mu = 2 \ldots S). \end{aligned} \tag{S55}$$

Note that we could have made other choices as well—we could have made $\mathcal{R}_{\mu>1} = \sum_{k<\mu} N_k$ or even just $\mathcal{R}_{\mu>1} = N_\mu$, as all these choices satisfy the criterion that keeping their values artificially fixed leads to the density-independence of the growth rates r_i. However, performing the necessary calculations may be easy with some choices and hard or even impossible with others. In our case, it turns out that Eq. (S55) lends itself to analytical treatment much better than the other choices (see below). The model equations, rewritten in terms of the regulating factors, are

$$\begin{aligned} r_1 &= f_1(\mathcal{R}_1) - m_1^0, \\ r_i &= f_i(\mathcal{R}_1) - m_i^0 + d_i(1 - \mathcal{R}_i) \qquad (i = 2 \ldots S). \end{aligned} \tag{S56}$$

We can see that our choice of regulating factors is valid, because fixing their values would make the per capita growth rates density-independent.

Step 2. The impact vectors $\mathcal{I}_{j,\mu}$ and sensitivity vectors $\mathcal{S}_{i,\mu}$ are calculated using Eq. (S54):

$$\mathcal{I}_{j,\mu} = \frac{\partial \mathcal{R}_\mu}{\partial N_j} = \left(\frac{\partial \mathcal{R}_1}{\partial N_j}, 0, \ldots, 0, \underbrace{-\theta \mathcal{R}_{j+1}}_{\mu=j+1}, -\theta \mathcal{R}_{j+2}, \ldots, -\theta \mathcal{R}_S\right), \tag{S57}$$

$$\mathcal{S}_{i,\mu} = \frac{\partial r_i}{\partial \mathcal{R}_\mu} = \left(\frac{\partial f_i}{\partial \mathcal{R}_1}, 0, \ldots, 0, \underbrace{-d_i}_{\mu=i}, 0, \ldots, 0\right), \tag{S58}$$

where all quantities are evaluated at equilibrium.

Step 3. We calculate the two volumes. This is where our particular choice for the regulating factors proves useful: it would be impossible to do the calculation using other choices. The volumes are calculated via Eq. (S70) (see the Appendix). The impact volume reads

$$\mathcal{V}_{\mathcal{I}} = \left| \det \begin{pmatrix} \frac{\partial \mathcal{R}_1}{\partial N_1} & -\theta \mathcal{R}_2 & -\theta \mathcal{R}_3 & \cdots \\ \frac{\partial \mathcal{R}_1}{\partial N_2} & 0 & -\theta \mathcal{R}_3 & \cdots \\ \frac{\partial \mathcal{R}_1}{\partial N_3} & 0 & 0 & \cdots \\ \vdots & \vdots & \vdots & \ddots \end{pmatrix} \right| = \left| \frac{\partial \mathcal{R}_1}{\partial N_S} \right| \theta^{S-1} \prod_{i=2}^{S} \mathcal{R}_i, \tag{S59}$$

and the sensitivity volume is

$$\mathcal{V}_{\mathcal{S}} = \left| \det \begin{pmatrix} \frac{\partial f_1}{\partial \mathcal{R}_1} & 0 & 0 & \cdots \\ \frac{\partial f_2}{\partial \mathcal{R}_1} & -d_2 & 0 & \cdots \\ \frac{\partial f_3}{\partial \mathcal{R}_1} & 0 & -d_3 & \cdots \\ \vdots & \vdots & \vdots & \ddots \end{pmatrix} \right| = \left| \frac{\partial f_1}{\partial \mathcal{R}_1} \right| \prod_{i=2}^{S} d_i. \tag{S60}$$

The especially simple form of these matrices allowed for the direct calculation of the determinants.

The product of these volumes is

$$\begin{aligned} \mathcal{V}_{\mathcal{I}} \mathcal{V}_{\mathcal{S}} &= \left| \frac{\partial f_1}{\partial \mathcal{R}_1} \frac{\partial \mathcal{R}_1}{\partial N_S} \right| \theta^{S-1} \left(\prod_{i=2}^{S} d_i \right) \left(\prod_{i=2}^{S} \mathcal{R}_i \right) \\ &= \left| \frac{\partial f_1}{\partial \mathcal{R}_1} \frac{\partial \mathcal{R}_1}{\partial N_S} \right| \theta^{S-1} \left(\prod_{i=2}^{S} d_i \right) \mathrm{e}^{-\theta N_1} \mathrm{e}^{-\theta (N_1 + N_2)} \cdots \mathrm{e}^{-\theta (N_1 + \cdots + N_{S-1})} \\ &= \left| \frac{\partial f_1}{\partial \mathcal{R}_1} \frac{\partial \mathcal{R}_1}{\partial N_S} \right| \theta^{S-1} \left(\prod_{i=2}^{S} d_i \right) \mathrm{e}^{-\theta \left((S-1) N_1 + (S-2) N_2 + \cdots + N_{S-1} \right)}. \end{aligned} \tag{S61}$$

Let N be the smallest of the equilibrium densities $N_1, N_2, \ldots, N_{S-1}$. Then we can write the inequality

$$\begin{aligned} \mathcal{V}_{\mathcal{I}} \mathcal{V}_{\mathcal{S}} &\leq \left| \frac{\partial f_1}{\partial \mathcal{R}_1} \frac{\partial \mathcal{R}_1}{\partial N_S} \right| \theta^{S-1} \left(\prod_{i=2}^{S} d_i \right) \mathrm{e}^{-\theta \left((S-1) N + (S-2) N + \cdots + N \right)} \\ &= \left| \frac{\partial f_1}{\partial \mathcal{R}_1} \frac{\partial \mathcal{R}_1}{\partial N_S} \right| \theta^{S-1} \left(\prod_{i=2}^{S} d_i \right) \mathrm{e}^{-N \theta S (S-1)/2}. \end{aligned} \tag{S62}$$

This expression asymptotically depends on the number of species as $\exp(-N\theta S^2/2)$. It converges to zero faster than exponential in the number of species (unless N decreases even faster—but in that case the equilibrium population densities would soon get so close to zero that, from a practical point of view, extinctions would be inevitable). Then, due to the above inequality, the product of the volumes spanned by the impact and sensitivity vectors must also converge to zero at least as fast as $\exp(-N\theta S^2/2)$.

Note also that in this model, the product of the volumes is exactly equal to the determinant of the generalized community matrix a_{ij} in absolute value. From Eq. (S54), this determinant can be written

$$\det(a_{ij}) = \det\left(\sum_{\mu=1}^{S} \frac{\partial r_i}{\partial \mathcal{R}_\mu} \frac{\partial \mathcal{R}_\mu}{\partial N_j}\right) = \det\left(\frac{\partial r_i}{\partial \mathcal{R}_\mu}\right) \det\left(\frac{\partial \mathcal{R}_\mu}{\partial N_j}\right) = \det\left(\mathcal{S}_{i,\mu}\right) \det\left(\mathcal{I}_{j,\mu}\right), \tag{S63}$$

where we used two facts: 1) that the number of regulating factors happens to be equal to the number of species and therefore $\mathcal{I}_{j,\mu}$ and $\mathcal{S}_{i,\mu}$ are square matrices, and 2) that the determinant of a product of square matrices is the product of the determinants. Due to the well-known geometrical interpretation of the determinant (see also the Appendix),

$$\left|\det(a_{ij})\right| = \left|\det\left(\mathcal{I}_{j,\mu}\right) \det\left(\mathcal{S}_{i,\mu}\right)\right| = \mathcal{V}_{\mathcal{I}} \mathcal{V}_{\mathcal{S}}, \tag{S64}$$

which is what we wanted to show.

The bound on the number of coexisting species

We have shown above that the product $\mathcal{V}_{\mathcal{I}} \mathcal{V}_{\mathcal{S}}$—and therefore, due to Eq. (S64), the determinant of a_{ij}—converges to zero as S increases. It is tempting to jump to the conclusion that coexistence of a large number of species is extremely unlikely. Some additional care is needed, however: since introducing a new species will also increase the dimensionality of the problem, $\mathcal{V}_{\mathcal{I}} \mathcal{V}_{\mathcal{S}}$ approaching zero does not automatically imply decreasing robustness.

To illustrate why, consider S noninteracting species. Assume each of them may have a mortality rate between 1 and 2, and only species with mortality lower than 1.5 are viable. The parameter range allowing for the persistence of a single species is 0.5. For S independent species, the total parameter volume allowing for the persistence of all species is then equal to 0.5^S, which converges to zero for large S. Yet, the robustness of the community need not be vanishing: if, for instance, all species have a mortality of 1.25, then no species will go extinct in response to small perturbations of any of these mortalities. Indeed, it is intuitively obvious that the number 0.5 is the "true" measure of robustness here, which is the Sth root of the total volume 0.5^S.

To avoid measuring the trivial artifact of parameter volumes shrinking due to an increasing number of species, we observe from Eq. (S62) that the Sth root of the determinant still converges to zero exponentially:

$$\sqrt[S]{\mathcal{V}_{\mathcal{I}} \mathcal{V}_{\mathcal{S}}} \sim \sqrt[S]{\theta^S \exp\left(-N\theta S^2/2\right)} = \theta \exp\left(-N\theta S/2\right) \to 0 \tag{S65}$$

(only the leading term in S was kept in the exponents). That is, the robustness of the community is still lost for large S, even when accounting for the above trivial effect.

The above intuitive argument can be pitched more formally. The determinant of a matrix is the product of its eigenvalues. The eigenvalues describe the robustness of the community in specific directions, while their product measures overall robustness. An eigenvalue that is nearly zero means that the corresponding eigendirection is extremely sensitive, since a small perturbation could push that eigenvalue over to the right half plane, destabilizing the system. If the product of the eigenvalues approaches zero, this need not mean that any one particular eigenvalue does—e.g., if each eigenvalue is equal to 0.5, none of them are very small, but their product does converge to zero for large S. But now let us consider not just the determinant, but the Sth root of the determinant. This quantity is simply the geometric mean of the eigenvalues. If the geometric mean goes to zero, then the smallest eigenvalue must also approach zero, as the geometric mean is necessarily greater than or equal to the smallest eigenvalue.[†] That is, when the Sth root of the determinant becomes small, one can be certain that robustness is lost in some of the individual directions as well. In our case, we can see from Eq. (S65) that this is exactly what happens.

From Eq. (S65) we can see that S cannot be much larger than $1/(N\theta)$, otherwise the likelihood of coexistence becomes exponentially small. To make this conclusion more transparent, let us consider a dimensional analysis of robustness. If N is measured in units of biomass, then θ is of dimension inverse biomass. Their product $N\theta$ is then a dimensionless quantity. We may rescale Eq. (S65) by multiplying it with N:

$$\sqrt[S]{\mathcal{V}_I \mathcal{V}_S} \sim N\theta \exp\left(-N\theta S/2\right). \tag{S66}$$

This expression will still converge to zero whenever S is large, and—unlike Eq. (S65)—is a dimensionless measure of robustness. It clearly converges to zero exactly when Eq. (S65) does; all we have done is a rescaling of the expression by the constant N. In this form it is clear that robustness is lost whenever the dimensionless quantity $N\theta$ is much larger or much smaller than 1. Therefore, S cannot be much larger than 1. (See also Meszéna *et al.* 2006, Eq. 52 for the calculation of the probability of coexistence as a dimensionless quantity, using the non-dimensionless determinant.)

Figure S2 plots the right hand side of Eq. (S66) for fixed values of S as a function of $N\theta$. The curves reach their unique maximum at $N\theta = 2/S$; the value at the maximum is $2/(\mathrm{e}S)$, as is easily seen by differentiating Eq. (S66) with respect to $N\theta$ and requiring the result to be zero. Therefore $\sqrt[S]{\mathcal{V}_I \mathcal{V}_S}$ goes to zero with the inverse of S even if one manages to fine-tune the parameters such that $N\theta$ remains at its optimal value for each S—a fairly unrealistic situation to begin with.

Our take-home message is that the coexistence of more than a few species through the cascade of facilitation in the Gross model is a highly unlikely outcome. Moreover, this result was obtained by a simple argument which did not take variation in specific parameters into account. More specific evaluation of the coexistence bandwidth for any fixed value of the species number could be carried out like we did in the case of the Levine–Rees model.

[†] One might worry that the eigenvalues may be complex numbers. How do we interpret "smaller" or "greater" in this case? The problem is easily resolved: since a_{ij} is necessarily a real matrix, its eigenvalues come in complex conjugate pairs, whose product is $(a+\mathrm{i}b)(a-\mathrm{i}b) = a^2+b^2 = (\text{length})^2$. So in this case it is the length of the shortest eigenvalue that will approach zero.

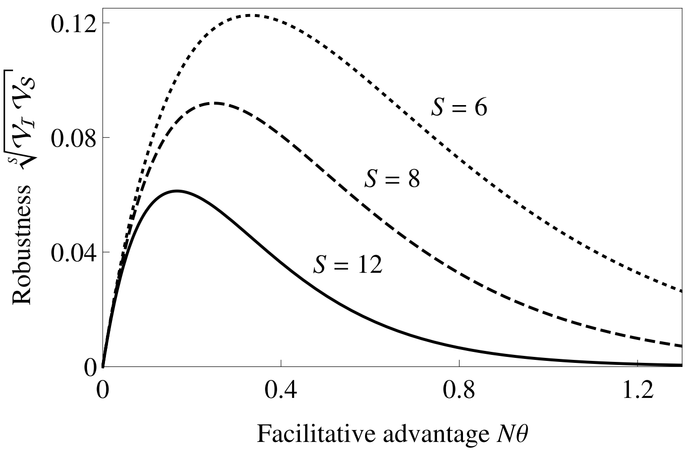

Figure S2: The robustness $\sqrt[S]{\mathcal{V}_I \mathcal{V}_S}$ as a function of the (scaled) facilitative advantage $N\theta$ for various values of S, based on Eq. (S66). The most robust scenario always happens at an intermediate $N\theta$ value.

Appendix: the volume spanned by a set of vectors

Suppose we are given a set of S vectors, with $\mathcal{W}_{i,\mu}$ referring to the μth entry of the ith vector ($i = 1 \ldots S$). We assume without loss of generality that $\mu = 1 \ldots L$, i.e., each vector has L entries (L is not necessarily equal to S). To calculate the volume $\mathcal{V}_{\mathcal{W}}$ of the parallelotope spanned by these vectors, define the following matrix of scalar products:

$$W_{ij} = \sum_{\mu=1}^{L} \mathcal{W}_{i,\mu} \mathcal{W}_{j,\mu}. \tag{S67}$$

Note that, in case μ is a continuous as opposed to a discrete index (i.e., when we have functions $\mathcal{W}_i(\mu)$ instead of vectors $\mathcal{W}_{i,\mu}$), the summation above becomes integration with respect to μ:

$$W_{ij} = \int_{\mu_0}^{\mu_1} \mathcal{W}_i(\mu) \mathcal{W}_j(\mu) \,\mathrm{d}\mu, \tag{S68}$$

where μ_0 and μ_1 are the appropriate limits of integration. Using W_{ij}, the volume $\mathcal{V}_{\mathcal{W}}$ may now be calculated with the help of the so-called *Gram determinant* $\det(W_{ij})$ (Gantmacher 1959):

$$\mathcal{V}_{\mathcal{W}} = \sqrt{\left|\det\left(W_{ij}\right)\right|}. \tag{S69}$$

There are two special cases for which this expression can be simplified. First, $\mathcal{V}_{\mathcal{W}} = 0$ whenever $L < S$. Second, for $L = S$, the formula simplifies to

$$\mathcal{V}_{\mathcal{W}} = \left|\det\left(\mathcal{W}_{i,\mu}\right)\right| \tag{S70}$$

(Meszéna *et al.* 2006, Appendix C), where $\mathcal{W}_{i,\mu}$ is treated as a (square) matrix with row index i and column index μ.

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