The Robustness of Ecological Communities: Theory and Application

by

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Abstract

The Robustness of Ecological Communities: Theory and Application
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As ecologists, we frequently rely on mathematical models to formulate and test our hypotheses concerning ecological communities. An important problem is whether and why interacting species coexist. Once our hypothesis for why coexistence happens is translated into the form of a model, we check to see whether the proposed mechanism could indeed lead to coexistence. Usually, the golden standard for evaluating coexistence has been to check whether the model possesses an all-positive, stable stationary state (where this state may be an equilibrium point, a limit cycle, or a chaotic or otherwise aperiodic orbit). This perspective, however, ignores another important aspect of the same problem: the robustness of the stationary state against parameter changes. We may find coexistence in a model, but if that coexistence collapses after even very slight parameter perturbations, it is not actually expected to hold. The purpose of this dissertation is fourfold. First, it aims at working out the quantitative, formal mathematical machinery for evaluating the robustness of ecological communities under complex circumstances, such as ones involving population structure or nonequilibrium community dynamics. Second, it applies this machinery to various ecological problems, ranging from the theoretical to the applied, to demonstrate the kinds of uses robustness analysis has. Among the models discussed are the sensitivity of a field-parametrized model of annual plant competition to parameter changes, the analysis of coexistence in the tolerance-fecundity tradeoff model, and predicting species diversity in a model of interspecific facilitation. Third, it takes a look at some of the consequences of robustness analysis for community patterns, arguing that the elementary biological fact that species are by and large discrete, well-defined entities is a natural consequence of the basic structure of ecological interactions, not of any model details. Fourth, the dissertation synthesizes some of the general conclusions of robustness analysis to formalize the concept of the ecological niche, revealing a fundamental unity between functional, temporal, and spatial mechanisms of diversity maintenance.

Chapter 0

Introduction

0.1 The concept of community robustness

Community patterns and species coexistence are both usually discussed from the point of view of stability. When we ask the question “can a given set of species coexist?”, we implicitly understand that the word “coexistence” means something more than mere co-occurrence (Leibold and McPeek 2006): it means that, even in the face of disturbance to the species’ densities, the system has some potential to compensate for the adverse effects. Indeed, the criterion for stability has become the acid test to decide whether species coexistence or a given community pattern is expected or not.

This perspective, however, ignores another important aspect of community dynamics: its *robustness* against changes in external conditions. Robustness analysis asks the question how the stationary state of the community responds to a change in some external parameter, such as a shift in the weather, an increase in chronic predation, or a novel evolutionary adaptation in one of the species – any change is “external” as long as it influences the dynamics, but is in turn unaffected by the system’s behavior.

Figure 0.1 demonstrates the basic idea of robustness for a two-species community. On panel A, we see that the stationary state is a simple point equilibrium whose position on the phase plane depends on the ambient temperature. High robustness (panel B) means that altering the temperature causes only a slight change in the position of the equilibrium on the phase plane. On the other hand, low robustness (panel C) means that even a small temperature change causes an erratic swing in the equilibrium densities, potentially causing species extinctions.

Notice that the equilibrium point is always stable in this example. Therefore, it could be tempting to conclude that this community is safe from extinctions. As we

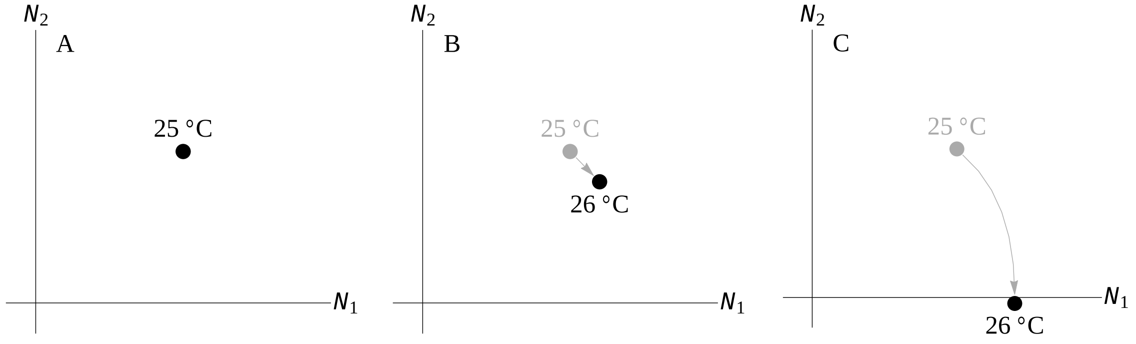

Figure 0.1: The idea behind robustness analysis. On panel A we see a community of two species that stably coexist at the indicated point when the temperature is 25 °C. Panel B demonstrates what happens if we increase temperature by 1 °C, and the community has *high* robustness. The equilibrium densities change after the perturbation, but not much – therefore, in this case, the system is not very sensitive to temperature variations. On the other hand, panel C shows what happens if the same 1 °C increase is applied to a *low* robustness community. The same change in temperature causes an erratic swing in the equilibrium densities, causing the extinction of species 2. In this case, the system is oversensitive to temperature variations – therefore, unless something is keeping the temperature constant, coexistence is *not* expected to happen, despite the fact that the equilibrium is stable.

just saw, considering the robustness of the community may completely overthrow this premature conclusion: in the situation depicted on panel C, coexistence could only be expected if the natural fluctuations in temperature are less than 1 °C. This might be possible to achieve under laboratory conditions, but the number of natural circumstances in which temperature can remain so constant are probably few and far between.

Clearly, the concept of robustness is relevant in an age when global climate change is altering parameters, such as the mean and the variance in annual temperature and precipitation levels, or the frequency of disturbance events. If we would like to predict the consequences of such changes, a sole emphasis on stability is not going to be enough. But, apart from addressing such applied problems, there is even more to be gained from studying community robustness. Namely, robustness analysis sheds new light on some of the classic theoretical problems in community ecology. Competitive exclusion, limiting similarity, the ecological niche – these can be given a solid, unified underpinning by relying on the concept of robustness.

This dissertation attempts to develop the theory of community robustness and to explore its consequences for coexistence and expected community patterns. Along the way, it tries to demonstrate the various uses of robustness analysis within community ecology, both theoretical and applied. Much of the material is rather technical, developing the mathematical machinery for being able to calculate robustness in complex ecological scenarios; e.g., when the environment fluctuates or the interacting populations are physiologically structured. This, however, is necessary to be able to move beyond the simplest ecological scenarios. Taking these complexities into consideration, one can move beyond the analysis of simple toy models, and explore coexistence and community structure in real-world situations.

0.2 Setting the stage

Classically, coexistence and its implications for observed community patterns have been discussed from the point of view of stability. As reviewed in Chapter 1, this proved to be a blind alley, leading to no clear conclusions: a careful scrutiny of the very same models that were used to establish limiting similarity in the first place has revealed that in fact it is always possible for arbitrarily similar species to stably coexist. This, of course, presents a problem in a world where we take natural selection and its capacity to generate all the marvelous adaptations of our biosphere for granted. Natural selection, after all, is what ultimately leads to competitive exclusion between competing similar mutants. If competitive exclusion is truly as easy to circumvent as stability analysis suggests, then although diversity becomes much easier to explain, we have actually thrown out the baby with the bath water: yes, coexistence of many species is possible, but how did they actually adapt to their environments? Our current understanding is that without competitive exclusion (and hence natural selection), adaptive complexity cannot be brought about[1].

This is where the perspective inspired by robustness analysis comes into the picture. The basic argument upon which the results of this dissertation stand can be found in Sections 3.3 and 4.2 and also, in a simplified and condensed form, in Box 1 and Figure 1.1 of Chapter 1. This argument concludes that, though stable coexistence of similar species is possible, it is unlikely, because the parameter range allowing for that coexistence will be very small – i.e., coexistence is going to be unrobust.

While this argument is very general, it does have certain limitations. First, it only applies to communities of unstructured populations at a fixed point equilibrium. The framework therefore needs to be extended to deal with additional complexities.

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[1] Short of miracles or certain limited mechanisms such as Lamarckism – none of which seem to be actually operating.

For instance, seasonality is a common driver of community dynamics, but in order to assess the robustness of coexistence in such communities, we need to move beyond the simple point equilibria of Figure 0.1 and analyze the robustness of periodic orbits. Similarly, population structure based on age, stage, or spatial position (or any combinations thereof) can and will complicate robustness calculations. Second, the purpose of robustness analysis is more than a mere derivation of formulas – it should also indicate what kinds of species differences would lead to more robust coexistence. The formulas should connect back to the biology of the organisms we are modeling. Third, the fact that coexistence of a set of species which are overly similar is unrobust does not say much about what kinds of community patterns one should expect to see in nature. Coexistence of such species is unlikely and therefore will be broken – but how exactly? Will species be spaced out, as in classical limiting similarity-type statements, or will some species go extinct, but in such a way that there will be no limits to similarity?

We set out to answer these questions in the rest of the dissertation, as outlined in the section below.

0.3 Dissertation structure

I have tried to keep the discussion of the material as deductive in its style as possible: I start out with the most general points and gradually work my way towards the details and applications.

Chapter 1 (based on Barabás et al. 2012b) reviews the large historical body of thought related to species coexistence and limiting similarity, and attempts at a reconciliation of the various viewpoints. It establishes the robustness-based approach to coexistence, and then inquires what kind of expectation one should have for the distribution of species traits in communities. In doing so, it systematically demonstrates that some kind of limiting similarity is the expected behavior, although no hard limits to similarity exist – coexistence of similars is unlikely, but not impossible. There could be things that would lead to a violation of this expectation (transients, considering coexistence at too small spatial scales, etc.), but the theory reviewed in the chapter does establish the picture of discretely many, separate species coexisting as a baseline expectation. This means that wherever the theory's assumptions are met, it provides strong qualitative and quantitative insights and predictions, and where these predictions are not met, it narrows down the underlying reasons to a handful of testable hypotheses for further empirical investigations.

Chapter 2 discusses one particular theoretical challenge to the expectation of limiting similarity (Barabás et al. 2013). Robust coexistence of arbitrarily similar species can arise if competition between species is modeled as a nonsmooth function of their trait differences – specifically, if the competition kernel (differential response of species' growth rates to changes in the density of other species along the trait axis) has a nondifferentiable sharp peak at zero trait difference (a "kink"). Both an intuitive and a more mathematical explanation is given why the behavior of such kernels is anomalous. Then the mechanisms that would lead to kinked kernels in the first place are investigated: it turns out that discontinuities in resource utilization generate them. It is then argued that such sudden jumps in the utilization of resources are unrealistic and therefore one should expect kernels to be smooth in reality. In other words, the apparent theoretical challenge to limiting similarity as a baseline expectation is not a challenge at all. Rather, the importance of this finding is in interpreting results from well-known models, e.g. the competition-colonization or tolerance-fecundity tradeoff models (Kinzig et al. 1999, Muller-Landau 2010, D'Andrea et al. 2013), where such kernels are uncritically used.

The next two chapters develop the theory of community robustness in periodically fluctuating environments, for continuous-time (Chapter 3) and discrete-time (Chapter 4) dynamics (Barabás et al. 2012a, Barabás and Ostling 2013). Temporal environmental variation has long been considered as one of the potential factors that could promote species coexistence. A question of particular interest is how the ecology of fluctuating environments relates to that of equilibrium systems. We already know that equilibrium systems lose robustness with increasing species similarity. Here we attempt to generalize this statement to temporally varying situations, and establish the precise mathematical relationship between the two. We provide a coherent theoretical framework for defining measures of species similarity and calculating community robustness. Our main conclusion is that time within one period of oscillation will effectively behave like a resource axis. In particular, a single resource becomes a resource continuum, along which species may segregate in the same manner as along classical resource continua. The chapters therefore provide a mathematical underpinning for considering fluctuation-mediated coexistence as temporal niche segregation.

Chapter 5 develops the theory of community robustness for interacting structured populations at point equilibria (Barabás et al. under review). The result is used to determine how robustness is influenced by the distribution of individual states. As an illustration, the theory is then applied to a two-species model of ontogenetic niche shift where each species has two stage classes, juveniles and adults. In this model, stable and robust coexistence is possible even if the adults compete for the same resource, and so if the species were unstructured and composed entirely of adults, they would not be able to coexist. This effect can be offset by the juveniles partitioning their resources.

Finally, Chapter 6 (in preparation as an Ideas & Perspectives piece for Ecology Letters) demonstrates the uses of robustness analysis through a set of carefully selected example applications. Examples are used throughout the other chapters as well, but their purpose is pedagogical: it is to show how to use the results in the simplest possible context. Here we apply the robustness framework to situations with either more realism, or to ones that have particularly important theoretical implications. An example of the first is a model describing competition between forbs and grass on a California grassland (Levine and Rees 2004), where coexistence is maintained by environmental fluctuations. An example of the latter is the Gross model of interspecific facilitation (Gross 2008), where the theoretical difference between the stability versus the robustness perspective comes out most sharply: from the point of view of stability, there is no limit to diversity in this model, while our robustness calculations show that there is in fact an effective limit to the number of species that can coexist.

This final chapter ends with a summary and synthesis of the results of this dissertation, aiming at discussing and solidifying the biological big picture emerging from robustness analysis applied in the context of community ecology.

Chapter 1

Continuous coexistence or discrete species? A new review of an old question

1.1 Introduction

It is an elementary fact of biology that species are – by and large – discrete entities. Why is this so? The question has both an ecological and a genetic aspect (Maynard Smith and Szathmáry 1995). Here we are interested in the ecological one: does ecology dictate the discreteness of species? Assumption of discrete niches would lead us to an answer of trivial "yes" without confronting the real problem. Therefore, we will consider the possibility of species coexistence along a continuous niche axis. For the purposes of this review, a species' niche is described by its position in the trait space that needs to be considered for determining the competitive effects between species. In this review, we focus on one-dimensional trait spaces. To disregard the effects that genetics may bear on this problem, we consider clonal reproduction only.

Investigations of coexistence along a niche axis were initiated by the seminal paper of MacArthur and Levins (1967). They examined a Lotka–Volterra model with the assumption that the strength of competition decreased as the difference in niche position. It was found that a minimal niche distance between two species was needed to allow a third one with a niche position in the middle of the two to invade the community. They summarized their results by coining the term "limiting similarity". However, more careful analysis revealed the *lack* of a clear minimum to species dissimilarity (Abrams 1975, 1983; May 1973, ch. 6), where species similarity is measured by the distance between two species along the niche axis. May and MacArthur (1972) resorted to environmental stochasticity to rescue the idea of limiting similarity, a result that was questioned by Abrams (1976) and Turelli (1978).

Moreover, even if the argument by May and MacArthur were correct, it would imply that that limiting similarity could not be expected to exist in the absence of such stochasticity (Rosenzweig 1995, p. 127).

Meanwhile, the attention of ecologists began to broaden beyond analyses of Lotka–Volterra models, which became regarded as being overly simplistic and as maintaining too little connection with empirical reality (Schoener 1976, 1978). Instead, more mechanistic models became established in research on population and community dynamics (e.g., Tilman 1982). These studies revealed a significantly richer parameter-dependence of the possibility for coexistence, and often found markedly different behavior relative to the Lotka–Volterra model (e.g., Abrams 1980a,b, 1998, Abrams et al. 2008, Abrams and Rueffler 2009). In his hallmark review, Abrams (1983) concluded that there was no such thing as a universal limit to similarity. He suggested that the relationship between an appropriate measure of relative competitiveness of the species and their similarity in resource use has to be studied on a model-to-model basis. The term "coexistence bandwidth" was coined for the parameter range allowing coexistence by Armstrong and McGehee (1976). This range was generally expected to shrink to zero when the difference in resource use disappears (Abrams 1983).

In an independent development, Roughgarden (1979, pp. 534-536) demonstrated the possibility of *continuous* coexistence, involving infinitely many ecological types that are continuously distributed along a niche axis and yet stably coexist. His model was not meant to describe an ecological community of species; instead, he interpreted the considered coexisting types as phenotypes within a single species. It might be for this reason that Roughgarden's result appears to have escaped the attention of many community ecologists: it is not usually cited in discussions of limiting similarity. This distinction is irrelevant, however, if we are considering the mathematical side of the problem.

Indeed, the model investigated by Roughgarden was mathematically identical to the one used by MacArthur and Levins (1967). As the very same model that provided the original inspiration for the notion of limiting similarity was thus shown also to produce continuous coexistence, it is no surprise that no clear conclusion could be drawn about whether or not to expect a lower limit to species similarity in nature. The possibility of continuous coexistence in the Lotka–Volterra model seems to be in agreement with the lack of a universal limit of similarity, but at odds with the general modeling experience of finding specific lower limits to similarity in specific ecological models.

Our goal is to offer a resolution to this potentially confusing situation. The last decade has seen a renewed interest in the classical problem of coexistence. On the specific side, Lotka–Volterra models have been reinvestigated by several authors using more sophisticated mathematical tools. After all, the empirical relevance of Lotka–Volterra models aside, if we do not even sufficiently understand the simplest of ecological models, we cannot possibly expect to understand more complicated ones. On the general side, new mathematical possibilities have emerged for reaching model-independent conclusions based on general mathematical conditions instead of model-specific assumptions. This chapter reviews these new developments. We mostly concentrate on Lotka–Volterra models, to explain all salient considerations in the simplest possible context. At the same time, we always highlight when there are reasons to consider a result as being more general. In particular, Appendix A presents a new result about the generic impossibility of continuous coexistence. In the following section, we introduce our central concepts: we explain the important distinction between the dynamical stability and structural robustness of coexistence, consider the scope of population dynamics described by Lotka–Volterra models, and introduce the main model underlying our further analyses. After reviewing and discussing existing results on the stability and structural robustness of coexistence in the subsequent two sections, we close with a discussion of the general conclusions these results enable us to draw.

1.2 Preliminaries

1.2.1 Dynamical stability and structural robustness of coexistence

In line with the classical research on species coexistence, we first concentrate on coexistence based on dynamically stable fixed points in constant environments, before remarking on coexistence based on nonequilibrium population dynamics in the next section.

A collection of species can coexist if their joint population dynamics has a dynamically stable fixed point at which all species are present with positive density. This gives two conditions that together are sufficient for ensuring coexistence: (1) the existence of an all-positive fixed point and (2) its dynamical stability. The second condition ensures that small perturbations of the densities away from the fixed point are damped, so that the densities return to the fixed point. Traditionally, most theoretical studies of coexistence have concentrated on such conditions of dynamical stability. However, as we see below, the mere existence of an all-positive fixed point is already a nontrivial issue.

For structurally stable population dynamics, an all-positive fixed point, if it exists, does so for a finite volume in the space of model parameters. The conditions under which this volume shrinks to zero in parameter space (or in one of its subspaces) thus define a biologically important reference case. To illustrate this point, we can consider as an example competing species without niche segregation (with no equality of demographic parameters assumed). Generically, one of them will win the competition, while all other species are destined to extinction. Still, in a theoretical model, an all-positive neutral manifold can be brought into existence if the modeler artificially fine-tunes the fitnesses of all species to be exactly equal (as population densities may drift along a line made up of neutrally stable fixed points, adding demographic stochasticity to the model would lead to the eventual extinction by drift of all but one species – but no extinctions will happen in the deterministic limit). Naturally, such a precise equality of all fitnesses is a structural assumption that is not plausible in the real world. If one were confronted with such a population dynamics a priori, it would therefore be critical to check its robustness to a relaxation of this structural assumption. In the considered example, this is straightforward: when the modeler gives even the tiniest advantage to any one species, by increasing its fitness relative to those of the others, coexistence is lost. Accordingly, the considered model is said not to be structurally stable.

In general, a fixed point is structurally unstable if an *arbitrarily* small perturbation of the model parameters will qualitatively change its dynamics (e.g., Rosen 1970, Yodzis 1989; such parameter perturbations are also referred to as "structural perturbations of the model"). To apply this criterion, it must be appreciated that not all structural perturbations that are mathematically possible are biologically plausible; the notion of structural stability as used in ecological theory is therefore always implicitly referring to biologically plausible perturbations. The hallmark of structural stability is that, for all parameters whose change is biologically realistic, a model's dynamics is qualitatively unchanged by any small parameter variation in the neighborhood of the parameter combination describing the unperturbed model.

Applied to the question of coexistence, this means that both the existence and the dynamical stability of the considered fixed point must be unchanged across an entire neighborhood of parameter values surrounding the unperturbed model. The likelihood of coexistence in the real world is directly related to this structural robustness: if the range of parameters allowing for coexistence, sometimes called the "coexistence bandwidth" (Armstrong and McGehee 1976), is known, the probability of coexistence can in principle be calculated from the empirical probability density of the parameter values, by integrating the latter over the entire coexistence bandwidth. A vanishing coexistence bandwidth therefore implies that coexistence is impossible, while a small coexistence bandwidth implies that it is unlikely.

Owing to these similar, but subtly different biological implications, it is helpful to formally distinguish between structural stability, a long-established notion in the mathematical theory of dynamical systems, and what throughout this chapter we refer to as structural robustness. While any finite range of parameters within which the dynamics is qualitatively unchanged makes a model structurally stable, such coexistence has weak structural robustness whenever that range is small. Whereas the lack of structural stability and the lack of structural robustness are hence equivalent, as both refer to a vanishing parameter range, structural stability and structural robustness are not, as they convey different information about a finite parameter range: the former is a binary notion that just tells us that this range is finite, even though it may be extremely small, whereas the latter can be weak or strong, depending on the actual range of a model's parameters that leave the qualitative dynamics unchanged relative to biologically relevant parameter ranges. It turns out that this extra information makes the notion of structural robustness considerably more biologically relevant and informative than that of structural stability, which is why we consistently employ it throughout this chapter.

Figure 1.1 and Box 1 describe the concepts of dynamical stability and structural robustness for the well-known two-species Lotka–Volterra model. This shows that concentrating exclusively on dynamical stability would miss two important points: the sensitivity of the position of the fixed point to changes in model parameters (i.e., structural robustness; middle column of Figure 1.1) and the fact that a dynamically stable fixed point is not necessarily all-positive (left and middle columns of Figure 1.1).

The figure also demonstrates the relationship between structural robustness and dynamical stability. Transition from dynamical stability to dynamical instability along a parameter change is accompanied by the loss and reappearance of the structural robustness of an all-positive fixed point. The fixed point is structurally unstable at the bifurcation point separating the dynamically stable and unstable regime. As explained in Box 1, this structural instability of the fixed point is nothing else than the above-mentioned structural instability of coexistence of species without niche segregation. The overall picture emerging from these mathematical considerations coincides with the expectation by Abrams (1983): structural robustness

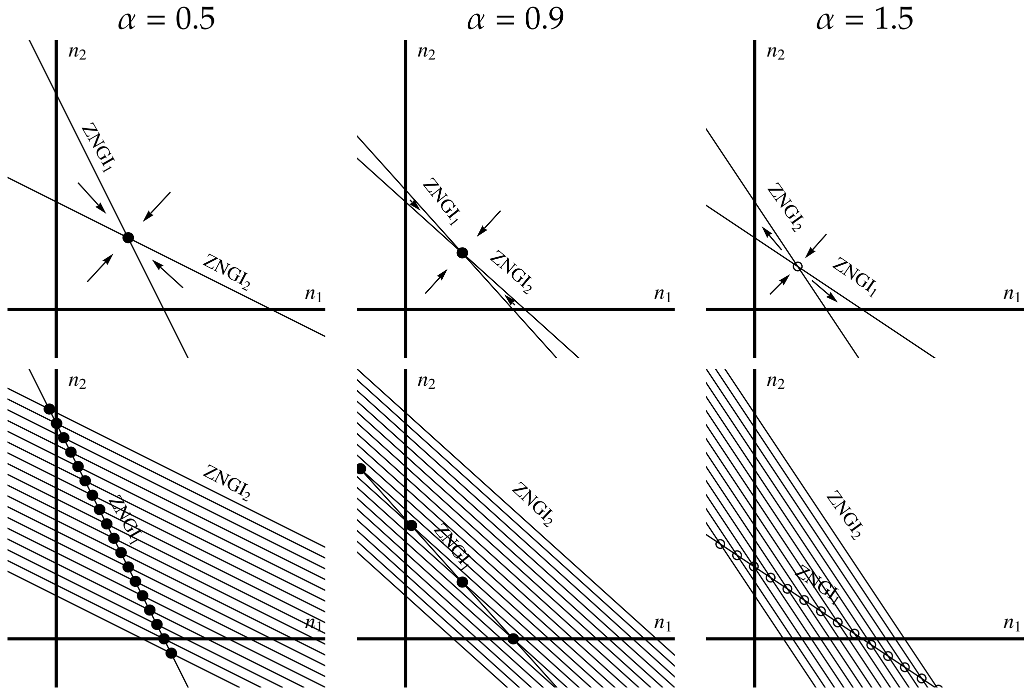

Figure 1.1: Dynamical stability (upper row) and structural robustness (lower row) of coexistence for the two-species competitive Lotka–Volterra model described in Box 1 (see also Figure 12.3 in Krebs 2001). In each panel, the population densities n_1 and n_2 of Species 1 and 2, respectively, vary along the axes. The tilted lines are the zero-net-growth isoclines (ZNGIs). The circles indicate the intersections of ZNGIs, and thus the fixed points of the population dynamics; they are filled (open) when the fixed point is dynamically stable (unstable). Arrows depict the qualitative flow of the dynamics. In the upper row, with $r_1 = r_2 = 1$, the fixed point is dynamically stable for $\alpha < 1$ (left column) and dynamically unstable for $\alpha > 1$ (right column). In the middle column, where α approaches 1 from below, the fixed point is still dynamically stable, but only weakly so, as the smaller eigenvalue of the Jacobian matrix approaches 0. This is depicted with shorter arrows in the weakly stable direction, i.e., in the direction of changes only affecting the relative density n_1/n_2. Notice that dynamical stability remains strong in the direction of the joint density $n_1 + n_2$. In the bottom row, r_2 changes from 0.4 to 2.1 in increments of 0.1, representing a disadvantage, or advantage, of Species 2 relative to Species 1, for which r_1 remains at 1: the ZNGI of Species 2 (parallel lines, with the lowest line corresponding to $r_2 = 0.4$) and the resultant fixed point move in accordance with this changing relative advantage. Only density combinations within the positive quadrant represent coexistence, provided they are dynamically stable. Species 2 (Species 1) goes extinct when r_2 is too small (too large). Observe again the peculiarity of the weakly stable case in the middle row: when α approaches 1 from below, the fixed point moves rapidly and therefore remains in the positive quadrant only for a narrow range of r_2. We call coexistence structurally robust when the fixed point exists in the positive quadrant for a wide range of the parameters describing relative advances/disadvantages. The figure therefore illustrates that structural robustness and dynamical stability of coexistence are different yet related properties, and why weak dynamical stability or instability imply low structural robustness.

of coexistence shrinks, and its dynamical stability weakens, when species become similar. Robustness and stability disappear altogether when the species become identical. (The shrinking of the coexistence bandwidth with increasing similarity needs to be monotonic only for sufficiently small niche differences; see Abrams and Rueffler 2009 for an example where both very small and very large differences lead to shrinking, with intermediate differences maintaining the largest possible coexistence bandwidth.) Meszéna et al. (2006) established the behavior of losing robustness with similarity for several species in a model-independent way, beyond the Lotka–Volterra model.

Box 1: Dynamical stability and structural robustness in two-species Lotka–Volterra models

As a point of reference, here we discuss the dynamical stability and structural robustness of coexistence in two-species competitive Lotka–Volterra models; see also Figure 1.1. Lotka–Volterra models for two species with population densities n_1 and n_2 are given by the following dynamical equations:

$$\frac{\mathrm{d}n_1}{\mathrm{d}t} = f_1(n_1, n_2)n_1 = (r_1 - a_{11}n_1 - a_{12}n_2)\, n_1,$$

$$\frac{\mathrm{d}n_2}{\mathrm{d}t} = f_2(n_1, n_2)n_2 = (r_2 - a_{21}n_1 - a_{22}n_2)\, n_2.$$

The density dependence of the growth rates f_1 and f_2 can also be conveniently expressed in vector form:

$$\mathbf{f} = \mathbf{r} - \mathbf{a}\mathbf{n}.$$

The solution for the equilibrium population densities is obtained by setting these growth rates to zero, $\mathbf{f} = 0$, which yields

$$\mathbf{n} = \mathbf{a}^{-1}\mathbf{r} = \frac{\mathrm{adj}(\mathbf{a})}{\det(\mathbf{a})}\mathbf{r},$$

where adj($\mathbf{a}$) is the adjoint of the matrix $\mathbf{a}$ and det($\mathbf{a}$) is its determinant (Cramer's rule). Note that $\det(\mathbf{a}) = 0$ when the two species are identical in their effects, i.e., $a_{11} = a_{12}$ and $a_{21} = a_{22}$.

The requirement for the unique existence of a fixed point $\mathbf{n}$ is $\det(\mathbf{a}) \neq 0$. As the determinant appears in the denominator, the fixed point becomes sensitive to changes in $\mathbf{r}$ for small det($\mathbf{a}$). Only a small range of the parameters r_1 and r_2 then allows the fixed point to remain in the biologically meaningful positive quadrant, $\mathbf{n} > 0$. Therefore, structurally robust existence of the positive solution requires det($\mathbf{a}$) to be not only non-zero, but *significantly* different from zero. For det($\mathbf{a}$) = 0, coexistence is structurally unstable: it occurs only for one special combination of r_1 and r_2.

The Jacobian matrix determining the dynamical stability (Otto and Day 2007, p. 306) of the fixed point $\mathbf{n}$ is $\mathbf{A} = (A_{ij})$ with

$$A_{ij} = \frac{\partial(\mathrm{d}n_i/\mathrm{d}t)}{\partial n_j} = f_i\delta_{ij} - a_{ij}n_i = -a_{ij}n_i,$$

where the Kronecker symbol δ_{ij} equals one if $i = j$ and zero otherwise. Notice that the term $f_i\delta_{ij}$ vanishes, since the partial derivatives comprising $\mathbf{A}$ have to be taken at the fixed point $\mathbf{n}$, where $f_i = 0$. The two eigenvalues of $\mathbf{A}$ describe the exponential rates at which perturbations away from the fixed point in the direction of the corresponding two eigenvectors grow or shrink. Therefore, the fixed point is dynamically stable if and only if both eigenvalues of $\mathbf{A}$ are negative. Equivalently, the eigenvalues of $\mathbf{a}$ must be positive for dynamical stability.

As the determinant is the product of the eigenvalues, dynamical stability requires det($\mathbf{a}$) to be positive. When det($\mathbf{a}$) approaches zero, indicating a gradual loss of structural robustness, and becomes negative, dynamical stability is also lost. For negative determinants, the existence of the fixed point can be structurally stable, even though the fixed point is dynamically unstable. We can conclude that weak dynamical stability or instability implies low structural robustness, since the dynamics are then so close to a structurally unstable configuration that small structural perturbations of the model can qualitatively alter the dynamical outcomes.

As det($\mathbf{a}$) = 0 holds for ecologically identical species, these arguments establish that structural robustness of coexistence is gradually lost when the two species become ecologically indistinguishable (see Meszéna et al. 2006).

This is demonstrated in Figure 1.1 for the simplest possible combination of parameters: $r_1 = r_2 = a_{11} = a_{22} = 1$ and $a_{12} = a_{21} = \alpha$. A simple calculation shows that the two eigenvalues of $\mathbf{a}$ are $\lambda_\pm = 1 \pm \alpha$, while the determinant is det($\mathbf{a}$) $= 1 - \alpha^2 = \lambda_+\lambda_-$. The larger eigenvalue is always positive. The dynamical stability condition $\lambda_+, \lambda_- > 0$ thus holds if and only if $\alpha < 1$. When dynamical stability holds, structural robustness requires α to be *significantly* smaller than 1.

These results have the well-known biological interpretation that interspecific competition must be (significantly) weaker than intraspecific competition. In turn, this requires sufficient ecological differentiation between the species. Increasing similarity leads to diminished structural robustness and weakened dynamical stability.

In the rest of the chapter we concentrate on extending this understanding on the coexistence of several but finitely many species to the problem of continuous coexistence.

1.2.2 Lotka–Volterra models and the real world

Lotka–Volterra models were the original framework for examining ecological coexistence (continuous coexistence in particular), and shaped the way ecologists think about species competition. This role had arisen from an appealing combination of simplicity and versatility offered by these models. More recently, however, both the relevance of Lotka–Volterra models and the validity of the biological picture was questioned in light of more mechanistic models. Here we argue that Lotka–Volterra models, when considered with proper care, may be used to glean out biological conclusions that are far more general than the specific models would suggest. Also, we warn about the possible over-interpretation of the Lotka–Volterra results.

Lotka–Volterra models were introduced by linearizing the per capita growth rates of an arbitrary population dynamics near a fixed point (Lotka 1932); see Section 2.2 for the technical details. Therefore, one can expect it to be realistic near any such population equilibrium (MacArthur 1970): while per capita growth rates may depend on population densities in nonlinear and intricate ways, this dependence reduces to a simple linear relationship near any fixed point (see also Durinx et al. 2008 about the special role of Lotka–Volterra models in evolutionary analyses). This linearization is the basis for the generality of our conclusions. However, there are a number of subtleties involved that need to be discussed.

First of all, the traditional way of studying Lotka–Volterra models is to define it with specific ingredient functions, such as a Gaussian competition kernel. Obviously, the linearization of mechanistic models will rarely lead to a Gaussian kernel, or any other generic kernel shape. The linearization argument lends generality only to the general form of the equations, which are independent of the specific shapes of the ingredient functions.

Second, linearization is of course a locally valid approximation. Results emerging from the analysis of the Lotka–Volterra model obtained via linearizing some other model can characterize the original model only in the local sense. Linearization at different points of the dynamical state space will lead to different Lotka–Volterra models, i.e., the competition coefficients will not be constant (Abrams 1980a). Moreover, the Lotka–Volterra model obtained from linearization is not necessarily the same as the intuitive Lotka–Volterra analogue of the underlying mechanistic model. This can lead to an apparent inconsistency between Lotka–Volterra and consumer-resource models (e.g., Abrams et al. 2008, Abrams and Rueffler 2009). It is therefore important to consider the actual, mathematically rigorous linearization of the model.

Fortunately, dynamical and structural stability as defined in the previous section are local properties, and so local analysis of models is sufficient to establish them. This will lend generality to our main result that a fixed point containing continuous coexistence is structurally unstable in any model. Since all such fixed points will prove to be (locally) structurally unstable, the system will have to converge to a fixed point which does not contain such a continuum.

The same does not hold for structural robustness, i.e., structural robustness is not strictly a local property. The structural robustness of coexistence, in particular, is intimately connected to the question of an extinction threshold – but extinction is in general not close to the all-positive equilibrium point. Despite this fact, local analyses are indicative of global robustness as well: if for a given parameter combination the linear analysis finds a lack of robustness in all points of the state space, then one can expect loss of robustness globally as well (see Meszéna et al. 2006 for the detailed analysis).

Third, the more detailed ecological models usually have more dynamical variables than just the total densities of the focal populations. For example, explicit representation of the dynamics of resources, consumers, and population structure all lead to additional dynamical variables. Averaging over temporal fluctuations may also introduce such additional dynamical variables (Levins 1979, Kisdi and Meszéna 1993, Chesson 1994, 2009, Szilágyi and Meszéna 2010). Fortunately, if one is interested only in the existence, position, and structural robustness of fixed points, any unwanted variables can be eliminated from a dynamical model by setting their rates to zero in the corresponding differential equations and by using the resultant algebraic equations to eliminate the unwanted variables from the remaining differential equations, which may thus be expressed among total population densities alone (Abrams 2009, Szilágyi and Meszéna 2009a). The resulting model can then be linearized into Lotka–Volterra form around a fixed point. If the original model has a fixed point, the corresponding reduced model will have a corresponding fixed point. Therefore, the existence and structural robustness of such a fixed point will in general be unaffected by the elimination of additional variables.

Unfortunately, the same equivalence applies to the dynamical stability of the fixed point only when 1) the dynamics of the population densities are slow relative to that of other variables (such as resources) which we want to eliminate, and 2) the fast dynamics converge to a stable fixed point. In this case one can study the slow dynamics separately with the assumption that the equilibrated fast variables remains in their slowly changing fixed point. Therefore, Lotka–Volterra models are more indicative of the existence and structural robustness of fixed points of approximated community dynamics than of their dynamical stability.

Fourth, linearization around a fixed point assumes that the dynamics converges to a fixed point, instead of exhibiting cycles, chaos, or other complex behavior. Indeed, experience shows that models of competition along single niche axes often converge to fixed points and do not exhibit complex dynamics. For Lotka–Volterra models with symmetric interactions among species, this has been proven by MacArthur (1970). Beyond this, different models of competition–colonization tradeoffs (Adler and Mosquera 2000, Kinzig et al. 1999, Parvinen and Meszéna 2009), tolerance–fecundity tradeoffs (Muller-Landau 2010, D'Andrea et al. 2013), seed-size evolution (Geritz et al. 1999), and superinfection (Levin and Pimentel 1981) are all based on single niche axes, and all of these models converge to fixed points, at least for the parameter combinations that were explored in the aforementioned studies.

However, we do not expect completely different behavior with respect to our interest even for models with cyclic, chaotic, or stochastically fluctuating population dynamics. No matter how complicated these dynamics, we can usually find a longer timescale on which the suitably time-averaged dynamics is stationary. On that timescale, the average per-capita growth rates are therefore zero (Turelli 1978, Chesson 1994, Szilágyi and Meszéna 2010, Hofbauer and Schreiber 2010, Schreiber et al. 2011). This will come to replace the original equilibrium conditions, to which the arguments above apply. The resultant conclusions can then be carried over to the original model with non-equilibrium behavior, since on the longer timescale the time-averaged model is an accurate representation of the original one; see Chapters 3 and 4 for the case of cyclic oscillations and Szilágyi and Meszéna (2010) for random-noise fluctuations. Note, however, that we do not claim that the effect of fluctuation are irrelevant, or small. The long-timescale, averaged-out model can be completely different from the original one. In particular, the effect of fluctuations can be the introduction of whole new niche axes (Chapter 3), leading out of our assumption of a single regulating continuum. We will therefore not consider models exhibiting complex dynamics in this chapter.

The present review attempts to connect the results from specific studies with an emerging general picture. Naturally, our specific examples will assume specific forms of the ingredient functions. Most of our discussion will be based on the general Lotka–Volterra model (see below). Results that go beyond linearization around an equilibrium are mentioned only briefly in the main text. The new theorem in Appendix A on the other hand is a more general result pertaining to structural stability, and it does not rely on Lotka–Volterra approximations at all.

1.2.3 Lotka–Volterra models along a niche axis

In this review we mostly focus on Lotka–Voltera models along a niche axis described by the following equation:

$$\frac{\mathrm{d}n(x,t)}{\mathrm{d}t} = n(x,t)\left(r(x) - \int_{x_\mathrm{A}}^{x_\mathrm{B}} a(x,y)n(y,t)\,\mathrm{d}y\right), \tag{1.1}$$

for all $x_\mathrm{A} \leq x \leq x_\mathrm{B}$. Here x varies along the niche axis and measures a quantitative trait influencing competition between different types, x_A and x_B are the minimum and maximum values x can take, $n(x,t)$ is the density of individuals with trait value x while $n(x,t)\,\mathrm{d}x$ is the infinitesimal number of individuals with trait values between x and $x + \mathrm{d}x$, $r(x)$ is the intrinsic growth rate of individuals with trait x, and a is the competition kernel, with $a(x,y)$ measuring the interaction strength between individuals with trait y on those with trait x. As we are mostly interested in competitive interactions, in our particular examples we will usually assume a to be nonnegative, i.e., $a(x,y) \geq 0$ for all x and y. However, this assumption is a purely didactic one, and the general conclusions concerning the dynamical stability and structural robustness of coexistence are insensitive to whether a describes purely competitive interactions. Note that the standard textbook form of these equations is obtained by setting $K(x) = r(x)/a(x,x)$ and $\alpha(x,y) = a(x,y)/a(x,x)$. For brevity, we will refer to the collection of individuals with trait x as "species x".

The mathematical analyses considered below are often simpler for the homogeneous case $a(x,y) = a(x-y)$, i.e., when the strength of competition between individuals depends only on the difference between their traits, so we largely restrict our treatment to this situation (again, this assumption will not be essential for our main conclusions later). At a fixed point of the dynamics above, $\mathrm{d}n(x,t)/\mathrm{d}t = 0$ for all x. Since the population densities then become time-independent, we omit t from the argument of $n(x,t)$, writing $n(x)$ when referring to such a steady state.

All coexisting species x have positive population density, $n(x) > 0$, which leads to the equilibrium condition

$$r(x) = \int_{x_\mathrm{A}}^{x_\mathrm{B}} a(x,y)n(y)\,\mathrm{d}y \qquad \text{for all } x \text{ with } n(x) > 0. \tag{1.2}$$

It is worthwhile to stress the mathematical nontriviality of this seemingly simple condition. While it states that the growth rate of each coexisting species must be zero, the condition need not hold for species that went extinct and thus have zero density: this is because in Eq. (1.1) the left-hand side will be zero for a given x either if Eq. (1.2) holds for x or if $n(x) = 0$. If we *assume* that all possible species are present with positive population density, then condition (1.2) yields an equation for each possible x. The solution to the resultant set of equations is called the "natural" solution by Hernandez-Garcia et al. (2009). However, after finding a solution to Eq. (1.2) by assuming $n(x) > 0$ for all possible x, one must not forget to check whether $n(x) > 0$ indeed holds for all x. If so, a fixed point of the dynamics has been found that corresponds to a community in which all possible species coexist. If not, i.e., if $n(x) \leq 0$ for some x in the natural solution, then the initial assumption of $n(x) > 0$ for all possible x is not feasible, and thus wrong. In the latter case, one must then not just remove the species with negative population densities and retain the positive part of the natural solution as a solution to the coexistence problem. Instead, the natural solution must be discarded altogether, as it was derived from a wrong assumption.

Therefore, analyzing the coexistence problem is difficult. One first has to guess at a set of coexisting species, solve the equilibrium conditions for them, and then check whether the resultant solution is indeed all-positive. If not, then that specific set of species cannot coexist. Adding to this complexity is the fact that even if an all-positive solution has been found for a particular set of species, removing some of those species and keeping the rest may still lead to an all-positive solution. This means that it can be very difficult to ensure that the set of species underlying a successfully identified all-positive solution is maximally large. No simple analytical mathematical procedure is known to bypass this trial-and-error search for all-positive and maximal all-positive solutions.

The simplest model for continuous coexistence is that of Roughgarden (1979). In this model, the niche axis encompasses the whole real line, i.e., $x_\mathrm{A} = -\infty$ and $x_\mathrm{B} = \infty$. The competition kernel is chosen to be homogeneous, symmetric, and Gaussian, with variance σ^2,

$$a(x, y) = \exp\left(-\frac{(x-y)^2}{2\sigma^2}\right), \tag{1.3a}$$

and the intrinsic growth rates are chosen also to vary across traits x according to a Gaussian function with variance ω^2,

$$r(x) = \exp\left(-\frac{x^2}{2\omega^2}\right). \tag{1.3b}$$

For $\omega > \sigma$, the equilibrium density distribution satisfying Eq. (1.2) is

$$n(x) = \frac{\omega/\sigma}{\sqrt{2\pi(\omega^2 - \sigma^2)}} \exp\left(-\frac{x^2}{2(\omega^2 - \sigma^2)}\right). \tag{1.3c}$$

This continuous-coexistence solution exists only when the distribution of intrinsic growth rates is wider than the competition kernel. For $\omega \leq \sigma$, no continuous coexistence is possible.

Observe that in the analysis above continuous coexistence seems to appear quite naturally: we find it in the simplest type of competition (described by Lotka–Volterra models) with the most convenient choice of ingredient functions (given by Gaussians). It is also extremely easy to construct infinitely many further mathematical examples of continuous coexistence: choose $a(x, y)$ and $n(x)$ arbitrarily and then calculate the appropriate intrinsic rates $r(x)$ from Eq. (1.2). Importantly, however, nature works the other way around: $r(x)$ and $a(x, y)$ are determined by the considered ecological circumstances and *then* one can ask whether a natural solution for $n(x)$ exists and whether it is dynamically stable.

1.3 Dynamical stability

In this section, we discuss the conditions under which a continuous-coexistence solution is dynamically stable. This means that here we treat the model structure and all model parameters as being fixed, while only perturbing the population densities. We assume that a natural solution to Eq. (1.2) has been found.

1.3.1 Positive-definite kernels

Hernandez-Garcia et al. (2009) proved that positive definiteness of the competition kernel is sufficient for the local dynamical stability of the natural solution. Positive definiteness of a means that the double integral $\iint f(x)a(x, y)f(y)\,\mathrm{d}x\,\mathrm{d}y$ is positive for any function f. When a is symmetric, i.e., $a(x, y) = a(y, x)$ for all x and y, its positive definiteness even implies the natural solution's global dynamical stability (Hernandez-Garcia et al. 2009). Although the latter result does not extend to asymmetric competition, a general nonlinear model of community dynamics is approximated well by a Lotka–Volterra model only near a fixed point anyway, so results for local dynamical stability are the best we can use in most situations to begin with.

1.3.2 Fourier analysis

The intuitive interpretation of the aforementioned result is easier to explain for homogeneous kernels and unlimited trait axes, because it turns out that in this case the requirement of positive definiteness is mathematically equivalent to the competition kernel possessing a Fourier transform whose real part is positive everywhere (Sasaki 1997, Pigolotti et al. 2007, Leimar et al. 2008, Hernandez-Garcia et al. 2009). In general, the construction of Fourier transforms relies on the remarkable mathematical fact that any function (with certain exceptions that are unimportant in applications) can be uniquely represented as a sum of sine waves of suitable frequency, amplitude, and phase (note that "frequency" here has nothing to do with temporal change: the frequency of a sine wave is simply the inverse of its period length, which in the models we consider here has the dimension, not of time, but of trait difference). The Fourier transform $\tilde{f}$ of a function f is given by $\tilde{f}(z) = \int_{-\infty}^{\infty} f(x)e^{-2\pi i x z}\,\mathrm{d}x$, where $i = \sqrt{-1}$ is the imaginary unit. This formula indeed decomposes the original function into a sum of simple sine waves, as $e^{ix} = \cos(x) + i\sin(x)$ by Euler's formula. Reflected by the fact that i appears in the Fourier transform, the resulting function is usually complex – but it turns out that symmetric kernels always have real Fourier transforms, so in our examples we stick to such kernels for simplicity's sake.

Figure 1.2 presents the Fourier transforms of four competition kernels. To understand what these figures mean biologically, we consider some arbitrary perturbation of the population densities $n(x)$ across all traits x and apply the idea that whatever the shape of this perturbation, it can be uniquely decomposed into a sum of simple sine waves. Then, the Fourier transform $\tilde{a}$ of the kernel a at frequency z gives the factor by which the corresponding Fourier component of the perturbation is amplified over time. Some care is needed in interpreting this factor: in Eq. (1.1) the sign of the interaction term is negative, so a *positive* Fourier amplitude of the kernel results in the damping out, or *negative* growth, of the given perturbation component. From this it is evident that if the Fourier transform of the kernel is positive for all possible frequencies, then no matter how we combine those frequencies into a perturbing function, they will all be damped out and so the system will return to its original fixed point: the natural solution is dynamically stable.

Figure 1.3 illustrates the effects of adding a low-frequency versus a high-frequency perturbation to the kernel. In the Fourier transform, such an addition is extremely simple: the transformed function simply acquires a sharp peak at the frequency we perturb. In the kernel itself, such a perturbation appears as an extra oscillation

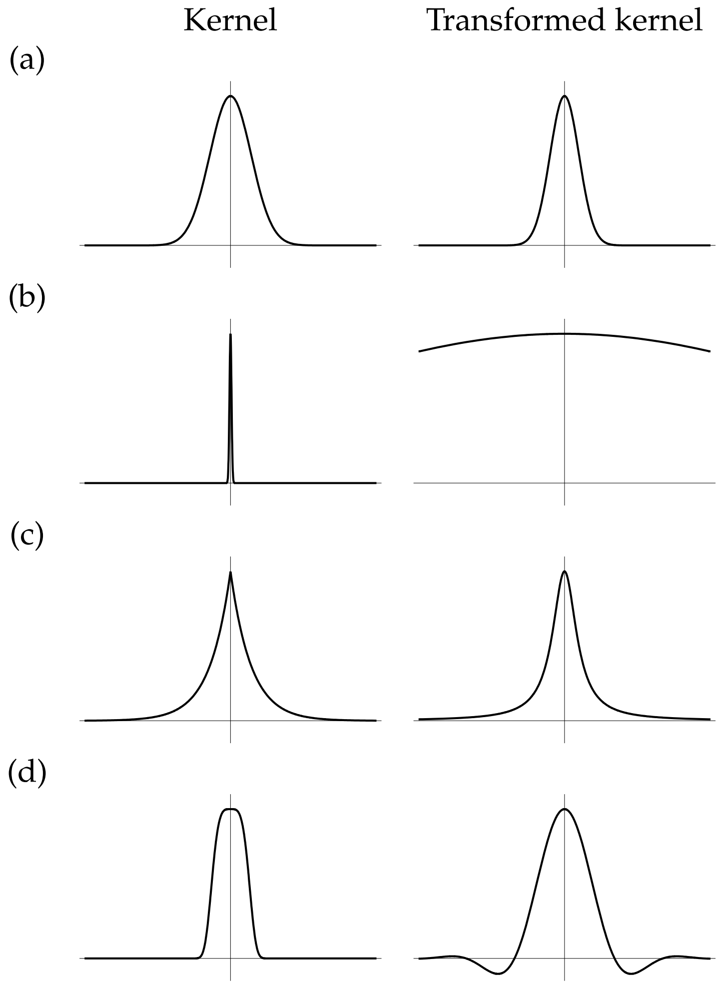

Figure 1.2: Examples of different homogeneous competition kernels a (left column) and their Fourier transforms $\tilde{a}$ (right column). The shown examples are focusing on symmetric kernels, whose Fourier transforms are real-valued symmetric functions. Interpretation of the values $\tilde{a}(z)$ for continuous z is analogous to that of the eigenvalues of the Jacobian matrix $\mathbf{A}$ for a discrete set of species (Box 1): the continuous-coexistence solution under a competition kernel a is dynamically stable against a small perturbation of frequency z if and only if $\tilde{a}(z) > 0$, so it is dynamically stable against all small perturbations if and only if $\tilde{a}(z) > 0$ holds for all z. (a) The Fourier transform of a Gaussian kernel is a Gaussian function with inverse width: as $\tilde{a}(z) > 0$ holds for all z, all such kernels are positive-definite. (b) The Fourier transform of a very narrow Gaussian kernel is a very wide Gaussian function. In the biologically unrealistic limit of an infinitely narrow Gaussian kernel (known as a Dirac delta function), the Fourier transform is therefore flat. (c) The Fourier transform of a kinked kernel also goes to zero for large z, but does so more slowly than for a Gaussian kernel with equal standard deviation. (d) The Fourier transform of a platykurtic kernel, which is more "box-like" than a Gaussian kernel, also goes to zero for large z, but is negative for a range of intermediate frequencies z, implying dynamical instability against small perturbations of those frequencies.

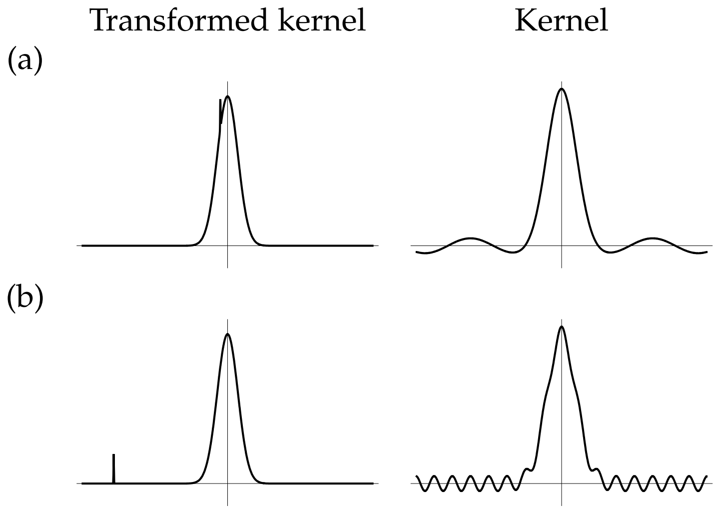

Figure 1.3: The effects of small- versus high-frequency perturbations in the Fourier transform on the original function. The first column contains the Fourier transforms: a Gaussian (whose backtransform is also a Gaussian; see Figure 1.2) and an extra, very narrow Gaussian added on top of it. Due to the narrowness of the perturbation, this corresponds roughly to amplifying a single, well-defined frequency in the Fourier transform. (a) When this frequency is relatively low, the kernel will attain some slow oscillatory behavior on top of the original Gaussian shape. (b) When the perturbing frequency is larger, the kernel exhibits much more rapid oscillations.

added to the original function. Notice how the frequency of the induced oscillation corresponds to the frequency with which we perturbed the Fourier transform.

It is worth mentioning at this point that the method of decomposing a perturbation's dynamics into sine waves is nothing but the generalization of the ideas of linear stability analysis (Box 1) to the case of infinitely many coexisting species. The analogue of the matrix **a** in Box 1 is the competition kernel itself, the eigenvectors in Box 1 correspond to sine waves of varying frequencies, and the eigenvalues in Box 1 are analogous to the amplitudes and phases associated with those frequencies in the Fourier transform of the kernel. Therefore, although the discussion of the dynamical stability of continuous-coexistence solutions requires some new language and a few mathematical tricks, it does not require any new ideas.

1.3.3 Marginal stability

All Fourier transforms in Figure 1.2 approach zero for $|z| \to \infty$. This is true for the Fourier transform of *any* function that has no singularities (Riemann-Lebesgue lemma; see, e.g., Bochner and Chandrasekharan 1949). This means that the large-frequency components (if any) of a perturbation will be damped out only very slowly. Therefore, dynamical stability becomes weaker and weaker for larger frequencies z. In the limit of infinitely high frequencies, there is no true dynamical stabilization anymore, as a zero value of the Fourier-transformed kernel means that perturbations are neither damped nor amplified.

We can consider the Gaussian kernel (1.3a) of Roughgarden's model as an example (Figure 1.2a). We know that the corresponding natural solution (1.3c) exists. The Fourier transform of a Gaussian kernel with standard deviation σ turns out to be another Gaussian with standard deviation $1/\sigma$. This immediately leads to two conclusions. First, as $\tilde{a}(z)$ is positive for all frequencies z, the continuous-coexistence solution in Roughgarden's model is dynamically stable. Second, as $\tilde{a}(z)$ becomes very small for large z, dynamical stability becomes very weak for large z, i.e., for perturbations of high frequency. In the limit of $z \to \infty$, $\tilde{a}(z)$ approaches zero, implying so-called "marginal" stability.

Marginal stability is not just a mathematical curiosity: it is closely related to the discreteness of species along the niche axis. As explained above, dynamical stabilization is effective only against low-frequency perturbations, but not against high-frequency ones. Here, the terms "high" and "low" are considered relative to the inverse niche width $1/\sigma$: the population densities of different species are strongly self-regulated, each almost only by its own population density, and thus almost entirely separately, when their niche differences are much larger than the niche width, i.e., when competition between them is weak. In contrast, their population densities are weakly regulated when their niche positions differ by less than the niche width: in that case, competition between them is strong, and it is only their joint population density that is strongly regulated.

A competition kernel with narrower niche width has a wider Fourier transform (Figure 1.2b). With this in mind, it is instructive to consider the hypothetical extreme case of zero niche width. Then the competition kernel is described by a so-called Dirac delta function, which can be understood as a Gaussian function whose standard deviation approaches zero. Accordingly, its Fourier transform is an infinitely wide Gaussian function – that is, a constant function. As the Dirac delta function is singular at $x = 0$, the Riemann-Lebesgue lemma no longer applies. For such perfectly local competition, dynamical stability would remain strong for perturbations with arbitrarily high frequencies, as the strength of competition would remain zero even between two arbitrarily similar species. Accordingly, there would be no need for species to remain discrete. Obviously however, zero niche width is impossible in the real world: realistic competition kernels are always nonsingular (Geritz et al. 1999, Adler and Mosquera 2000, Rueffler et al. 2007 and Chapter 2; see also Section 1.4.4 below, arguing that any nonsmooth competition kernel is in fact biologically unrealistic). Therefore, dynamical stability is marginal at best for any realistic example of continuous coexistence.

1.3.4 Nondifferentiable positive-definite kernels

To move beyond the realm of Gaussian functions, the following property of Fourier transforms is helpful. As mentioned before, all nonsingular functions have Fourier transforms that eventually approach zero for large frequencies. However, not all of them approach zero at the same rate. More specifically, a function that is differentiable k times has a Fourier transform that for large z approaches zero as fast as z^{-k-2} (Brychkov and Shirokov 1970). Therefore, the more differentiable a function is, the faster its Fourier transform approaches zero and, accordingly, the less stable continuous coexistence will be for competition described by such kernels. One example is provided by Gaussian functions, which are differentiable infinitely many times and whose Fourier transforms therefore approach zero faster than any power function. Other types of competition kernels are not differentiable so many times. For instance, Pigolotti et al. (2010) analyzed kernels that are nondifferentiable at $x = 0$, i.e., at the point of self-competition: these have been dubbed "kinked" kernels. See Figure 1.2c for an example. By comparing Figure 1.2c with Figure 1.2a, it is evident that the Fourier transform of such kinked kernels approach zero much more slowly than that of Gaussian kernels of similar width. This means that the continuous-coexistence solution has nonmarginal stability for a much wider range of frequencies, and therefore for a much wider class of perturbations.

1.3.5 Overlap kernels

So far we have examined only positive-definite competition kernels, as the continuous-coexistence solution is dynamically unstable for other kernels. It is thus important to understand how positive-definite and non-positive-definite kernels might arise in nature (Figure 1.2d). One simple result is that if the competition kernel is exactly determined by the overlap between the resource-utilization functions of the two competing species (as, e.g., in MacArthur and Levins 1967), then it will always be positive-definite (Roughgarden 1979, p. 520, Hernandez-Garcia et al. 2009, Pigolotti et al. 2010). However, as pointed out in the last two references and by Meszéna et al. (2006), analyzing such overlaps between resource-utilization functions is but one special, if particularly popular, approach to the formation of competition kernels. Non-positive-definite kernels arise just as naturally from other approaches.

1.3.6 Platykurtic kernels

One feature many non-positive-definite kernels have in common is that they are more platykurtic, or "box-like", than positive-definite ones, as a quick visual comparison of Figure 1.2d with the other three examples in the same figure immediately reveals. This makes intuitive sense given the link between continuous coexistence and positive definiteness: a more box-like competition kernel means that similar species compete more strongly, making their coexistence more difficult to achieve. Conversely, kinked kernels reduce competition even between very similar species to tolerable levels, making their coexistence easier.

1.3.7 Summary

The dynamical stability of the natural solution, and thus of continuous coexistence, hinges on the positive definiteness of the competition kernel, i.e., the double integral $\iint f(x)a(x,y)f(y)\,\mathrm{d}x\,\mathrm{d}y$ has to be positive for any function f. For homogeneous kernels, where $a(x,y) = a(x-y)$, positive definiteness is equivalent to the positivity of the competition kernel's Fourier transform. In the homogeneous case even when this requirement is met, dynamical stability is always only marginal for perturbations involving frequencies approaching infinity.

1.4 Structural robustness

After having studied the dynamical stability of the natural solution, in this section we now turn our attention to the structural robustness of the all-positive fixed point describing continuous coexistence.

1.4.1 Two aspects of structural robustness

The Lotka–Volterra models in Eq. (1.1) have two ingredient functions: the competition kernel a and the distribution r of intrinsic growth rates. Structural stability and robustness therefore needs to be analyzed with respect to perturbations of each of these ingredients.

Robustness with respect to perturbations of the competition kernel is easier to understand than robustness with respect to perturbations of the distribution of intrinsic growth rates. As we have seen in the previous section, positive definiteness of the kernel is required for dynamically stable continuous coexistence. For homogeneous kernels, this translates to the Fourier transform having to be positive. In this case, we have also seen that the transformed kernel always approaches zero for large frequencies. Therefore, if we perturb the competition kernel by a sinusoidal function of high enough frequency, its Fourier transform will turn negative at some points regardless of how small the strength of this perturbation is. Therefore, there always exists a perturbation of arbitrarily small strength that turns a dynamically stable fixed point (corresponding to dynamically stable continuous coexistence) into a dynamically unstable one (corresponding to the loss of continuous coexistence). The conclusion for homogeneous and positive-definite competition kernels is that the fixed point of continuous coexistence is *always* structurally unstable with respect to perturbations of such kernels.

Below, we therefore focus on the much more important aspect of robustness against perturbations of the intrinsic rates r. There are two reasons why this is more important. First, it is easier to provide general results for structural robustness rather than dynamical stability, as there are powerful model-independent theorems that can inform us about structural robustness. Second, as we shall see, continuous coexistence will prove to be unrobust to perturbations of the intrinsic rates r in any realistic model, irrespective of the properties of the competition kernel.

The topic was initiated by the landmark paper of Sasaki and Ellner (1995): while these authors investigated mixed evolutionarily stable strategies (ESS, Maynard Smith and Price 1973) in fluctuating environments, the mathematical structure of their problem was similar to the problem of coexistence in Lotka–Volterra models (see Eq. E4 of Sasaki and Ellner 1995). They concluded that a mixed ESS with a continuous distribution was exceptional, i.e., structurally unstable. Haccou and Iwasa (1998) studied the transition between the continuous and the discrete solutions. The issue of generic discreteness was further established by Sasaki (1997) (in the formally analogous context of spatial rather than phenotypic distributions of individuals), who explicitly demonstrated the lack of structural robustness of Lotka–Volterra models to small random-noise perturbations of the intrinsic rates r.

Based on these earlier findings, Gyllenberg and Meszéna (2005) have proven a result that is independent of Lotka–Volterra models: continuous coexistence is inevitably structurally unstable. It is beyond the scope of the current chapter to specify the precise mathematical assumptions underlying this result. In essence, the theorem is based on two biologically natural assumptions: a finite niche volume (for instance, a finite interval $[x_A, x_B]$ along a niche axis describing variation in a quantitative trait x) and continuous ingredient functions (therefore, the theorem does not exclude the possibility of structurally robust continuous coexistence for an infinitely narrow competition kernel, as such a kernel is not continuous). However, there is one limitation in the way the theorem treats coexistence, as it focuses on the structurally robust coexistence of a predefined set of strategies: while the theorem shows that there always exists an arbitrarily small perturbation that destroys coexistence of any specific infinite set of species, it leaves open the possibility that *another* infinite set of species can coexist after the perturbation.

These considerations assumed that the functions a and r can be perturbed independently of one another. This will not be necessarily so when the Lotka—Volterra approximation is derived as the linearization to an underlying model: a perturbation of the original model will in general modify both the kernel a and the intrinsic rates r (Ackermann and Doebeli 2004, Rueffler et al. 2006). However, it is always possible to modify the intrinsic rates r independently in *any* underlying model, as this would simply correspond to species-specific increased mortality rates, possibly due to chronic predation or any other ecological mechanism. Adding such extra mortalities modify the intrinsic rates r but not the kernel a. This extra freedom can also be used to keep r constant when a is perturbed. Putting it differently, if the underlying model builds a fine-tuned connection between r and a such that the arguments above lose validity, then that fine-tuning is structurally unstable.

1.4.2 Analytic kernels

A stronger statement can be derived if we assume analytic ingredient functions. A function is called analytic if it can be substituted by its Taylor series around any value of its argument. Consequently, such functions are differentiable infinitely many times, so that analyticity can be seen as an especially high degree of “smoothness”. The use of analyticity arguments in the context of continuous coexistence was initiated by Sasaki and Ellner (1995).

With the assumption of analyticity, any model that allows an infinite set of species to coexist on a finite interval along a single niche axis can be perturbed by an arbitrarily small perturbation in such way that the perturbed model no longer allows for the coexistence of *any* infinite set of species. This theorem was proved by Gyllenberg and Meszéna (2005) for the special case of Lotka–Volterra models with homogeneous competition kernels (with key elements of the mathematical argument closely corresponding to those underlying Proposition 2 of Appendix E in Sasaki and Ellner 1995). With the proof being presented in Appendix A, here we provide a model-independent generalization of this theorem.

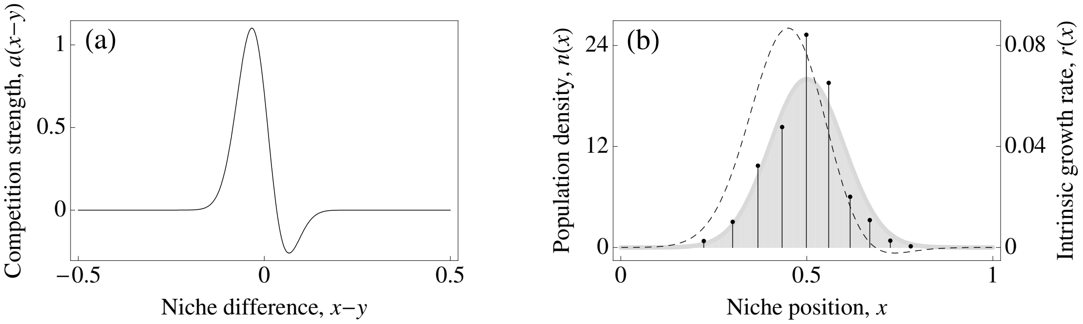

Figure 1.4: Coexistence under an analytic competition kernel. (a) The competition kernel a is obtained as $a(x-y) = e^{-225(x-y)^2}(1-30(x-y))/\sqrt{2}$. One can show that this kernel is positive definite. Note that the kernel does not attain its maximum at zero niche difference, and that the species interactions described by this kernel are not purely competitive. (b) The distribution r of intrinsic growth rates (dashed curve) is constructed so as to yield the continuous-coexistence solution $n(x) = \exp(-(x-0.5)^2/0.02)$ (gray curve and area) in conjunction with this particular competition kernel. This is achieved by inserting the kernel and the desired continuous-coexistence solution into Eq. (1.2). We perturb this distribution r with a small and very narrow perturbation at $x = 0.5$. The outcome is obtained by following the dynamics of Eq. (1.1), approximated by 400 equidistant species, until equilibrium is reached, from a uniform initial condition. Even though the perturbation is small, it completely collapses continuous coexistence, leaving only ten discrete, more-or-less evenly spaced surviving species (vertical lines).

Figure 1.4 provides an example. The kernel is homogeneous, but that is just for the sake of easier presentation: nonhomogeneous kernels are more difficult to plot and to interpret. The kernel used in this example does not peak at zero niche difference (competition does not increase monotonically with increasing species similarity), and the interactions described by this kernel are not purely competitive. Maximal competition at zero niche difference and purely competitive kernels are popular assumptions, but are not necessarily biologically realistic (Ackermann and Doebeli 2004, Abrams and Rueffler 2009). In our example, the original continuous coexistence pattern collapses into the coexistence of ten distinct species after perturbing the intrinsic rates r – just as the theory predicts.

Reinterpreting the classical results on species coexistence and similarity in light of the theorem in Appendix A reinforces some of the original conclusions, while overcoming the mathematical limitations of the original analyses. For example, Szabó and Meszéna (2006) considered the continuous-coexistence solution of Roughgarden and tried to break it by changing the distribution of intrinsic growth rates in a variety of ways. They found that the original "2σ-rule" of MacArthur and Levins (1967) for the minimum distance between coexisting species can be retained as a rule of thumb, i.e., the coexistence of species at a niche distance that is smaller than twice their niche width has sufficiently low structural robustness to be unlikely to be observed. On this basis, Barabás and Meszéna (2009) investigated whether and how continuous-coexistence solutions are recovered in the limit of infinitely small perturbations to the distribution of intrinsic growth rates. The main results can be summarized as follows. First, the shape of the perturbing function is largely irrelevant; it is only its amplitude that matters. Second, the average niche distance between nearest neighbors is proportional to $((2\sigma)^{-1} - \beta \ln \epsilon)^{-1}$, where σ is the standard deviation of the competition kernel, β varies with the shape of the perturbing function, but can be approximated by 1 without incurring a large error, and ϵ is the perturbation's amplitude. Here, ϵ is measured relative to the maximum of the unperturbed intrinsic rates r and σ is measured relative to the width of the unperturbed r (ω in Eq. (1.3b)). This expression predicts that for small σ the average nearest-neighbor niche distance rises very steeply with ϵ, towards an intermediate plateau at 2σ (the spacing exactly equals 2σ for $\epsilon = 1$). For example, for $\sigma = 0.01$, a spacing of 90% of 2σ is reached already for perturbation amplitudes as small as $\epsilon \approx 0.4\%$. For very small values of ϵ, species packing can be very tight. As $\epsilon \to 0$, continuous coexistence is recovered, as mathematically required. But since such very tight packing can be achieved only when perturbations remain exceedingly small, in reality we are approximately observing the classical 2σ-rule.

These results are in line with the aforementioned theorem by Gyllenberg and Meszéna (2005), which establishes that analytic competition kernels preclude any structurally robust continuous coexistence, so that the emergence of finitely many, discrete species is the expected equilibrium community pattern. A remaining question is what happens when the intrinsic rates $r(x)$ are perturbed and the competition kernel is *not* analytic.

1.4.3 Smooth nonanalytic kernels

Since assuming analyticity requires a degree of "smoothness" that is biologically unrealistic, we now turn to competition kernels that are not analytic, but just differentiable at least once. In mathematics, such functions are called “smooth”[1]. While there are no such powerful theorems as in the case of analytic kernels to rule out structurally robust continuous coexistence, smooth nonanalytic kernels are visually similar to analytic ones and there is no obvious argument to discard them a priori as being biologically unrealistic.

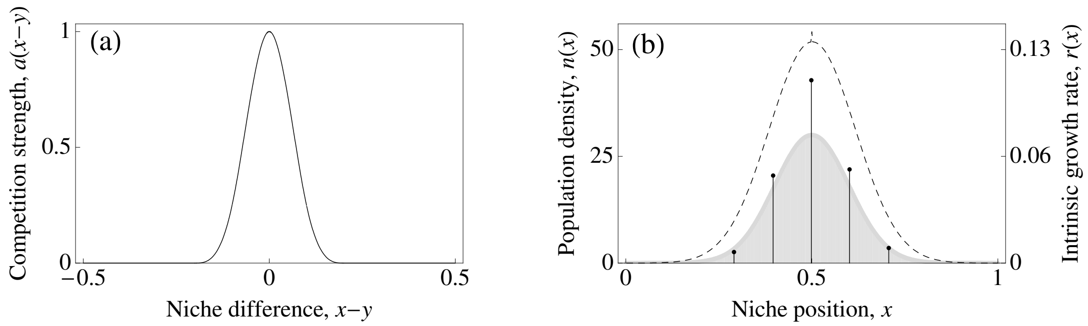

Figure 1.5: Coexistence under a smooth nonanalytic competition kernel. (a) The competition kernel a is obtained as $a(x-y) = \int u(x-z)u(y-z)\,\mathrm{d}z$ with a resource-utilization function u that equals $u(x) = 1 - |10x|$ for $x \leq 1/10$ and zero otherwise. The construction of this kernel as an overlap kernel guarantees its positive definiteness. It is smooth enough to be twice differentiable, but not smooth enough to be analytic, as its third derivative is already discontinuous. (b) The distribution r of intrinsic growth rates (dashed curve) is constructed so as to yield the continuous-coexistence solution $n(x) = \exp(-(x-0.5)^2/0.02)$ (gray curve and area) in conjunction with this particular competition kernel, just as in Figure 1.4. We perturb this distribution r with a small and very narrow perturbation at $x = 0.5$ (tiny peak at the top of the dashed curve). The outcome is obtained by following the dynamics of Eq. (1.1), approximated by 400 equidistant species, until equilibrium is reached, from a uniform initial condition. Even though the perturbation is small, it completely collapses continuous coexistence, leaving only five discrete, more-or-less evenly spaced surviving species (vertical lines). Observe that the distance between neighboring surviving species roughly equals twice the standard deviation of the competition kernel.

In Chapter 2 extensive numerical analyses are performed to clarify what kinds of coexistence patterns are to be expected under such conditions. We choose smooth nonanalytic kernels a and intrinsic rate distributions $r(x)$ that produced continuous-coexistence solutions, and then numerically solved Eq. (1.1) for small localized perturbations of $r(x)$ and initial conditions $n(x,0) = n_0(x) = \text{const}$. In all studied cases, continuous coexistence proved to be structurally unstable, which

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[1] In the mathematics literature, “smooth” is often synonymous with “differentiable infinitely many times”. We deviate from this convention by calling those functions “smooth” that are differentiable at least once.

means that the model behaved in every way as if the competition kernel were analytic (Figure 1.5; see also Figure 2.2).

Based on these results, we tentatively accept the conclusion that smooth nonanalytic kernels also do not allow for structurally robust continuous coexistence: for all practical purposes, they behave as if they were analytic.

1.4.4 Kinked kernels

As stated before, we refer to a competition kernel as being “kinked” if it is nondifferentiable at the point of self-competition (kernels possessing nondifferentiabilities at other points are not called “kinked” according to this convention). The competition dynamics resulting from kinked kernels turns out to be vastly different from what we have discussed above. In Chapter 2 we numerically analyze many instances of Lotka–Volterra models with kinked kernels, the result invariably being that continuous coexistence turned out to be structurally robust (Figure 1.6; see also Figure 2.3). Certain species might go extinct, but the pattern of infinitely closely packed species remains intact.

An intuition of why this happens can be gained by examining the coexistence of just two species. For two species with similar niche positions competing according to a smooth competition kernel, the strength of interspecific competition will almost equal that of intraspecific competition. More precisely, the ratio between both types of competition is exactly 1 to a first-order approximation for small niche distances. The reason is that, since the two species are so close together, the competition kernel needs to be considered only for very small niche differences, i.e., very near its peak – where, to first-order approximation, a smooth function does not change. Since dynamically stable coexistence requires that intraspecific competition be greater than interspecific competition, coexistence at very small niche distance will then not be structurally stable, i.e., it can occur only for very particular parameter choices. To coexist structurally robustly, the two species will thus have to differ somewhat more in their niche traits, such that the quadratic term of the Taylor expansion of the competition kernel plays a nonnegligible role in reducing interspecific competition. In contrast, if the kernel is kinked, then no matter how similar the two species are, competition between them is reduced linearly with their niche distance, rendering their coexistence structurally robust. The fact that a kinked kernel decays linearly with the distance from its maximum – as opposed to a smooth kernel which decays only quadratically – is the key to the capacity of kinked kernels to generate structurally robust coexistence among

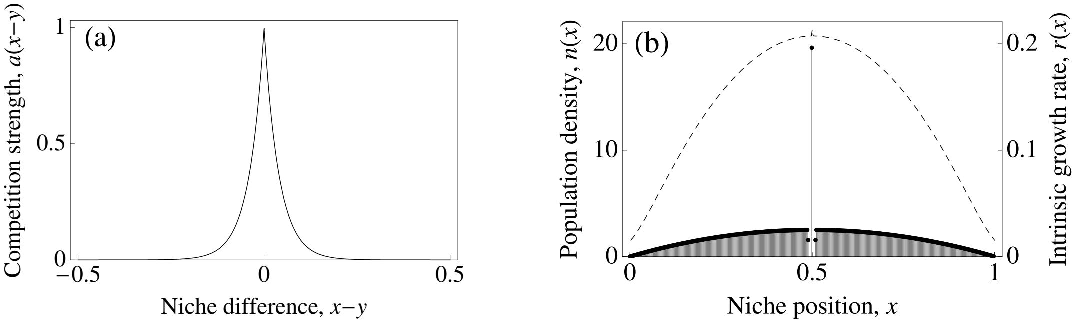

Figure 1.6: Coexistence under a kinked competition kernel. (a) The competition kernel a is given by $a(x-y) = \exp(-|x-y|/0.04)$. This kernel is kinked (not differentiable) at $x = 0$. (b) The distribution r of intrinsic growth rates (dashed curve) is constructed so as to yield the continuous-coexistence solution $n(x) = 10(0.25 - (x-0.5)^2)$ for $0 \leq x \leq 1$ and $n(x) = 0$ otherwise in conjunction with this particular competition kernel. We perturb this distribution r with a small and very narrow perturbation at $x = 0.5$ (tiny peak at the top of the dashed curve). The outcome is obtained by following the dynamics of Eq. (1.1), approximated by 400 equidistant species, until equilibrium is reached, from a uniform initial condition. Under this perturbation, the original community is almost perfectly retained, except for a narrow range of species that go extinct near the central species at $x = 0.5$, which the perturbation furnishes with a relative advantage. Therefore, although the community as a whole is not structurally stable with respect to the perturbation of r – since some extinctions did happen, as is guaranteed by the theorem by Gyllenberg and Meszéna (2005) – the general pattern of continuous coexistence turns out to be structurally robust. This structural robustness of continuous coexistence, however, is an artifact of the competition kernel being kinked: as explained in the text, such kernels are not biologically realistic, so the coexistence patterns they generate are of no real significance.

arbitrarily similar species. Therefore, not only are there good intuitive reasons to expect structurally robust continuous coexistence under kinked competition kernels, but every numerical example we have considered so far confirms this expectation.

However, it has been argued (see Chapter 2) that kinked kernels provide an unrealistic representation of trait-dependent competition, arising from overly idealized ecological assumptions. In particular, it has been shown that intraspecific variation in traits (*any* intraspecific variation at all, not just continuous or smooth ones), as well as environmental variability, will smooth out any nondifferentiabilities in the competition kernel. Therefore, the structurally robust continuous-coexistence patterns produced by kinked kernels turn out to be mere model artifacts. This has important implications for models using such kernels, like the hierarchical competition-colonization and competition-mortality tradeoff models (Kinzig et al.

1999, Adler and Mosquera 2000; in these models, competition kernels are discontinuous, making structurally robust continuous coexistence even easier to achieve than in models in which competition kernels are merely kinked), the tolerance-fecundity tradeoff model (Muller-Landau 2010), and models of superinfection (Levin and Pimentel 1981). It must therefore be expected that any smoothing out of trait-dependent competition in these models will lead to qualitative differences in their behavior. For instance, D'Andrea et al. (2013) have investigated the tolerance-fecundity and competition-colonization tradeoff models to ascertain whether the proposed coexistence mechanisms in these models would still operate after smoothing the assumed competition kernels, and to examine how other aspects of the model, such as species richness, would be affected. These analyses showed that the proposed coexistence mechanisms still work as such, but also that they generate significantly less coexistence than their nonsmooth counterparts, even if the smoothed kernels were still changing very abruptly (i.e., they had large negative second derivatives at the point of self-competition; with the corresponding absolute value being infinitely large for a kinked kernel). Very similar results were obtained by Adler and Mosquera (2000) for the competition-mortality tradeoff model, and by Geritz et al. (1999) for a model of seed-size evolution. In particular, continuous coexistence was always ruled out after smoothing the competition kernels of these models.

Note that the importance of the shape of the competition kernel has already been emphasized by Abrams (1975); his results are easy to interpret within the context above. He studied the coexistence bandwidth for two species as a function of niche difference in three different models. The first model employed the usual smooth overlap kernel. Accordingly, the coexistence bandwidth shrunk to zero quadratically, which means that beyond a certain level of similarity the bandwidth shrinks so fast that it becomes essentially zero. In the other two models the strength of competition was related to the area in common under the two utilization curves, instead of the overlap-integral of the curves. In can be shown (Chapter 2) that these kinds of kernels are kinked. Therefore, the coexistence bandwidth goes to zero only linearly in these cases, meaning that the bandwidth can still be appreciably large even for very similar species. From this angle, too, the result is that kinked kernels allow for the coexistence of similar species.

1.4.5 Kinked non-positive-definite kernels

For the sake of completeness and theoretical interest, we finally consider what happens when a competition kernel is kinked, but not positive-definite. We know that kinked kernels can produce structurally robust continuous coexistence, but we also know that non-positive-definite kernels destabilize continuous coexistence. What happens when these two opposing effects are occurring together?

Once again, only numerical analyses are available for addressing this question. Such analyses consistently show a special coexistence pattern in which exclusion zones are interspersed with trait intervals of continuously coexisting species (Figure 1.7). These findings are compatible with the interpretation that local dynamics along the trait axis are dominated by the kernel's kink, whereas the global pattern is determined by the kernel's non-positive-definiteness. In summary, continuous coexistence is still observed, although not for all trait values along the niche axis. With this qualification, kinked non-positive-definite kernels produce structurally robust continuous coexistence just as kinked positive-definite kernels do.

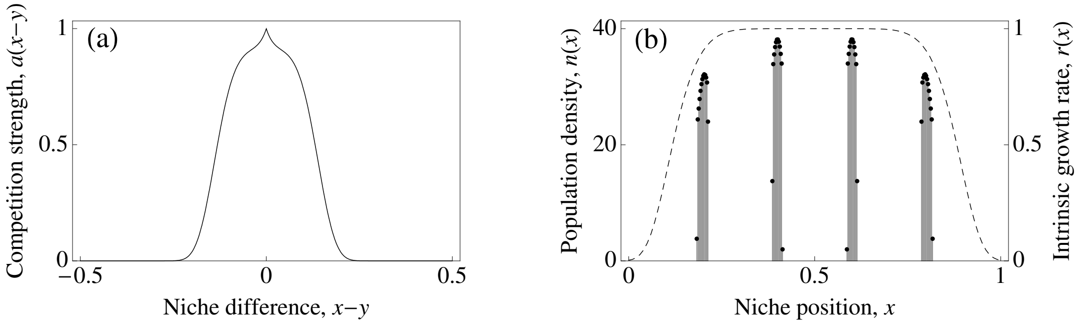

Figure 1.7: Coexistence under a kinked non-positive-definite competition kernel. (a) The competition kernel a is given by $a(x-y) = 0.9\exp(-(x-y)^4/0.15^4) + 0.1\exp(-|x-y|/0.02)$. This kernel is kinked (not differentiable) at $x = 0$, and its Fourier transform is negative for some frequencies. (b) The distribution r of intrinsic growth rates is given by $r(x) = \exp(-(x-0.5)^8/0.4^8)$ (dashed curve). The outcome is obtained by following the dynamics of Eq. (1.1), approximated by 400 equidistant species, until equilibrium is reached, from a uniform initial condition. This yields a coexistence pattern in which dynamically stable lumps of continuously coexisting species are alternating with exclusion zones in which no species exist. Interesting though these patterns are, they are of no real significance, as they critically depend on the biologically unrealistic assumption of a kinked competition kernel.

The relevance of these findings lies not just in future research: kinked non-positive-definite kernels have already been used in the literature, leading to the patterns described above (Scheffer and van Nes 2006, Hernandez-Garcia et al. 2009, Vergnon et al. 2012). In the study by Scheffer and van Nes (2006), the competition kernel was chosen to be Gaussian, for which the arguments presented in the previous sections clearly predict dynamically stable (but structurally unrobust) continuous coexistence. Pigolotti et al. (2010) elucidated how this discrepancy with the numerical results actually reported by Scheffer and van Nes (2006) can be ascribed to the implementation of periodic boundary conditions. When periodic boundary conditions are chosen, distances are not unambiguously defined, as the niche space is effectively a circle. Denoting the shortest niche distance between two species by d and the circle's length by L, the proper implementation of periodic boundaries requires that all distances $(jL + d)$ or $(jL - d)$ for arbitrary positive integers j be considered, corresponding to different numbers of winding clockwise or counterclockwise around the circle. Instead, Scheffer and van Nes (2006) implemented periodic boundaries by simply picking the shortest of all these distances. Such a simplification amounts to truncating the tails of the competition kernel at a niche distance of $d = L/2$. Because of the structural instability of models with Gaussian kernels discussed above, this truncated kernel has negative Fourier components, leading to the dynamical instability of continuous coexistence, and thus to the "clumpy" pattern observed by Scheffer and van Nes (2006): this pattern applies for very long transients, during which several additional species coexist around each of a few eventual surviving equally spaced species. As was highlighted already by Scheffer and van Nes (2006), these unusually long transients result when applying a perfectly uniform function for the intrinsic rates r – Figure 4 of their study shows faster convergence to the eventual equilibrium when r is not uniform. Crucially, Pigolotti et al. (2010) showed how the clumpy pattern disappears when periodic boundaries are implemented in the usual way: as the kernel then is not truncated, and hence remains positive-definite, no transient clumps of species are observed and continuous coexistence is retained.

Scheffer and van Nes (2006) also studied a case in which the same model is complemented by an enhanced self-interaction term – possibly describing species-specific predators or pathogens. The resulting effective competition kernel was therefore given by a Dirac delta function being added to the original Gaussian. The outcome of this setting can be understood as the combined effect of the negative Fourier components of the truncated Gaussian kernel, leading to the clumpy pattern, and of the Dirac delta function, which in analogy with the kinked kernels described above has the effect of stabilizing continuous coexistence within the clumps (Figure 1.7). To appreciate the connection, notice that the Dirac delta function can be defined as the limit of a kinked kernel, namely a symmetric tent function, in which the two flanks surrounding the kink become infinitely steep. (Earlier in the chapter we claimed that a Dirac delta can be thought of as a Gaussian with an infinitely narrow variance. There is no contradiction: both procedures lead to the same object in the limit of infinite steepness and infinitely small variance, respectively.)

It has been emphasized (Scheffer and van Nes 2006) that such patterns generated by kinked but non-positive-definite kernels fall neither into the domain of pure limiting similarity nor into that of pure continuous coexistence, but constitute an interesting separate case situated in between those extremes. Contrary to this interpretation, however, we would be cautious about assigning too great an importance to these mixed coexistence patterns, simply because kinked kernels are unbiological. Therefore, interesting though the patterns produced by kinked non-positive-definite kernels are from a purely theoretical perspective, they are practically irrelevant in a world in which all realistic competition kernels are smooth.

1.4.6 Summary

Analytic competition kernels never allow for structurally stable continuous coexistence, as is proved in Appendix A. Smooth nonanalytic kernels seem to behave exactly like their analytic cousins, though the evidence so far is purely numerical (see, e.g., Figure 1.5). While kinked kernels do lead to the robust possibility of arbitrarily many arbitrarily similar coexisting species, such kernels are biologically unrealistic, therefore this theoretical possibility cannot be realized in nature. In reality, competition kernels are always smooth. As long as no counterexamples are found to smooth kernels behaving just like analytic ones, this will rule out structurally robust continuous coexistence altogether.

1.5 Discussion

In this chapter we have reviewed the community patterns produced by the grandmother of all competition models, the family of Lotka–Volterra models. We were particularly interested in conditions for continuous coexistence, i.e., coexistence of arbitrarily many arbitrarily tightly packed species along a single niche axis. To address the biological relevance of dynamically stable patterns of continuous coexistence, we have investigated whether such patterns are also structurally stable, or robust: do small perturbations of a Lotka–Volterra model's ingredient functions – the competition kernel and the distribution of intrinsic growth rates – typically restore the discreteness of coexisting ecological types? The answer is that patterns of continuous coexistence are invariably structurally unstable to perturbations of the distribution of intrinsic growth rates if the competition kernel is analytic; this has been proven as a theorem (see Appendix A). We also find that smooth nonanalytic competition kernels behave exactly like their analytic counterparts in that any resultant continuous coexistence is structurally unstable. While there is no analytic proof of this latter finding, extensive numerical results are all pointing in this direction. Finally, competition kernels that are "kinked", i.e., are nondifferentiable at zero niche distance, lead to structurally robust continuous coexistence. However, such kernels are biologically unrealistic: in reality, we expect all competition kernels to be smooth. The emerging picture is that coexistence of a number of well-defined, separate species is expected in all realistic Lotka–Volterra models. Exceptions to this rule require either unrealistic biological assumptions or fine-tuned parameter values.

Two reasons motivate our focus on Lotka–Volterra models. First, as stated earlier, any model reduces to a Lotka–Volterra model near a fixed point, and many niche models indeed exhibit fixed-point equilibria. Therefore, Lotka–Volterra models are much more general than it seems at first sight: since dynamical and structural stability are local properties of a model, fixed point analysis suffices to establish them. Second, Lotka–Volterra models also have the advantage of providing the simplest possible framework for studying competition. Consequently, it is very important to gain a deep and thorough understanding of all possible dynamic behaviors and resultant community patterns such models can produce, as this provides a necessary solid starting point for understanding more complicated models.

The emerging picture is that the mathematical structure of ecological interactions alone is enough to dictate the discreteness of species. Yes, there exist specific models where a continuum of ecological types may coexist. Even more is true: continuous coexistence can be achieved in any model whatsoever by properly fine-tuning parameters. However, such coexistence is necessarily structurally unstable, and is dynamically marginally stable at best. Both dynamical and structural stability have a characteristic distance along the niche axis, determined by the asymptotic decay of the kernel's Fourier transform. The stabilizing effect of ecological interactions is based on the net interspecific competition weakening compared with intraspecific competition. Since we assume that the kernel is smooth, this weakening – an the stabilizing effect (Chesson 2000b) that comes with it – cannot be realized between types that are overly similar. The niche distance over which competition decreases sufficiently corresponds to the niche width of early competition models.

In general we cannot expect the competition kernel to be Gaussian, or even to decrease monotonically with increasing niche distance. The crucial fact on which the above intuitive picture hinges is that the strength of competition will significantly decrease for large enough niche differences. The distance over which this "significant decrease" happens is what we call the niche width. This definition is decidedly imprecise – but it is still a useful concept, yielding a rule of thumb for the approximate distance between coexisting species in the absence of fine-tuning (Szabó and Meszéna 2006, Barabás and Meszéna 2009).

Naturally, no fixed lower limit to the similarity of coexisting species exists: arbitrarily similars may coexist by properly adjusting parameters. Without such tinkering however, an effective lower limit to similarity appears, in line with the picture given by Abrams (1983) and already mentioned in the Introduction. In this case it is the niche width, defined above, which will determine that lower limit. In this way, we managed to unite the possibility for continuous coexistence, the intuition regarding limiting similarity, and the concept of the coexistence bandwidth into a single framework. This framework is independent of the underlying ecological details.

Our analyses were restricted to models with a single niche axis. Many of our results on the other hand still apply for multidimensional niche spaces as well. In particular, positive definiteness of the kernel as a requirement for dynamical stability, and its relation to (multidimensional) Fourier transforms for homogeneous kernels are retained. The theorem of Gyllenberg and Meszéna (2005) explicitly assumes a multidimensional niche space. Only the result assuming analyticity (the theorem of Appendix A) is restricted to a single niche dimension. Whether this theorem can be generalized to multiple niche axes is an open question. Nevertheless, we do not expect its conclusions to be violated on these grounds. At least so far, we have not seen any counterexamples to the claim that continuous coexistence is structurally unstable for multiple niche dimensions.

Needless to say, departures from the results reported here could occur for a number of reasons: e.g., equilibrium might not be reached, so some species may still be on their way to extinction; the spatial range to which the model is applied could be chosen too small, so immigration from outside that range, unaccounted for in the model, might dominate the observed coexistence patterns; or the salient niche spaces might be multi-dimensional (imagine two independent niche axes; if two species are segregated with respect to one but not the other axis, and we only look at that second axis, we will get the impression that the species coexist without niche segregation). But the theory summarized here still provides clear baseline expectations regarding community patterns, rejection of which would indicate that one or more of the aforementioned reasons are applicable in a studied empirical setting. That the theory reviewed in this chapter establishes the picture of discretely many, separate species coexisting as a baseline expectation makes it especially useful: where the theory's assumptions are met, it provides strong qualitative and quantitative insights and predictions, and where these predictions are not met, it narrows down the underlying reasons to a handful of testable hypotheses for further empirical investigations.

A central aspect of the debate concerning limiting similarity was the claim by May (1973) that limiting similarity is contingent on environmental fluctuations. This idea has been criticized by Abrams (1976), who showed that only those fluctuations can maintain limiting similarity which influence the competing species in different ways. Turelli (1978) introduced the method of averaging to study invasion dynamics, and built the stochastic theory from ground up, using stochastic differential equations. In light of their results one can say that May's argument is valid when the fluctuations are so slow as to make it biologically meaningless to take averages over it. In this case, species must be able to coexist for all parameter combinations produced by the fluctuating environment. May's argument is therefore effectively equivalent to an argument about structural robustness, leading to limits of similarity when the fluctuating parameters are varying the relative competitiveness of the competing species.

Discussions on the adequacy of Lotka–Volterra models are closely connected to broader questions about the role of theoretical models in ecology. After all, such models always oversimplify reality, the "validity" of underlying assumptions are difficult to ascertain, and different models may often lead to wildly different conclusions. The study of limiting similarity is especially sensitive in this respect: the very same family of Lotka–Volterra models motivated limiting similarity *and* was used for demonstrating the possibility of continuous coexistence. The history of theoretical ecology has shown that going beyond Lotka–Volterra models also did not help to clarify this confusingly ambiguous situation, which uncomfortably reminded researchers of the fact that they did not actually fully understand even the simplest models. In a nutshell, it has taken theoretical ecologists decades to unravel the subtleties associated with continuous coexistence in Lotka–Volterra models. Here we have attempted to demonstrate that a sufficiently careful analysis of Lotka–Volterra models, together with some general considerations, can largely settle the issue of continuous coexistence versus the discreteness of species – not just for one specific family of models, but as a broadly relevant biological conclusion.

Chapter 2

Species packing in nonsmooth competition models

2.1 Introduction

The Darwinian view of life can be summarized as follows: 1) competition between similars is too strong for coexistence to happen, and the ensuing competitive exclusion favors the more fit type, thus driving natural selection and the evolution of all the marvelous adaptations on our planet; and 2) competition between sufficiently dissimilars can be reduced to a level where there is no competitive exclusion, leading to coexistence and the fantastic diversity of life we see around us. Darwin's insight does lead to some natural questions: what do species have to be different in to coexist, and just how much dissimilarity is sufficient to avoid competitive exclusion?

The first question was the main focus of early competition theory (Volterra 1926, Gause 1934, Hardin 1960). The conclusion was that at equilibrium, no two species may consume the same resources. Later Levin (1970) noticed that, from a mathematical point of view, there is no essential difference between what we would call a "resource" and all other possible things that provide a negative feedback loop between growth rates and densities. These generalized resources (called limiting factors by Levin, and regulating factors by Krebs 2001, p. 288 and Case 2000, p. 146) are the things then that species have to utilize differently in order to coexist. Hence, traits associated with resource consumption (or, more generally, population regulation) are expected to differ amongst coexisting species: if bird populations are limited by seeds of various sizes, then differences in beak size would indicate specialization to different resources and therefore ecological differentiation.

The second question, how much interspecific dissimilarity is needed for coexistence, becomes important if there are infinitely many resource variables, as, e.g., in the case of a seed size continuum. The most important early result concerning this problem is by MacArthur and Levins (1967), who demonstrated that limiting similarity (i.e., a tendency towards the spacing of phenotypes along the trait axis with exclusion zones in between) is the expected equilibrium behavior. However, their conclusions came into doubt when later work (May and MacArthur 1972, May 1973, Roughgarden 1979) demonstrated that not only are there no strict limits to similarity, but it is even possible for a continuum of species to stably coexist. These results lead to the paradoxical situation where, on the one hand, competitive exclusion seemed to be an irrelevant idea for ecology, but on the other hand nobody ever questioned the reality of Darwinian natural selection, which is strictly dependent on the ecological process of competitive exclusion between similar heritable phenotypes.

However, later it has been observed that while there are no formal limits to similarity, the more tightly packed a community is, the less robust it is against perturbations of model parameters (Armstrong and McGehee 1976, Abrams 1983, Meszéna et al. 2006). In particular, it has been shown (Meszéna et al. 2006) that robustness (i.e., the volume in parameter space allowing for stable coexistence) always decays to zero with increasing similarity in *any* model of coexistence. Analogously, Gyllenberg and Meszéna (2005) proved an important theorem, demonstrating that if a continuum of species coexist, there always exists a perturbation of arbitrarily small amplitude that would destroy that coexistence. The extreme fragility of tightly packed communities leads to a reinterpretation of the old limiting similarity principle. Instead of asking how similar the species may be, we ask how robust any given coexistence pattern is. Since tightly packed species are so fragile, and random parameter variation is inevitable in a noisy environment, the default expectation for model behavior and empirical observations will still be limiting similarity — although the precise limits emerging will depend on model details. Thus, the apparent paradox of how natural selection could be a driving force in biology when there are no formal limits to similarity has been resolved by shifting the focus from the stability of coexistence to its robustness.

Here we show that there is another potential theoretical challenge to the expectation of limiting similarity. We demonstrate through numerical calculations that there are several cases where, though perturbations of arbitrarily small amplitude may still lead to the extinction of certain species (as is guaranteed by the Gyllenberg-Meszéna theorem), the general pattern of continuous coexistence is in fact quite robust. We will call situations where continuous coexistence is not entirely destroyed by perturbations *robust continuous coexistence*. What the models producing robust continuous coexistence have in common is that their competition kernels, defined as the differential response of the growth rate of the species with trait x to a change in the density of the species with trait y, is nondifferentiable whenever $x = y$, i.e., the kernel possesses a sharp peak or even a discontinuity at zero trait difference. This is in contrast with the classical practice of modeling the competition kernel as a strictly smooth function (and by smooth we will mean "differentiable at least once" throughout the chapter), usually of Gaussian form (but see Abrams et al. 2008, Pigolotti et al. 2010). We will say that such kernels possess a "kink" at the point of self-competition. We then further motivate our hypothesis that the property of possessing a kink is the key to robust continuous coexistence through two analytical arguments. The first one is based on a two-species coexistence scenario: we show that under this property of the competition kernel, limits to the similarity of two species disappear as long as certain (not very restrictive) conditions are satisfied. The second argument is based on the asymptotic properties of Fourier transforms, showing that models with smooth kernels tend to be more fragile than models with kinked ones. Finally, we discuss the mechanisms that lead to kinked kernels in the first place.

However, in light of these mechanisms, we argue that nonsmooth competition is unrealistic, i.e., it is not an accurate representation of competition that is expected to occur in nature. We base this argument on a demonstration that kinked kernels will not occur in the presence of intraspecific variation. Even in the absence of intraspecific variation, environmental variation would still lead to the smoothing out of kinked kernels. Therefore, we argue that one in fact should not expect kernels to be kinked, and therefore limiting similarity is still the expected behavior for stably coexisting species.

Competition kernels which are kinked according to our definition have been used in the context of the competition-colonization model (Tilman 1994, Kinzig et al. 1999), the competition-mortality tradeoff model (Adler and Mosquera 2000), a model of seed size evolution (Geritz et al. 1999), models of superinfection (Levin and Pimentel 1981), the Lotka–Volterra competition model (Scheffer and van Nes 2006, Hernandez-Garcia et al. 2009, Pigolotti et al. 2010), and the tolerance-fecundity tradeoff model (Muller-Landau 2010). Some of these studies (Adler and Mosquera 2000, Geritz et al. 1999, Hernandez-Garcia et al. 2009) point out that sharply asymmetric competition (in which the better competitors have a much larger influence on the poorer competitor than vice versa) may lead to higher diversity and therefore tighter species packing along the trait axis, and Geritz et al. (1999) and Adler and Mosquera (2000) also emphasize the compromised realism of the assumption of sharp asymmetry. However, none of this prior work has studied the robustness of coexistence patterns predicted by these kernels, or identified the key property of the competition kernel influencing predicted patterns and their robustness. Our results here suggest that for considering the question of how much coexistence can be robustly generated by a given mechanism, the model of that mechanism should be constructed with care. In particular, although kinked kernels can provide a simpler, more analytically tractable description of competition mechanisms (as in, e.g., the competition-colonization tradeoff model), they lead to a vastly different answer to how much coexistence is to be expected. Note however that a key theme emerging from prior work is unchanged: some system-specific limits to the similarity of species along trait axes should be expected in practice, i.e., there should exist a minimum trait distance between stably coexisting species in any model, but this minimum distance will be different from model to model. Hence our work here provides development of the theory supporting the search for patterns of dispersion in trait-based community ecology (Weiher et al. 1998, Stubbs and Wilson 2004, Mason and Wilson 2006, Pillar et al. 2009, Cornwell and Ackerly 2009).

The chapter is structured as follows. After building the model framework and reviewing some of the better-known results emerging from it in Section 2.2, we go on to show examples of the model with kinked kernels (Section 2.3), which invariably produce robust continuous coexistence. Next, in Section 2.4 we give some mathematical arguments for why kinked kernels would have this property, but not smooth ones. Finally, in Section 2.5 we derive the conditions that lead to kinked kernels, and demonstrate that under realistic circumstances one should always expect kernels to be smooth.

2.2 Background

2.2.1 Models of competition around equilibria

We wish to study the equilibrium patterns of competing organisms that vary in a single quantitative trait x. This trait parameter may assume any value within certain limits: $x \in [x_0, x_m] \subseteq \mathbb{R}$. We call the set of possible trait values x the *trait axis*. The canonical example for such a system is a community of birds with beak size x whose competition is mediated by the consumption of seeds of various sizes: this example is good to keep in mind, though our treatment will not be system specific. The most general continuous time, continuous density model within this framework reads

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x)\, r(n, E). \tag{2.1}$$

Here $n(x)$ is the abundance distribution of traits, $n(x)\,\mathrm{d}x$ measuring the number (or density) of individuals with trait values between x and $x + \mathrm{d}x$. While we write down differential equations to describe how $n(x)$ evolves as a function of time, we are primarily interested in $n(x)$ under equilibrium conditions — consequently, we simply write $n(x)$ instead of $n(x, t)$. The symbol r is the per-capita growth rate, which is a functional of the densities and all density-independent parameters, denoted by E (which could also depend on trait value). In principle, this equation could still produce arbitrarily complicated behavior. Therefore from here on we make the assumption that the system converges to some fixed point attractor. Then the per capita growth rates may be linearized around the fixed points. Denoting the equilibrium density distribution by n^*, we get

$$\begin{aligned}\frac{\mathrm{d}n(x)}{\mathrm{d}t} &\approx n(x)\Big(\underbrace{r(n^*, E)}_{0} + \delta r(n, E)\Big) \\ &= n(x)\left(\int_{x_0}^{x_m} \frac{\delta r(x)}{\delta E(y)}\delta E(y)\,\mathrm{d}y + \int_{x_0}^{x_m} \frac{\delta r(x)}{\delta n(y)}\delta n(y)\,\mathrm{d}y\right),\end{aligned} \tag{2.2}$$

where $r(x)$ is shorthand for $r\left(n(x), E(x)\right)$ and the δ denotes functional differentiation (for those unfamiliar with functional derivatives, note that the expression

$$\delta r(x) = \int \frac{\delta r(x)}{\delta n(y)}\delta n(y)\,\mathrm{d}y,$$

where x and y are continuous variables, is precisely analogous to the formula $\mathrm{d}r_i = \sum_j(\partial r_i/\partial n_j)\mathrm{d}n_j$ where i and j are discrete indices; see, e.g., Rudin 1973 for the precise definition). Denoting the first term of the expansion by $c(x)$ and the functional derivative $\delta r(x)/\delta n(y)$ by $-a(x, y)$, this may be rewritten as

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x)\left(c(x) - \int_{x_0}^{x_m} a(x, y)\delta n(y)\,\mathrm{d}y\right). \tag{2.3}$$

Using the fact that $\delta n(x) = n(x) - n^*(x)$, this dynamical equation can be brought to the usual Lotka–Volterra form:

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x)\left(c(x) - \int_{x_0}^{x_m} a(x, y)\Big(n(x) - n^*(x)\Big)\,\mathrm{d}y\right), \tag{2.4}$$

or

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x)\left(\underbrace{c(x) + \int_{x_0}^{x_m} a(x,y)n^*(y)\,\mathrm{d}y}_{r_0(x)} - \int_{x_0}^{x_m} a(x,y)n(y)\,\mathrm{d}y\right), \tag{2.5}$$

and so

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x)\left(r_0(x) - \int_{x_0}^{x_m} a(x,y)n(y)\,\mathrm{d}y\right), \tag{2.6}$$

where $r_0(x)$ is an effective density-independent growth term. (Note that the form of the equation preferred by most textbooks is recovered through the definitions $r(x) = r_0(x)$, $K(x) = r_0(x)/a(x,x)$, $\alpha(x,y) = a(x,y)/a(x,x)$). This equation applies around any fixed point equilibrium; the linearity of the approximation ensures equivalence with the Lotka–Volterra equations.

The function $a(x,y)$ is called the *competition kernel*. It measures the effect of a change in the abundance of species y on the growth rate of species x. In general it may be an arbitrary function of its arguments, but since we are interested in competitive systems, we shall make two assumptions. First, the kernel has to be nonnegative; this means that the growth of any one species necessarily inhibits the growth of the others and so there are no mutualistic and/or exploitative interactions present. Second, the kernel should decrease with increasing $|x - y|$: competition is assumed to be stronger between more similar phenotypes. Without this assumption, being sufficiently different in phenotype would not confer an advantage and so there would not be any interesting coexistence patterns to analyze in the first place.

2.2.2 The fragility of continuous coexistence solutions

As mentioned in the Introduction, the original idea of strict limits to similarity had to be abandoned when it was demonstrated that even in the original Lotka–Volterra model (where the idea was first proposed) it is possible to have the stable coexistence of a continuum of species (Roughgarden 1979). However, such coexistence is extremely sensitive to perturbations of model parameters and is therefore not expected to occur under realistic circumstances. Let us investigate the original example of Roughgarden and its behavior under model perturbations. From Eq. (2.6), the equilibrium condition reads

$$r_0(x) = \int_{x_0}^{x_m} a(x,y)n(y)\,\mathrm{d}y \tag{2.7}$$

for any species with positive density. Assuming $x_0 = -\infty$, $x_m = \infty$, and the functional forms

$$r_0(x) = \exp\left(-\frac{(x-x^*)^2}{2w^2}\right), \tag{2.8}$$

$$a(x,y) = \exp\left(-\frac{(x-y)^2}{2\sigma^2}\right) \tag{2.9}$$

for the parameters, it can be shown that the solution $n(x)$ will also assume the Gaussian form

$$n(x) = \frac{w}{\sigma\sqrt{w^2-\sigma^2}} \exp\left(-\frac{(x-x^*)^2}{2(w^2-\sigma^2)}\right) \tag{2.10}$$

as long as $w > \sigma$.

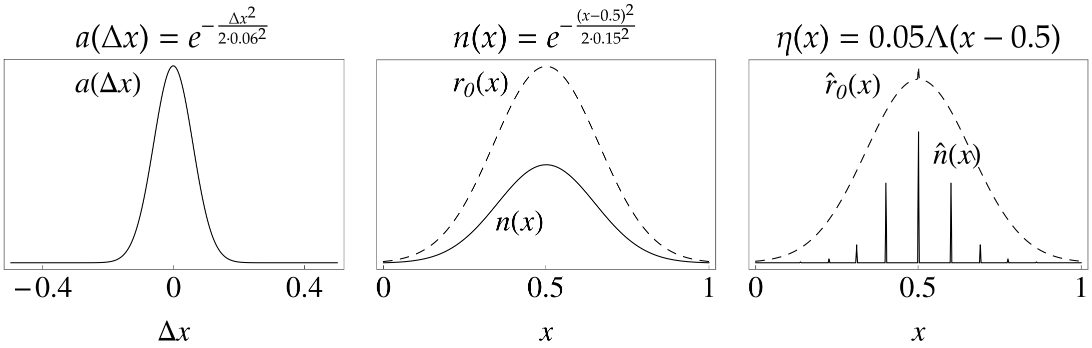

Figure 2.1: Equilibrium patterns produced by a Gaussian competition kernel. The first panel shows the equation and the graph of the competition kernel used; $\Delta x = x - y$. The second panel gives the formula for $n(x)$ and the curves of $n(x)$ and $r_0(x)$ (which can be obtained by substituting the given forms of $a(x-y)$ and $n(x)$ into Eq. (2.7) and performing the integration). The third panel presents what happens to the equilibrium state when $r_0(x)$ is perturbed. We obtained the perturbed equilibrium $\hat{n}(x)$ by first adding a small perturbing function $\eta(x)$ to the original $r_0(x)$ to obtain the perturbed intrinsic rates $\hat{r}_0(x) = r_0(x) + \eta(x)$, then simulating the dynamics via Eq. (2.6) until it reached its stable equilibrium. The function $\Lambda(x)$ involved in the perturbation in panel 3 is defined as $400(1-|x|)$ for $-1 < x < 1$ and zero otherwise. The argument is multiplied by 400 since this was the number of bins the trait axis was divided into in our simulations — this way the perturbation is effectively point-like, i.e., zero everywhere except at $x = 0.5$. In panels 2 and 3, $r_0(x)$ and $\hat{r}_0(x)$ have been scaled so they would fit on the same plot as the densities.

This solution is structurally unstable, i.e., a perturbation of arbitrarily small amplitude may destroy it (Gyllenberg and Meszéna 2005). Figure 2.1 shows an example where the continuous coexistence pattern collapses completely, even though the perturbation amplitude is small. Note that the spacing between surviving species is almost perfectly even, as expected in this model for the type of perturbation we employed (Barabás and Meszéna 2009).

It is instructive to look at these results in light of the Gyllenberg-Meszéna theorem (Gyllenberg and Meszéna 2005). As a matter of fact, this theorem is a collection of several related results. But, for our purposes, we only need to distinguish between two cases. The first one concerns the equilibrium condition Eq. (2.7) in its full generality. It first assumes that, given the continuous parameters $r_0(x)$ and $a(x, y)$, an equilibrium solution $n(x)$ is produced whose support (i.e., values of x for which $n(x)$ is nonzero) includes a domain of continuous coexistence. Then the theorem states that there exists a positive function $\eta(x)$ such that for an arbitrarily small ε, if one replaces $r_0(x)$ by $r_0(x) + \varepsilon\eta(x)$, the resulting perturbed solution $\hat{n}(x)$ will not have the same support as $n(x)$. In other words, some species are bound to go extinct, no matter how small the disturbance is: continuous coexistence is, in this sense, fragile. Notice that the theorem does *not* say that continuous coexistence *as a whole* is going to collapse, merely that certain species will go extinct. However, a stronger version of the theorem, guaranteeing that an arbitrarily small perturbation can break down all continuous coexistence and lead to strict spacing can be proven for the special case of $a(x, y) = a(x - y)$, where $a(x - y)$ and $r_0(x)$ are analytic functions of their arguments.

This second, stronger theorem applies to the example in Figure 2.1, since the parameters are all analytic. Therefore it is no surprise that continuous coexistence is completely destroyed. The next section will explore what happens if the parameters are not chosen to be analytic. It will be shown that spacing is still expected for kernels that are *smooth*, i.e., differentiable at least once: though technically speaking the stronger version of the Gyllenberg-Meszéna theorem does not apply, the results look as if it did. However, when the kernel becomes nondifferentiable at zero trait difference, the situation changes drastically.

2.3 Demonstrating robust continuous coexistence under kinked kernels

Figure 2.2 presents several examples of smooth nonanalytic kernels (column 1) that support continuous coexistence (column 2). Our method for generating these solutions was to first choose a positive $a(x, y)$ and $n(x)$ arbitrarily, then use the equilibium condition Eq. (2.7) to obtain the corresponding $r_0(x)$ by performing the integration. Then the function $r_0(x)$ was perturbed and we obtained the solution to the perturbed problem by numerically integrating Eq. (2.6) (column 3). The four examples presented differ in whether the kernel is a function of trait diference only

($a(x,y) = a(x-y)$, rows 1 and 2, or $a(x,y) \neq a(x-y)$, rows 3 and 4), and in whether the kernel is symmetric or not ($a(x,y) = a(y,x)$, rows 1 and 3, or $a(x,y) \neq a(y,x)$, rows 2 and 4).

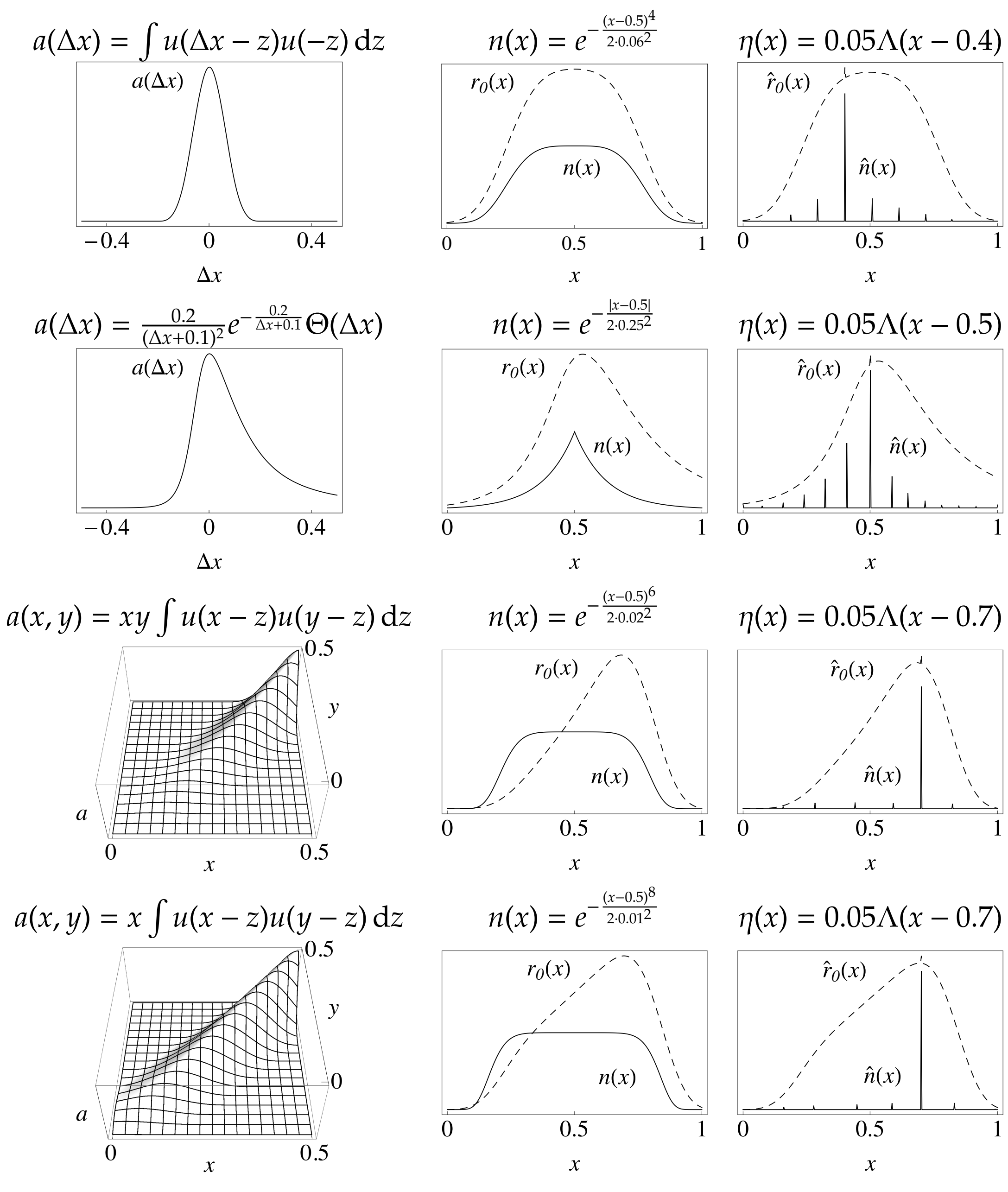

Figure 2.2: Equilibrium patterns produced by smooth nonanalytic competition kernels. Layout and notation and methods as in Figure 2.1, with four rows instead of one; $u(x) = 1 - |x/0.1|$ if $|x| \leq 0.1$ and zero otherwise; $\Theta(x)$ is the Heaviside unit step function. The four rows present four different examples of continuous coexistence and the coexistence pattern obtained by slightly perturbing the intrinsic rates of growth. Continuous coexistence collapses in all cases following perturbation.

In all cases, continuous coexistence is completely lost following the perturbation, and only a finite number of phenotypes persist, more-or-less evenly spaced out. The behavior of these models is therefore indistinguishable from the one we expect when the kernel $a(x, y) = a(x - y)$ is analytic (to which the strong version of the Gyllenberg-Meszéna theorem applies). We did not prove it mathematically, but based on our simulation results we will take it for granted that in all cases when the competition kernel is a smooth function of its arguments continuous coexistence collapses after perturbation and limiting similarity is recovered. In other words, a tightly packed community is extremely fragile to model perturbations, both with smooth and analytic kernels.

The situation is entirely different if the kernels are kinked (nondifferentiable at zero trait difference). Figure 2.3 is analogous to Figure 2.2, except that all kernels are kinked, which is evident from their graphs in column 1 (they all possess a sharp peak at each point where $x = y$). In these examples, though a few species do go extinct after perturbation, continuous coexistence itself is not eliminated: most regions on the trait axis still have arbitrarily similar species coexisting. This is exactly the situation we called robust continuous coexistence in the Introduction. Nondifferentiability at zero trait difference therefore has a tremendous impact on the robustness of the coexistence of similar species.

The perturbed densities in column 3 of Figure 2.3 are not very different from their unperturbed counterparts (column 2), except in the direct vicinity of the perturbation. The effects of the perturbation therefore seem to be very local: beyond a certain distance, the coexistence pattern behaves as if no perturbation would have occurred at all. This distance depends on perturbation size, as Figure 2.4 demonstrates: the larger the perturbation, the larger the exclusion zone in which species are driven extinct. Beyond that zone, however, coexistence is unaffected.

2.4 Kinked kernels and robust continuous coexistence

Why do kinked kernels lead to robust continuous coexistence while smooth kernels do not? We present two mathematical arguments why this is so: a two-species coexistence analysis and a multispecies one based on simple properties of Fourier transforms.

Consider two species that are extremely similar along the trait axis. The difference in their $r_0(x)$ values may then be expanded to linear order in the trait difference, neglecting higher order terms. If the competition kernel is smooth, then the smallest

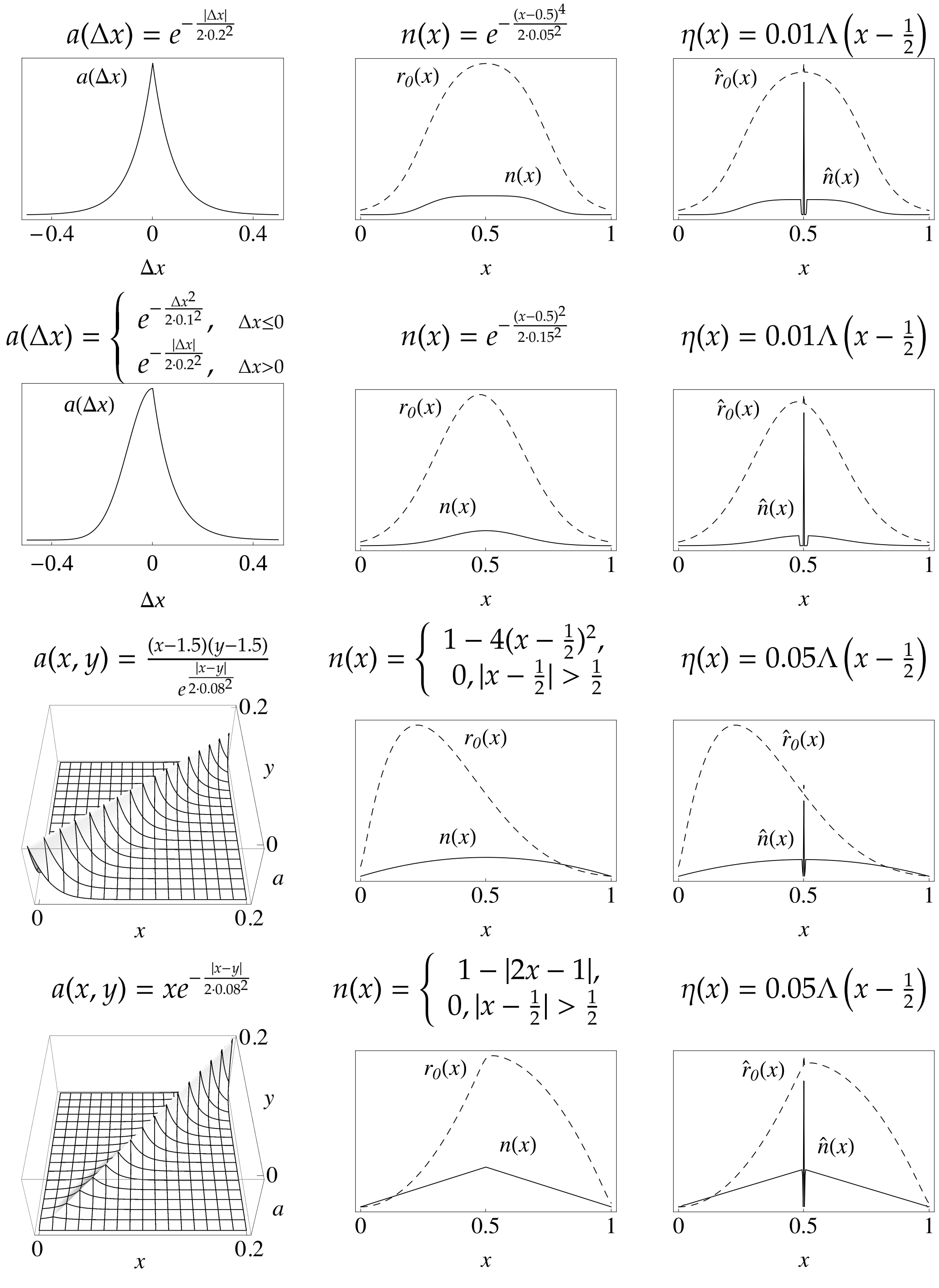

Figure 2.3: Equilibrium patterns produced by kinked competition kernels. Layout, methods, and notation as in Figure 2.2. Although certain species go extinct following perturbation in all cases, continuous coexistence does not disappear.

nontrivial order of expansion of the kernel around zero trait difference is quadratic, since the kernel has a maximum there. Hence, to first order, the competitive effect of

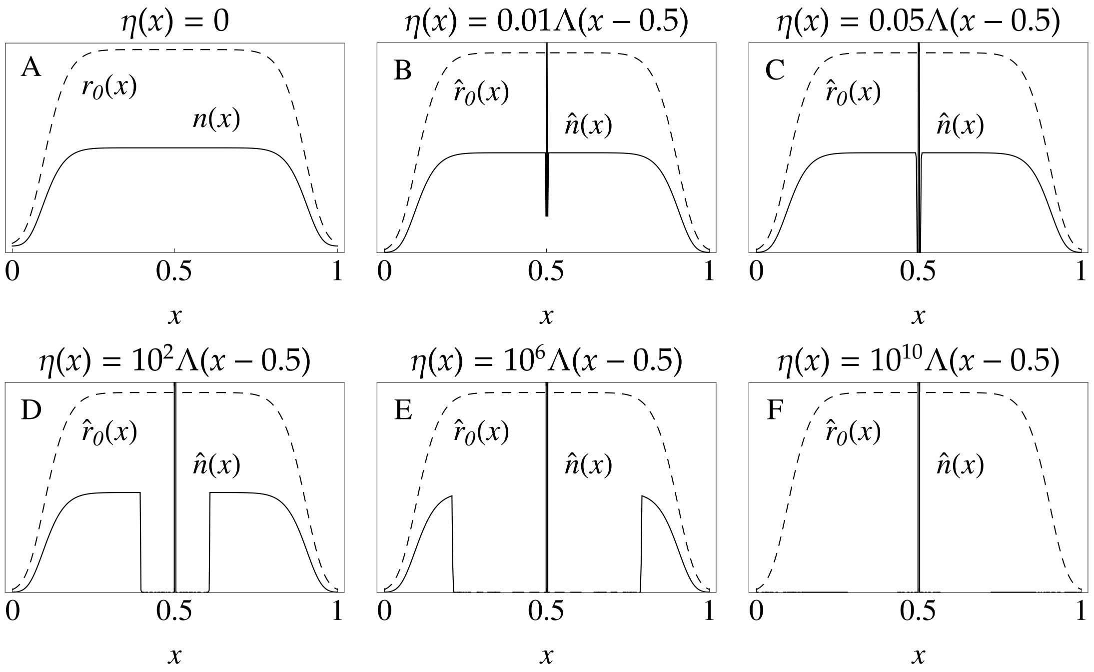

Figure 2.4: The effects of increasing perturbation size on a model with a kinked kernel. The kernel used is $a(\Delta x) = \exp(-|x|/(2 \cdot 0.1^2))$ (its general shape is given by the top left corner of Fig 2.3), and the unperturbed densities are $n(x) = \exp(-(x-1/2)^{10}/(2 \cdot 0.0083^2))$. Notation is as in the previous figures. Panel A depicts the unperturbed solution. For sufficiently small perturbations (panel B) the equilibrium abundances are altered but no extinctions occur. For larger perturbations (panels C, D and E), some species go extinct, but beyond a well-defined exclusion zone coexistence is just like it was without the perturbation. As the perturbation size increases, the exclusion zone progressively increases until all but one single species are excluded (panel F). Note that this happens when the perturbation size is approximately 10^{10} larger than the original function, i.e., the perturbation is astronomically large compared to the original $r_0(x)$.

one species on itself is equal to its effect on the other and vice versa. Competition is therefore not reduced between the species: coexistence will in general not be possible (MacArthur 1962, Metz et al. 2008). On the other hand, if the kernel is kinked, the linear-order decrease in competition is not zero anymore and so competition may immediately be reduced to tolerable levels where the two species can coexist, even for arbitrarily similar trait values. The abrupt decrease in competition in the case of kinked kernels brings about the possibility of the competitive coexistence of arbitrarily similar species. The precise, quantitative form of this argument is found in Appendix B.

Suggestive as it is, this result only applies for two competing species. We know and have seen in Sections 2.2 and 2.3 that smooth kernels do sometimes allow for continuous coexistence, so the limiting similarity condition obtained for the two-species case does not directly apply. However, the extreme fragility of such solutions signals that limiting similarity is still to be expected in all cases where the parameters have not been precisely fine-tuned. No such fine-tuning is required for retaining continuous coexistence in the case of kinked kernels. In the remainder of this section we demonstrate the extra fragility of continuous coexistence with smooth kernels via an argument based on Fourier transforms. This comes at a price though: only the $a(x, y) = a(x - y)$ homogeneous case may be treated in this manner.

For the special case $a(x, y) = a(x - y)$, the equilibrium condition Eq. (2.7) reads

$$r_0(x) = \int_{-\infty}^{\infty} a(x-y)n(y)\,\mathrm{d}y, \tag{2.11}$$

where the limits of integration have been extended from minus to plus infinity for future convenience (since $r_0(x)$ can be arbitrarily small outside a relevant domain of trait values, this assumption is not really restrictive). Assume the equation has a positive solution $n_0(x)$. Now we perturb the left hand side with the arbitrary function $\eta(x)$, multiplied by the small parameter ε:

$$r_0(x) + \varepsilon\eta(x) = \int_{-\infty}^{\infty} a(x-y)n(y)\,\mathrm{d}y. \tag{2.12}$$

This equation can be solved via Fourier transforms, invoking the convolution theorem. Defining the transform of a function $f(x)$ as $\mathcal{F}(f) = \int_{-\infty}^{\infty} f(x)\exp(-i\omega x)\,\mathrm{d}x$, we get

$$\mathcal{F}(r_0) + \varepsilon\mathcal{F}(\eta) = \mathcal{F}(a)\mathcal{F}(n), \tag{2.13}$$

which yields the solution

$$n(x) = \mathcal{F}^{-1}\left(\frac{\mathcal{F}(r_0)}{\mathcal{F}(a)}\right) + \varepsilon\mathcal{F}^{-1}\left(\frac{\mathcal{F}(\eta)}{\mathcal{F}(a)}\right) = n_0(x) + \varepsilon\mathcal{F}^{-1}\left(\frac{\mathcal{F}(\eta)}{\mathcal{F}(a)}\right). \tag{2.14}$$

The new solution is the sum of the unperturbed densities plus a perturbing term. As a side note, the solution is clearly unstable if the transform of the kernel is zero for any given frequency. This, however, will not happen if the kernel is chosen to be *positive definite*, i.e., $\iint f(x)a(x-y)f(y)\,\mathrm{d}x\,\mathrm{d}y > 0$ for all functions f, a simple consequence of which is that the Fourier transform of the kernel is strictly positive (Leimar et al. 2008, Hernandez-Garcia et al. 2009). Therefore we assume now that the kernel $a(x - y)$ is indeed positive definite.

The ratio $\mathcal{F}(\eta)/\mathcal{F}(a)$ is therefore finite for any given frequency, but might increase without bounds as frequencies go to infinity. If the Fourier transform of the kernel decays faster asymptotically than the transform of $\eta(x)$, then no matter how small ε is, there will always exist some frequency for which the ratio $\mathcal{F}(\eta)/\mathcal{F}(a)$ is large enough to make the solution $n(x)$ nonpositive for certain x values, destroying the original coexistence pattern.

We are going to use the following simple property of the Fourier transform (e.g., Brychkov and Shirokov 1970). A function proportional to a Dirac delta has a transform which does not decay to zero asymptotically for large frequencies. A function with a finite jump (discontinuity) has a transform that decays asymptotically to zero as ω^{-1}. A continuous nondifferentiable function's transform decays as ω^{-2}, a function which is differentiable once has a transform decaying as ω^{-3}, and so on: the Fourier transform of a k-differentiable function decays asymptotically as ω^{k-2}.

Returning to the ratio $\mathcal{F}(\eta)/\mathcal{F}(a)$: due to the above property of the Fourier transform, if the kernel is differentiable k times, then the perturbing function $\eta(x)$ has to be differentiable $j > k$ times, otherwise the perturbing term in Eq. (2.14) will grow arbitrarily large, irrespective of the value of ε.

To give a specific example, let us define the perturbing function as

$$\eta(x) = \int_{-\infty}^{\infty} \frac{u(x-z)u(-z)}{\int_{-\infty}^{\infty} u(y)u(y)\,\mathrm{d}y}\,\mathrm{d}z, \tag{2.15}$$

where $u(x) = 1 - |x/\sigma|$ for $|x| \leq \sigma$ and zero otherwise (the general shape of $u(x)$ is given in the top left corner of Figure 2.2). It is easily seen that $\eta(x)$ is differentiable twice, therefore we expect its Fourier transform to decay asymptotically as ω^{-4}. This is indeed the case, since the transform of $\eta(x)$ is

$$\mathcal{F}(\eta) = \frac{3e^{-2i\omega\sigma}(e^{i\omega\sigma}-1)^4}{2\sigma^3\omega^4}. \tag{2.16}$$

Now we choose a competition kernel that is differentiable more than twice, e.g., a Gaussian one:

$$a(x-y) = \exp\left(-\frac{(x-y)^2}{2\sigma^2}\right). \tag{2.17}$$

Its Fourier transform is also Gaussian:

$$\mathcal{F}(a) = \sigma\sqrt{2\pi}\exp\left(-\frac{\omega^2\sigma^2}{2}\right). \tag{2.18}$$

The ratio $\mathcal{F}(\eta)/\mathcal{F}(a)$ is

$$\frac{\mathcal{F}(\eta)}{\mathcal{F}(a)} = e^{\frac{1}{2}\sigma^2\omega^2} \frac{3e^{-2i\omega\sigma}(e^{i\omega\sigma}-1)^4}{2\sqrt{2\pi}\sigma^4\omega^4}, \tag{2.19}$$

which clearly gets larger and larger for high frequencies. Therefore the solution cannot remain positive for all x: the perturbation will break the coexistence pattern, no matter how small ε is.

If, on the other hand, we assume a different form of the competition kernel, one that is kinked:

$$a(x-y) = \exp\left(-\frac{|x-y|}{\sigma}\right), \tag{2.20}$$

then $\eta(x)$ will never be able to break the coexistence pattern for ε sufficiently small. The Fourier transform of this kernel is

$$\mathcal{F}(a) = \frac{2\sigma}{1+\sigma^2\omega^2}, \tag{2.21}$$

decaying asymptotically as ω^{-2}, as it should (since this kernel is continuous nondifferentiable); $\mathcal{F}(a)$ therefore decays more slowly than $\mathcal{F}(\eta)$. Their ratio is

$$\frac{\mathcal{F}(\eta)}{\mathcal{F}(a)} = \frac{3e^{-2i\omega\sigma}(e^{i\omega\sigma}-1)^4(1+\sigma^2\omega^2)}{4\sigma^4\omega^4}, \tag{2.22}$$

asymptotically decaying as ω^{-2}. It is well-behaved, its inverse Fourier transform will be finite — and therefore there exists a sufficiently small ε such that the original coexistence pattern is unaffected.

Our result says that the more differentiable the competition kernel is, the larger the class of perturbations that can break the continuous coexistence pattern it generates. More specifically, if the kernel is differentiable k times, then a perturbation differentiable $j < k$ times will destroy the coexistence for any value of ε. Kinked kernels are nondifferentiable and so the patterns they generate cannot be broken for an arbitrarily small ε by differentiable perturbations: only nondifferentiable or discontinuous perturbations will be able to do that.

2.5 How do kinked competition kernels emerge?

2.5.1 Discontinuous utilization curves lead to kinked kernels

So far we have been discussing the impact of kinked kernels on the outcome of competition models. What biological factors would lead to such kernels in the first place is a question that remains to be answered. In this section we answer the question in the context of resource overlap models, i.e., we assume that if $u(x, z)$ is the rate at which a resource item of size z is consumed by a member of the species with trait x, then the kernel will read

$$a(x, y) = \int_{z_0}^{z_m} u(x, z) u(y, z) \, \mathrm{d}z, \tag{2.23}$$

where z_0 and z_m are the maximum and minimum resource size, respectively (MacArthur and Levins 1967, MacArthur 1970, Chesson 1990b). We also assume that the utilization function is bounded and only depends on the difference between resource type and trait: $u(x, z) = u(x - z)$. Then the competition kernel will also be a function of only the trait difference, since the amount of overlap depends only on how far the two traits are from each other, not on their absolute positions along the trait axis. (Appendix C generalizes the overlap picture to arbitrary ecological models, where it turns out that it is always possible to write the kernel as the overlap of two *different* functions, called the sensitivity and the impact; see also Meszéna et al. 2006).

With these assumptions we show that simple jump discontinuities in the resource utilization function are responsible for generating kinked kernels. The general analysis, not dependent on any of these assumptions about $a(x, y)$, is found in Appendix D, yielding very similar results and interpretation.

A kinked kernel is nondifferentiable at zero trait difference, therefore its second derivative at that point is infinite. Our strategy is to take the second derivative of the kernel and determine the conditions under which it would be infinitely large. First we fix the trait value y to be zero without loss of generality, so that $a(x - y) = a(x)$ is a function of a single variable. The second derivative will read

$$a''(x) = \int_{z_0}^{z_m} u''(x - z) u(-z) \, \mathrm{d}z, \tag{2.24}$$

where the prime denotes differentiation with respect to the argument. Now let us fix x to be zero as well:

$$a''(0) = \int_{z_0}^{z_m} u''(-z)u(-z)\,\mathrm{d}z = -\int_{z_0}^{z_m} u''(z)u(z)\,\mathrm{d}z \tag{2.25}$$

after a convenient change of variables $z \to -z$. Since in general the integral of the second derivative of a function is finite if the function is continuous but infinite if it possesses a jump discontinuity, we can already see that such discontinuities in u will make the kernel kinked. Let us assume now that the function u is continuous except at a point z^*. This means that u can be written as

$$u(z) = \alpha\Theta(z - z^*) + \eta(z), \tag{2.26}$$

where Θ is the Heaviside unit step function, α is a constant and $\eta(z)$ is a continuous function. Substituting this form into Eq. (2.25) we get

$$a''(0) = -\alpha \int_{z_0}^{z_m} \delta'(z - z^*)u(z)\,\mathrm{d}z + \ldots, \tag{2.27}$$

where δ' is the derivative of the Dirac delta function, and the ellipsis means all other terms the derivative produces that have not been written out. (The derivative of a Dirac delta might seem like a strange construct, but not only is well defined, it also behaves in exactly the way one would intuitively expect, i.e., $\int \delta'(x - y)u(y)\,\mathrm{d}y = -u'(x)$; see Rudin 1973 for the rigorous definition.) The integral of these other terms denoted by the ellipsis is necessarily finite and so they cannot contribute to the nonsmoothness of the kernel. Performing the integration with the help of the δ' function yields

$$a''(0) = -\alpha u'(z^*) + \ldots = -\alpha^2\delta(0) + \ldots, \tag{2.28}$$

which is infinitely large. Note that if u has more than one discontinuity, $a''(0)$ will be a sum of similar terms, i.e., each discontinuity contributes minus infinity times a constant squared to the expression above. Thus we have shown that the competition kernel is kinked if the utilization function has one or more discontinuities somewhere in its domain. Since we assumed u to be bounded, the converse will also be true (the most singular way a bounded function may behave is to be discontinuous, and the integral of a continuous function is differentiable). We therefore conclude that the competition kernel is kinked if and only if u has discontinuities. Finally, note that this result applies even if u is not a function of the difference of its arguments, and holds even if the kernel is not expressible via the overlap of utilization functions; see Appendix D for the generalization.

2.5.2 Mechanisms inhibiting discontinuous resource utilization

How is this result to be interpreted? A discontinuity in the resource utilization function means a species utilizing a certain resource is suddenly incapable of utilizing another, arbitrarily similar resource with similar efficiency. Expanding on the example of the competing bird species, one might imagine that each species has a box-like utilization curve: within a certain range σ of the beak size, all seeds are equally consumable, but outside of that limit, none at all ($u(x-z) = u_0$ if $|x-z| \leq \sigma$ and zero otherwise). Then, no matter how similar two species are, one will have access to seeds of certain sizes that the other does not, and vice versa (Figure 2.5). Thinking of the various resources as the factors regulating the populations, this means that no matter how similar, the two species will still be independently regulated, which is the key to species coexistence in general (Levin 1970, Meszéna et al. 2006). It follows that two species very similar along the trait axis are not really similar in the relevant sense of the word: no matter how close they are in their traits, their way of relating to the available regulating factors will be different, meaning that they are ecologically differentiated and thus can coexist.

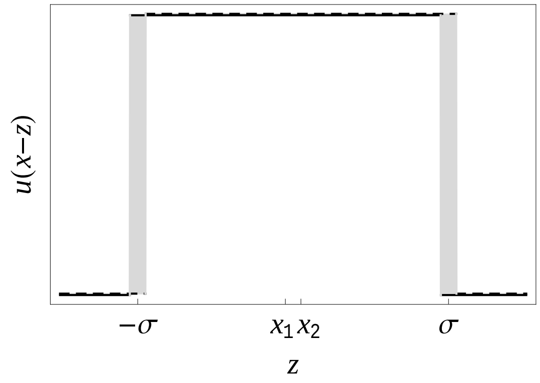

Figure 2.5: Utilization curves of two species with traits x_1 (solid line) and x_2 (dashed line), respectively. For the given box-like utilization function $u(x-z)$, no matter how similar the two species are, there will always be a range of resources (shaded in gray) that are utilized exclusively by only one of them. This leads to the independent regulation of the species and therefore to their coexistence, regardless of how close x_1 is to x_2.

This simple interpretation is not quite watertight because any discontinuity will lead to kinked kernels and therefore robust coexistence of arbitrarily similar species, not just those discontinuities that occur between some finite value and zero. Still, even if the jump occurs between two nonzero values, one can say that the species relate to arbitrarily similar resources in a qualitatively different way, bringing about their automatic ecological differentiation.

Natura non facit saltus — or does it? The question remains: what biological mechanisms would lead to sharp discontinuities in the resource utilization curves of species? Although one should not take the old Leibnitzian principle for granted (at least not in ecology), the question raised by Meszéna (2005) is still a serious challenge: what qualitative difference could there be between two bird species which only differ in that one has a beak 1μm larger than the other, when clearly no one would even notice that there are two separate species to begin with? The question may be analyzed more clearly if, instead of asking whether nature exhibits jumps, we ask whether the kinds of *models* we use would exhibit them. Here we give two arguments supporting the assertion that sudden jumps will in fact never occur in the kinds of deterministic competition models we have been considering.

The first thing that has a smoothing effect is intraspecific variation in traits. Even if the utilization function of an individual with a given trait is discontinuous, one must not forget that not all individuals of a species are alike: as with all quantitative traits, there is some variation around a mean trait value. Let the "raw" utilization function be $u(x-z)$, assumed to be discontinuous, and let the trait distribution within a species be $p(\overline{x}, x)$, where $\overline{x}$ is the mean trait value. Then the species-level utilization function $u_s(\overline{x}, z)$ will be the sum of the contributions of all individuals to consuming the resources, i.e.,

$$u_s(\overline{x}, z) = \int_{x_0}^{x_m} p(\overline{x}, x) u(x-z) \,\mathrm{d}x. \tag{2.29}$$

This function is continuous even if the trait distribution $p(\overline{x}, x)$ is not, since the integral of a bounded discontinuous function is continuous. The only case when the original discontinuities in $u(x-z)$ are retained is when $p(\overline{x}, x) = \delta(\overline{x} - x)$, i.e., when all individuals are exactly the same. In reality, most quantitative traits follow a normal distribution (e.g., Falconer 1981), where the variance may depend on the mean trait $\overline{x}$:

$$p(\overline{x}, x) = \frac{1}{\sqrt{2\pi\sigma^2(\overline{x})}} \exp\left(-\frac{(\overline{x}-x)^2}{2\sigma^2(\overline{x})}\right). \tag{2.30}$$

The effective, species-level utilization function is then given by

$$u_s(\overline{x}, z) = \int_{x_0}^{x_m} \frac{u(x - z)}{\sqrt{2\pi\sigma^2(\overline{x})}} \exp\left(-\frac{(\overline{x} - x)^2}{2\sigma^2(\overline{x})}\right) \mathrm{d}x, \tag{2.31}$$

which is continuous even if $\sigma(\overline{x})$ is not.

The second smoothing mechanism comes from environmental variability. Even if all members of a given species are perfectly identical, there is an inherent randomness in their individual fates due to the unpredictability of their surroundings. Just as individuals of a species are not exactly identical, no two seeds of the same size are identical either: one may be a little softer and thus may be opened by a bird with a slightly smaller beak, to give an example. Then, even if for the time being we do assume all individuals of the species to be identical, the discontinuity of the utilization curve will disappear, for the following reason. Let us denote the "raw" utilization function, which now becomes a function of the environment, by $u(x - z, E)$, where E specifies the state of the environment. Moreover, let us assume, as a worst-case scenario, that all individuals are perfectly identical: everyone has trait x. But, since each individual experiences a given environment, the species-level utilization curve will be the normalized sum of the raw curves over all individuals. Since continuous-density models inherently assume very large population sizes, the sum may be thought of as an integral over the probability distribution of E — which, by the logic of the previous paragraph, will smooth out any discontinuities in resource utilization.

Consequently, discontinuous utilization curves are not to be expected in any realistic ecological scenario. Since the emergence of kinked competition kernels is conditional on those discontinuities, it follows that in reality competition kernels are always smooth. kinked kernels emerge when model assumptions are too idealized or simplified. As we have seen, there is a major difference between the behavior of smooth versus nonsmooth models, which suggests siding with the more realistic smooth models when applying ecological theory.

2.6 Discussion

We have considered the effects of kinked competition kernels on species packing and coexistence along a trait axis. Kernels possess a "kink" if they are nondifferentiable when two species have the exact same trait value. It turns out that such kernels are able to produce patterns of continuous coexistence that are not entirely destroyed by model perturbations, in contrast to what one would expect based on limiting similarity arguments. The intuitive explanation for this behavior is the rapid decrease in competition between similar species: nondifferentiability at zero trait difference means that a small change in the trait of one of the species will lead to an immediate linear decrease in competition between them, as opposed to the much slower quadratic decrease of smooth kernels. The mechanism that produces kinked kernels to begin with is the sudden, discontinuous change in the resource utilization functions of the species. We also concluded that such discontinuities are unrealistic and that any real ecological situation would lead to continuous utilization functions and therefore smooth competition kernels.

Our treatment relied heavily on the Lotka–Volterra equations. Though Lotka–Volterra models have mostly fallen out of favor and have been replaced by more mechanistic models in modern ecological literature, one must not forget that any model may be linearized and brought to a form equivalent to a Lotka–Volterra system near a fixed point equilibrium. Then, as long as the system does not exhibit cycles, chaos, or other complex dynamics, local analysis of the fixed points will lead to the understanding of the global behavior of the model. This justifies having restricted our attention to Lotka–Volterra-type equations.

The argument that kernels decreasing faster around zero niche difference will lead to more coexistence than smooth ones is the generalization of the intuitive argument given by Pigolotti et al. (2010), who were comparing the diversity predicted by a restricted set of kernels. In particular, they were considering the class of kernels $a(x-y) \sim \exp(|x-y|^p)$, which is smooth for $p \geq 2$ but kinked for $0 < p < 2$. In their simulations 200 species were randomly thrown onto a niche axis with fully periodic boundary conditions, then their dynamics was simulated assuming Lotka–Volterra competition. What they found was that, for $0 < p < 2$, species thrown arbitrarily closely on the niche axis could stably coexist, while for $p > 2$ there were always zones of exclusion between prevailing species, i.e., limiting similarity was recovered. This result was interpreted in light of the fact that $p > 2$ kernels are more box-like than $0 < p < 2$ ones, and therefore competition between similars is stronger. The authors' main concern was the analysis of the limiting case $p = 2$ (Gaussian kernel), which lies on the borderline between box-like and peaked kernels. In our parlance, $p \geq 2$ kernels are a subcategory of smooth kernels, while $0 < p < 2$ ones are kinked. Work by the same authors determined that positive definiteness of the kernel is required for the stability of continuous coexistence solutions (Hernandez-Garcia et al. 2009), and it so happens that for $p < 0 \leq 2$ the kernel is positive definite, but not for $p > 2$.

Similarly, Adler and Mosquera (2000) analyzed the existence and stability of fixed point solutions in the competition-mortality tradeoff model. They pointed out that the competition kernel's discontinuity allows for the coexistence of a continuum of species, but when the kernel is smoothed out, continuous coexistence is impossible. They correctly identified the discontinuity of the kernel as the key property generating continuous coexistence, and also argued that in reality the kernel should be smooth.

These results are all in agreement with ours, but are not the same. We were investigating robustness, not stability: what happens to a given solution if model parameters are perturbed? In the work of Adler and Mosquera (2000) robustness of continuous coexistence solutions with the smooth kernel did not even come up, as they demonstrated that such a solution does not exist in the first place. However, they did not analyze the robustness of the continuous coexistence solution when the kernel is unsmoothed and therefore kinked. In light of our work, they would have found that continuous coexistence is robust (see also D'Andrea et al. 2013). In the case of the work of Pigolotti et al. (2010), they assigned the same r_0 value for all species and stuck to that choice, so the issue of robustness was not investigated. We can now say that they would have found robust continuous coexistence for $0 < p < 2$ kernels and unrobust one for $p = 2$, the Gaussian case. For $p > 2$ the fixed point is unstable and so the issue of robustness does not even arise.

The difference in behavior between smooth and kinked kernels is relevant in the context of the debate over the relative importance of stabilizing vs. equalizing mechanisms (Adler et al. 2007). Chesson (2000b) showed that the invasion growth rate of a species can be approximated as a sum of two terms, as long as the interactions within the community are purely competitive and all species but the invader are at their stationary equilibria. The first ("equalizing") term is always proportional to the difference (or ratio, in discrete time) of the intrinsic rates of growth, while the second ("stabilizing") term depends on the equilibrium densities of the resident species. Without stabilization, two species may only coexist if their intrinsic growth rates are exactly equal under all circumstances — a nongeneric scenario. However, as Adler et al. (2007) pointed out, if the intrinsic rates are nearly equal, then even a very slight amount of stabilization will be enough to guarantee long-term coexistence. This seems to suggest that coexistence by virtue of species similarities, as opposed to differences, could lead to stable coexistence: although similar species would only have very weak stabilizing terms, their intrinsic growth rates will also be very similar and so the weak stabilization will still be enough to ensure a positive invasion growth rate for all species. This idea has spurred a body of literature on the coexistence and evolutionary emergence of similar species (Scheffer and van Nes 2006, Holt 2006, Hubbell 2006, terHorst et al. 2010).

The concept that species with almost-equal intrinsic growth rates can coexist via relatively weak stabilization is surely uncontroversial. However, the situation is not that simple when the trait-dependence of the two terms is considered. We have seen in Section 2.4 (with the mathematical underpinning in Appendix B) that the equalizing term (difference in r_0) and the stabilizing, frequency dependent term do *not* approach zero at the same rate in general: the former is proportional to the difference in trait, while the latter is proportional to the square of the difference in trait. The stabilizing term is therefore incapable of overcoming differences in r_0 if the species are too similar — *except* when the competition kernel is kinked. For kinked kernels the stabilizing term changes linearly with trait difference, just like the equalizing term, and so it can compensate for differences in r_0. In conclusion, only models with kinked kernels can allow for the robust coexistence of similar species; for instance, in the work of Scheffer and van Nes (2006), only transient coexistence of similars was possible with a Gaussian competition kernel, but stable coexistence was observed when an extra term was added to the equations that rendered the kernel kinked.

Does the conclusion that models should be smooth mean one should avoid models possessing kinked kernels? As mentioned before, several well-known models exhibit this property, e.g., the hierarchical competition-colonization tradeoff model (Tilman 1994, Kinzig et al. 1999), the competition-mortality tradeoff model (Adler and Mosquera 2000), a model of superinfection (Levin and Pimentel 1981; in these three models the kernel is not even continuous), and the tolerance-fecundity tradeoff model (Muller-Landau 2010, D'Andrea et al. 2013). Despite their nonsmoothness, they do capture important features of the world. In particular, they drive attention to potential coexistence-enhancing tradeoffs which could operate in smooth models as well, although the precise amount of diversity predicted by the two approaches will be different. Smooth versions of these models, along with some consequences of the smoothing (in agreement with our results) are given in D'Andrea et al. (2013). It turns out that the smoothed models are somewhat more inconvenient to handle, both analytically and numerically. Therefore even if nonsmooth models are less realistic, they could be good as a first proxy to assess the consequences of certain assumptions because they are simpler to solve. Perhaps the main lesson to be learned is not that kinked models should be eschewed, but rather that one should be careful not to push the simplifying assumptions too far: when a model like the competition-colonization tradeoff model produces arbitrarily tight species packing (Kinzig et al. 1999) and even robust continuous coexistence (D'Andrea et al. 2013), we know that this result is just an artifact produced by the kernel and that in reality the kernel is smooth and no robust continuous coexistence is expected.

Of course it is possible to have kernels which, though not kinked in the technical sense, are "very peaked", meaning that their second derivative at zero trait difference is large. Continuous coexistence would be unrobust with these kernels, but still, we would expect their behavior to approach that of kinked kernels. Although we have not looked into the implications of such kernels in a rigorous way, both past results and common sense suggest that the more peaked the kernel is, the tighter species packing it will allow for. For instance, in the case of Gaussian kernels, tightness of packing depends on the competition width (MacArthur and Levins 1967, May 1973, Szabó and Meszéna 2006), which in turn is proportional to the kernel's second derivative at zero trait difference. In this way, one would expect the spacing between species to shrink as the kernel gets more and more peaked. Finally, in the limit where the second derivative of the kernel goes to infinity, the nearest-neighbor distances shrink to zero, i.e., robust continuous coexistence is recovered. Thus, though kinked kernels are unrealistic, it might still be possible to have fairly tight species packing via kernels that are close to being kinked.

Needless to say, the theoretical expectation of limits to similarity may be violated in particular cases for several reasons. One obvious possibility is that the system has not yet reached its equilibrium and so some of the species are still on their way to extinction. Also, it might be that coexistence is maintained through multiple trait axes. If there are several important axes and we concentrate on only one of them, what we see is the projection of all species onto a single axis and depending on how traits map onto regulating factors the distribution of species expected along one trait axis may differ from a spaced pattern. Yet another reason why spacing could be obscured is that metacommunity processes may play a role as well: there is a constant stream of immigrants to a particular site, replenishing those species that are on their way to extinction (MacArthur and Wilson 1967). In this case the spatial scale at which the observation is carried out could be too small to see the effects of competition on community structure as a whole. Finally, it is certainly possible that the trait under consideration does not map onto any niche axis, i.e., a linear array of regulating entities. We usually think that the beak size of Darwin's finches corresponds to the size of the food they eat, and since we think of food of a certain size as providing potentially independent regulation from all the other types of food, we may justifiably claim that beak size as a trait is an indicator for niche differentiation. But in other cases such trait differences might not be indicative of adaptation to different regulating factors. The drought-tolerance of plant species coexisting in arid regions does not display limiting similarity, because drought acts as an environmental filtering agent and not as a regulating factor, let alone a whole continuum of them.

Despite these caveats, if spacing is always expected in competitive guilds then work aimed at discovering spacing patterns in data could lead to a better understanding of which trait differences allow for niche differentiation. Apart from the difficulties already mentioned, the problem of discerning limiting similarity from data is complicated by the fact that there are no universal, system-independent limits to similarity (Abrams 1983, Meszéna et al. 2006) and that even when one has limiting similarity the spacing between adjacent species need not be uniform (Szabó and Meszéna 2006, Barabás and Meszéna 2009). Discussion of the methodological tools needed to overcome these problems is beyond the scope of this chapter. Empirical as well as methodological research of limits to similarity, however, remains an important direction within community ecology (Weiher et al. 1998, Stubbs and Wilson 2004, Mason and Wilson 2006, Pillar et al. 2009, Cornwell and Ackerly 2009), and should remain so in the future.

Chapter 3

Community robustness and limiting similarity in periodic environments

3.1 Introduction

Much of the early theory on coexistence concerned equilibrium situations (Volterra 1926, Gause 1934, Hardin 1960); the main conclusion was that if two or more species consume the same resources, only one will persist. Later Levin (1970) and Levins (1974) realized that this inference generalizes from resources to all those factors that are involved in a density-dependent feedback loop. After Krebs (2001, p. 288), Case (2000, p. 146), and Meszéna et al. (2006) we will call these factors regulating variables (they are equivalent to what Levin 1970 and Chesson 1994 call limiting factors, and what Chesson and Huntly 1997 call competitive factors). The competitive exclusion principle then states that at equilibrium the number of coexisting species cannot exceed the number of regulating factors. This simple picture emerging from equilibrium theory came under attack, however, from at least two quarters. First, the practical utility of the principle came into doubt. Second, the question arose whether fluctuating dynamics would invalidate the competitive exclusion principle, something that seems to depend on the equilibrium assumption crucially.

The problem of practical usefulness arises when there are infinitely many regulating factors and therefore there is no upper limit to the number of coexisting species. Though MacArthur and Levins (1967) argued persuasively that limiting similarity is the expected behaviour in the context of the Lotka–Volterra model, the work of May and MacArthur (1972), May (1973) and Roughgarden (1979) demonstrated that it is always possible to have arbitrarily tight species packing, suggesting that the competitive exclusion principle is more of a mathematical curiosity than an empirically relevant idea (Rosenzweig 1995). On the other hand, it has been observed mathematically that while there is no fixed lower bound to similarity, not all configurations are equally robust: certain coalitions of species are more sensitive to external perturbations than others. While coexistence of similars is possible, it is restricted to a narrow range of environmental parameters. Therefore, the limiting similarity principle can be recovered by shifting the emphasis from analyzing the *stability* of coexistence to looking at its *likelihood*, i.e., how wide or narrow is the range of parameters that allow for the persistence of all populations within the system ("coexistence bandwidth", Armstrong and McGehee 1976). Large volumes of parameter space allowing for coexistence are called robust systems; narrow ranges are called unrobust. A system with a very narrow coexistence bandwidth, i.e., one that is unrobust is unlikely to persist for long, and therefore some sort of limits to similarity are expected to emerge after all. This new, reformulated limiting similarity principle will only be useful though if robustness decreases with increasing similarity, independent of model details, at least for species that are already similar enough. That this is so has been demonstrated rigorously for fixed point models by Meszéna et al. (2006). They showed that as species get more similar in how they relate to the regulating factors (more specifically: if species growth rates show similar sensitivity to a change in the regulating variables, or the species have similar impacts on the regulating factors) then the robustness of their coexistence declines to zero. Hence the criticism of the competitive exclusion principle that it is unable to address the question of how similar two species may become has been resolved through considering the robustness, as opposed to the stability, of coexistence.

However, there remains the second important criticism of the competitive exclusion principle, namely that the ubiquity of temporal fluctuations in real ecosystems calls the equilibrium assumptions behind the principle (and behind the more modern theory of robustness of coexistence) into question. The consequences of the equilibrium conditions were thought to lose validity in a fluctuating system (Hutchinson 1961). Presumed invalidity of the competitive exclusion principle was developed into an ecological world view by Huston (1979). However, as Abrams (1983) and Chesson (1991) pointed out, the need for ecological segregation is not alleviated by environmental fluctuations: it just seems to be that way if we look at segregation strictly in the sense of resource partitioning. Chesson and Huntly (1997) not only argued for the verity of the need for ecological segregation but demonstrated the flaws inherent in those theories that look upon fluctuations as a means to invalidate the competitive exclusion principle.

Rigorous theories of coexistence in a fluctuating environment also imply the need for ecological segregation. Levins (1979) established the role of higher moments as effective regulating factors in situations where the densities are fluctuating arbitrarily in a bounded region of phase space. This means that, e.g., the time-average and variance of a resource both act like effective resources and thus two species could stably coexist on them — provided that interspecific competition between the two species "consuming" the mean and the variance of the resource is lower than intraspecific competition within each of the species. Chesson (1994, 2000b, 2009) provided a classification scheme for the coexistence maintaining mechanisms. Beyond fluctuation-independent niche segregation, he established the "effect of relative nonlinearity" (which occurs when species have different nonlinear responses to competition) and the "storage effect", which is based on species-specific responses to the environment, covariance between the environment and competition, and buffered population growth. His approach is based on a small-fluctuation approximation. Intuitively, the storage effect is considered a mathematical representation of temporal niche segregation (Chesson and Huntly 1997, Chesson 2000b).

In this chapter we aim to provide a solid ground for the concept of temporal niche segregation and its role in maintaining coexistence. That is, we intend to formalize the commonality between temporal and more conventional types of niche segregation. Our starting point is Meszéna et al. (2006), that has already provided that commonality in a stable environment. We restrict our attention to externally forced periodic dynamics with a fixed period T. Moreover, we assume the dynamics of the regulating variables to be fast compared to population dynamics. Within these restrictions we keep our considerations general. In particular, we do not need the assumption of small fluctuations. In Meszéna et al. (2006) the common ground was segregation with respect to the regulating variables. In line with this biological intuition, here we consider the regulating variables at different instants of time to be different regulating variables. In this scheme temporal niche segregation is also a type of differentiation with respect to regulating variables. Therefore, all considerations in Meszéna et al. (2006), especially decreasing robustness with increasing similarity, carry over to the fluctuating case. We will discuss the realationship between our and Chesson's (1994) formalization as well.

We begin by introducing the fundamental concept of regulating factors (Section 3.2), and then reviewing the basic framework for fixed points in Section 3.3.

Then, in Section 3.4 we extend the theory to periodic orbits in phase space and rederive the basic formulas in a periodically fluctuating environment. Finally, as a demonstration we apply the results to a simple example in Section 3.5.

3.2 Regulating factors

Populations with fixed demographic parameters grow exponentially — but, since the parameters usually dependent on density and external influences, population growth can take on virtually any form. However, one may still treat any change in population densities as locally exponential in time, where the instantaneous growth rate is a function of both density dependent and independent variables. Taking density dependence into account, one can introduce the concept of regulating factors: the set of variables involved in the feedback between growth rates and densities. In other words, *all* interactions between the individuals of the populations have to be mediated by the regulating variables: fixed values of these factors would lead to the exponential growth of all species in the community.

In this context, the growth of any population in any model may be written as

$$\frac{\mathrm{d}x_i(t)}{\mathrm{d}t} = r_i\left(\mathbf{R}(x_1(t), \ldots, x_L(t)), E, t\right) \qquad (i = 1, \ldots, L), \tag{3.1}$$

where $x_i(t) = \ln(n_i(t))$ is the natural logarithm of the ith population's density $n_i(t)$ at time t (the logarithmic scale having been introduced for future convenience), r_i is the growth rate of the ith population, E is the collection of environmental and all other density-independent parameters (the "external" variables), L is the total number of species in the system and $\mathbf{R}$ is the vector of regulating factors (the same as $\mathbf{I}$ in Meszéna et al. 2006), which of course is a function of the densities. In case one has environmental parameters that fluctuate with time, only the time-independent parts go into E and the rest should be considered as an explicit time dependence of the growth rates. For example, if a certain ecological situation causes the (density-independent) intrinsic rate of growth r_0 to fluctuate as $r_0 = a(1 + \varepsilon \cos(\omega t))$, then the vector E refers to the parameters a, ε and ω, not r_0 as a whole. One does not lose generality by this choice of convention, and it will make differentiation of r_i with respect to E more convenient later on.

There are two things neglected by Eq. (3.1). First, it considers unstructured populations only. Second, it assumes that $\mathbf{R}$ depends on the instantaneous values of the population densities — in other words, it disregards time lags in the regulation of populations. Apart from these restrictions however, these population dynamical equations are general: any continuous time, continuous density model may be stated in the form of Eq. (3.1).

The vector of regulating factors **R** deserves special attention. In general, its elements will include resources, predators, and other discrete entities. But the number of regulating factors is not necessarily finite. The paradigmal example for infinite dimensional regulation is the resource continuum, e.g., the continuum of foods of different sizes. In this case, the function $q \mapsto R(q)$ constitutes the vector **R**, where $R(q)$ denotes the concentration of food with size q. One can consider q as a continuous index of the vector **R**. In general, the continuous index variable can be more than one dimensional (e.g., describing size and hardness of the food). It is also possible to have discrete and continuous indices at the same time, e.g., if two different kinds of food both have size-distributions, or if a food size continuum *and* various predators function to regulate the populations. To emphasize the role these indices play in our analysis, here we adopt the notational convention that the **boldface** type will be reserved for quantities that carry the same indices as **R**.

3.3 Summary of the fixed point theory

3.3.1 Limiting similarity of species

The idea behind Meszéna et al.'s (2006) general theory of niche and limiting similarity is to realize that any system will behave like the Lotka–Volterra model near a stable fixed point. One therefore has to linearize the growth rates around the equilibrium point and analyze the robustness (i.e., the range of parameters where all densities are positive) of the simpler linear model (May 1973, Vandermeer 1975). Dynamical stability of the community, i.e., negative real parts of the eigenvalues of the community matrix, is assumed (there is no point in looking at the robustness of a dynamically unstable system). To obtain the set of parameters that allows for coexistence, one calculates the response of the densities to a change in the external variables E. A wild response even to small changes indicates unrobust coexistence, one that is oversensitive to external perturbations and is therefore unlikely to persist for long.

So we have to take the set of equilibrium equations and differentiate them with respect to E. At a fixed point attractor Eq. (3.1) becomes time-independent so that the left hand side is zero, and the growth rates on the right hand side are independent of time. Since at a fixed point all growth rates are zero, we have L algebraic equations:

$$r_i\Big(\mathbf{R}(x_1^*, \ldots, x_L^*), E\Big) = 0, \tag{3.2}$$

where the asterisk in the superscript refers to equilibrium values. Implicit differentiation with respect to E yields

$$\frac{\partial r_i}{\partial E} + \sum_{j=1}^{L} \frac{\partial r_i}{\partial \mathbf{R}} \frac{\partial \mathbf{R}}{\partial x_j} \frac{\mathrm{d}x_j^*}{\mathrm{d}E} = 0, \tag{3.3}$$

where summation (integration) for all discrete (continuous) indices of $\mathbf{R}$ is understood in the scalar product $(\partial r_i / \partial \mathbf{R})(\partial \mathbf{R} / \partial x_j)$. This formula yields the linearized growth rates as a function of the perturbations of the densities, and as such, connects an arbitrary ecological model with the classic Lotka–Volterra equations.

The first factor of this scalar product describes the response of the ith growth rate to a change in the regulating variables, i.e., the sensitivity of the population to changes in regulation; the second describes the impact of a change in population densities on the regulating factors. These two vectors turn out to be very important in our analysis. The first one,

$$\mathbf{S}_i = \frac{\partial r_i}{\partial \mathbf{R}}, \tag{3.4}$$

is the *sensitivity niche vector*. Originally it was defined with an extra minus sign in Meszéna et al. (2006) to imply resource depletion — but, since the generalized regulating factors could be anything, not just resources, we will not use this convention here. The other quantity,

$$\mathbf{I}_j = \frac{\partial \mathbf{R}}{\partial x_j}, \tag{3.5}$$

is the *impact niche vector* (the $\mathbf{C}$ of Meszéna et al. 2006). Again, we use a slightly different convention: originally the impact vector was the derivative of $\mathbf{R}$ with respect to $n_j = \exp(x_j)$, not x_j. This is to make the formalism consistent with what will follow in Section 3.4. These vectors may be calculated for any population size, but their real utility comes through when evaluated at equilibrial densities, as they are in Eq. (3.3).

Let us define the community matrix as the product of the two niche vectors:

$$a_{ij} = \mathbf{S}_i \mathbf{I}_j = \frac{\partial r_i}{\partial \mathbf{R}} \frac{\partial \mathbf{R}}{\partial x_j} = \frac{\partial r_i}{\partial x_j}, \tag{3.6}$$

where, as before, summation or integration for all indices of **R** is assumed.

With these notations and conventions established, Eq. (3.3) can be rewritten as

$$\frac{\partial r_i}{\partial E} + \sum_{j=1}^{L} a_{ij} \frac{\mathrm{d}x_j^*}{\mathrm{d}E} = 0. \tag{3.7}$$

Rearranging and inverting the community matrix solves this system of equilibrium equations:

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L} a_{ij}^{-1} \frac{\partial r_j}{\partial E}, \tag{3.8}$$

or

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\frac{1}{J} \sum_{j=1}^{L} \hat{a}_{ij} \frac{\partial r_j}{\partial E}, \tag{3.9}$$

where J and $\hat{a}_{ij}$ are the determinant and the classical adjoint of a_{ij}, respectively. Also, it is understood that the inverse operation a_{ij}^{-1} always refers to inverting the whole matrix as opposed to calculating the inverses of the individual matrix elements.

Small values of $|J|$ indicate weak community regulation and strong dependence on population densities so that even a slight change in abundance may drive certain populations to extinction. This means that in this case coexistence is only possible for a narrow range of environmental parameters and is thus not robust. Since the determinant is simply the product of the eigenvalues, knowing all eigenvalues of a_{ij} is equivalent to knowing the determinant. More importantly, the largest eigenvalue (which will still be negative for a stable system) may be used as a proxy for the loss of robustness: as the largest eigenvalue approaches zero, so does the determinant, signaling that the system has approached a bifurcation point.

3.3.2 Niche

The biologically more intuitive sensitivity and impact niche vectors also have the capacity to measure robustness besides the determinant of the matrix a_{ij}. As shown in Meszéna et al. (2006), it is always true that

$$|J| \leq \mathcal{V}_\mathrm{S} \mathcal{V}_\mathrm{I}, \tag{3.10}$$

where $\mathcal{V}_\mathrm{S}$ and $\mathcal{V}_\mathrm{I}$ refer to the volume of the parallelepipeds spanned by the sensitivity and the impact vectors of each species, respectively. Note that these volumes remain finite dimensional even if there are infinitely many regulating factors, because they are spanned by as many vectors as the number of species considered. The volume $\mathcal{V}_\mathrm{S}$ ($\mathcal{V}_\mathrm{I}$) will be zero if the collection of all sensitivity (impact) vectors is a linearly dependent set, and will be small in the case of near linear dependence. A corollary of this is that the volumes will be small if any two vectors are nearly parallel to one another. Therefore *coexistence will not be robust if either the sensitivity or the impact vectors are too similar to each other, making* $\mathcal{V}_\mathrm{S}$ *or* $\mathcal{V}_\mathrm{I}$ *and thus the product of the two volumes small*. In theory it would be possible that a small $\mathcal{V}_\mathrm{S}$ is compensated by a large $\mathcal{V}_\mathrm{I}$ leading to robust coexistence, but in practice this probably never happens. On the contrary, a small (large) value of one of the volumes usually implies a small (large) value of the other, since corresponding sensitivity and impact vectors tend to be similar — a mathematical way of saying the biological fact that a population will generally use and therefore influence the same resources that it depends upon for its survival. In conclusion, species have to differ in their responses to the regulating factors as well as in the way they modify them if they are to coexist robustly. Similarity of species is measured by the volumes spanned by the sensitivity and impact vectors, two quantities that can mechanistically and very simply be obtained from the model definition (though usually the numerical values of the equilibrium densities also need to be known). The more orthogonal the vectors of the species, the less similar they are. Coexistence of similars is not impossible but sensitive to perturbations of the environment, as is the coexistence of species that are weakly regulated (indicated by niche vectors of small length), since in both cases the volumes defined by the vectors will be small. The general way of making this instability more robust is to make regulation stronger and the coexisting species less similar, i.e., making the vectors longer and more orthogonal to one another.

Leibold (1995), and Chase and Leibold (2003) already introduced a modernized ecological niche concept that was based on the two-way interaction between a population and its environment. Their version of the impact vector is almost identical to ours. Our sensitivity vector is the normal vector of the zero net growth isocline (ZNGI) describing Leibold's concept of the requirement niche. We consider only the slope, but not the location, of the ZNGI as a descriptor of the niche, because the impact and sensitivity niche vectors thus defined are the proper generalizations of the Hutchinsonian resource utilization function describing the partitioning of the niche space: their scalar product (overlap) yields the competition coefficients (see Pigolotti et al. 2008 for the case of classical resource continua).

The essential aspect of the Hutchinsonian niche space is that coexisting species avoid competitive exclusion via partitioning that space (Hutchinson 1978). In the context of the described theory, the species should differ with respect to the regulating variables. Therefore, the proper concept of niche space is that of *the set of all regulating factors*. The impact and sensitivity niche vectors can be seen as the generalization of the resource utilization function. In the case of a continuum of regulating variables, the continuous index (like the food size q in the example in Section 3.2) constitutes the "niche variable" or "niche axis". To allow for generality while keeping the spirit of Hutchinson's parlance, one may want to refer to the discrete indices of the regulating variables also as (discrete) niche variables. Then, the niche space to be partitioned is the space spanned by the niche variables. It should not be confused with the space of regulating factors (or regulation space), which is the space of all the possible combination of values the regulating factors may assume. For instance, in the case of the food size continuum, niche space is one dimensional, while regulation space is the infinite dimensional function space of the functions $R(q)$ (see Figure 3.1 for a visual representation of this difference).

3.4 Extending the theory to periodic orbits

Recall the general continuous-time dynamical equations of the system (Eq. 3.1):

$$\frac{\mathrm{d}x_i(t)}{\mathrm{d}t} = r_i\left(\mathbf{R}(x_1(t), \ldots, x_L(t)), E, t\right) \qquad (i = 1, \ldots, L). \tag{1}$$

Now we shall assume that the L-component vector field defined by the right hand side of Eq. (3.1) induces a unique, stable, periodic flow $\varphi_i(x_1^0, \ldots, x_L^0, E, t)$ with period T and initial conditions $x_i^0 = x_i(0)$, where the initial moment t_0 was chosen to be zero without loss of generality. It is a very important restriction at this point however that we assume T not to change in response to perturbations — in other words, we assume that it is independent of E. This assumption is more or less reasonable when the source of the periodicity is external forcing like seasonality, but usually breaks down if the cycles are internally generated by the dynamics.

Now, if we were able to translate the system into an equivalent *discrete* model with time step T, then this new system would possess a fixed point to which one could apply the formalism of the previous section. More specifically, let us write the logarithms of the discrete rates of growth $\bar{r}_i$ that we obtain by stroboscopically recording the state of the system defined by (3.1) every time T. Various expressions

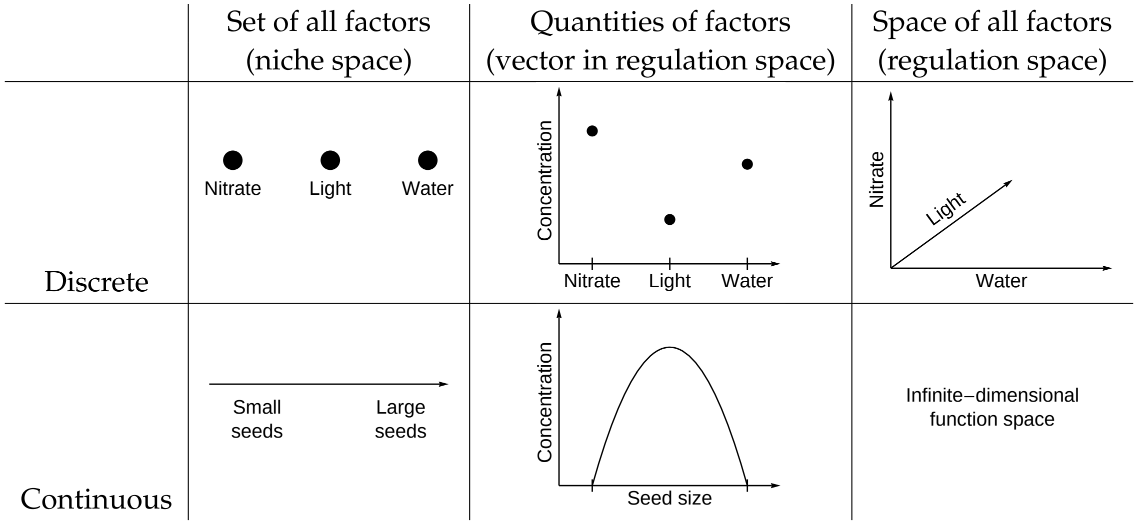

Figure 3.1: Niche space and regulation space for the cases of discrete (upper row) and continuous (lower row) resources. The discrete case is exemplified by three resources (regulating factors): nitrate, light, and water. Now the niche space (defined as the set of regulating factors) is a 3-element set (left figure). These resources are always present in specific quantities; the central figure in the upper row plots these three numbers. They form a vector of three components, a specific realization of the vector **R**. The regulation space (figure on the right) is the vector space that contains all possible vectors **R**. Having three distinct regulating factors (i.e., a 3-element niche space) means that the regulation space is three dimensional. In the continuous case we assume the existence of a fine gradation of various seed sizes that a hypothetical bird community may consume. That is, between the limits defined by the smallest and largest possible size, all seed sizes are available and are potentially regulating. The niche space therefore has infinitely many elements: one for each seed size. These elements are linearly ordered, creating a one-dimensional space (left figure of lower row). As in the discrete case, one may plot resource availabilities for all seed sizes — but this time, instead of a vector, one obtains a function (central figure of lower row). The space that contains all these possible functions has infinitely many dimensions and thus it is impossible to visualize on paper (right figure of lower row). Notice however that while the regulation space is infinite dimensional, niche space has only one dimension and is easily visualizable.

are possible, the more useful of which are

$$\bar{r}_i(x_1^0, \ldots, x_L^0, E) = \int_0^T r_i(\tau)\,\mathrm{d}\tau \tag{3.11}$$

and

$$\bar{r}_i(x_1^0, \ldots, x_L^0, E) = \Pi_i(x_1^0, \ldots, x_L^0, E) - x_i^0, \tag{3.12}$$

where r_i are the growth rates as defined by the right hand side of Eq. (3.1), τ is the time integration variable and Π_i is the so-called stroboscopic (or Poincaré) map.

This map transforms the initial densities into the densities one period later, so that by definition

$$\Pi_i(x_1^0, \dots, x_L^0, E) = \varphi_i(x_1^0, \dots, x_L^0, E, T) = x_i(T). \tag{3.13}$$

When the dynamics is flowing on the periodic attractor, $\bar{r}_i(x_1^*, \dots, x_L^*, E) = 0$, where x_i^* are the equilibrium initial conditions (to which the system returns after time T). Naturally, all the x_i^* are functions of E. Implicit differentiation of this condition with respect to E yields

$$\frac{\partial \bar{r}_i}{\partial E} + \sum_{j=1}^{L} \frac{\partial \bar{r}_i}{\partial x_j^0} \frac{\mathrm{d}x_j^*}{\mathrm{d}E} = 0. \tag{3.14}$$

Rearranging the equation and inverting the matrix multiplying the second term above, we get

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L} \left(\frac{\partial \bar{r}_i}{\partial x_j^0} \right)^{-1} \frac{\partial \bar{r}_j}{\partial E}. \tag{3.15}$$

Now the only thing left to be done is to express the derivatives of $\bar{r}_i$ in terms of the continuous dynamics. The response of $\bar{r}_i$ to changes of the external parameters is expressible from Eq. (3.11) as

$$\frac{\partial \bar{r}_i}{\partial E} = \int_0^T \frac{\partial r_i(\tau)}{\partial E} \, \mathrm{d}\tau. \tag{3.16}$$

The derivative of $\bar{r}_i$ with respect to the initial conditions may be obtained using the stroboscopic map:

$$\frac{\partial \bar{r}_i}{\partial x_j^0} = \frac{\partial \Pi_i}{\partial x_j^0} - \frac{\partial x_i^0}{\partial x_j^0}, \tag{3.17}$$

which is shown to be

$$\frac{\partial \bar{r}_i}{\partial x_j^0} = \mathcal{T}\mathrm{Exp} \left(\int_0^T \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)} \, \mathrm{d}\tau \right) - \delta_{ij} \tag{3.18}$$

in Appendix E. Apart from the calculation leading to the above Jacobian for the stroboscopic map, Appendix E also contains the definitions for the time-ordering operator $\mathcal{T}$ and the matrix exponential Exp therein (δ_{ij} is the identity matrix). As before, summation or integration for all indices of $\mathbf{R}$ is assumed in the exponent above.

Substituting Eqs. (3.16) and (3.18) into Eq. (3.15), we finally arrive at

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L} \left(\mathcal{T}\mathrm{Exp} \left(\int_0^T \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)} \, \mathrm{d}\tau \right) - \delta_{ij} \right)^{-1} \int_0^T \frac{\partial r_j(\tau)}{\partial E} \, \mathrm{d}\tau. \tag{3.19}$$

This formula looks considerably more complicated than its equilibrium analogue (Eq. 3.8), but the interpretation will turn out to be the same. Let us define the time-dependent niche vectors in the following way. The sensitivity will be

$$\mathbf{S}_i(\tau) = \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \tag{3.20}$$

for every moment $\tau \in [\,0, T)$. Similarly, the impact for any moment will be

$$\mathbf{I}_j(\tau) = \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)} = \frac{\partial \mathbf{R}(\tau)}{\partial n_j(\tau)} n_j(\tau), \tag{3.21}$$

where the form of the vector has also been indicated on the linear scale, since that will be more useful for applications later on.

We shall see that these vectors have the capacity to measure the robustness of the system — just as they did in the fixed point case. The scalar product of these two vectors for all indices of the regulating factors will yield a community matrix for every moment τ:

$$a_{ij}(\tau) = \mathbf{S}_i(\tau)\mathbf{I}_j(\tau) = \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)}. \tag{3.22}$$

Notice however that the exponent in Eq. (3.19) contains not just the scalar product of the sensitivity and impact vectors, but this product integrated over time. Let us denote the integral of $a_{ij}(\tau)$ with A_{ij}:

$$A_{ij} = \int_0^T a_{ij}(\tau) \, \mathrm{d}\tau = \int_0^T \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)} \, \mathrm{d}\tau. \tag{3.23}$$

In this formula we sum or integrate over all indices of **R**, plus integrate over time. The time integration is in principle no different from all the other integrals/summations involved: as a matter of formal analogy, we could even say that τ is just another continuous quantity indexing the vector of regulating factors, for which we need to integrate over the interval $[\,0, T)$. This observation allows us to redefine the concept of a regulating factor. Instead of considering $\mathbf{R}(\tau)$ a different vector for every moment τ, we can regard the function $\tau \mapsto \mathbf{R}(\tau)$ as a *single* vector of regulating factors with the extra continuous index τ. If we accept this formal analogy between resource continua and time, then the cyclic time variable τ itself becomes a niche variable. Let us call the vector $\mathbf{R}(\tau)$ at any one particular moment τ the *instantaneous* vector of regulating factors, and $\mathbf{R}(\cdot)$, where τ plays the role of an index, the *temporal* vector of regulating factors. All quantities carrying these same indices (i.e., time-dependent boldface ones) should inherit this nomenclature, therefore we may talk about instantaneous and temporal sensitivity and impact vectors as well. For the purposes of our theory, the temporal niche vectors are the ones we need, as opposed to the instantaneous ones.

Eq. (3.19) can be rewritten in terms of A_{ij}:

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L} \Big(\mathcal{T}\mathrm{Exp}(A_{ij}) - \delta_{ij}\Big)^{-1} \int_0^T \frac{\partial r_j(\tau)}{\partial E}\,\mathrm{d}\tau. \tag{3.24}$$

The matrix A_{ij} is the scalar product of the *temporal* sensitivity and impact vectors for all indices of $\mathbf{R}(\cdot)$ (which therefore includes time). If any two species have very similar temporal sensitivity (impact) vectors, the determinant of A_{ij} will be small. The question is: does a small $\det A_{ij}$ imply that $\det(\mathcal{T}\mathrm{Exp}(A_{ij}) - \delta_{ij})$ will also be small and thus the response of the equilibrium densities large? This question is answered affirmatively in Appendix F, implying that *the product of the volumes spanned by the temporal sensitivity and impact vectors — cf. Inequality (3.10) — is the proper measure of robustness in our context*. Therefore we may conclude that the biological content of Eq. (3.19) is exactly equivalent to the meaning of Eq. (3.8). Treating every regulating factor at every moment within one period as a *different* regulating factor defines the full space of regulating variables now, and each species has a fixed *temporal* sensitivity and impact vector in this extended space. This linear space of functions is the one in which the volumes spanned by the niche vectors have to be calculated. We will refer to the corresponding extended niche space (the *set* of regulating factors) as the temporal niche space (see Figure 3.2).

Naturally, the regulating factors at different times cease to be different from one another in the absence of fluctuations. This intuitively obvious fact can be demonstrated mathematically by showing that Eq. (3.19) simplifies to the time-independent Eq. (3.8) if the attractor of the dynamics is a fixed point instead of a limit cycle. In that case, the "period" T can be chosen arbitrarily, so let us choose an

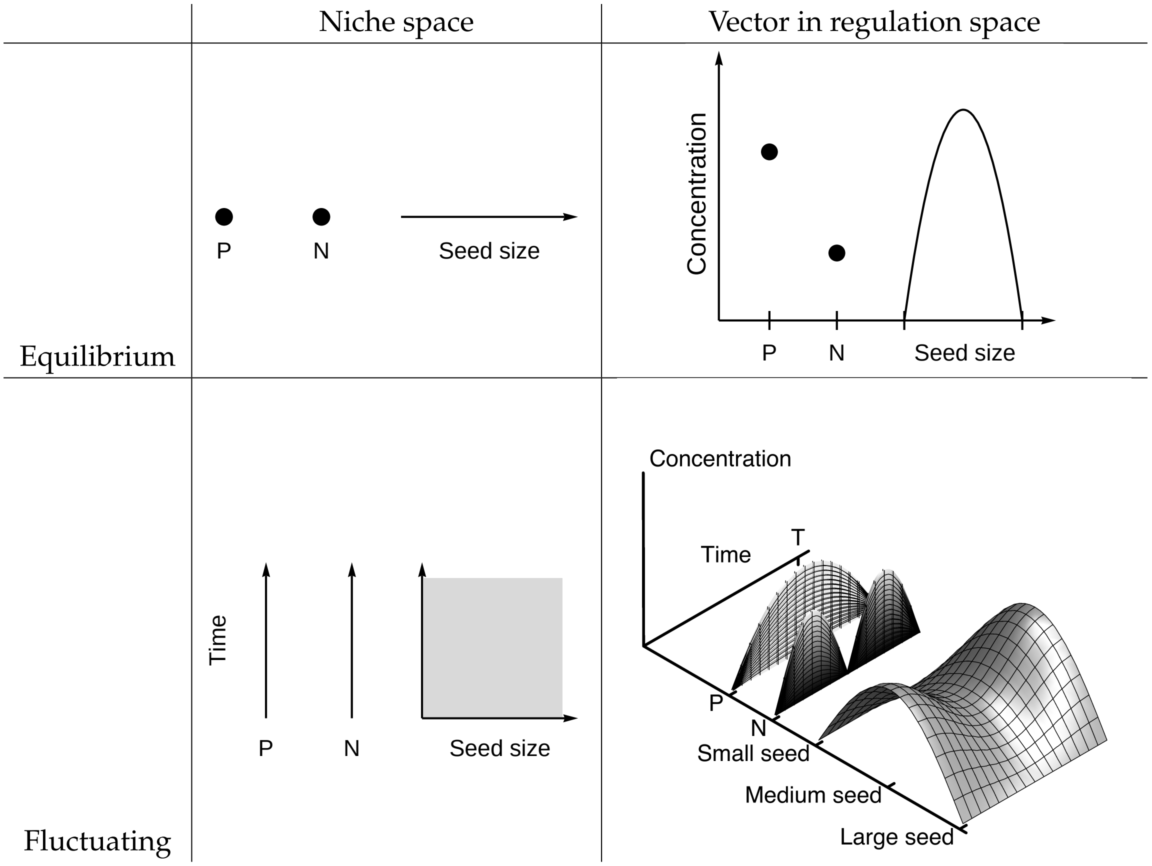

Figure 3.2: Instantaneous and temporal niche and regulation space for a hypothetical bird community. The birds feed on seeds of various sizes, use specific nesting sites (N), and are preyed upon by a predator (P). The first row depicts an equilibrium community: the left side shows the niche space, the right side shows a sample element of regulation space (i.e., a specific vector **R**). The second row does the same, but for the temporal niche and regulation spaces, where every regulating factor at every moment is a different factor, leading to the temporal **R**(·) on the right side. Notice that the dimension of the niche space has increased by one.

infinitesimal $\mathrm{d}\tau$ for the period. Then Eq. (3.19) will read

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L}\left(\mathcal{T}\,\mathrm{Exp}\left(\frac{\partial r_i}{\partial \mathbf{R}}\frac{\partial \mathbf{R}}{\partial x_j}\,\mathrm{d}\tau\right)-\delta_{ij}\right)^{-1}\frac{\partial r_j}{\partial E}\,\mathrm{d}\tau. \tag{3.25}$$

Since the matrix in the exponent is now a constant, time-ordering (see Appendix E) does not play a role and thus the exponential function can be Taylor expanded to linear order in time:

$$\begin{aligned}\frac{\mathrm{d}x_i^*}{\mathrm{d}E} &= -\sum_{j=1}^{L}\left(\delta_{ij} + \frac{\partial r_i}{\partial \mathbf{R}}\frac{\partial \mathbf{R}}{\partial x_j}\,\mathrm{d}\tau - \delta_{ij}\right)^{-1}\frac{\partial r_j}{\partial E}\,\mathrm{d}\tau = \\ &= -\sum_{j=1}^{L}\left(\frac{\partial r_i}{\partial \mathbf{R}}\frac{\partial \mathbf{R}}{\partial x_j}\right)^{-1}\frac{\partial r_j}{\partial E},\end{aligned} \tag{3.26}$$

which is identical to Eq. (3.8). As expected, our theory contains the equilibrium situation as a special case.

3.5 A minimal model of purely fluctuation-maintained coexistence

Here we apply our formalism to a minimal model of temporal niche segregation. It is a two-species Lotka–Volterra model with periodic $r_0(t)$ and $K(t)$ parameters, and competition coefficients that are all equal to one. This means that the determinant of the community matrix will be zero at any one moment: coexistence is maintained purely by fluctuations. This assumption is not necessary for fluctuations to have a stabilizing effect — however, we want to focus strictly on the effects of fluctuations and not have any other mechanisms that might contribute to coexistence; hence the choice for our competition coefficients.

Formally, the model is defined as

$$\frac{1}{n_i(t)}\frac{\mathrm{d}n_i(t)}{\mathrm{d}t} = r_{0i}(t)\left(1 - \frac{n_1(t) + n_2(t)}{K_i(t)}\right) \qquad (i = 1, 2) \tag{3.27}$$

with

$$r_{0i}(t) = \varrho_i(1 + r_\mathrm{e}\cos(\omega t + \phi_i)) \tag{3.28}$$

and

$$K_i(t) = \kappa_i(1 + K_\mathrm{e}\cos(\omega t + \phi_i)). \tag{3.29}$$

Here ϱ_i and κ_i measure the time averages of the intrinsic rate of growth and the carrying capacity of the ith population, respectively; r_e and K_e are the relative amplitudes of their fluctuations with angular frequency ω (so the period is $T = 2\pi/\omega$). Note that r_{0i} and K_i oscillate in-phase for each population. The difference $\Delta\phi = \phi_2 - \phi_1$ of the phase shifts characterizes the relative timing of the two populations.

The two populations are regulated by the same, single regulating variable:

the sum of the densities. The fact that there is only one regulating factor can be made transparent by reparametrizing the model (MacArthur 1972) as a two-species competition model for a single resource $R(t)$:

$$\frac{1}{n_i(t)}\frac{\mathrm{d}n_i(t)}{\mathrm{d}t} = b_i(t)\,R(t) - m_i(t) \qquad (i = 1, 2), \tag{3.30}$$

and

$$R(t) = R_0 - n_1(t) - n_2(t). \tag{3.31}$$

Here we assumed fast resource dynamics; R_0 corresponds to the maximum possible amount of resource. The factor

$$b_i(t) = \frac{r_{0i}(t)}{K_i(t)} \tag{3.32}$$

characterizes the resource dependence of the population and

$$m_i(t) = \left(\frac{R_0}{K_i(t)} - 1\right) r_{0i}(t) \tag{3.33}$$

can be seen as the resource-independent mortality rate.

For constant parameters the single regulating factor allows for the robust persistence of only one species. In this situation the model reduces to the well-known case of density-dependent selection (Metz et al. 2008): competition is won by the species with the higher K_i value (K-selection, MacArthur 1962), or — equivalently — by the species with the lower equilibrium resource level (R^* rule, Tilman 1982).

The issue of interest is that oscillations of the parameters result in a periodic solution. In turn, periodicity of the solution transforms the single regulating variable R into the *continuum* of regulating factors $R(\cdot)$. With this in mind, let us calculate the temporal sensitivity and impact vectors (functions) from Eqs. (3.30) and (3.31):

$$\mathbf{S}_i = S_i(t) = \frac{\partial r_i(t)}{\partial R(t)} = b_i(t), \tag{3.34}$$

and

$$\mathbf{I}_j = I_j(t) = \frac{\partial R(t)}{\partial n_j(t)} n_j(t) = -n_j(t). \tag{3.35}$$

The sensitivities are equivalent to the birth rates at each moment, assuming the available total resource is unity (see Eq. 3.30). The populations are more sensitive when their per-unit-resource birth rates are high and less so when they are low.

The magnitudes of the impacts are simply measured by the population densities. This in effect means that the per capita impacts are all the same: each individual consumes exactly one unit of resource in a unit time, therefore the total consumption per unit time is simply the total density. The negative sign of the impacts indicates that the populations *reduce* the amount of resource available. Should our model be formulated for two populations who compete indirectly via a shared predator (apparent competition, Holt 1977) instead of a shared resource, the impacts would be positive, since the presence of the populations will tend to increase the predator population, not reduce it.

The community matrix will be the scalar product of $S_i(t)$ and $I_j(t)$ in time:

$$\begin{aligned} A_{ij} &= \int_0^T S_i(\tau)\, I_j(\tau)\, \mathrm{d}\tau = \\ &= -\int_0^T b_i(\tau) n_j(\tau)\, \mathrm{d}\tau = \\ &= -T\, \overline{b_i\, n_j} = \\ &= -T\left(\overline{b_i}\;\overline{n_j} + \operatorname{Cov}\left(b_i, n_j\right)\right), \end{aligned} \tag{3.36}$$

where we used the identity $\overline{pq} = \overline{p}\;\overline{q} + \operatorname{Cov}(p, q)$, the overline denoting time averaging and $\operatorname{Cov}(p, q)$ being the covariance of p and q. Note that a lack of covariance between b_i and n_j leads to $\det A_{ij} = \det\left(-T\,\overline{b_i}\,\overline{n_j}\right) = 0$. Therefore, nonzero covariance between the densities and the b_is is a requirement for robust coexistence. Obviously, the constant case violates this requirement. This covariance is the same one that is so essential to Chesson's (1994) general theory of the temporal storage effect.

It is instructive to calculate $b_i(t)$ for small fluctuations, i.e., for small r_e and K_e:

$$\begin{aligned} b_i(t) &= \frac{\varrho_i(1 + r_\mathrm{e}\cos(\omega t + \phi_i))}{\kappa_i(1 + K_\mathrm{e}\cos(\omega t + \phi_i))} \approx \\ &\approx \frac{\varrho_i}{\kappa_i}\left(1 + (r_\mathrm{e} - K_\mathrm{e})\cos(\omega t + \phi_i)\right). \end{aligned} \tag{3.37}$$

Observe that $b_i(t)$ oscillates in-phase with $r_{0i}(t)$ and $K_i(t)$ for $r_\mathrm{e} > K_\mathrm{e}$, but in opposite phase for $r_\mathrm{e} < K_\mathrm{e}$. The other constituent of the covariance, n_i, would reach K_i in a constant environment. In the case of a fluctuating $K_i(t)$, one can expect $n_i(t)$ to follow the changes in $K_i(t)$ with some phase delay. Therefore, if $r_e > K_e$ and the r_{0i}s are large enough to minimize the delay of the n_is, then b_i and n_i oscillate nearly in phase. In this case, each population becomes sensitive to resource concentration levels at the time period when it uses the resource most intensively. If $\Delta\phi$ differs from zero significantly, this situation corresponds exactly to the traditional concept of niche segregation: the resources at different instants of time are considered different, and each population depends on the very same resource which it uses. Consequently, we expect robust coexistence with the described parameter combination.

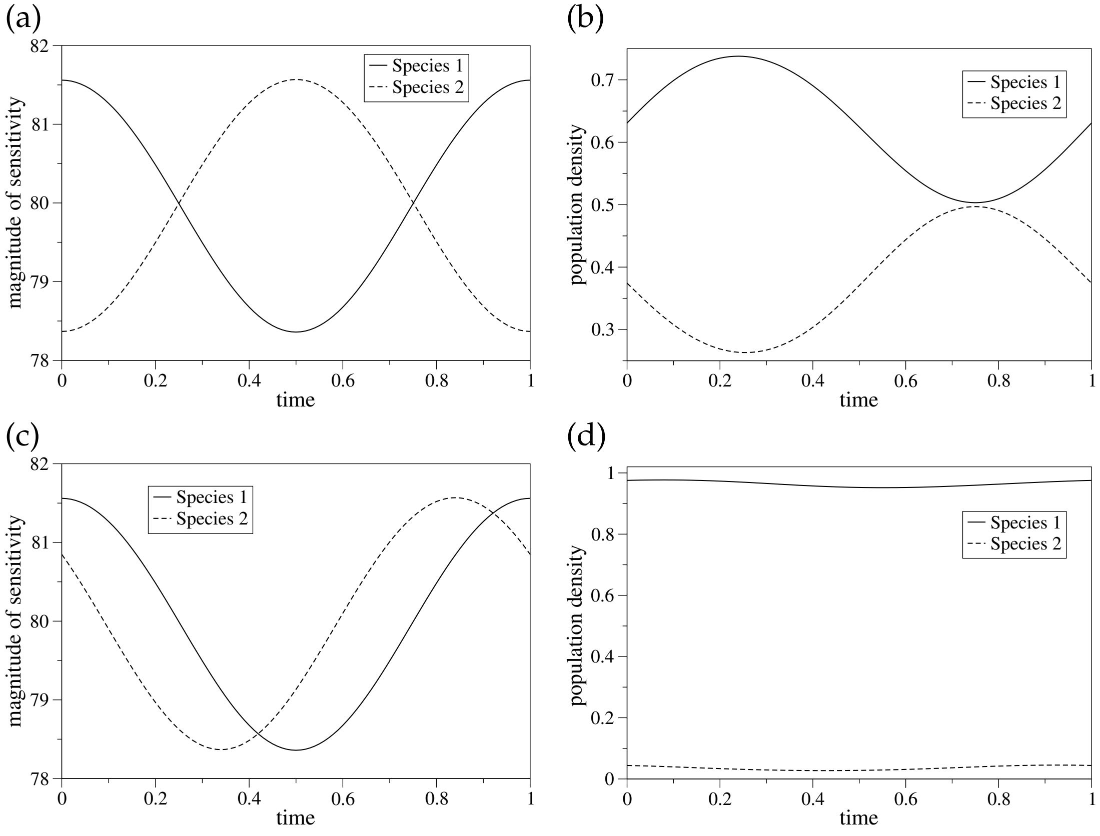

Figure 3.3: Top row: robust coexistence maintained by out-of-phase oscillations ($\Delta\phi = \pi$). The sensitivities $S_1(t)$ and $S_2(t)$ are shown in (a) over one full period; (b) shows the population densities $n_1(t)$ and $n_2(t)$, which are equal to the impacts $I_1(t)$ and $I_2(t)$ times (-1). Since both of these quantities oscillate out of phase, they exhibit reduced similarity, leading to robust coexistence. Bottom row: unrobust coexistence with a smaller phase difference ($\Delta\phi = 0.32\pi$). Observe on (c) that the sensitivities $S_1(t)$ and $S_2(t)$ have almost maximal similarity, and on (d) that the density $n_2(t)$ of Species 2 is very small: any further decrease of the phase difference could cause it to go extinct. Parameters: $\kappa_1 = 1.0001$, $\kappa_2 = 1$, $K_\mathrm{e} = 0.02$, $\varrho_1 = \varrho_2 = 80$, $r_\mathrm{e} = 0.04$, $T = 1$, $\phi_1 = 0$ (therefore $\phi_2 = \Delta\phi$).

These results are in line with a more Chessonesque analysis of the same model. The application of Chesson's framework to this model can be found in Appendix G. There we find that the only coexistence mechanism operating is the storage effect, which reads

$$\Delta I = \frac{\varrho_i}{\kappa_i}(r_e - K_e)\Big(\mathrm{Cov}(E_r n_r) - \mathrm{Cov}(E_i n_r)\Big) \tag{3.38}$$

in our model. Compare the two covariance terms above with the expression for the community matrix A_{ij} that we obtained with Eq. (3.36). At first they might look different, but if one applies the small fluctuation approximation in Eq. (3.37) to the community matrix then $A_{11} - A_{21}$ ($r = 1$, $i = 2$) will precisely correspond to ΔI. In Chesson's approach, the difference of the elements in one column of A_{ij} gives the storage effect; in ours, robustness is determined by $\det A_{ij}$. The difference in our approaches has its roots in the fact that Chesson uses invasion criteria to assess coexistence, whilst we are interested in stability only in the vicinity of the attractor. Calculating the difference of the column elements corresponds to the first approach, since the invasibility criterion in the Lotka–Volterra model is that intraspecific competition has to be greater than interspecific competition within the resident (so $A_{11} - A_{21} > 0$ means Species 2 can invade Species 1). On the other hand, we also know that the fixed point of stable coexistence in the same model disappears precisely when the determinant of the community matrix becomes zero, so what we are doing is simply measuring how close the system is to this critical point. Therefore, the difference between the two approaches is the particular coexistence criterion they consider, which are equivalent in the context of the Lotka–Volterra model.

The simulations (not shown) confirmed that if the two populations have identical parameters except for $\Delta\phi$, their average densities are the same, and only the relative phases in which they oscillate varies. Then we gave a small relative advantage of 10^{-4} to Species 1 by increasing κ_1. In the various runs the phase difference $\Delta\phi$ was gradually decreased from π to near zero. As expected, decreasing $\Delta\phi$ increases the response of the average densities to the perturbation of κ_1 (Figure 3.3 (a) and (b)). Coexistence proved to be robust when the two oscillations were out of phase ($\Delta\phi = \pi$, corresponding to the kind of parameter combination described above). Lower values of $\Delta\phi$ resulted in significant reduction of the average density of the species with the smaller κ, however (Figure 3.3 (c) and (d)). Having obtained the community matrix A_{ij} by numerically integrating over one full period, its determinant was calculated as a function of $\Delta\phi$ (Figure 3.4). Observe that the determinant becomes very small around $\Delta\phi \sim 0.32\pi = 1$. This is consistent with the results in the lower row of Figure 3.3, where the 10^{-4} relative disadvantage of Species 2 almost leads to its extinction at $\Delta\phi = 0.32\pi$.

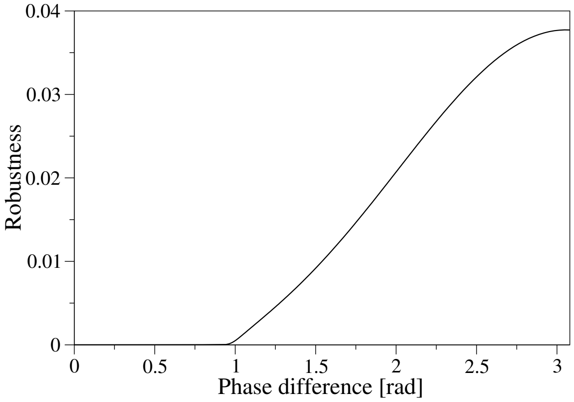

Figure 3.4: Loss of robustness with increasing similarity. Horizontal axis: phase difference $\Delta\phi$ in radians; vertical axis: determinant of A_{ij} as a measure of robustness. For practical purposes, $\det A_{ij}$ becomes almost zero when $\Delta\phi \lesssim 1$; it becomes exactly zero at $\Delta\phi = 0$. The curve is smooth everywhere, though it does change very rapidly around $\Delta\phi \approx 1$.

3.6 Discussion

In this chapter we extended Meszéna et al.'s (2006) theory of coexistence and niche from fixed point dynamics to cycles of constant period, without any constraints on the amplitude of the fluctuations. The emerging picture is a formalization of the concept of temporal niche segregation. The original theory required species to segregate with respect to the variables involved in their regulation as a condition for robust coexistence. Accordingly, temporal niche segregation means segregation with respect to the timing of population regulation within the cycle: this is done by considering the values of a given regulating variable at different instants of time within the period as different regulating variables. Generally, the niche of a species is characterized by the species' impact on and sensitivity towards the regulating variables. For the cyclic case it means that the time-courses of the impacts and the sensitivities within a period should differ between the species.

In principle, our treatment was independent of whether the cyclic dynamics originates from external forcing or from the internal dynamics of the system. However, we assumed that the period T was unaffected by the perturbations, with respect to which robustness was considered. This condition is naturally satisfied in the case of external forcing, but is usually invalid otherwise, i.e., when the cycles are generated internally by the dynamics.

Our study was motivated by the wish to have a unified mathematical theory of the ecological niche. After the Lotka–Volterra model had fallen out of favor because of its uneasy relationship with empirical details, it became the prevailing attitude to study coexistence in specific mechanistic models and have generalized conclusions only on a verbal level. As the assumptions and conclusions of the different models are often difficult to compare, and no model is immune to the criticism of neglegting important details, the predictive power of this approach is limited. Instead we prefer to have a consistent theory with clear mathematical foundations on the general level that maintains a well-defined connection to verbal theory as well as to specific models of arbitrary detailedness. Adaptive dynamics (Geritz et al. 1998, Meszéna et al. 2005) and the theory of structured populations (Caswell 2001, Diekmann et al. 2003) demonstrated the possibility and usefulness of such a framework within the context of population biology. Within such a framework, there is a clean way of incorporating additional details whenever it is necessary.

The perturbation approach makes a general theory of coexistence possible. It was demonstrated that robustness of coexistence against the change of external parameters is tied to niche segregation in a well-defined sense (Meszéna et al. 2006). As it is sufficient to consider small perturbations only, no generality is lost by carefully made linearization. This linearization establishes a general connection between an arbitrarily complicated model of coexistence and the Lotka–Volterra model. Unfortunately, the concept of a resource utilization function as a descriptor of the niche of a species does not generalize: one has to linearize the two legs of population regulation separately, leading to the concept of impact and sensitivity niches.

Intuitively, three distinct types of niche segregation can and have been distinguished: functional, habitat, and temporal segregation (Christiansen and Fenchel 1977). Functional segregation is covered by the basic fixed point theory. Habitat segregation requires the handling of the spatial structure of populations — this has been achieved by Szilágyi and Meszéna (2009a,b), not just for spatial but for arbitrary population structure as well. Finally, temporal niche segregation in a periodic environment is what this chapter was about. Parvinen and Meszéna (2009) studied a different kind of temporal segregation, one that is inherently tied to spatial structure as well: the coexistence of successional species. Szilágyi and Meszéna (2010) applied the framework to fluctuation-mediated coexistence by the effect of relative nonlinearity.

Today the reference point for any theory of coexistence in a fluctuating environment is the framework of Chesson (1994), both because of its completeness and its generality. Chesson distinguishes between two types of coexistence-affecting mechanisms that are specifically induced by environmental fluctuations (Chesson 2000b): the storage effect and the effect of relative nonlinearity. The storage effect is essentially a result of temporal niche segregation, whilst the effect of relative nonlinearity emerges from a difference between the species' (nonlinear) competitive effect curves as a function of their densities. One very important question is how these mechanisms (and Chesson's whole framework) relate to ours. For one thing, the two approaches differ in their coexistence criteria: Chesson considers mutual invasibility; we only require that the population dynamical attractor be locally stable (note that mutual invasibility is a sufficient but not a necessary condition for coexistence, at least when demographic stochasticity can be ignored; see Szilágyi and Meszéna 2010). A second difference is that, strictly speaking, Chesson's theory is only valid for small fluctuations. In our framework, however, there is no limit on the amplitude of population oscillations. Regardless of the small-fluctuation approximation though, a more formal analogy can be drawn between the two approaches. If the growth rates are linear functions of the population densities, neglecting higher-order terms will not affect this property. Therefore, the resulting model in Chesson's scheme will be equivalent to a Lotka–Volterra model with fluctuating parameters. In fact, it will be the very same model as the one we used in our example (Eq. 3.27), provided that the amplitudes of the fluctuating parameters are not very large — i.e., after linearization according to Eq. (3.37). The analysis of this model using Chesson's framework is performed in Appendix E, where the results from the two approaches can be compared. This comparison formally establishes the fact that Chesson's storage effect can be seen as temporal niche segregation, something that has often been stressed by Chesson himself (Chesson 1991, 1994, 2000b).

When the growth rates are nonlinear functions of the densities, the analysis is more complicated, since relative nonlinearity might also contribute to species coexistence. Unfortunately, we cannot as yet provide a detailed formal analogy between the two frameworks in this case. We would like to emphasize, however, that our methodology does apply to models with relative nonlinearity, as long as the period of the oscillations remains fixed. This basically precludes the analysis of indigenously generated cycles, since their period will in general depend on the perturbed parameters. But other models, where periodicity is externally forced, may be analized in our way. One example is provided by the model of Szilágyi and Meszéna (2010), who considered the simplest possible model that produces relative nonlinearity. Their choice for the environmental fluctuations was a Gaussian white noise, but no essential part of the model is altered if one replaces the white noise with some periodic function. In this case, both their conclusions and ours hold simultaneously. We are thus provided with a specific model which may be studied using our method, and in which only relative nonlinearity is operating as a coexistence-affecting mechanism, to use Chesson's terminology.

We close our discussion by commenting on the status of niche theory in a nonequilibrium environment. Our framework assumes periodic dynamics. Nevertheless, we conjecture that the underlying idea, the concept of temporal niche segregation, generalizes for all stationarily fluctuating environments and ergodic situations as well, be it aperiodic stationary fluctuations or seasonally forced chaotic dynamics. The crucial point is to have an "equilibrium" condition, which then can be subjected to perturbation analysis. In the periodic case this happened to be the periodicity condition $\bar{r}_i = 0$. For arbitrary stationarily fluctuating environments it is the condition that the long-term average growth rate should be zero (Turelli 1978, Chesson 1994, Szilágyi and Meszéna 2010; see Hofbauer and Schreiber 2010, Schreiber et al. 2011 for the formal proof). On the other hand, existence of a long-term environmental trend (i.e., departure from stationarity, as in the case of global climate change) invalidates our approach in an essential way. Then, our formulation applies only as an approximation. It could be a very good approximation, however. If a population survives for a sufficiently long time T, then the average growth rate $\ln(n(T)/n(0))/T$ for that time period is close to zero even if the initial and final densities $n(0)$ and $n(T)$ differ considerably. Therefore, the existence of long-term environmental trends does not essentially invalidate niche theory. It remains a null model: the real process can be seen as a perturbation of the presented theory.

Chapter 4

Community robustness in periodic environments for discrete-time dynamics

4.1 The importance of robustness analysis for the coexistence problem

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

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

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

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

This chapter develops a general robustness analysis of discrete-time limit cycles of fixed period length. We deal with robustness exclusively: existence, stability, and positivity of the cycle are therefore all assumed. First, in Section 4.2, we discuss some preliminaries on the robustness of fixed points, its connection to deeper concepts in ecology such as the ecological niche, and the extension of these results to continuous-time limit cycles (Chapter 3). Next, we derive the robustness formulas for discrete-time cycles in Section 4.3. We then go on in Section 4.4 to present a general approximation scheme, based on the celebrated framework of Peter Chesson (1994), which allows for simplified robustness calculations. Finally, we apply our results in Section 4.5 to a two-cycle in a model of annual plant competition with seed banks.

4.2 Preliminaries

4.2.1 Robustness of fixed points

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

$$x_i(t+1) = x_i(t) + r_i(\mathbf{R}(x_1(t), \ldots, x_L(t)), \mathbb{E}, t) \qquad (i = 1, \ldots, L), \tag{4.1}$$

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

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

$$r_i(\mathbf{R}(x_1^*, \ldots, x_L^*), \mathbb{E}) = 0 \tag{4.2}$$

equilibrium conditions will hold. These are L algebraic equations for the equilibrium log-densities x_i^*. What we are interested in is how much the position of this fixed point is expected to shift after perturbing the external parameters $\mathbb{E}$. Since the equilibrium densities are functions of $\mathbb{E}$, differentiating Eq. (4.2) with respect to the parameters yields

$$\frac{\partial r_i}{\partial \mathbb{E}} + \sum_{j=1}^{L} \frac{\partial r_i}{\partial x_j} \frac{\mathrm{d}x_j^*}{\mathrm{d}\mathbb{E}} = 0. \tag{4.3}$$

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

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}\mathbb{E}} = -\sum_{j=1}^{L} \left(\frac{\partial r_i}{\partial x_j} \right)^{-1} \frac{\partial r_j}{\partial \mathbb{E}}, \tag{4.4}$$

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

We would also like to emphasize the generality of our approach. Recently, it has been stressed that model robustness should be checked not just against parameter perturbations, but also against changes in the functional forms of the model's ingredient functions (Gross et al. 2009, Cordoleani et al. 2011, Adamson and Morozov 2012; see also Chapters 1 and 2). An example of such a structural perturbation would be changing the functional response curve of a predator from a Michaelis-Menten (Holling 1959) to an exponential (Ivlev 1961) function (which look very similar to the naked eye). We emphasize that, as long as a family of functions can be parametrized in a smooth manner (and this assumption is already there e.g. in the work of Cordoleani et al. 2011 and Adamson and Morozov 2012), there is nothing to stop one from assigning that parameter to be part of $\mathbb{E}$ and analyzing the robustness of the model with respect to it, using Eq. (4.4). Or, to go even further: Eq. (4.4) remains formally valid even if $\mathbb{E}$ contains functions and not just numbers – the only thing to modify is to replace differentiation with respect to $\mathbb{E}$ by functional differentiation. Note that this extension to infinitely many parameters comes at a price though: since the concept of a volume is not well defined in function spaces, one can no longer talk about the set of parameters supporting coexistence being "large" or "small". We therefore lose the intuitive notion of the "volume in parameter space allowing for coexistence" when $\mathbb{E}$ is a continuum of parameters.

4.2.2 Ecological implications

Eq. (4.4) can be made more useful and biologically interpretable by further expanding the partial derivative of r_i with respect to x_j via the chain rule:

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}\mathbb{E}} = -\sum_{j=1}^{L} \left(\frac{\partial r_i}{\partial \mathbf{R}} \frac{\partial \mathbf{R}}{\partial x_j} \right)^{-1} \frac{\partial r_j}{\partial \mathbb{E}}, \tag{4.5}$$

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

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

$$\frac{\partial r_i}{\partial x_j} = \sum_{m=1}^{L} S_{im} I_{mj}. \tag{4.6}$$

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

$$\det\left(\frac{\partial r_i}{\partial x_j} \right) = \det(S_{ij}) \det(I_{ij}). \tag{4.7}$$

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

$$\left| \det\left(\frac{\partial r_i}{\partial x_j} \right) \right| = \mathcal{V}_\mathbf{S} \mathcal{V}_\mathbf{I}. \tag{4.8}$$

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

$$\left|\det\left(\frac{\partial r_i}{\partial x_j}\right)\right| \leq \mathcal{V}_{\mathrm{S}}\mathcal{V}_{\mathrm{I}} \tag{4.9}$$

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

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

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

The classical niche concept thus finds a natural implementation via the modern theory of community robustness. The Hutchinsonian "niche space" is then identified with the set of all regulating factors because, as we have seen, these are the variables species have to be different in to coexist robustly. This is true regardless of whether this space is discrete (e.g., two noninteracting resources) or continuous (as in the case of a resource gradient). Classically, the niche of a species within niche space was assumed to be given by a resource utilization function (MacArthur and Levins 1967, Hutchinson 1978). The overlap of these functions measured the strength of competition (the derivative $\partial r_i/\partial x_j$) between two species. Unfortunately, being a phenomenological construct, the resource utilization function lacks a mechanistic underpinning which would allow it to be generalized beyond the confines of the simplest competition models. However, looking at Eq. (4.5), we see that the strength of competition, $\partial r_i/\partial x_j$, is always necessarily given by the overlap of $\mathbf{S}_i$ and $\mathbf{I}_j$. Therefore, the resource utilization function needs to be replaced by *two* functions: the sensitivity and the impact. Together, they fully characterize the niche of any species within niche space, and they also inherit the fundamental property ascribed to resource utilization functions: too much similarity (i.e., overlap) of the sensitivities and/or the impacts makes coexistence unlikely by rendering it unrobust. And this is not an intuitive, phenomenological statement, but a powerful, general conclusion that will hold regardless of any model details.

4.2.3 Robustness of continuous-time limit cycles

The above results for the robustness of fixed points have been extended to continuous-time limit cycles (Chapter 3). The formulas are not really important for us per se, but we summarize the main conclusions. In brief, it turns out that all results from the fixed point case, in particular Eq. (4.9), carry over, provided that we treat each regulating factor at each moment in time as a *separate* regulating factor. Putting it another way, time becomes another quantity indexing the vector of regulating factors. Robust coexistence may therefore be achieved, not just through resource partitioning or species-specific natural enemies, but by the proper timing of resource use or predator-avoidance. Moreover, the mathematical structure of time-partitioning is equivalent to that of resource-partitioning. In this way, the extension of robustness analysis to continuous-time limit cycles formalizes the concept of temporal niche segregation (Christiansen and Fenchel 1977, Levins 1979, Chesson 1994, 2000b, Szilágyi and Meszéna 2010).

4.3 Robustness of discrete-time limit cycles

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

Let us start with Eq. (4.1) as our community model and assume it induces a T-cycle with initial conditions $x_i^* = x_i(0)$. We convert this periodic dynamics into an equivalent fixed point dynamics by recording the state of the system stroboscopically at every time T. The cumulative growth rates $\bar{r}_i$ over one cycle read

$$\bar{r}_i = \sum_{\tau=0}^{T-1} r_i(\tau) = 0, \tag{4.10}$$

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

$$x_i(t+T) = x_i(t) + \bar{r}_i, \tag{4.11}$$

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

$$\frac{\partial \bar{r}_i}{\partial \mathbb{E}} + \sum_{j=1}^{L} \frac{\partial \bar{r}_i}{\partial x_j^*} \frac{\mathrm{d}x_j^*}{\mathrm{d}\mathbb{E}} = 0, \tag{4.12}$$

and rearranging the result yields the analogue of Eq. (4.4):

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}\mathbb{E}} = -\sum_{j=1}^{L} \left(\frac{\partial \bar{r}_i}{\partial x_j^*} \right)^{-1} \frac{\partial \bar{r}_j}{\partial \mathbb{E}}. \tag{4.13}$$

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

$$\Phi_{ij}(\tau) = \frac{\partial x_i(\tau)}{\partial x_j^*}, \tag{4.14}$$

and

$$a_{ij}(\tau) = \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)}. \tag{4.15}$$

In $a_{ij}(\tau)$, summation/integration for all discrete/continuous indices of the vector $\mathbf{R}(\tau)$

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

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

$$\frac{\partial\bar{r}_i}{\partial x_j^*} = \frac{\partial}{\partial x_j^*}\sum_{\tau=0}^{T-1} r_i(\tau) = \sum_{\tau=0}^{T-1}\sum_{k=1}^{L}\frac{\partial r_i(\tau)}{\partial\mathbf{R}(\tau)}\frac{\partial\mathbf{R}(\tau)}{\partial x_k(\tau)}\frac{\partial x_k(\tau)}{\partial x_j^*} = \sum_{\tau=0}^{T-1}\sum_{k=1}^{L} a_{ik}(\tau)\Phi_{kj}(\tau). \tag{4.16}$$

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

$$\Phi_{ij}(\tau) = \frac{\partial x_i(\tau)}{\partial x_j^*} = \frac{\partial}{\partial x_j^*}\left(x_i^* + \sum_{t=0}^{\tau-1} r_i(t)\right) = \delta_{ij} + \sum_{t=0}^{\tau-1}\sum_{k=1}^{L} a_{ik}(t)\Phi_{kj}(t), \tag{4.17}$$

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

$$\Phi_{ij}(\tau+1) - \Phi_{ij}(\tau) = \sum_{k=1}^{L} a_{ik}(\tau)\Phi_{kj}(\tau) \tag{4.18}$$

immediately follows. Now Eq. (4.16) can be simplified:

$$\frac{\partial\bar{r}_i}{\partial x_j^*} = \sum_{\tau=0}^{T-1}\sum_{k=1}^{L} a_{ik}(\tau)\Phi_{kj}(\tau) = \sum_{\tau=0}^{T-1}\Big(\Phi_{ij}(\tau+1) - \Phi_{ij}(\tau)\Big) = \Phi_{ij}(T) - \Phi_{ij}(0). \tag{4.19}$$

Note that $\Phi_{ij}(0) = \delta_{ij}$ from Eq. (4.14). To make use of this expression, we need to solve for $\Phi_{ij}(T)$ explicitly. Switching to matrix notation for better readability, Eq. (4.17) with $\tau \to T$ reads

$$\Phi(T) = 1 + \sum_{\tau=0}^{T-1} a(\tau)\Phi(\tau), \tag{4.20}$$

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

$$\Phi(T) = \prod_{\tau=T-1}^{0}\Big(1 + a(\tau)\Big) \tag{4.21}$$

for all $T \geq 1$. Since $\Phi(0) = 1$, for $T = 1$ Eq. (4.20) gives $\Phi(1) = 1 + a(0)\Phi(0) = 1 + a(0)$, which is the same as the result from Eq. (4.21). Therefore, the conjecture holds for $T = 1$. We now show it holds for $T + 1$ if it holds for T. Substituting the conjectured solution into Eq. (4.20), we get

$$\prod_{\tau=T-1}^{0}\Big(1 + a(\tau)\Big) = 1 + \sum_{\tau=0}^{T-1} a(\tau) \prod_{\tau'=\tau-1}^{0}\Big(1 + a(\tau')\Big). \tag{4.22}$$

Let us call the terms on either side of the equality sign in Eq. (4.22) D. For $T + 1$ we have

$$\prod_{\tau=T}^{0}\Big(1 + a(\tau)\Big) = 1 + \sum_{\tau=0}^{T} a(\tau) \prod_{\tau'=\tau-1}^{0}\Big(1 + a(\tau')\Big). \tag{4.23}$$

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

$$\begin{aligned}&\Big(1 + a(T)\Big) \underbrace{\prod_{\tau=T-1}^{0}\Big(1 + a(\tau)\Big)}_{D}\\ &= a(T) \underbrace{\prod_{\tau=T-1}^{0}\Big(1 + a(\tau)\Big)}_{D} + \underbrace{1 + \sum_{\tau=0}^{T-1} a(\tau) \prod_{\tau'=\tau-1}^{0}\Big(1 + a(\tau')\Big)}_{D},\end{aligned} \tag{4.24}$$

or

$$\Big(1 + a(T)\Big)D = a(T)D + D, \tag{4.25}$$

the two sides clearly being equal. This proves by induction that Eq. (4.21) is indeed the solution giving $\Phi(T)$ for all $T \geq 1$. Now Eq. (4.19) can be written as

$$\frac{\partial \bar{r}_i}{\partial x_j^*} = \prod_{\tau=T-1}^{0}\Big(\delta_{ij} + a_{ij}(\tau)\Big) - \delta_{ij}. \tag{4.26}$$

This expression is the discrete-time analogue of Eq. (3.19); notice that in the limiting case of infinitely many infinitesimal time steps, this formula becomes identical to the continuous-time one. The full formula for the robustness of the periodic orbit is then obtained by substituting this expression into Eq. (4.13):

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}\mathbb{E}} = -\sum_{j=1}^{L}\left(\prod_{\tau=T-1}^{0}\Big(\delta_{ij} + \mathbf{S}_i(\tau)\mathbf{I}_j(\tau)\Big) - \delta_{ij}\right)^{-1} \sum_{t=0}^{T-1} \frac{\partial r_j(t)}{\partial \mathbb{E}} \tag{4.27}$$

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

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

If $a_{ij}(\tau)$ has an eigenvalue of zero for each τ corresponding to the same eigenvector α, $(\delta_{ij}+a_{ij}(\tau))$ will have an eigenvalue of 1 for each τ, and the product of these matrices will also have an eigenvalue of 1 (because the matrices share the eigendirection α). Then, subtracting off the identity matrix from this product as in Eq. (4.26), the expression as a whole has an eigenvalue of zero. Then, as seen from Eq. (4.27), the equilibrium densities become infinitely sensitive to perturbations in $\mathbb{E}$: the system is structurally unstable. Also, since eigenvalues are continuous functions of matrix elements, near-linear dependence of sensitivities or impacts will result in $\partial \bar{r}_i / \partial x_j^*$ having an eigenvalue that is nearly zero, which means the system is nearly structurally unstable, i.e., it lacks sufficient robustness.

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

4.4 A method for analytically estimating the sensitivity vectors

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

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

One possible way of doing this is to connect our robustness analysis with the general framework of Chesson (1994) for multispecies competition in variable environments. In that framework we start out from Eq. (4.1) and take the growth rates r_i to be functions of density-independent (environmental) parameters E_i and density-dependent (competitive) factors C_i, so $r_i = r_i(E_i, C_i)$. We define "equilibrium" values for the environmental and competitive parameters, E_i^* and C_i^*, such that $r_i(E_i^*, C_i^*) = 0$. They are usually not unique, but fixing one will fix the other (also, there are often natural, biologically motivated choices for their values). Next, the r_i are approximated. Since the growth rates are allowed to fluctuate (if E_i and C_i depend on time), a linear approximation will not suffice. Instead, Chesson tells us to perform a quadratic expansion:

$$r_i \approx \alpha_i(E_i - E_i^*) - \beta_i(C_i - C_i^*) + \zeta_i(E_i - E_i^*)(C_i - C_i^*), \tag{4.28}$$

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

$$r_i(t) \approx \mathcal{E}_i(t) - \mathcal{C}_i(t) + \gamma_i \mathcal{E}_i(t) \mathcal{C}_i(t). \tag{4.29}$$

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

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

$$\sum_{t=0}^{T-1} r_i(t) \approx \sum_{t=0}^{T-1} \mathcal{E}_i(t) - \sum_{t=0}^{T-1} C_i(t) + \gamma_i \sum_{t=0}^{T-1} \mathcal{E}_i(t) C_i(t) = 0. \tag{4.30}$$

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

$$\mathbf{S}_i(t) = S_{ik}(t) = \frac{\partial r_i(t)}{\partial C_k(t)} = \delta_{ik} \left(\gamma_i \mathcal{E}_i(t) - 1 \right), \tag{4.31}$$

while the impacts will depend on the particular form of the $C_i(t)$ and their dependence on the log-densities:

$$\mathbf{I}_j(t) = I_{kj}(t) = \frac{\partial C_k(t)}{\partial x_j(t)}. \tag{4.32}$$

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

$$\mathbf{S}_i(t) = S_{ik}(t) = \frac{\partial r_i(t)}{\partial \mathrm{C}_k(t)} = \delta_{ik} \beta_k \left(\gamma_i \mathcal{E}_i(t) - 1 \right). \tag{4.33}$$

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

This derivation did not depend on whether we have a continuous or discrete time model. In continuous time, the sums are replaced by integrals in Eq. (4.30) and the partial derivative by a functional derivative in the sensitivities, but the final forms of the sensitivities and impacts will be unchanged.

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

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

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

4.5 Application: the seedbank model

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

$$N_i(t+1) = N_i(t)\left(s_i(1-E_i(t)) + \frac{Y_i E_i(t)}{E_1(t)N_1(t) + E_2(t)N_2(t)}\right), \tag{4.34}$$

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

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

$$r_i(t) = \log\left(s_i(1 - E_i(t)) + \frac{Y_i E_i(t)}{\exp(R(t))}\right). \tag{4.35}$$

This choice for $R(t)$ immediately reveals an important property of the system: if the environment is constant and the densities settle down to a fixed point equilibrium, coexistence is impossible. This is because in that case there is a single regulating factor $R = \log(E_1 N_1 + E_2 N_2)$ for both species, and so the sensitivities and the impacts are confined to a one-dimensional space. Since two vectors on the same line necessarily span an area (i.e., 2D volume) of zero, by Eq. (4.9) the robustness of the system is lost. The conclusion is that fluctuations are strictly necessary for the two species to coexist, a known result for this model (Chesson 1994).

We shall assume that the $E_i(t)$ oscillate between "good" and "bad" years and rely on these fluctuations to generate coexistence that would otherwise be impossible in a constant world. What counts as a good year for species 1 will be considered a bad year for species 2, and vice versa. Let $P(t)$ be a parity function, equal to -1 if t is odd and to 1 if t is even. Then our choices for the $E_i(t)$ are

$$E_1(t) = \epsilon_{10}\left(1 - \epsilon_{1a} P(t)\right) \tag{4.36}$$

and

$$E_2(t) = \epsilon_{20}\left(1 + \epsilon_{2a} P(t)\right), \tag{4.37}$$

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

To obtain the robustness of the stationary cycle against parameter perturbations, we first choose numerical values for all eight model parameters (Table 4.1). Next, we obtain the stationary two-cycle of the system by iterating the model twice and solving for the densities. The resulting algebraic equations yield $N_1(0) = 0.56$, $N_2(0) = 0.9$ for the initial, and $N_1(1) = 0.41$, $N_2(1) = 0.95$ for the final point in the two-cycle. Finally, we calculate the linear responses of these equilibrium densities to perturbations of each model parameter using Eq. (4.27); the results are shown in Table 4.1.

From these values it is possible to estimate the amount of parameter change that would cause the extinction of at least one of the species. Of course, this is based on our local approximation; when extrapolating the effects for non-infinitesimal

Parameter ($\mathbb{E}$)	Value of $\mathbb{E}$	$\frac{dN_1(0)}{d\mathbb{E}}$	$\frac{dN_2(0)}{d\mathbb{E}}$	$\frac{dN_1(1)}{d\mathbb{E}}$	$\frac{dN_2(1)}{d\mathbb{E}}$
ϵ_{10}	0.5	4.13	−5.31	3.93	−3.72
ϵ_{20}	0.5	−4.94	4.97	−4.35	2.97
ϵ_{1a}	0.2	−1.33	1.55	−1.42	1.51
ϵ_{2a}	0.2	4.26	−4.43	3.27	−3.15
s_1	0.5	2.50	−2.73	2.51	−1.74
s_2	0.6	−1.89	3.12	−1.80	1.97
Y_1	1	3.47	−3.46	3.09	−2.29
Y_2	1	−2.90	4.36	−2.68	3.24

Table 4.1: The parameters of the two-species seedbank model (column 1), their numerical values (column 2), and the sensitivities of the species' densities to each parameter at both points within the two-cycle, calculated from Eq. (4.27) (last four columns). Since $N_i = \log(x_i)$, we have converted back to the linear scale by using $dx_i/d\mathbb{E} = (1/N_i)(dN_i/d\mathbb{E})$. The sensitivity values are to be thought of as multipliers: if the parameter gets perturbed away from its original value by a small $\Delta\mathbb{E}$, the population density of species i at time t within the cycle will be modified by $\Delta N_i(t) = (dN_i(t)/d\mathbb{E})\Delta\mathbb{E}$.

parameter perturbations, this might not give very accurate results. To explore the accuracy of our predictions, we compared them to explicit simulation results, where we numerically solved the model for a wide range of parameter values, recording those where one of the species went extinct (the extinction threshold was $N_{\text{ex}} = e^{-10}$). A graphical depiction of the parameter ranges that support coexistence can be seen on Figure 4.1. On this plot, we shaded the domain for each parameter in which both populations oscillate with all-positive densities. The gray shading represents the "true" coexistence range, obtained via simulations, while the white shading is the estimated coexistence range based on Eq. (4.27). Outside the gray-shaded regions, at least one species will have gone extinct. Note that we vary one parameter at a time, not multiple ones simultaneously.

Based on the correspondence between the gray and white regions, the approximation of Eq. (4.27) clearly does a very good job of predicting where coexistence can happen. It does, however, seem to yield conservative estimates, slightly underestimating the endpoints of the coexistence-yielding parameter range in all cases except for the lower bound on ϵ_{2a}. As the local approximation measures the slope of the cycle's position in phase space as a function of the parameters, the implication is that this function must have been concave-down for every parameter except ϵ_{2a}. One possible way to explore the curvature of this function would be to consider the second-order perturbations – i.e., the derivative $d^2x_i^*/d\mathbb{E}^2$. The sign of this

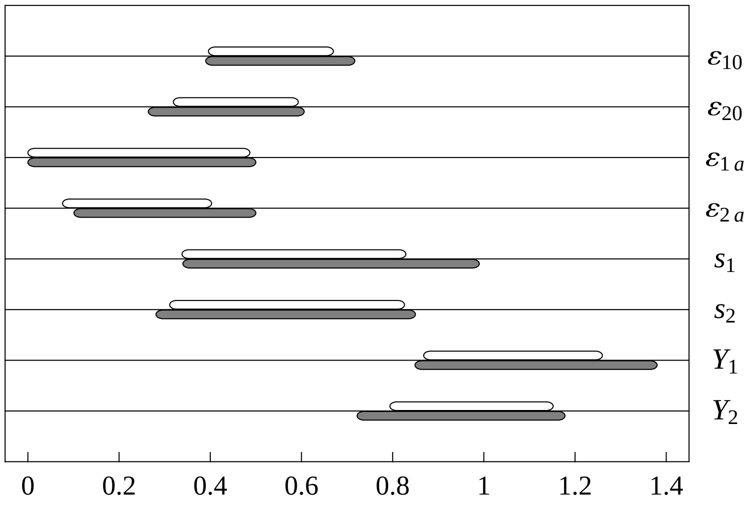

Figure 4.1: The range of each parameter allowing for the coexistence of the two competitors in the seedbank model. Since the parameters all have comparable magnitudes, they have been put on the same scale. The gray bars represent the "true" ranges, obtained via simulation, while the white bars are obtained by applying Eq. (4.27) and extrapolating the effects of this linear approximation to see where extinction is predicted to happen. Note the strong correspondence between the simulated and calculated results.

second derivative will inform us about the local convexity of the function, and so will give information about whether and how much the linear approximation is expected to under- or overestimate the true parameter range where coexistence can happen. Developing the quadratic perturbation formula is, however, beyond the scope of this chapter; for now, we will have to be content with the (already good) approximation our linear formula provides.

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

$$S_i(t) = \frac{\partial r_i(t)}{\partial R(t)} = \frac{Y_i}{s_i\left(E_1(t)N_1(t) + E_2(t)N_2(t)\right)\left(1 - 1/E_i(t)\right) - Y_i}, \tag{4.38}$$

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

$$I_j(t) = \frac{\partial R(t)}{\partial x_j(t)} = \frac{\partial R(t)}{\partial N_j(t)} N_j(t) = \frac{E_j(t)N_j(t)}{E_1(t)N_1(t) + E_2(t)N_2(t)}. \tag{4.39}$$

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

One final thing to do is to see how well the approximation scheme of the previous section for the sensitivity vectors works in practice. First we calculate the analytical approximation to the sensitivities. We choose $C(t) = R(t)$ for the competitive factor. A natural choice for C^* is $C^* = 0$; substituting this into Eq. (4.35) with $R(t) \to C^*$ and requiring the growth rates to be zero yields $E_i^* = (1 - s_i)/(Y_i - s_i)$. We use the definitions for α_i, β_i, γ_i, and $\mathcal{E}_i(t)$ given in the previous section to obtain

$$\alpha_i = \left.\frac{\partial r_i(t)}{\partial E_i(t)}\right|_{E_i^*,C^*} = Y_i - s_i, \tag{4.40}$$

$$\beta_i = -\left.\frac{\partial r_i(t)}{\partial C(t)}\right|_{E_i^*,C^*} = Y_i \frac{1 - s_i}{Y_i - s_i}, \tag{4.41}$$

$$\gamma_i = -\frac{1}{\alpha_i \beta_i} \left.\frac{\partial^2 r_i(t)}{\partial E_i(t) \partial C(t)}\right|_{E_i^*,C^*} = \frac{s_i}{1 - s_i}, \tag{4.42}$$

$$\mathcal{E}_i(t) = \alpha_i \left(E_i(t) - E_i^*\right) = (Y_i - s_i) \left(E_i(t) - \frac{1 - s_i}{Y_i - s_i}\right). \tag{4.43}$$

The approximated sensitivity vectors then read, from Eq. (4.33), as

$$S_i(t) = \beta_i \left(\gamma_i \mathcal{E}_i(t) - 1\right) = s_i Y_i E_i(t) - Y_i \frac{1 - s_i^2}{Y_i - s_i}. \tag{4.44}$$

Figure 4.2 compares the volumes spanned by the true and the approximated sensitivity vectors as functions of the parameters. To obtain the true sensitivities given by Eq. (4.38), the model has to be simulated numerically for the stationary densities (the main advantage of the approximation is precisely that it obviates the need for this step). The volumes are calculated as the absolute value of the determinant of the 2 × 2 matrix obtained by stacking the sensitivity vectors of the two species on top of one another in two rows. On each plot, the abscissa represents about one third of the total range of one of the parameters, while the ordinate measures the volume spanned by the sensitivity vectors. The solid lines are the volumes spanned by the true sensitivity vectors, the dashed lines are the volumes spanned by the approximated ones from Eq. (4.44). We see that the approximation is fair for a reasonably wide range of all the parameters.

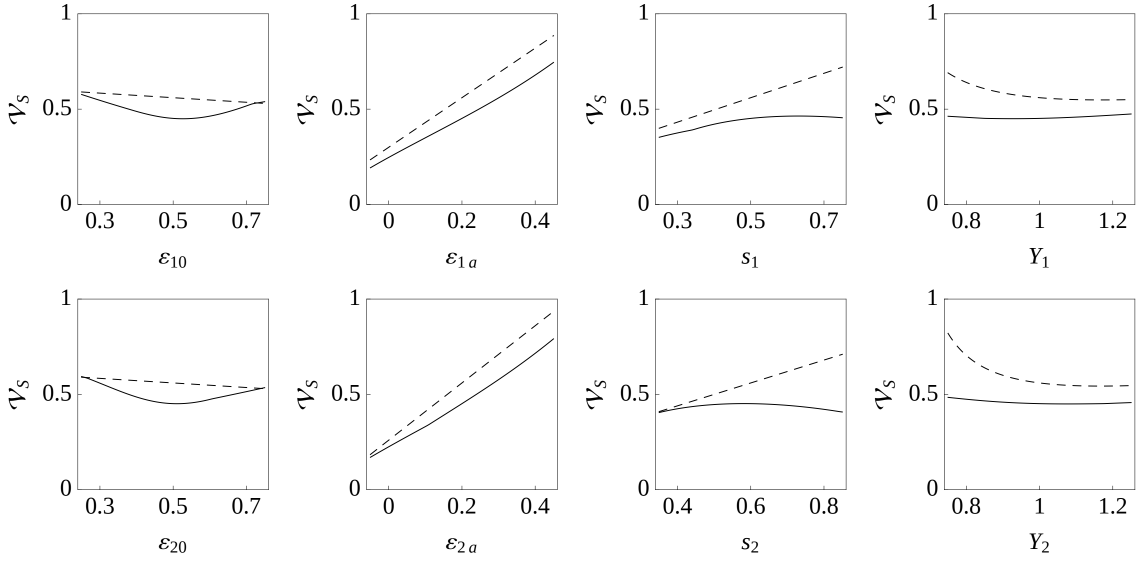

Figure 4.2: Volumes spanned by the temporal sensitivity vectors of the two species as a function of the parameters. The volumes are calculated as the absolute value of the determinant of the 2×2 matrix obtained by stacking the sensitivity vectors of the two species on top of one another in two rows. On each plot a different parameter is varied in a ±0.25 range of its original value (Table 4.1, column 1). The solid lines are the actual sensitivity volumes obtained via simulation; the dashed lines are the approximated sensitivities from Eq. (4.44).

4.6 Discussion

In this chapter we have developed the machinery to evaluate the robustness of discrete-time limit cycles to parameter perturbations. The result, in line with earlier findings (Chapter 3), is that every regulating factor at each point in time within the cycle is effectively a separate regulating factor, independent utilization of which will enhance the robustness of the system. Each species' sensitivity and impact vectors have to be considered at every point in time within the T-cycle; small volumes spanned by these vectors will lead to unrobust coexistence that cannot be expected to hold over an appreciable range of parameter space. These volumes will always be small if the vectors are nearly collinear – therefore, sufficient segregation of the niche vectors is a necessary condition for coexistence. We also developed, based on the formalism of Chesson (1994), an approximation scheme that allows for the analytical treatment of the sensitivity vectors. Finally, we demonstrated how our machinery works by applying it to the two-species seedbank model.

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

Species' relationships to the regulating factors dictate community robustness, but there is no unambiguous way of picking the regulating variables. For instance, in our seedbank model, we could have chosen the two population densities as regulating factors (this would have made the impact vectors trivial: $I_{mj} = \delta_{mj}$), or the two growth rates themselves (which makes the sensitivities trivial: $S_{im} = \delta_{im}$). Needless to say, we could have chosen any function of the weighted sum of densities as well, not just their logarithm – the number of choices is infinite. Importantly however, robustness itself is invariant to the choice of regulating factors: as is seen from Eq. (4.5), the matrix whose inverse determines robustness does not ultimately depend on this choice. Whatever differences there would be in the sensitivities due to choosing the regulating factors in a certain way, they will be compensated by corresponding differences in the impacts. Therefore, choosing the set of regulating factors is as much an art as a science: one should strive to make a choice that makes the niche vectors as simple and as biologically informative as possible. In the seedbank model for instance, the fact that there is a single regulating factor immediately reveals that coexistence is impossible – unless fluctuations increase this number. Since in the fluctuating framework every regulating factor at every moment in time counts as a different factor, the two-cycle increases the number of factors to two. Two-species coexistence therefore becomes possible, but not the coexistence of three or more species. Also, by making the seemingly arbitrary decision of putting the regulating factors on the log scale, it turned out that the impact volumes become bounded this way, making the volumes spanned by the sensitivities (which can be analytically approximated) more meaningful.

The present state of the theory of community robustness is rather incomplete. On the practical side, applications to real-world communities and data will be necessary to assess just how useful the theory is in practice. On the theoretical side, here is how we stand. Fixed-point robustness analysis of unstructured populations is available (Meszéna et al. 2006, summarized earlier in this chapter). An extension to structured populations at fixed points is found in Szilágyi and Meszéna (2009a), but the types of perturbations this framework can analyze is rather restricted, so a generalization of those results will be needed. The theory for periodically fluctuating unstructured populations is covered in Chapter 3 and in the present chapter. The framework for arbitrary stationary fluctuations with unstructured populations and (the most complicated case) with structured ones is still lacking. Working these cases out is the next step in developing the robustness framework further.

Chapter 5

Fixed point sensitivity analysis of interacting structured populations

5.1 Introduction

Sensitivity analysis has been a long-standing and distinguished tool in population ecology. It asks the question what is the linear response of some variable of interest to a change in some parameter. Though the concept is very general, arguably the most successful branch of applications came from linear structured population models (Caswell 2001, chapter 9). Sensitivity analysis of this deceptively simple class of models has led to deep ecological and evolutionary insights into the theory of senescence (Hamilton 1966, Gleeson 1984, Caswell 2011), life history tradeoffs (Templeton 1980, Caswell 1982, 1984), classification of plant strategies (Silvertown et al. 1992, Franco and Silvertown 1996), the analysis of transient population dynamics (Caswell 2007), and the assessment of extinction risk and suggestion of viable conservation measures (Crouse et al. 1987, Silvertown et al. 1993, Noon and McKelvey 1996, Forsman et al. 1996, Seamans et al. 1999, Fujiwara and Caswell 2001, Hunter et al. 2010).

Indeed, sensitivity analysis of linear structured population models has been generating so many interesting results that, ironically, extensions of this methodology to other types of models have been somewhat lagging behind. Nevertheless, Takada and Nakajima (1992, 1998) took the lead on developing the sensitivity analysis of density-dependent structured population models. Behind their extension lies an important insight. Although calculating the sensitivity of any quantity to any parameter is straightforward in linear models, it has usually been the leading eigenvalue's sensitivity that has received most attention. The leading eigenvalue is a measure of the long-term growth rate of the population. However, in density-dependent models, populations eventually reach a stationary state where there is no long-term growth. Therefore, eigenvalue sensitivities are not very informative (but see Caswell et al. 2004); instead, it is the sensitivity of the stationary state itself that is of great interest. Takada and Nakajima (1992, 1998) analyzed the sensitivity of the position of a fixed point attractor in phase space: when perturbing a parameter, how much is the fixed point expected to shift? Their approach did have some technical limitations concerning the form of the density dependence, but these were overcome by Caswell (2008), who provided a completely general sensitivity formula for fixed points in density-dependent structured population models. Moreover, by extension, this result may also be used to yield the sensitivity of discrete-time limit cycles, as a periodic model can be converted into one with a fixed point by repeated composition.

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

For the simplest case of fixed points with unstructured populations, the extension of sensitivity analysis to communities has been done by Levins (1974) and Meszéna et al. (2006). This has subsequently been generalized to (unstructured) community dynamics in random (Szilágyi and Meszéna 2010) and periodic (Chapters 3 and 4) environments, and – partially – to structured community dynamics with fixed point attractors (Szilágyi and Meszéna 2009a,b). Potential practical applications aside, these studies revealed that the sensitivity analysis of coexistence maintains a surprisingly deep connection with some fundamental concepts in ecology, such as that of the ecological niche (Grinnell 1914, Elton 1927, MacArthur and Levins 1967, Hutchinson 1978, Leibold 1995, Chesson 2000b, Chase and Leibold 2003, Meszéna et al. 2006). Indeed, based on their results, Meszéna et al. (2006), Szilágyi and Meszéna (2009a), and Barabás et al. (2012a) have proposed a niche concept that unifies functional, temporal, and spatial modes of niche segregation (Christiansen and Fenchel 1977), keeping in the spirit of but generalizing the classical Hutchinsonian notion of the niche.

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

In this chapter, after fixing notational conventions in Section 5.2, we derive a general formula for the sensitivity of a fixed point describing coexistence of interacting structured populations in Section 5.3. The formula can handle generic perturbations of any lower-level parameter E, assuming the projection matrices depend on E differentiably. It also allows for the sensitivity analysis of any function of the abundance vectors. Finally, in Section 5.4, we apply our findings to a two-species model of competing structured populations, where both species are assumed to undergo an ontogenetic niche shift. After obtaining the sensitivities of the equilibrium densities to all model parameters, we check to see what happens when relaxing the assumptions that the system is at its equilibrium, and that the parameter perturbations are infinitesimal. As our results prove sensitive to neither of these assumptions, we have good indication that our framework is applicable even to systems not close to their equilibria, and to perturbations that are not very small.

5.2 Model framework, notation, and normalization conventions

A general model of interacting structured populations reads

$$\mathbf{n}_i(t+1) = \mathbf{A}_i(\mathcal{R}_\mu(\mathbf{n}_j), E)\,\mathbf{n}_i(t) \qquad (i = 1 \ldots S) \tag{5.1}$$

in discrete time, and

$$\frac{\mathrm{d}\mathbf{n}_i(t)}{\mathrm{d}t} = \mathbf{A}_i(\mathcal{R}_\mu(\mathbf{n}_j), E)\,\mathbf{n}_i(t) \qquad (i = 1 \ldots S) \tag{5.2}$$

in continuous time. Here S is the total number of species in the community, $\mathbf{n}_i(t)$ is the population structure vector of the ith species at time t, E is the collection of external (density-independent) parameters, $\mathbf{A}_i$ is the projection matrix of the ith species as a function of density-dependent and density-independent parameters, and $\mathcal{R}_\mu$ is the collection of regulating factors (Levin 1970, Meszéna et al. 2006). By definition, the regulating factors mediate all interactions between individuals, so that artificially keeping their values fixed would lead to the density-independent increase or decrease of each population. They may include resources, predators, pathogens, refuge availability, or any other thing which provides a feedback between a population's growth rate and density.

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

The identity matrix is denoted by the Kronecker symbol δ_{ij}, equal to 1 if $i = j$

and to 0 otherwise. When inverting matrices, $\left(M_{ij}\right)^{-1}$ always refers to the (i, j)th element of the inverse matrix, never to the inverse of the (i, j)th element (for that purpose, the notation $1/M_{ij}$ would be used).

For the population structure we employ matrix notation, where vectors and matrices are denoted in boldface by lowercase and uppercase letters, respectively. The number of distinct stage classes for species i is s_i. The inner product of two vectors $\mathbf{a}$ and $\mathbf{b}$ is written simply as $\mathbf{ab}$. Their outer product $\mathbf{a} \otimes \mathbf{b}$ is by definition the matrix such that $(\mathbf{a} \otimes \mathbf{b})\mathbf{c} = \mathbf{a}(\mathbf{bc})$ for any vector $\mathbf{c}$. The s_i-dimensional identity matrix is $\mathbf{I}_i$. The one-norm (absolute sum of components) of a vector $\mathbf{a}$ is denoted $|\mathbf{a}|$.

The algebraic multiplicity of each eigenvalue of each matrix $\mathbf{A}_i$ is assumed to be one. The kth eigenvalue of the ith population projection matrix is λ_i^k. For $k = 1$ we simply write λ_i, and it is understood that this is the leading eigenvalue of $\mathbf{A}_i$. In discrete time, the existence of such an eigenvalue is ensured by the Perron-Frobenius theorem (Caswell 2001, chapter 4). In continuous time, as long as we define the "leading" eigenvalue as the one with the largest real part as opposed to the largest modulus, its existence is still guaranteed (Szilágyi and Meszéna 2009a). The kth right and left eigenvectors of species i are denoted $\mathbf{w}_i^k$ and $\mathbf{v}_i^k$, respectively. Again, for $k = 1$ we simply write $\mathbf{w}_i$ and $\mathbf{v}_i$ and it is understood that these are the vectors corresponding to the leading eigenvalue, i.e., are the stable stage distribution and the reproductive value.

The normalization of the eigenvectors is such that

$$\mathbf{w}_i^k \mathbf{v}_i^l = \delta_{kl} \qquad (k, l = 1 \ldots s_i) \tag{5.3}$$

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

$$|\mathbf{w}_i| = 1. \tag{5.4}$$

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

$$n_i = \mathbf{q}_i \mathbf{n}_i \tag{5.5}$$

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

$$\mathbf{p}_i = \frac{\mathbf{n}_i}{n_i}. \tag{5.6}$$

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

$$\mathbf{p}_i = \frac{\mathbf{n}_i}{n_i} = \frac{\mathbf{n}_i}{\mathbf{q}_i\mathbf{n}_i} = \frac{\mathbf{w}_i}{\mathbf{q}_i\mathbf{w}_i}, \tag{5.7}$$

as $\mathbf{w}_i$ is just the normalized version of $\mathbf{n}_i$. This only holds at equilibrium, however.

5.3 Deriving the sensitivity formula

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

When the community described by Eq. (5.1) or Eq. (5.2) is at a fixed point, the following condition on the leading eigenvalue λ_i holds:

$$\lambda_i(\mathcal{R}_\mu(\mathbf{n}_j), E) = \begin{cases} 1 & \text{for discrete time} \\ 0 & \text{for continuous time} \end{cases} \tag{5.8}$$

Here the $\mathbf{n}_j$ assume their equilibrium values, and the dependence of the leading eigenvalues on the regulating factors and the external parameters is explicitly noted. In either of these cases, expanding the equations in their arguments leads to

$$\sum_\mu \frac{\partial\lambda_i}{\partial\mathcal{R}_\mu}\mathrm{d}\mathcal{R}_\mu + \frac{\partial\lambda_i}{\partial E}\mathrm{d}E = 0. \tag{5.9}$$

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

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

$$\mathrm{d}\mathcal{R}_\mu = \sum_{j=1}^{S} \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \mathrm{d}\mathbf{n}_j = \sum_{j=1}^{S} \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \left(\mathbf{p}_j \mathrm{d}n_j + n_j \mathrm{d}\mathbf{p}_j \right). \tag{5.10}$$

According to chapter 9 of Caswell (2001) and Appendix B of Szilágyi and Meszéna (2009a),

$$\mathrm{d}\mathbf{w}_j = \mathbf{Q}_j \mathrm{d}\mathbf{A}_j \mathbf{w}_j, \tag{5.11}$$

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

$$\mathbf{Q}_j = \sum_{k=2}^{s_j} \left(\frac{\mathbf{w}_j^k - |\mathbf{w}_j^k| \mathbf{w}_j}{\lambda_j - \lambda_j^k} \right) \otimes \mathbf{v}_j^k. \tag{5.12}$$

However, Eq. (5.10) is expressed in terms of $\mathrm{d}\mathbf{p}_j$, not $\mathrm{d}\mathbf{w}_j$. We therefore need to connect these two quantities. This can easily be done by taking differentials in Eq. (5.7):

$$\mathrm{d}\mathbf{p}_j = \frac{\mathrm{d}\mathbf{w}_j}{\mathbf{q}_j \mathbf{w}_j} - \frac{\mathbf{w}_j \left(\mathbf{q}_j \mathrm{d}\mathbf{w}_j \right)}{\left(\mathbf{q}_j \mathbf{w}_j \right)^2} = \frac{1}{\mathbf{q}_j \mathbf{w}_j} \left(\mathbf{I}_j - \frac{\mathbf{w}_j \otimes \mathbf{q}_j}{\mathbf{q}_j \mathbf{w}_j} \right) \mathrm{d}\mathbf{w}_j. \tag{5.13}$$

Using the notation

$$\mathbf{P}_j = \frac{1}{\mathbf{q}_j \mathbf{w}_j} \left(\mathbf{I}_j - \frac{\mathbf{w}_j \otimes \mathbf{q}_j}{\mathbf{q}_j \mathbf{w}_j} \right), \tag{5.14}$$

this is written as

$$\mathrm{d}\mathbf{p}_j = \mathbf{P}_j \mathrm{d}\mathbf{w}_j. \tag{5.15}$$

Then, using Eq. (5.11), we get

$$\mathrm{d}\mathbf{p}_j = \mathbf{P}_j \mathbf{Q}_j \mathrm{d}\mathbf{A}_j \mathbf{w}_j \tag{5.16}$$

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

$$\begin{aligned} \mathbf{T}_j = \mathbf{P}_j \mathbf{Q}_j &= \frac{1}{\mathbf{q}_j \mathbf{w}_j} \left(\mathbf{I}_j - \frac{\mathbf{w}_j \otimes \mathbf{q}_j}{\mathbf{q}_j \mathbf{w}_j} \right) \left(\sum_{k=2}^{s_j} \frac{\left(\mathbf{w}_j^k - |\mathbf{w}_j^k| \mathbf{w}_j \right) \otimes \mathbf{v}_j^k}{\lambda_j - \lambda_j^k} \right) \\ &= \frac{1}{\mathbf{q}_j \mathbf{w}_j} \sum_{k=2}^{s_j} \frac{1}{\lambda_j - \lambda_j^k} \left(\mathbf{w}_j^k - \frac{\mathbf{q}_j \mathbf{w}_j^k}{\mathbf{q}_j \mathbf{w}_j} \mathbf{w}_j \right) \otimes \mathbf{v}_j^k. \end{aligned} \tag{5.17}$$

Then, Eq. (5.16) can be written as

$$\mathrm{d}\mathbf{p}_j = \left(\frac{1}{\mathbf{q}_j \mathbf{w}_j} \sum_{k=2}^{s_j} \frac{1}{\lambda_j - \lambda_j^k} \left(\mathbf{w}_j^k - \frac{\mathbf{q}_j \mathbf{w}_j^k}{\mathbf{q}_j \mathbf{w}_j} \mathbf{w}_j \right) \otimes \mathbf{v}_j^k \right) \mathrm{d}\mathbf{A}_j \mathbf{w}_j, \tag{5.18}$$

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

We now expand $\mathrm{d}\mathbf{A}_j$ as

$$\mathrm{d}\mathbf{A}_j = \sum_{\nu} \frac{\partial \mathbf{A}_j}{\partial \mathcal{R}_\nu} \mathrm{d}\mathcal{R}_\nu + \frac{\partial \mathbf{A}_j}{\partial E} \mathrm{d}E. \tag{5.19}$$

Substituting this into Eq. (5.16) and in turn substituting the result into Eq. (5.10) yields

$$\mathrm{d}\mathcal{R}_\mu = \sum_{j=1}^{S} \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \mathbf{p}_j \mathrm{d}n_j + \sum_{j=1}^{S} n_j \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \mathbf{T}_j \left(\sum_{\nu} \frac{\partial \mathbf{A}_j}{\partial \mathcal{R}_\nu} \mathrm{d}\mathcal{R}_\nu + \frac{\partial \mathbf{A}_j}{\partial E} \mathrm{d}E \right) \mathbf{w}_j. \tag{5.20}$$

To simplify notation, we introduce the function

$$\mathcal{G}_\mu(\mathcal{R}_\nu, E) = \sum_{j=1}^{S} n_j \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \mathbf{T}_j \mathbf{A}_j(\mathcal{R}_\nu, E) \mathbf{w}_j, \tag{5.21}$$

where we emphasize that the dependence of $\mathcal{G}_\mu$ on $\mathcal{R}_\nu$ and E comes exclusively from the dependence of the matrix $\mathbf{A}_j$ on these variables, as denoted; all other factors are evaluated at the unperturbed equilibrium. This function is summed over all species and so is the property of the community as a whole. Using this notation, Eq. (5.20) becomes

$$\mathrm{d}\mathcal{R}_\mu = \sum_{j=1}^{S} \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \mathbf{p}_j \mathrm{d}n_j + \sum_{\nu} \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \mathrm{d}\mathcal{R}_\nu + \frac{\partial \mathcal{G}_\mu}{\partial E} \mathrm{d}E. \tag{5.22}$$

Rearranging and solving for $\mathrm{d}\mathcal{R}_\mu$ yields

$$\mathrm{d}\mathcal{R}_\mu = \sum_{\nu} \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \left(\sum_{j=1}^{S} \frac{\partial \mathcal{R}_\nu}{\partial \mathbf{n}_j} \mathbf{p}_j \mathrm{d}n_j + \frac{\partial \mathcal{G}_\nu}{\partial E} \mathrm{d}E \right). \tag{5.23}$$

We now substitute this expression for $\mathrm{d}\mathcal{R}_\mu$ into Eq. (5.9):

$$\sum_\mu \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \sum_\nu \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \left(\sum_{j=1}^{S} \frac{\partial \mathcal{R}_\nu}{\partial \mathbf{n}_j} \mathbf{p}_j \mathrm{d}n_j + \frac{\partial \mathcal{G}_\nu}{\partial E} \mathrm{d}E \right) + \frac{\partial \lambda_i}{\partial E} \mathrm{d}E = 0. \tag{5.24}$$

Differentiation by E yields

$$\sum_\mu \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \sum_\nu \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \left(\sum_{j=1}^{S} \frac{\partial \mathcal{R}_\nu}{\partial \mathbf{n}_j} \mathbf{p}_j \frac{\mathrm{d}n_j}{\mathrm{d}E} + \frac{\partial \mathcal{G}_\nu}{\partial E} \right) + \frac{\partial \lambda_i}{\partial E} = 0, \tag{5.25}$$

or

$$\begin{aligned} &\sum_{j=1}^{S} \sum_{\mu,\nu} \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \frac{\partial \mathcal{R}_\nu}{\partial \mathbf{n}_j} \mathbf{p}_j \frac{\mathrm{d}n_j}{\mathrm{d}E} \\ &+ \sum_{\mu,\nu} \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \frac{\partial \mathcal{G}_\nu}{\partial E} + \frac{\partial \lambda_i}{\partial E} = 0. \end{aligned} \tag{5.26}$$

Solving for $\mathrm{d}n_i/\mathrm{d}E$, we obtain

$$\begin{aligned} \frac{\mathrm{d}n_i}{\mathrm{d}E} = -\sum_{j=1}^{S} &\left(\sum_{\mu,\nu} \frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \frac{\partial \mathcal{R}_\nu}{\partial \mathbf{n}_j} \mathbf{p}_j \right)^{-1} \\ \times &\left(\frac{\partial \lambda_j}{\partial E} + \sum_{\sigma,\varrho} \frac{\partial \lambda_j}{\partial \mathcal{R}_\sigma} \left(\delta_{\sigma\varrho} - \frac{\partial \mathcal{G}_\sigma}{\partial \mathcal{R}_\varrho} \right)^{-1} \frac{\partial \mathcal{G}_\varrho}{\partial E} \right). \end{aligned} \tag{5.27}$$

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

$$\frac{\partial \lambda_i}{\partial \mathcal{R}_\mu} = \frac{\partial \lambda_i}{\partial \mathbf{A}_i} \frac{\partial \mathbf{A}_i}{\partial \mathcal{R}_\mu} = \mathbf{v}_i \frac{\partial \mathbf{A}_i}{\partial \mathcal{R}_\mu} \mathbf{w}_i \tag{5.28}$$

(and analogously for $\partial \lambda_i / \partial E$), where we used the fact that the derivative of the leading eigenvalue with respect to the matrix elements is the outer product of the reproductive value vector and the stable stage distribution (Caswell 2001, chapter 9). The derivative of $\mathbf{A}_i$ with respect to the regulating factors or the parameters E is of course directly calculable from the model definition. Substitution of these expressions into Eq. (5.27) yields our final result:

$$
\begin{aligned}
\frac{\mathrm{d}n_i}{\mathrm{d}E} = -\sum_{j=1}^{S} &\left(\sum_{\mu,\nu} \left(\mathbf{v}_i \frac{\partial \mathbf{A}_i}{\partial \mathcal{R}_\mu} \mathbf{w}_i \right) \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \frac{\partial \mathcal{R}_\nu}{\partial \mathbf{n}_j} \mathbf{p}_j \right)^{-1} \\
&\times \left(\mathbf{v}_j \frac{\partial \mathbf{A}_j}{\partial E} \mathbf{w}_j + \sum_{\sigma,\varrho} \left(\mathbf{v}_j \frac{\partial \mathbf{A}_j}{\partial \mathcal{R}_\sigma} \mathbf{w}_j \right) \left(\delta_{\sigma\varrho} - \frac{\partial \mathcal{G}_\sigma}{\partial \mathcal{R}_\varrho} \right)^{-1} \frac{\partial \mathcal{G}_\varrho}{\partial E} \right),
\end{aligned}
\tag{5.29}
$$

where

$$
\mathcal{G}_\mu(\mathcal{R}_\nu, E) = \sum_{j=1}^{S} \left(\frac{n_j}{\mathbf{q}_j \mathbf{w}_j} \frac{\partial \mathcal{R}_\mu}{\partial \mathbf{n}_j} \sum_{k=2}^{s_i} \frac{1}{\lambda_i - \lambda_i^k} \left(\mathbf{w}_i^k - \frac{\mathbf{q}_i \mathbf{w}_i^k}{\mathbf{q}_i \mathbf{w}_i} \mathbf{w}_i \right) \otimes \mathbf{v}_i^k \right) \mathbf{A}_j(\mathcal{R}_\nu, E) \mathbf{w}_j. \tag{5.30}
$$

To interpret Eq. (5.29), observe that, since all other indices are summed over, the inverted matrix possesses only the two indices i and j. These are species indices, therefore the rows and columns of the matrix express properties of the species: the ith row is a property of species i, and the jth column is a property of species j. The inverse of a matrix is proportional to the inverse of its determinant, and the determinant will be close to zero if any two rows or columns of the matrix are nearly linearly dependent. Therefore, it is immediately seen that the fixed point will become overly sensitive if any two species become very similar, as that will lead to similar rows/columns in the matrix to be inverted. This property can be used to give a more biological interpretation to the formula (see the Discussion).

A simple corollary of Eq. (5.29) is that the sensitivity of any function of the population structure vectors $\mathbf{n}_i$ may now be calculated. As a first step, notice from Eq. (5.5) that n_i will simply be the kth component of $\mathbf{n}_i$ by setting $\mathbf{q}_i$ to be a vector whose kth component is 1 and the rest are 0. In this way, the sensitivity $\mathrm{d}\mathbf{n}_i/\mathrm{d}E$ can be obtained using Eq. (5.29). Then, if we are interested in the sensitivity of some nonlinear function $f(\mathbf{n}_i)$ of the stage classes (e.g., the sensitivity of the ratio of adults to juveniles), we simply use the chain rule:

$$
\frac{\mathrm{d}f}{\mathrm{d}E} = \sum_{i=1}^{S} \frac{\mathrm{d}f}{\mathrm{d}\mathbf{n}_i} \frac{\mathrm{d}\mathbf{n}_i}{\mathrm{d}E}. \tag{5.31}
$$

This method works for any differentiable function $f(\mathbf{n}_i)$ – though for linear functions it is somewhat of an overkill, since in that case properly setting the $\mathbf{q}_i$s will also do the job. For instance, if we are interested in the sensitivity of the biomass of species

i, we can set $\mathbf{q}_i$ to express the per capita biomasses for each stage class, and then use Eq. (5.29) directly.

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

$$\Delta n_i = \left(\frac{\mathrm{d}n_i}{\mathrm{d}E}\right)\Delta E, \tag{5.32}$$

where the derivative is calculated from Eq. (5.29). As this is a local approximation, two consequences follow. First, the formula will be more accurate with ΔE being smaller. Whether it yields acceptable results for non-infinitesimal parameter perturbations is a question we will examine in the next section. Second, if multiple parameters are perturbed simultaneously, the total effect of these perturbations will be the sum of the individual effects:

$$\Delta n_i = \sum_k \left(\frac{\mathrm{d}n_i}{\mathrm{d}E_k}\right)\Delta E_k, \tag{5.33}$$

where E_k is the kth parameter. This additivity of the individual effects of each parameter is a consequence of the linearization in Eq. (5.9).

5.4 Application: a model of ontogenetic niche shift

5.4.1 The model

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

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

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

$$\mathcal{R}_0 = n_{1,2} + n_{2,2}, \tag{5.34a}$$

$$\mathcal{R}_1 = \beta_{11} n_{1,1} + \beta_{12} n_{2,1}, \tag{5.34b}$$

$$\mathcal{R}_2 = \beta_{21} n_{1,1} + \beta_{22} n_{2,1}. \tag{5.34c}$$

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

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

$$\mathbf{A}_i = \begin{pmatrix} (1 - p_i)\dfrac{z_i}{1 + \mathcal{R}_i} & \dfrac{F_i}{1 + \mathcal{R}_0} \\ p_i \dfrac{z_i}{1 + \mathcal{R}_i} & \dfrac{s_i}{1 + \mathcal{R}_0} \end{pmatrix}, \tag{5.35}$$

where z_i is the probability of juvenile survival, p_i the probability of morphing into an adult, F_i is adult fertility, and s_i is the adult survival probability (all probabilities are per capita per time step). As seen from Eq. (5.35), the fertility, juvenile survival, and adult survival are density-dependent through the regulating factors with a Beverton–Holt-style density dependence. Notice that while the juveniles of the two species are affected by two different regulating factors, $\mathcal{R}_1$ and $\mathcal{R}_2$, the adults are affected by the same factor $\mathcal{R}_0$. With the projection matrices thus specified, the dynamics evolves according to Eq. (5.1), the discrete-time model.

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

5.4.2 Results

The first step is to choose values for all model parameters (see Table 5.1). These parameter values lead to the equilibrium population vector $\mathbf{n}_i = (0.899,\ 0.114)$ for both species. The fact that $\mathbf{n}_1 = \mathbf{n}_2$ should not be surprising, as the species are symmetric with respect to their assigned parameters (but they are not equivalent due to $\beta_{12} = \beta_{21} = 0.8$; therefore the fixed point is stable, not neutrally stable). Then, after obtaining the eigenvalues and eigenvectors of the two projection matrices, calculation of the sensitivities via Eq. (5.29) is a straightforward exercise – see Table 5.1 for the results. We will use the total population density as the weighted population size, i.e., $\mathbf{q}_i = (1,\ 1)$ for both species. The total equilibrium population densities are then $n_i = \mathbf{q}_i \mathbf{n}_i = 1.013$.

Parameter (E)	Value of E	$\mathrm{d}n_1/\mathrm{d}E$	$\mathrm{d}n_2/\mathrm{d}E$
F_1	8	0.83	−0.69
F_2	8	−0.69	0.83
p_1	0.36	16.23	−13.89
p_2	0.36	−13.89	16.23
s_1	0.3	7.12	−6.07
s_2	0.3	−6.07	7.12
z_1	0.7	11.40	−9.68
z_2	0.7	−9.68	11.40
β_{12}	0.8	−2.74	2.31
β_{21}	0.8	2.31	−2.74

Table 5.1: Parameter values and their sensitivities in our model of ontogenetic niche shift. The first column lists all the parameters of the model; the second shows their numerical values. The third and fourth columns are the respective sensitivities of the total population sizes of species 1 and 2 to perturbations of each model parameter, calculated from Eq. (5.29).

When interpreting the sensitivity values in Table 5.1, the same considerations apply as in standard eigenvalue sensitivity analyses of single populations. Namely, the numbers alone will not tell us whether the model is "sensitive" to a given parameter or not: the biologically realistic variation of that parameter also needs to be known. The sensitivity values are merely amplifiers: perturbations of the parameters are multiplied by those numbers to yield the change in equilibrium densities via Eq. (5.33). For instance, our model shows great sensitivity to changes in the probability of morphing into adults (the p_is), but if this probability is a parameter that is evolutionarily set and the environment has little or no effect on it, then the model can be quite robust even with those large sensitivity values, as long as selection is negligible. Conversely, small sensitivities may be lethal to a species if the natural variation of the parameter is too large.

There are some natural questions arising from our results:

1. How much do the sensitivity values in Table 5.1 depend on our particular choice of parameters?

2. Sensitivity analysis is of course a locally valid approximation. As stated before, Eq. (5.33) is in principle only accurate for small ΔE values. How much is this accuracy compromised when the parameter perturbations are not infinitesimally small?

3. To use Eq. (5.29), the equilibrium stage distribution needs to be known, but this cannot usually be analytically obtained except in the simplest of models. Instead, field data may be used to estimate this distribution – which may be difficult to do, not to mention the problem that the system might not be at or even near its equilibrium point at the time of measurement. Assuming that the stage distribution is off of its true equilibrium value (which we have the benefit of knowing due to our *in silico* approach), how much are the sensitivity values of Table 5.1 altered?

To answer the first question, we randomized the parameters by simultaneously changing them within a ±10% band of their original values with a uniform probability distribution. Then the model was simulated with these new parameters until equilibrium was reached. The equilibrium condition was that the leading eigenvalues of the two species cannot differ from 1 by more than 10^{-5}. Then, Eq. (5.29) was used to obtain the sensitivities to each parameter. This procedure was then repeated 1000 times. The results are seen on Figure 5.1. While there certainly is variation around the original sensitivities, it is immediately seen that they still give a good general idea of how much sensitivity there is to be expected.

For the second question we performed the same randomization of parameters, ran the model on the computer until equilibrium, and then calculated the difference between the densities predicted by the local sensitivity analysis and the actual densities obtained via simulation. By "predicted" change we mean the following. We determined ΔE for each parameter (the difference between the randomly generated value and the original one in Table 5.1). Then, using the already determined sensitivity values (also in Table 5.1), the contribution of all parameters to Δn was calculated using Eq. (5.33). One thousand such comparisons of simulated and

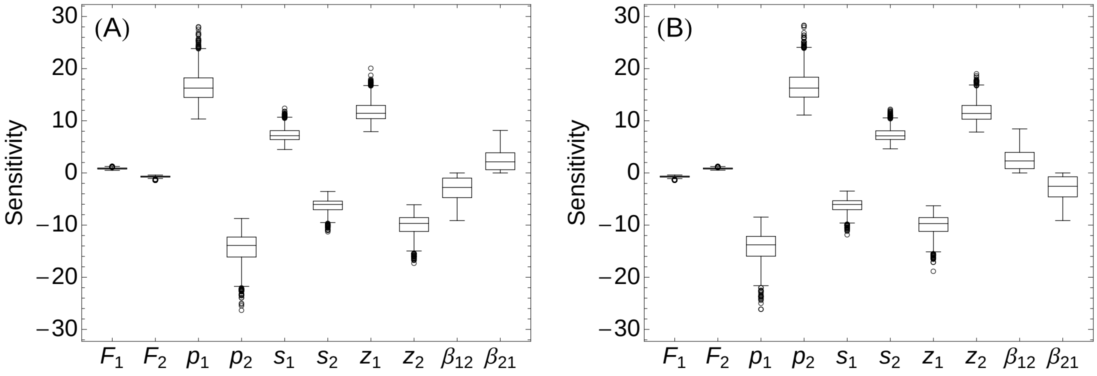

Figure 5.1: Distribution of sensitivity values in parameter space for the ontogenetic niche shift model. First all the parameters are randomly changed within a ±10% range of their original values in Table 5.1. Then the sensitivity to each parameter is calculated using Eq. (5.29). Repeating this process a thousand times, we get a distribution of sensitivities for each parameter, depicted here using box plots. Panel (A) shows the sensitivities for species 1, panel (B) for species 2. The median markers may either be interpreted as the median, or as the sensitivity with the original set of parameters in Table 5.1 – the difference is invisibly slight in all cases.

predicted densities are seen on Figure 5.2. The implications are clear: in the majority of cases, local sensitivity analysis did a good job predicting densities for the ±10% parameter variation we introduced in each parameter.

One manual correction was used in making Figure 5.2. If predicted densities turned out negative, we tested to see whether the species in question indeed went extinct. If so, we took the predicted density to have precisely matched the simulated one, i.e., registered such a case as a perfect prediction. This procedure might in principle be sensitive to the extinction threshold, but we found that the results were essentially unchanged for extinction threshold values between 10^{-3} and 10^{-14}. Incidentally, the fraction of simulations in which at least one species went extinct also showed the same insensitivity to the extinction threshold: it was always about 15% of all cases.

Finally, to answer the third question we kept the original parameter values fixed but randomized the stable stage distribution in a ±30% band of their original values. Applying Eq. (5.29) to the randomized values as if they were the true equilibria of the model, we calculated the (modified) sensitivities to each parameter. Repeating the process 1000 times, we ended up with the variation depicted on Figure 5.3. The error due to an incorrect assessment of the equilibrium is slight even for very large

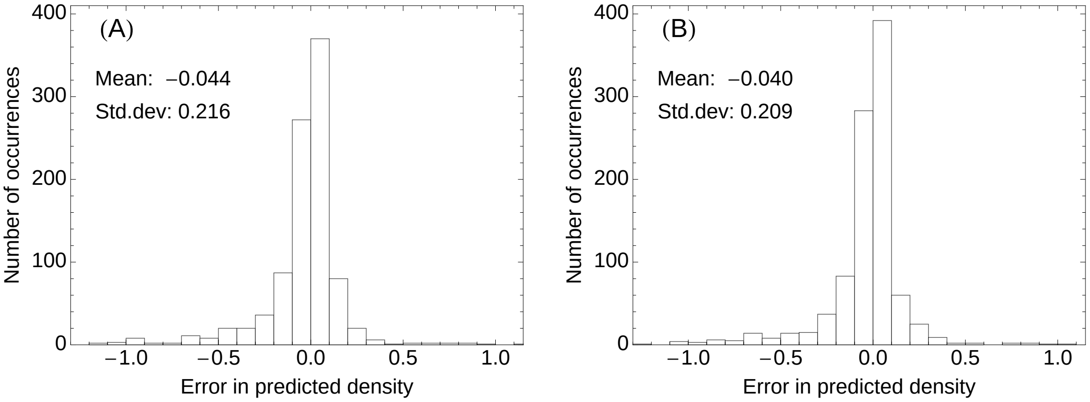

Figure 5.2: Histograms of the difference between predicted and actual changes to equilibrium densities in the ontogenetic niche shift model. First, all the parameters are randomly changed within a ±10% range of their original values in Table 5.1. The difference between the random values and the original ones is ΔE. We used these ΔEs along with the sensitivity values in Table 5.1 to calculate the predicted change in the equilibrium densities from Eq. (5.33). We then simulated our model with the randomized parameter values, recording the equilibrium densities. The difference between the simulated and calculated densities is a measure of how well the sensitivity formula captures the actual change in equilibrium abundances. The histograms summarize a thousand such comparisons; panel (A) is the difference for species 1, panel (B) for species 2. Note that with the original parameter values the total population size is $n_i = 1.013 \approx 1$ for both species, so the abscissas of the histograms can be interpreted as proportional errors relative to that size.

errors in the densities. This suggests that in field studies, it is acceptable to use measured data as a proxy for the actual equilibrium distributions, as the error due to the fact that the measured values are not the actual equilibrium densities will be small – at least for the model in question.

5.5 Discussion

In this chapter we derived a general perturbation formula for the equilibrium densities of interacting structured populations to changes in density-independent model parameters. Each population may be age- or stage-structured with arbitrarily many stage classes, and species' projection matrices may depend on those stage classes in arbitrarily complicated ways. Our formula yields the response of any function of the stage class abundances to perturbations of any model parameter. We applied our results to a model of two competing species undergoing ontogenetic niche shifts. After obtaining the sensitivity of each species' density to each model

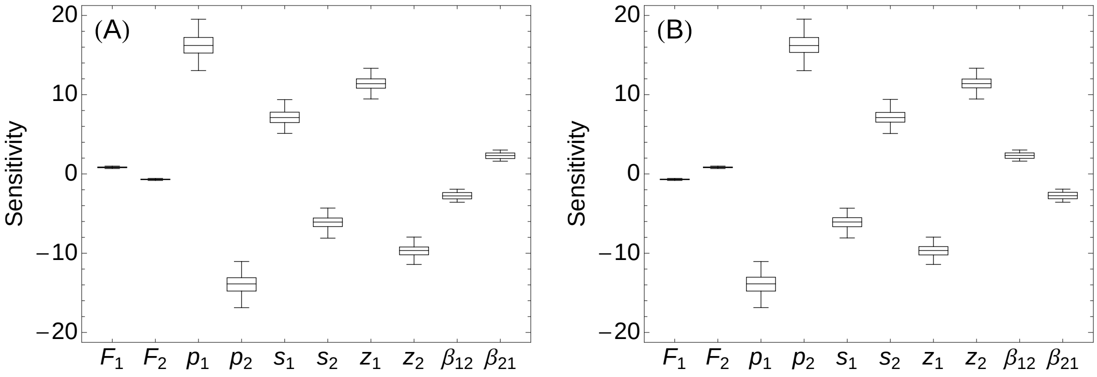

Figure 5.3: Distribution of sensitivity values in the ontogenetic niche shift model when randomizing the equilibrium abundance vectors $\mathbf{n}_i$. We fix the parameters at the values in Table 5.1, which lead to $\mathbf{n}_i = (0.899,\ 0.114)$ at equilibrium for both species. Now, as a first step, we randomize each stage class of each species within a ±30% band of these values. We then use Eq. (5.29) to calculate the sensitivities as if the randomized abundance vectors represented the true equilibrium point. Repeating this process a thousand times, we get the distribution of sensitivities shown by the box plots. Panel (A) is for species 1, panel (B) is for species 2. As in Figure 5.1, the median markers may stand for either the median or the original sensitivities of Table 5.1.

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

Elasticities (Caswell et al. 1984) also enjoy considerable popularity as measures of how sensitive models are to parameter perturbations. The difference is that sensitivities describe the effects of additive perturbations, while elasticities the effects of multiplicative ones. Our sensitivities are easily converted into elasticities. By definition, the derivative of $\log n_i$ with respect to $\log E$ is the elasticity, therefore $(E/n_i)(\mathrm{d}n_i/\mathrm{d}E)$ will yield the elasticities. Or, if we are interested in the elasticity of $f(n_i)$ with f being an arbitrary function, we get $(E/f(n_i))(\mathrm{d}f(n_i)/\mathrm{d}E)$, where the derivative of f with respect to E is given by Eq. (5.31). As in conventional eigenvalue elasticity analysis of linear models, the elasticity to a parameter whose value is zero will be 0. However, elasticities of equilibrium densities cannot be thought of as contributions of matrix elements to the n_is, as that property hinges on Euler's homogeneous function theorem (Mesterton-Gibbons 1993), and the n_is are not homogeneous functions of matrix elements in general (and, even in the realm of eigenvalue elasticities, thinking of the elements as "contributions" to λ_i requires considerable care of interpretation). Even though this property is lacking, there is no obstacle to using our formulas to get at the effects of proportional as opposed to additive perturbations.

We can give a more biological interpretation to Eq. (5.29), the formula for the perturbation of the weighted population densities. We start out from the already stated fact that the rows and columns of the inverted matrix express properties of the species themselves, and that therefore too much similarity in the species leads to similar rows or columns in the matrix to be inverted, making the fixed point overly sensitive to parameter perturbations. The rows and columns are not just some complicated summary of the species' properties; they have straightforward biological interpretations. The row index i appears in the derivative of the projection matrix with respect to the regulating factors, weighted by the reproductive value and the stable stage distribution: it is therefore a measure of how sensitive species i is to the regulating factors (not to be confused with "sensitivity" as a measure of the robustness of the fixed point). The column index j appears in the derivative of the regulating factors with respect to the population structure vector, averaged over the reduced population structure vector: this is a measure of the impact of species j on the regulating factors (Szilágyi and Meszéna 2009a). Our earlier statement that near-linear dependence of the rows or columns leads to an overly sensitive fixed point thus translates into the following: species that are too similar in either their sensitivities to or their impacts on the regulating factors will make the fixed point unrobust to parameter perturbations. In the limiting case where two species share exactly the same sensitivities and/or impacts, the system becomes infinitely sensitive, signaling the destabilization of the system.

The biological interpretation arising from our expression for the fixed point sensitivity of interacting populations is consistent with interpretations arising in existing formulas for the sensitivity of interacting populations (Meszéna et al. 2006, Szilágyi and Meszéna 2009a, 2010; see also Chapters 3 and 4). No two species that are too similar in their way of regulation can realistically coexist on the long run because, even if stability can be ensured (a necessary condition for coexistence), the smallest change in E may result in an erratic swing of the equilibrium population densities, leading to the elimination of at least one of the species. This recasting of the familiar competitive exclusion principle (Hardin 1960, Levin 1970) therefore shifts the emphasis from the stability of coexistence to its sensitivity: coexistence of similar species is not impossible (stability can be forced by careful choice of model parameters), just extremely unlikely, precisely because of the required fine-tuning.

This property connects sensitivity analysis with niche theory. Modern reinterpretations of the niche concept, based on the expectation of stable coexistence (Leibold 1995, Chesson 2000b, Chase and Leibold 2003) have essentially two components. The first, inspired by Levin (1970), is that the niche of a species is to be identified, in some way or another, with the factors it is regulated by. The second is the realization of the importance of the two-way interaction between species and the factors that regulate them. Leibold (1995) and Chase and Leibold (2003) emphasize that resources, predators/pathogens, or the two combined may serve as the niche. They also distinguish requirements (effect of regulator on species) and impacts (effect of species on regulator), and show that only a proper consideration of both can give a full account of the niche. In Chesson's (2000b) terminology, niche space has four "main" axes (each of which may in turn be constituted of multiple axes): resources, predators/pathogens, space, and time. Space and time as niche dimensions mean that each regulating factor at each spatial location and/or point in time may serve as a more-or-less independent factor (spatial and temporal storage effect, Chesson and Warner 1981, Chesson 1991, 1994, Chesson and Huntly 1997, Chesson 2000a, Snyder and Chesson 2004, Chesson 2009, Chapters 3 and 4). Indeed, the main goal of Szilágyi and Meszéna (2009a), whose work we extended here, was to establish the role of space as a niche axis. Chesson stresses that the niche of a species is not a Hutchinsonian hypervolume, but are given by both the effect of a species on each point in niche space, and the response of the species to each point (again, the two-way paradigm). This is of course entirely correct, but it may be added that this replacement of terminology could also be seen as part of a progression of more and more formal niche descriptions. The hypervolume (crudest level) has been made more realistic with the introduction of resource utilization functions (MacArthur and Levins 1967). These in turn have been superseded by the sensitivity/impact picture, one that is both formal and generally applicable in any ecological scenario.

In our framework the two-way nature of regulation is apparent: species have sensitivities to and impacts on the regulating factors. Therefore, one can identify niche space with the set of all regulating factors, and the sensitivities and impacts describe the two-way relationship between species and points in this niche space, in complete agreement with the picture suggested by Chesson (2000b). With the shift in focus from the stability (the fundamental basis for Leibold 1995 and Chesson 2000b) to the sensitivity of coexistence, the original intuition behind niche theory is retained: too much niche overlap – i.e., too much similarity in either the sensitivities or the impacts – confines any coexistence to a very limited range of parameter space, making it unrealistic. Note that this niche interpretation is carried over from Szilágyi and Meszéna (2009a): the reason is that the niche theoretical conclusions hinge on the properties of the inverted matrix in Eq. (5.29), and this matrix has the same general form here as it did in the original study. This is why the impact-sensitivity conclusions have not been changed. However, the whole perturbation story has changed significantly: perturbations can have a direct effect on the population structure, and this direct effect induces further, indirect effects through population interactions. The perturbations of different species' population structures are therefore not independent: instead, they are intrinsically correlated.

In terms of future directions, there are several ways in which sensitivity analyses of interacting populations still have to be developed. One open avenue is the sensitivity analysis of transient community dynamics where, instead of concentrating on the stationary state, the focus is on the parameter dependence of short-term dynamics (Caswell 2007 has followed this approach but only for single populations). But even in the realm of the analysis of stationary states, there is work to do. Although fixed point (Meszéna et al. 2006) and limit cycle (Chapters 3 and 4) analysis of unstructured models is available, and here, by extending the results of Szilágyi and Meszéna (2009a), we have obtained a general formula for fixed point analysis of structured community models, sensitivity calculations for communities in general aperiodic environments is still lacking, both for the unstructured and the structured case. Developing the formalism to deal with these extra complexities will be the next step in the theory of community-wide sensitivities.

Chapter 6

Applications and general conclusions

6.1 Introduction

One of the most common ways of thinking about complex ecological communities is in terms of their stability: given some stationary behavior of the system (stable equilibrium, periodic oscillations, etc.), will it tend to return to that behavior after a disturbance event or not? There is, however, another important aspect to the same problem. To illustrate this, imagine a stable community. In such a community the system will return to its stable state after disturbance (at least from those that are not too large). Can we draw the conclusion that this community is safe from extinctions? Not at all, because we also need to consider how the stable state depends on external environmental influences. Will it still remain stable if the average annual temperature rises by 1 °C? Or will it change in a way that leads to the extinction of some of the species? Since there is no way of knowing the answer to these questions *a priori*, we are simply not thinking about dynamics in a complete enough way without considering the dependence of the stationary states to changes in external conditions.

We are interested in the response of stationary densities to parameter changes. The formal treatment of this type of question belongs to the realm of sensitivity analysis. This methodology has enjoyed tremendous popularity in the context of population ecology (Caswell 2001, chapter 9), and has lead to deep insights both in a theoretical context, especially in terms of life history theory (Hamilton 1966, Templeton 1980, Caswell 1982, 1984, Gleeson 1984, Silvertown et al. 1992, Franco and Silvertown 1996, Caswell 2011), and in a more applied context, for population viability analyses, conservation, and management (Crouse et al. 1987, Silvertown et al. 1993, Noon and McKelvey 1996, Forsman et al. 1996, Seamans et al. 1999, Fujiwara and Caswell 2001, Hunter et al. 2010). Recently, a systematic extension of sensitivity analysis to communities of interacting species has been taking place (Meszéna et al. 2006, Szilágyi and Meszéna 2009a,b, 2010, Barabás et al. 2012a,b, 2013, Barabás and Ostling 2013, Barabás et al. under review and the previous Chapters of this dissertation; but see Levins 1974, 1975 for some early applications). Development of the methodology is work in progress, with more and more complexity being incorporated into the community-wide sensitivity formulas.

In this chapter we suggested that this merging of community ecology with sensitivity analysis opens up a new and vital perspective, with a lot to be gained from both a theoretical and a practical point of view. For should the response of stationary densities be very abrupt – i.e., oversensitive to changing parameters – the likelihood increases that even a slight parameter alteration will lead to the extinction of at least some of the species. By enabling us to explicitly determine what parameter perturbations will lead to such extinctions, community-wide sensitivity analysis allows community ecologists to consider not only which biological scenarios lead to coexistence that is stable against small perturbations of population densities (as is typically done), but also which lead to coexistence that is robust against varying environmental conditions.

In fact, there are at least three different types of questions and problems that community-wide sensitivity analysis can address and illuminate. These range from the applied to the theoretical, and we shall address them in that order throughout the chapter.

First, we demonstrate through a model of annual plant competition (Levine and Rees 2004) how community-wide sensitivity analysis can be used to assess extinction risk in response to changing environments and to make informed management decisions. Our purpose with this example is twofold. First, it shows how community-wide sensitivity analysis can be applied in the spirit of more traditional sensitivity analyses from population ecology. Second, as diversity in our system of study is maintained purely by fluctuation-dependent mechanisms, it demonstrates how community-wide sensitivity analysis is capable of dealing with this kind of complexity, treating it in a unified manner with other, more conventional diversity-maintaining mechanisms.

Second, we employ community-wide sensitivity analysis as an addition to the fundamental toolkit of model analyses typically carried out to understand species interactions. We present two model studies, the tolerance-fecundity tradeoff (Muller-Landau 2010, D'Andrea et al. 2013) and one of interspecific facilitation (Gross 2008), in which the method provides limits to diversity and species similarity not obtainable via standard methods such as stability analysis. In addition, since the tolerance-fecundity tradeoff model is spatially structured, we demonstrate how this additional complexity is incorporated into and handled by community-wide sensitivity analysis.

Finally, we synthesize our results and interpret them within a general framework. Irrespective of the particular mechanisms maintaining diversity or model details, a simple geometric picture emerges for quantifying community-wide sensitivities which is able to incorporate various complexities, such as environmental fluctuations or population structure, in a unified manner. This geometric picture can be used to draw a general conclusion about the coexistence of similar species: beyond some level of similarity, coexistence gets more unlikely as the species get more similar. Moreover, this likelihood of coexistence can be precisely quantified using the geometric picture emerging from the community-wide sensitivity framework. Coexistence of similar species is not impossible, just unlikely to happen, requiring the precise fine-tuning of parameters. Current theoretical frameworks aimed at classifying coexistence are based mainly on the dynamical stability of coexistence (Gause 1934, Leibold 1995, Chesson 2000b, Chase and Leibold 2003). We suggest that shifting the focus from the stability of coexistence to its sensitivity makes the classification much more streamlined and is in fact a better way of looking at the same problem.

The chapter is structured as follows. After reviewing some necessary background for community-wide sensitivities in section 6.2, we go on to apply this theory to our model examples: the model of annual plant competition (section 6.3), the tolerance-fecundity tradeoff (section 6.4), and the Gross model of interspecific facilitation (section 6.5). We close by a synthesis and summary in section 6.6.

6.2 Community-wide sensitivity analysis: a field guide

Imagine a community of interacting (unstructured) populations. Their population dynamics can be written in the form of the general equation

$$\frac{1}{N_i}\frac{\mathrm{d}N_i(t)}{\mathrm{d}t} = r_i\left(\mathcal{R}_\mu\left(N_j(t), t\right), \mathbb{E}, t\right) \qquad (i = 1\dots S), \tag{6.1}$$

where $N_i(t)$ is the abundance of species i at time t, S is the number of species in the community, and r_i is species i's per capita growth rate – the “species fitness” of Chesson (2000b) – which is a function of:

- t, time. Any change in the external environment (the vagaries of the weather) applied to the system will result in an explicit time dependence.
- $\mathbb{E}$, the collection of all density-independent model parameters. They are, by definition, never time-dependent. For instance, if the community is subjected to a regular sequence of "good" and "bad" seasons described by the function $a\cos(\omega t)$, then the vector $\mathbb{E}$ will include the amplitude a and the frequency ω as its components, but the time-dependence will be treated as an explicit dependence of r_i on t.
- $\mathcal{R}_\mu$, the collection of all variables that mediate 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 refer to this vector as the collection of *regulating factors* (Levin 1970, Case 2000, p. 146, Krebs 2001, p. 288, Meszéna et al. 2006): $\mathcal{R}_\mu$ therefore measures the quantity/concentration of the μth regulating factor. Regulating factors may include resources, predators, pathogens, refuge availability, or any other thing that is involved in the feedback between population densities and growth rates. The important point is that *all* density-dependent effects have to be mediated by the $\mathcal{R}_\mu$. Also, since the regulating factors may be time-dependent, the same regulating factor is considered to be a different factor at different moments in time.

The model thus specified, we look at the long-term stationary behavior it produces. In the stationary state the long-term average per capita growth rates $\bar{r}_i$ of the species are all zero. For sake of simplicity, let us look at the case when the stationary state is a fixed point. Then the "average" growth rates are simply the growth rates evaluated at the equilibrium point. The equilibrium densities will be functions of the model parameters $\mathbb{E}$, therefore we have, at equilibrium,

$$\bar{r}_i\left(\mathcal{R}_\mu\left(N_j(\mathbb{E})\right),\mathbb{E}\right) = 0. \tag{6.2}$$

If this system of algebraic equations could be solved for the $N_j(\mathbb{E})$, then we would have a complete knowledge of the parameter combinations allowing for a community where all densities are positive, and thus would be able to address questions such as whether the response of the community to climate change would lead to species extinctions on the long run or not, or what the consequences of some management plan would be. Unfortunately, this system, as it is, cannot be generically solved to yield $N_j(\mathbb{E})$ except in the simplest of scenarios. This is not some overly pessimistic statement, but a simple acknowledgement of the mathematical fact that a generic system of nonlinear algebraic equations has no closed-form solution. The overambitious plan of finding the functions $N_j(\mathbb{E})$ thus has to be abandoned.

The next best thing one can do is to determine the local response of a given stationary state to perturbations of the model parameters. In other words, we are looking for the sensitivities $\partial N_j(\mathbb{E})/\partial\mathbb{E}$. Fortuitously, it turns out that there actually is a general formula one can derive for these sensitivities – see Eq. (B1).

Even more fortuitously, the state of the art does not stop at fixed point dynamics of communities of unstructured populations. The methodology can be extended to incorporate much more complexity (Box 1). These include the sensitivity analysis of limit cycles (Chapters 3 and 4), communities of structured populations at fixed points (Szilágyi and Meszéna 2009a and Chapter 5), and – partially – communities in stationary aperiodic environments (Szilágyi and Meszéna 2010). The ultimate goal would be the ability to analyze the sensitivity of the most general conceivable scenario: communities composed of structured populations experiencing aperiodic stationary fluctuations. Such a formula is, as yet, unavailable. Still, what we have so far does allow us to incorporate much real-life complexity in our sensitivity analyses, as the examples in the subsequent sections aim to demonstrate.

Box 1: Community-wide sensitivity formulas

Below we give a catalogue list of the sensitivity formulas for various dynamical scenarios. In each case we state the applicability of the given formula, reference where it is derived, and indicate the impact and sensitivity vectors $\mathcal{I}_{j,\mu}$ and $\mathcal{S}_{i,\mu}$.

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

$$\frac{\mathrm{d}N_i}{\mathrm{d}\mathbb{E}} = -\sum_j \left(\sum_\mu \underbrace{\frac{\partial r_i}{\partial \mathcal{R}_\mu}}_{\mathcal{S}_{i,\mu}} \underbrace{\frac{\partial \mathcal{R}_\mu}{\partial N_j}}_{\mathcal{I}_{j,\mu}} \right)^{-1} \frac{\partial r_j}{\partial \mathbb{E}} \tag{B1}$$

- Limit cycle of fixed period length T in continuous time, for communities of unstructured populations (Chapter 3):

$$\frac{\mathrm{d}N_i(0)}{\mathrm{d}\mathbb{E}} = -\,N_i(0)\sum_{j=1}^{S}\left(\mathcal{T}\mathrm{Exp}\left(\int_0^T \sum_{\mu} \underbrace{\frac{\partial r_i(\tau)}{\partial\mathcal{R}_\mu(\tau)}}_{\mathcal{S}_{i,\mu}(\tau)} \underbrace{\frac{\partial\mathcal{R}_\mu(\tau)}{\partial N_j(\tau)}N_j(\tau)}_{\mathcal{I}_{i,\mu}(\tau)}\,\mathrm{d}\tau\right) - \delta_{ij}\right)^{-1} \times \int_0^T \frac{\partial r_j(t)}{\partial\mathbb{E}}\,\mathrm{d}t \tag{B2}$$

- Limit cycle of fixed period length T in discrete time, for communities of unstructured populations (Chapter 4):

$$\frac{\mathrm{d}N_i(0)}{\mathrm{d}\mathbb{E}} = -\,N_i(0)\sum_{j=1}^{S}\left(\prod_{\tau=T-1}^{0}\left(\delta_{ij} + \sum_{\mu} \underbrace{\frac{\partial r_i(\tau)}{\partial\mathcal{R}_\mu(\tau)}}_{\mathcal{S}_{i,\mu}(\tau)} \underbrace{\frac{\partial\mathcal{R}_\mu(\tau)}{\partial N_j(\tau)}N_j(\tau)}_{\mathcal{I}_{i,\mu}(\tau)}\right) - \delta_{ij}\right)^{-1} \times \sum_{t=0}^{T-1} \frac{\partial r_j(t)}{\partial\mathbb{E}} \tag{B3}$$

- Fixed point dynamics in either continuous or discrete time, for communities of structured populations (Szilágyi and Meszéna 2009a, Chapter 5):

$$\mathbf{q}_i\frac{\mathrm{d}\mathbf{N}_i}{\mathrm{d}\mathbb{E}} = -\sum_{j=1}^{S}\left(\sum_{\mu,\nu} \underbrace{\left(\mathbf{v}_i\frac{\partial\mathbf{A}_i}{\partial\mathcal{R}_\mu}\mathbf{w}_i\right)}_{\mathcal{S}_{i,\mu}} \left(\delta_{\mu\nu} - \frac{\partial\mathcal{G}_\mu}{\partial\mathcal{R}_\nu}\right)^{-1} \underbrace{\frac{\partial\mathcal{R}_\nu}{\partial\mathbf{N}_j}\mathbf{p}_j}_{\mathcal{I}_{i,\mu}}\right)^{-1} \times \left(\mathbf{v}_j\frac{\partial\mathbf{A}_j}{\partial\mathbb{E}}\mathbf{w}_j + \sum_{\sigma,\varrho}\left(\mathbf{v}_j\frac{\partial\mathbf{A}_j}{\partial\mathcal{R}_\sigma}\mathbf{w}_j\right)\left(\delta_{\sigma\varrho} - \frac{\partial\mathcal{G}_\sigma}{\partial\mathcal{R}_\varrho}\right)^{-1}\frac{\partial\mathcal{G}_\varrho}{\partial\mathbb{E}}\right) \tag{B4}$$

where

$$\mathcal{G}_\mu(\mathcal{R}_\nu,\mathbb{E}) = \sum_{j=1}^{S}\left(\frac{N_j}{\mathbf{q}_j\mathbf{w}_j}\frac{\partial\mathcal{R}_\mu}{\partial\mathbf{N}_j}\sum_{k=2}^{s_i}\frac{1}{\lambda_i - \lambda_i^k}\left(\mathbf{w}_i^k - \frac{\mathbf{q}_i\mathbf{w}_i^k}{\mathbf{q}_i\mathbf{w}_i}\mathbf{w}_i\right)\otimes\mathbf{v}_i^k\right)\mathbf{A}_j(\mathcal{R}_\nu,\mathbb{E})\mathbf{w}_j \tag{B5}$$

As seen from the summary in Box 1, the formulas do tend to get more complicated indeed as additional complexity is incorporated into the sensitivity analysis. However, all these formulas contain important generalities beneath their superficially different appearances. Regardless of their domain of applicability, all sensitivity formulas possess the following general structure:

$$\frac{\mathrm{d}N_i}{\mathrm{d}\mathbb{E}} = \sum_{j=1}^{S} \left(A^{-1}\right)_{ij} z_j, \tag{6.3}$$

where z_j is a vector analogous to $\partial \bar{r}/\partial \mathbb{E}$ (but not necessarily the same, e.g. in Eq. B4), and A_{ij} is analogous to a Jacobian matrix. The inverse of any matrix is always proportional to the reciprocal of its determinant (Cramer's rule), therefore the sensitivity itself will be proportional to $1/\det(A_{ij})$. Although this is just a proportionality that can and will be distorted by the other terms on the right hand side, there is one case when a definite statement about the sensitivity can be made purely on the basis of $\det(A_{ij})$: sensitivity will approach infinity as the determinant approaches zero. Formally, when $\det(A_{ij}) = 0$, the matrix can no longer be inverted: this signals the onset of a critical transition (bifurcation) in the system, such as an extinction event. Right before this critical point is reached, the system will become oversensitive to parameter perturbations: when $\det(A_{ij}) \approx 0$, its inverse is a very large number multiplying the right hand side of Eq. (6.3), causing erratic swings in the equilibrium densities for even slight changes in the parameters.

The determinant of A_{ij} can be thought of as a measure of the system's *robustness*. Robustness and sensitivity are thus roughly inversely related: high robustness means insensitivity to parameter changes, while low robustness implies high sensitivity. In accord with this terminology, "community-wide sensitivity analysis" is also referred to as "robustness analysis". Here we will use the two terms interchangeably.

As it turns out, $\det(A_{ij})$ can be connected to quantities that are both generally defined in any ecological scenario and are biologically meaningful. To understand these quantities, recall Eq. (6.2): the average growth rates depend on the regulating factors, which in turn depend on the (stationary) densities, thus completing the feedback loop. The two components of this feedback are:

- How do the regulating factors affect the growth rate of species i? Let us denote this quantity by $\mathcal{S}_{i,\mu}$ and call it the *sensitivity* of the ith species to the μth regulating factor[1].
- How are the regulating factors being affected by the density of species j? Let

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[1] There is an unfortunate clash of nomenclature here: "sensitivity" in this sense is not to be confused with the sensitivity of the dynamics to parameter perturbations, the main theme of this chapter. To avoid confusion, we will consistently refer to the quantity $\mathcal{S}_{i,\mu}$ as the "sensitivity vector" and to the quantity $\mathrm{d}N_i/\mathrm{d}\mathbb{E}$ as just the "sensitivity".

us denote this quantity by $\mathcal{I}_{j,\mu}$ and call it the *impact* of the jth species on the μth regulating factor.

Though the basic idea behind these vectors is always the same, the precise definitions do depend on the particular dynamical scenario being considered – see Box 1 for these definitions.

Let us now consider not these vectors by themselves, but the volumes they span: $\mathcal{V}_{\mathcal{S}}$ and $\mathcal{V}_{\mathcal{I}}$. By this we mean the following. Take the impact vectors of all the S species in the community. These vectors each have as many dimensions (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 of the impact vectors. See Figure 6.1 for a graphical depiction of what is meant by $\mathcal{V}_{\mathcal{S}}$ and $\mathcal{V}_{\mathcal{I}}$.

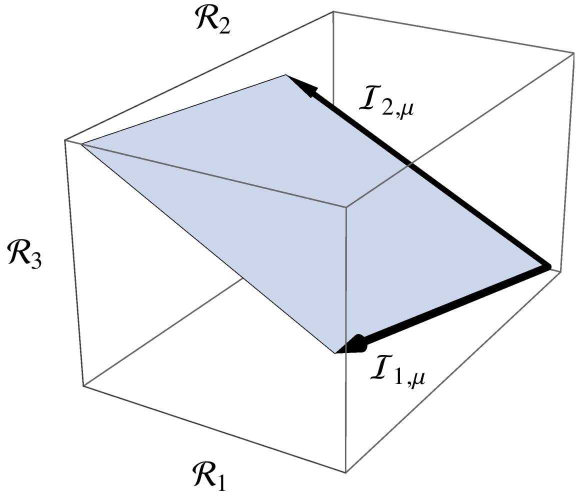

Figure 6.1: The volume spanned by the impact vectors of two interacting species. Let us assume that there are three regulating factors in the system (say, one resource, one pathogen, and a refuge). We draw the two impact vectors $\mathcal{I}_{1,\mu}$ and $\mathcal{I}_{2,\mu}$ (thick arrows) in the space spanned by the regulating factors. Since there are two species, we are interested in the two-dimensional volume, or area, that these vectors span (shaded region). The volume spanned by the sensitivity vectors $\mathcal{S}_{1,\mu}$ and $\mathcal{S}_{2,\mu}$ would be evaluated analogously.

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

$$\left|\det(A_{ij})\right| \leq \mathcal{V}_{\mathcal{S}}\mathcal{V}_{\mathcal{I}} \tag{6.4}$$

(Meszéna et al. 2006). In words, the product of the volumes spanned by the sensitivity and the impact vectors yields an upper bound to the magnitude of A_{ij}'s determinant. This implies that robustness is determined by $\mathcal{V}_S\mathcal{V}_I$: if these volumes are small, robustness will also be small. What could cause the impact and sensitivity vectors to span small volumes? There are two basic options. First, the volumes will be small if they are spanned by vectors of small length. Short vectors result from weak dependence of growth rates on regulating factors (sensitivity vectors), and weak dependence of the regulating factors on population densities (impact vectors). In short, *weak regulation* of the community will result in low community robustness. Second, the volumes will be small if the vectors spanning it are nearly collinear or, in general, linearly dependent.

This second possibility will be realized whenever two species are overly similar in the way they are being regulated. Robustness will then be low, implying that even small perturbations of the parameters will result in large, erratic swings of the population densities, increasing the likelihood of extinctions or other critical transition phenomena. Since both the impact and the sensitivity vectors are related to the ecologies of the species they describe, robustness will be low for species with overly similar ecologies. This is the property of community-wide sensitivity analysis that connects it to coexistence theory and the niche, to be discussed later.

One immediate corollary of the above is that robust coexistence of S species on less than S regulating factors is impossible. Consider for instance three species and two regulating factors. Then the three impact and sensitivity vectors are confined to a two-dimensional plane – and the three-dimensional volume of an area is always zero. Within the context of resource competition, this statement has been known for a long time: at equilibrium, no more species can coexist than the number of resources. For non-resource based competition, such as predator-mediated coexistence (apparent competition; Holt 1977), the statement has also been known for a long time (Levin 1970), though maybe it is not as well appreciated as it should be. Apart from our framework reproducing these classic results from the perspective of sensitivity analysis, there is another benefit: it considers the potential time-dependence of the interactions, and is therefore true even if the environment is fluctuating. As shown in Chapters 3 and 4, a single regulating factor at different moments in time actually behaves as that many independent regulating factors. Keeping track of the factors at various moments in time as separate factors in our bookkeeping generalizes the statement to fluctuating environments. See the example in Section 6.3, where the time-dependence of the regulating factor is of vital importance.

In summary, community-wide sensitivity formulas yield the responses of stationary densities to small perturbations of model parameters. Depending on the nature of the stationary state (fixed point, limit cycle, bounded aperiodic orbit,. . .), different formulas are to be used, as summarized in Box 1. No matter how complicated these formulas are however, it is always possible to introduce two quantities, the volumes spanned by the impact and sensitivity vectors, which are related to community robustness via Eq. (6.4). This can be used to infer when robustness is lost: if any of the volumes is zero or very close to zero, $\det(A_{ij})$ will be even closer to zero and so the system becomes oversensitive to external influences and therefore cannot remain stable for long.

6.3 An application of community-wide sensitivities to conservation and management

Our first example application of community-wide sensitivity analysis is in the spirit of traditional sensitivity analyses in population ecology: given a system, a model for that system, and data to parametrize the model, we attempt to forecast what would happen if parameters would change. Such forecasts, coupled with a knowledge of the actual range of parameter fluctuations at the place where the species coexist, can be used to assess extinction risk: are the fluctuations large enough to knock species densities to dangerously low values? Here we perform community-wide sensitivity analysis on a model that was proposed by Levine and Rees (2004) to describe competition between forbs and grass on a California grassland. The analysis may, in principle, be used to make informed management decisions to help prevent species extinctions.

The model of Levine and Rees (2004) is an annual plant model which can be written, after introducing the time-dependent regulating factor

$$\mathcal{R}(t) = \frac{g_1(t)N_1(t)}{\alpha} + g_2(t)N_2(t), \tag{6.5}$$

as

$$N_i(t+1) = \left((1 - g_i(t))(1 - d_i) + \frac{\lambda_i(t) g_i(t)}{1 + \alpha_i \mathcal{R}(t)} \right) N_i(t), \tag{6.6}$$

where i may be 1 (forb) or 2 (grass), and α_i is equal to α for $i = 1$ and to 1 for $i = 2$. See the Supplementary for more information.

Here we have two species and a single regulating factor. Considering the argument of the previous section about coexistence of S species on less than S regulating factors, does this mean that coexistence is impossible in this model? Indeed, it is true that no coexistence can happen *at a fixed point equilibrium*. However, as discussed in the previous section, if the system experiences periodic environmental variability, then the regulating factor at various moments within the cycle behaves like that many independent regulating factors. For instance, if the environment periodically fluctuates between good years and bad years (a discrete-time two-cycle), then the regulating factor in good years and the same regulating factor in bad years act as two *distinct* regulating factors. In this way, we will have two regulating factors for two species: coexistence therefore becomes possible in principle.

It is also worthwhile mentioning that, using the framework and terminology of Peter Chesson (1994, 2000b), coexistence in this model is maintained by pure storage effect. Relative nonlinearity is not operating because, by Eq. (6.5), $\mathcal{R}(t)$ is a linear function of the population densities, and fluctuation-independent mechanisms are also not operating because there is a single regulating factor for two species. Therefore the only stabilizing mechanism here is the temporal storage effect. The difference between the two approaches is that Chesson is interested in the invader's long-term growth rate to see whether coexistence is possible via mutual invasibility, while our approach quantifies coexistence via the range of parameters that will allow for it.

To obtain coexistence, we will make the above fluctuating assumption about the environment. Specifically, both the fraction of germinating seeds $g_i(t)$ and the annual fecundities $\lambda_i(t)$ are assumed to fluctuate periodically between "good" and "bad" years. We assume we have a bad year whenever t is even and a good year whenever t is odd. The parameter estimates of Levine and Rees (2004), along with a short description of each parameter, are found in Table 6.1.

At this point, a word of warning is in order. Though Levine and Rees (2004) did their best to estimate all parameter values, some of them were less easy to get at than others. For some, there was insufficient data. Also, our assumption about the simple periodicity of the environment above is clearly a simplification of what is going on in nature. Therefore, the particular numerical sensitivity values we calculate for each parameter are to be taken with a grain of salt: they can only be as accurate as the input. However, our main focus here is not so much the accurate reproduction of actual sensitivity values as to demonstrate how such an analysis has to be performed. With better data, the predictions would also become more reliable. Here we aim to explain how to use the methodology in principle, as opposed to

$\mathbb{E}$	Description	Value
α	Reciprocal interspecific competition coefficient	2
d_1	Forb death rate in the seed bank	0.1
d_2	Grass death rate in the seed bank	0.7
$\lambda_1(0)$	No. of forb seeds/individual in a bad year	5
$\lambda_1(1)$	No. of forb seeds/individual in a good year	30
$\lambda_2(0)$	No. of grass seeds/individual in a bad year	5
$\lambda_2(1)$	No. of grass seeds/individual in a good year	30
$g_1(0)$	Fraction of forb seeds germinating in a bad year	0.1
$g_1(1)$	Fraction of forb seeds germinating in a good year	0.7
$g_2(0)$	Fraction of grass seeds germinating in a bad year	0.9
$g_2(1)$	Fraction of grass seeds germinating in a good year	0.9

Table 6.1: Numerical value and description of each parameter in the Levine–Rees model. Every odd year (e.g., year $t = 1$) is a good year, and every even year (e.g., year $t = 0$) is a bad year, as shown by the decreased fecundities and germination probabilities. The symbol $\mathbb{E}$ stands for any one model parameter.

getting accurate answers. The exact same procedure will then yield better estimates once more data is accumulated, and the model is fitted better.

With that, we can perform the sensitivity calculations. As this model is a discrete-time model with a limit cycle, we simply take the appropriate sensitivity formula off the shelf – in our case, Eq. (B3) – and use the estimated parameter values to calculate the sensitivities of each species to each model parameter. The details of the calculation may be found in the Supplementary.

The results are seen on Figure 6.2. It is important to note that all the usual considerations apply when interpreting these sensitivity values. The sensitivity values by themselves are not enough: one also needs to know how much variation is to be expected in the parameters. For instance, the sensitivities to the λ_is are low, but their numerical values (and the presumable variation in them) are an order of magnitude larger than for the other parameters, therefore the effect of altering these parameters might have more serious effects than one might think. Conversely, we see an overwhelming sensitivity of the forb to its death rate in the seed bank. However, if this is a parameter that is not expected to fluctuate much, then the high sensitivity might not actually matter. Needless to say, there could be a plethora of different reasons why the death rates might be perturbed, from increased seed predation to the deterioration of soil quality. Therefore, one possible morale of our analysis is that the forb seed mortality is an important parameter that needs to be measured accurately and has to be carefully controlled, lest the system undergo an

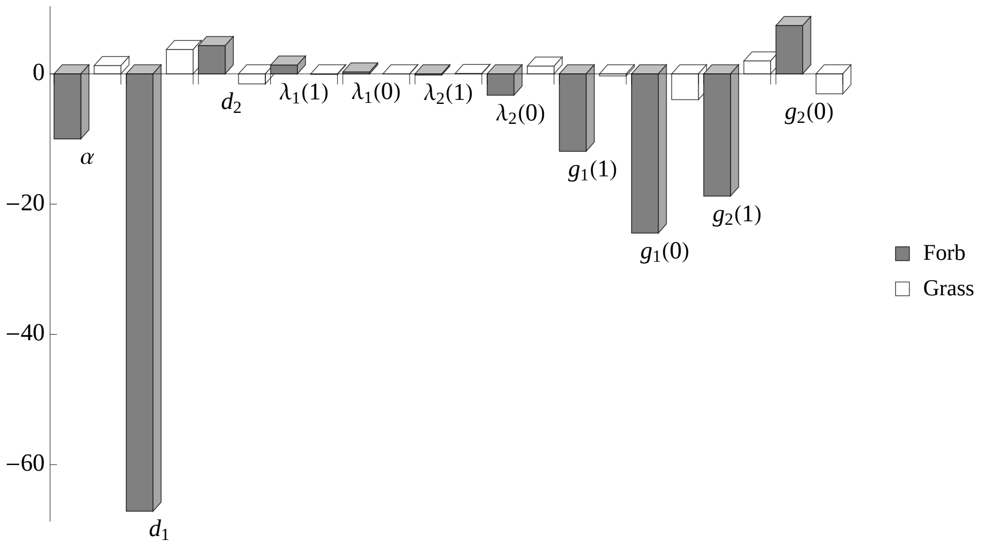

Figure 6.2: Sensitivities of the Levine-Rees model of forb-grass competition to each model parameter. The gray bars represent the sensitivity values of the forb; the white bars represent the sensitivity values of the grass. Note the extremely high sensitivity of the forb species to its death rate in the seed bank.

undesired critical transition, such as the extinction of the forb.

6.4 The tolerance-fecundity tradeoff model

We now turn our attention to a model where the interacting species of the community have population structure. This model, the tolefance-fecundity tradeoff, has originally been proposed by Muller-Landau (2010). Since then, D'Andrea et al. (2013) have generalized the model in a way that makes it much more general but less amenable to analytical treatment. In its generalized form the model is complicated enough that even calculating the equilibrium population structure of the species is an impossible task. One may therefore justifiably ask what kind of analysis is even possible on such a model (short of computer simulations). This is where the power of community-wide sensitivity analysis as an analytical tool manifests itself. Here we show that in this model it is possible to derive effective coexistence criteria and limits to species similarity using our framework. Community-wide sensitivity analysis may therefore be used as an addition to the theorist's toolbox which can make model analysis easier.

We now briefly outline the basic idea of the model; see the Supplementary for the full derivation. In the model individuals are sessile, occupying a single site.

Each site may have a different level of local environmental stress, ranging from s_1 (lowest) to s_M (highest). Individuals produce seeds that may randomly fall on any of the sites. If the site is already occupied, the seed dies; if it is not, it has a finite chance of survival depending on 1) the local stress level, and 2) species identity: some species are more tolerant of stress than others. Between the seeds that do survive on a given site, a lottery draw decides which one is going to germinate.

The tolerance-fecundity tradeoff itself is built into this model via the assumption that the more tolerant a species is to stressful conditions, the fewer seeds it produces. This might be thought of in terms of seed size: some plants produce large seeds that are more tolerant to stressful conditions but are in turn energetically expensive to produce, keeping their numbers low, and some other plants produce tons of cheap small seeds that are prone to dying under harsh environmental conditions. The stress tolerance of species i's seeds is given by the function $T_i(s)$. This function measures the probability that an individual seed of species i survives if it falls on a site with stress level s. We assume $T_i(s)$ to be a sigmoid function: each species is really good at tolerating a given range of stress levels (the more it tolerates, the lower its fecundity, in accord with the tradeoff), after which the tolerance quickly falls to very low values. Figure 6.3 shows a pictorial representation of these functions.

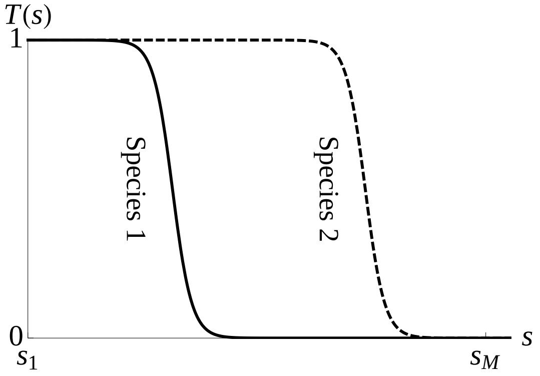

Figure 6.3: Tolerance functions of two species (solid and dashed curves). The abscissa represents stress, ranging from s_1 (minimum level) to s_M (maximum stress level). The ordinate is the probability that a seed survives the given stress level. The tolerance functions are sigmoid curves with a relatively sudden (but still smooth) transition from the tolerant to the intolerant regime. The tolerance-fecundity tradeoff is implemented by enforcing $f_1 > f_2$, i.e., the more fecund species is less tolerant by assumption.

As derived in the Supplementary, the governing equation for this system reads

$$\frac{\mathrm{d}N_{i,a}}{\mathrm{d}t} = \sum_{b=1}^{M} \Big(f_i T_i(s_a) \mathcal{R}(s_a) - m_i \delta_{ab} \Big) N_{i,b}, \tag{6.7}$$

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, respectively, δ_{ab} is the identity matrix (equal to 1 if $a = b$ and to 0 otherwise), and the regulating factors are given by the algebraic equation

$$\mathcal{R}(s_a) = \frac{c(s_a) - \sum_i N_{i,a}}{\sum_k f_k N_k T_k(s_a)}, \tag{6.8}$$

which is simply the density-dependent factor of the reproduction rate. 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. Notice that we now have separate regulating factors for all stress levels. That is, we have as many factors as there are different stress levels. If the gradation of various stress levels is infinitely fine-grained (i.e., we have a smooth stress gradient), then we have infinitely many regulating factors, in perfect analogy with the case of a resource continuum (e.g., MacArthur and Levins 1967).

To perform sensitivity analysis on this model, we first notice that it involves population structure, therefore the equation we need to take off the shelf for the analysis is Eq. (B4). In the Supplementary, both the impact and the sensitivity vectors are calculated. In particular, the sensitivity vectors have the especially simple form

$$\mathcal{S}_{i,\sigma} = f_i T_i(s_\sigma). \tag{6.9}$$

This expression has a very important property: *it is independent of the equilibrium population distributions $N_{i,a}$*. Therefore, it can be evaluated without actually having to solve the model. We have already seen in Eq. (6.4) that near-zero values of the volume spanned by these vectors is sufficient for the system to lose its robustness against parameter perturbations. The question is, under what conditions will the volume spanned by the vectors $\mathcal{S}_{i,\sigma}$ be very small? Let us consider just two competing species for a start. We can then plot the volume spanned by the vectors $\mathcal{S}_{1,\sigma}$ and $\mathcal{S}_{2,\sigma}$ as a function of the species' fecundities f_1 and f_2 (Figure 6.4; the methodology for calculating the volume spanned by two functions is described in the Supplementary).

It is clear from the Figure that coexistence will only be a reasonable option when one of the species has a high fecundity, while the other has an intermediate one:

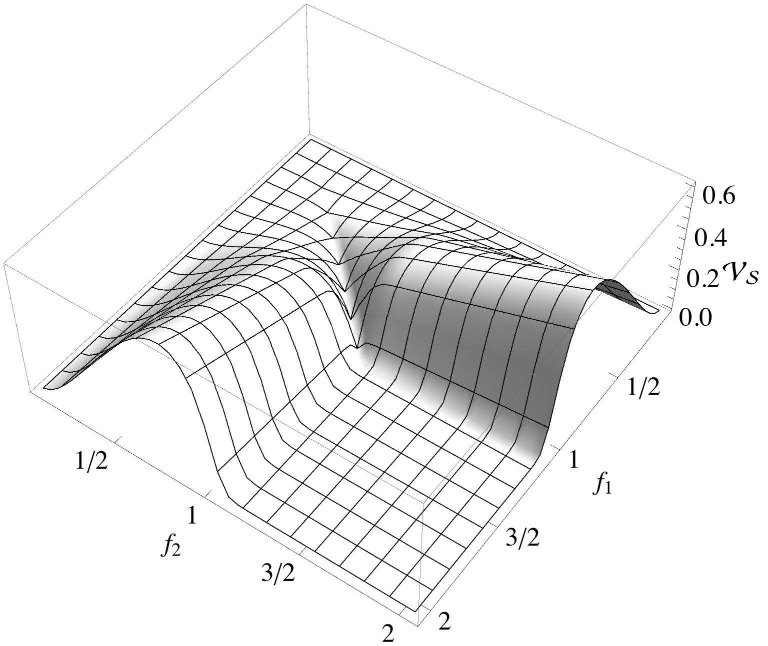

Figure 6.4: The volume $\mathcal{V}_\mathcal{S}$ spanned by the sensitivity vectors of two species as a function of their fecundities in the tolerance-fecundity tradeoff model. This volume only gets to be appreciably large around the two symmetric ridges, where one species has a high fecundity and the other an intermediate one. Both species possessing high fecundities leads to small volumes, as does an overly low fecundity of either species, irrespective of the other. We know from Eq. (6.4) that 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.

that is the only portion of the plot where the volume $\mathcal{V}_\mathcal{S}$ is appreciably different from zero. Also, observe that the volume is equal to zero along the line of identical fecundities $f_1 = f_2$. This is because the sensitivity vectors of identical species will be the same, and so they point in the same direction – the volume they span is therefore zero. Also, since these vectors are continuous functions of model parameters, near-equality of the fecundities will result in a near-zero volume, as can be seen on the Figure.

Two comments about our results are in order. First, one may be worried that we used $\mathcal{V}_\mathcal{S}$ as a proxy for robustness, when in fact it is the product $\mathcal{V}_\mathcal{S}\mathcal{V}_\mathcal{I}$ which is relevant. What if a small $\mathcal{V}_\mathcal{S}$ is compensated by a large $\mathcal{V}_\mathcal{I}$ and so our conclusions need revision? This, however, turns out not to be the case. In fact, we show in the Supplementary that the impact vectors, though they have a complicated form (and, unlike the sensitivity vectors, are dependent on the equilibrium stage distributions), they are actually proportional to the sensitivity vectors. Therefore, whenever $\mathcal{V}_\mathcal{S}$ is small, $\mathcal{V}_I$ will in turn be small as well. Considering the impact vectors does not weaken our conclusion; instead, it reinforces it.

In fact, though exceptions undoubtedly exist, it is probably a fairly general rule of thumb that species' sensitivity vectors and impact vectors will be more or less similar. Usually a species will impact those resources that it requires the most, and is therefore sensitive towards. Or, if predators are regulating, it will have an impact on the predators that are trying to hunt it down, making it sensitive to them. Therefore, if the sensitivity vector of a species is large in the direction of a particular regulating factor, its impact vector will probably also be large in that direction, and vice versa.

Second, though we have carried out the analysis just for a pair of species, the generalization to arbitrarily many interacting species is straightforward. We simply take all their sensitivity vectors $\mathcal{S}_{i,\sigma} = f_i T_i(s_\sigma)$ and consider the volumes they span as a function of all the fecundities. In principle, there is nothing problematic about this, though trying to depict the results as in Figure 6.4 might prove challenging when the number of dimensions is higher than three – i.e., when the number of species is higher than two.

6.5 The Gross model of interspecific facilitation

As our final example application, we analyze the sensitivity in a model of interspecific facilitation that was proposed by Kevin Gross (2008). In this section we demonstrate how big of a difference it makes to shift the emphasis from the stability of coexistence to its robustness against parameter perturbations: if one only considers stability, the expected diversity is very different than if one properly takes sensitivity analysis into account.

In the Gross model, there is a single resource and several consumer species. These species have facilitative effects on one another: an increase in the abundance of one species actually reduces the death rate of another. This facilitation actually allows for the stable coexistence of several consumer species on the same resource. How is this possible, when a single resource means a single regulating factor? The answer has already been provided by Gross (2008). Namely, due to the facilitative effects, certain combinations of species will also become regulating factors. Therefore, introducing another species into this system not only increases the number of consumers, but potentially also the number of regulating factors. In this way, the number of regulating factors can be larger than the original one, and so multispecies coexistence on a single resource at a fixed point equilibrium becomes possible.

The fact that the species themselves may act as regulating factors means this model offers something new relative to the usual picture of species occupying preexisting niches. If the introduction of a new species is potentially also the introduction of a new niche, then it is not clear what mechanism would be able to put a constraint on diversity. As we shall see, sensitivity analysis actually provides that limit.

Though this particular coexistence mechanism has not yet been studied in the field, it is difficult to overemphasize the potential importance of Gross's (2008) discovery. In his model, despite the facilitative effects, the *net* interaction is actually negative between all consumer species. It is an interesting avenue for future field studies of species-rich communities where the net pairwise interaction types are known to be competitive (such as tropical forests) whether this proposed mechanism is actually at work – it might considerably overhaul our expectations of how much diversity we should be seeing in these systems.

In the version of the model we will analyze here, there is one further assumption made: facilitation is *hierarchical*. This means that 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, until the last species, which is facilitated by all the other consumers. This assumption probably does not play out anywhere in nature and should be considered a toy model of facilitation. However, it is a very enlightening one, because using this assumption, Kevin Gross (2008) was able to prove a very important theorem: in this model, it is possible for an *arbitrary* number of consumers to stably coexist on a single resource. The hierarchical nature of the facilitation makes it clear that species k is regulated by the resource and by the combination of species $1 \ldots k-1$. Therefore, introduction of a new species automatically results in the introduction of a new regulating factor as well.

The equations for this model read

$$\frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} = f_i(R) - m_i^0 + d_i\left(1 - \exp\left(-\theta \sum_{k<i} N_k\right)\right) \tag{6.10}$$

for the consumer species ($i = 1 \ldots S$), and

$$\frac{\mathrm{d}R}{\mathrm{d}t} = g(R) - \sum_{i=1}^{S} c_i f_i(R) N_i \tag{6.11}$$

for the resource – see the Supplementary for more information. 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 is the maximum advantage it can gain from facilitation (we assume $d_i \leq m_i^0$), θ measures the facilitative advantage any species is able to give another, 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.

With the assumption of hierarchy, Kevin proved that an arbitrary number of consumers may stably coexist on a single resource. But do we expect truly no limit to the number of species? Is there nothing to stop the inflow of ever more consumer species short of energetic constraints? This is where community-wide sensitivity analysis comes into the picture. Although it is indeed possible to pack in more and more species, such a community will become ever more sensitive to parameter changes. Eventually, sensitivities get so high that even the slightest perturbation will cause the extinction of several species. In the Supplement, the robustness of the community is calculated asymptotically, for large S. The result is

$$\sqrt[S]{\mathcal{V}_{\mathcal{S}}\mathcal{V}_{\mathcal{I}}} = \exp\left(-\frac{\theta N}{2} S\right), \tag{6.12}$$

where N is the smallest of the equilibrium densities of the consumer species. Taking the Sth root of $\mathcal{V}_{\mathcal{S}}\mathcal{V}_{\mathcal{I}}$ is an important technical point which is explained in the Supplement in detail. In short, this is to compensate for artifacts caused by the constant increase in dimensionality when adding in further species to the system. Imagine an S-dimensional cube whose side is equal to one centimeter, or 1/100 meters. Its volume is then equal to $100^{-S}\mathrm{m}^S$, which approaches zero for large S – when in fact nothing is shrinking, and if we would measure distances in units of centimeter, the volume would be $1\mathrm{cm}^S$. By taking the Sth root, we remove this artifact of increasing dimensionality. Putting it differently, taking the Sth root ensures that we measure robustness in consistent units, regardless of the number of species.

The implications are clear: the robustness of this system decays exponentially with the number of species. Due to this exponential decay, a crude estimate for the maximum sustainable number of species can be given by $S_{\max} \approx 2/(\theta N)$ (an S larger than this will make the expression exponentially small). With the original parametrization of Gross (2008), $\theta = 0.28$, and the population densities are of the order of magnitude 1. Using these, we get $S_{\max} \approx 2/(0.28 \times 1) = 7.14$, therefore one could state, as a conservative rule of thumb, that in this model it is very unlikely to have more than $S_{\max} = 10$ species coexisting. Incidentally, this is exactly what was observed for this model when randomizing parameters: the average number of coexisting species was about 5, with the species count sometimes reaching but never exceeding ten survivors (Gross 2008, Figure 5d).

6.6 Synthesis: coexistence and community-wide sensitivities

In this chapter we have attempted to demonstrate through a handful of carefully selected examples the kind of benefits community-wide sensitivity analysis might hold for ecology. The examples were aimed at covering a diverse range of different situations: the sensitivity of fluctuation-mediated coexistence, spatially structured communities, and noncompetitive interactions. Yet behind the diversity of the applications underlies a fundamental unity in how the problems are approached and what methods are employed to arrive at their solution. The question of coexistence is viewed through the lens of sensitivity analysis. What are some of the generalities emerging from this new perspective?

First of all, in all of the examples considered, it proved to be a fruitful approach to think in terms of regulating factors. There are several benefits to doing this.

First, regulating factors offer a way of constructing and encourage the use of explicit, mechanistic models. For instance, in the logistic growth model, it is unclear what the mechanism is behind the linear decrease of the per capita growth rates with increasing density. Once we make the mechanism clear, e.g. via some simple consumer-resource model (Mallet 2012), the resource (or some function thereof, such as its depletion) can be designated as the regulating factor.

Second, the concept of a regulating factor is very general indeed, and this flexibility allows for the automatic treatment of seemingly very different types of interactions. Apart from being able to treat the familiar and well-understood area of resource competition (MacArthur 1970, Tilman 1982, Chesson 1990b), it can also incorporate predator-mediated effects such as apparent competition (Holt 1977), spatial effects (as in our analysis of the tolerance-fecundity model), and temporal segregation (as in the forb-grass competition model). There is no fundamental difference in how these various mechanisms are treated: the details do change (see Box 1 for the formulas), but their basic biological interpretation remains the same.

Third, since by definition the regulating factors mediate the feedback between population growth rates and densities, it brings attention to the necessity of considering both directions in the feedback loop: the effect of the species on the regulating factors (impact vector) and the response of species' growth rates to changes in the regulating factors (sensitivity vectors). As we have seen, both quantities are important when evaluating community-wide sensitivities.

Fourth, as we have already seen, the number of regulating factors puts an upper limit to the maximum number of species that can coexist in a way that is not infinitely sensitive to parameter perturbations (more species than regulating factors lead to zero sensitivity and impact volumes, therefore zero robustness, or infinite sensitivity). In certain cases, this immediately restricts how many species can coexist – for instance in the forb-grass competition model, where there were two regulating factors: resource availability (empty space) in good and bad years. Therefore two species could coexist at most. But sometimes the number of regulating factors is infinite, as in the tolerance-fecundity tradeoff model. Therefore, there is no "hard" limit to the number of coexisting species. Community-wide sensitivity calculations showed that even in this case, infitite diversity is not expected.

The second way in which community-wide sensitivity analysis offers a unified perspective is through the introduction of impact and sensitivity vectors. These quantities offered a way to treat completely different types of dynamical and ecological situations in a unified manner. Once the structure of the set of all regulating factors is established, these two vectors measured the sensitivity of the system, regardless of whether the example was equilibrium or nonequilibrium, or whether there was spatial structure, or noncompetitive interactions. More precisely, the volumes spanned by these vectors are what determined this sensitivity, not the individual vectors themselves. The volumes are clearly small whenever two species have very similar impact and/or sensitivity vectors, as mentioned before in Section 6.2. It is also clear that two species with exactly identical traits will have the exact same impact and sensitivity vectors. Their coexistence therefore has zero robustness: an arbitrarily small change in some parameter may be enough to ensure the extinction of the other.

This is nothing else than a restatement of classical ideas about competitive exclusion and natural selection: if two species are exactly identical, then the slightest advantage one gains over the other will result in the fixation of the advantageous type on the long run. It has to be emphasized however that the principle is reformulated in terms of sensitivities. It is not impossible for two similar species to stably coexist, just extremely unlikely, since unless all parameters are carefully fine-tuned to allow for their coexistence, the extreme sensitivity of the equilibrium densities will essentially guarantee that any parameter perturbation will cause at least one of the densities to hit zero.

Similar species have similar impact and sensitivity vectors, therefore $\mathcal{V}_I$ and $\mathcal{V}_S$ will be small, leading to reduced community robustness and reduced likelihood of coexistence. This connects community-wide sensitivity analysis to the classic idea of the ecological niche. A word of clarification is in order. The word "niche" is used in a wide array of often confusing or contradictory ways (see e.g. Chase and Leibold 2003 for a review), there are still, roughly speaking, two main camps of thought today. One of them uses the word "niche" in a sense that tries to predict the ranges of species based on their environmental tolerance levels (niche modeling, Colwell and Rangel 2009). The other takes the Hutchinson–MacArthur view on the niche and holds that the most important property of the niche is that no two species may occupy the same one – in other words, this niche concept is aimed at formalizing the competitive exclusion principle. *If* we consider competitive exclusion to be the defining property of the niche, *then* the impact-sensitivity vector formalism automatically conforms to this defining property. If two species are overly similar, either in their impact or in their sensitivity vectors, their coexistence can be fragile at best.

Is this an adequate statement for the purposes of niche theory? Instead of having a clear-cut statement that "coexistence is possible" or "coexistence is impossible", we have the statement "such-and-such amount of segregation in the impact and sensitivity vectors (i.e., niche segregation) results in this and this parameter range that can support coexistence". Classical ideas on the niche (Gause 1934, MacArthur and Levins 1967, Hutchinson 1978, Leibold 1995, Chesson 2000b, Chase and Leibold 2003) have always emphasized the stability of coexistence, as opposed to its sensitivity against parameter perturbations. In fact, one of the insights that community-wide sensitivity analysis has to offer is that the emphasis on the stability, as opposed to the sensitivity, of coexistence is a blind alley that will not lead to very clear conclusions in the end. The review in Chapter 1 shows how, when stability is the ultimate criterion for coexistence, not only are there no clear-cut limits to how similar various species can be: it is in fact possible to have continuous coexistence (Roughgarden 1979, pp. 534-536), i.e. coexistence of every possible phenotype along some niche axis, in the very same Lotka–Volterra model that was used to demonstrate the existence of such limits in the first place (MacArthur and Levins 1967). This continuous coexistence, however, proves to be structurally unstable (an arbitrarily small parameter perturbation will break it down); moreover, it has been proven mathematically that this will be the case in *any* realistic ecological model

(Gyllenberg and Meszéna 2005; see also Chapter 1 and Appendix A).

Shifting the emphasis from the stability to the sensitivity of coexistence is therefore not a step that reduces the power of our approach. Instead, stability in general is simply not the proper criterion when evaluating whether coexistence is expected. Coexistence studies therefore necessarily need to consider the sensitivity of coexistence. “How much niche segregation is needed for species to be able to coexist?” is not the proper question. Instead, we ask: “what is the range of parameters allowing for coexistence given a certain amount of niche differentiation?” The amount of differentiation is given by the impact and sensitivity vectors, while the sensitivity formulas yield the viable parameter range. Chapters 1 and 2 explored the implications of this statement for community patterns, establishing the null expectation of limiting similarity in any ecological model. Chapters 3 and 4 developed the proper notion of robustness in periodically fluctuating environments, and Chapter 5 did the same for communities of spatially or physiologically structured populations. In all cases, focusing on the sensitivity of coexistence cleans up controversies and puts the study of coexistence and niche theory on a solid foundation.

Appendices

Appendix A

An extension of the theorem by Gyllenberg and Meszéna (2005)

In this Appendix we state and prove an extension to Theorems 4 and 8 of Gyllenberg and Meszéna (2005).

Theorem 4 of that article proves that the coexistence of infinitely many species is structurally unstable (i.e., can be destroyed by an arbitrarily small modification of the underlying model) when the (possibly nonlinear) operator describing population interactions is compact in the sense defined below. This assumption is valid if, e.g., the trait values in niche space are constrained to a finite volume (like $[x_A, x_B]$ in the main text) and the model is constructed from continuous ingredient functions, as shown by Theorems 1-3 of Gyllenberg and Meszéna (2005). This assumption is therefore expected to hold for any realistic ecological model, rendering the result stated by the aforementioned Theorem 4 very general. However, as highlighted in the main text, that theorem does not exclude the possibility that a different set of infinitely many species can still coexist after the structural perturbation.

Theorem 8 of Gyllenberg and Meszéna (2005) rectifies this problem, but only for Lotka–Volterra models with a one-dimensional niche space and a homogeneous and *analytic* competition kernel. As now an infinite niche axis is allowed, robust coexistence of infinitely many species is possible. The theorem states that the set of coexisting species cannot contain a continuum (mathematically speaking, have a “limit point”) in a structurally robust way. In other words, if a model has a solution with a limit point, the model has a structurally perturbed version that does not have such a solution. As shown in Chapter 2, the assumption of analyticity is an important prerequisite for this theorem, as kinked kernels (which are nonanalytic) satisfy the conditions of Theorem 4, but not of Theorem 8.

The first theorem below proves an extension of Theorem 8 beyond the confines of Lotka–Volterra models, while retaining the assumptions of a one-dimensional niche space and of the analyticity of the ingredient functions. The second theorem below shows that if the original intrinsic growth rates $r(x)$ are positive and bounded away from zero, then the perturbed intrinsic growth rates can be chosen to be positive as well.

As in the main text, r and n are the distributions of intrinsic growth rates $r(x)$ and densities $n(x)$ of species with trait vales x. The densities n may describe continuous or discrete distributions, with the latter being composed of Dirac delta functions. Accordingly, n is not a continuous function, but a more abstract object known as a "measure" – a nuanced mathematical distinction we have avoided making in the main text. A is the operator describing population interactions, corresponding to the integral operator in Eq. (1.1). Then the growth rate of species x is given by $r(x) - A(n)(x)$, so the equilibrium condition is $r(x) = A(n)(x)$ for all x in the support of n.

With this introduction, we now rigorously state and prove the two theorems. Let the one-dimensional niche space $\mathcal{X}$ be an arbitrary subset of the real numbers. The Banach space of signed measures with the total-variation norm is denoted by $M(\mathcal{X})$.

Let Ω be an open and connected set in the complex plane $\mathbf{C}$ that contains $\mathcal{X}$. Let Z be the linear space of all functions on $\mathcal{X}$ that have a holomorphic extension to Ω. Equivalently, Z can be viewed as the space of all functions f that are holomorphic in Ω and have real values on $\mathcal{X}$. Alternatively, we consider the linear space Y of bounded holomorphic functions f on Ω such that $f(z)$ is real for all $z \in \mathcal{X}$.

Y equipped with the supremum norm is a Banach space; Z equipped with the locally convex topology of uniform convergence on compact subsets of Ω is a Fréchet space equipped with the metric

$$d(f,g) = \sum_{i=1}^{\infty} \frac{2^{-i} p_i(f-g)}{1 + p_i(f-g)}, \tag{A.1}$$

where

$$p_i(f) = \sup \left\{ \left| f(z) \right| : z \in K_i \right\}, \tag{A.2}$$

with $K_1 \subset K_2 \subset \cdots$ being a sequence of nonempty compact subsets of Ω such that K_i lies in the interior of K_{i+1} and $\Omega = \cup_{i=1}^{\infty} K_i$.

A (nonlinear) operator A between two topological vector spaces is said to be compact if A is continuous and the closure of $A(U)$ is compact for every bounded set U.

The following theorem hinges on Baire's theorem (Dugundji 1966, Theorem 10.5, p. 250), which states that in a Baire space a set of the first category has empty interior. As complete metric spaces are Baire spaces (Rudin 1973, Theorem 2.2, p. 42), we can take V to be either Y or Z in the following theorem.

Theorem 1. *Let $r \in V$ and suppose that $A : M(\mathcal{X}) \to V$ is compact. If there exists a solution n of*

$$r(x) = A(n)(x) \quad \text{for all } x \in \operatorname{supp}(n), \tag{A.3}$$

the support of which has a limit point in Ω, then in every neighborhood of r there exists an r' such that Eq. (A.3) *with r replaced by r' does not have any solution with a support with a limit point in Ω.*

Proof. Suppose Eq. (A.3) holds and $\operatorname{supp}(n)$ has a limit point in Ω. Then, because of analyticity,

$$r(x) = A(n)(x) \quad \text{for all } x \in \Omega. \tag{A.4}$$

V is an infinite-dimensional topological vector space and hence not locally compact. Let U_t be the ball of radius t in $M(\mathcal{X})$. Because A is compact, the interior of the closure of $A(U_t)$ is empty for all $t > 0$. It follows that the range of A is of the first category and hence has empty interior by Baire's theorem. As r is an element of the range of A, there exists an $r' \in V$ in an arbitrarily small neighborhood of r such that r' is not in the range of A, that is, no solution of (A.4) with r replaced by r' exists. Again, by analyticity, $r'(x) = A(n)(x)$ cannot hold in any set with a limit point. □

If r is strictly positive, then the r' of Theorem 1 can also be chosen strictly positive (under a small extra condition in the case of space Z).

Theorem 2. *Suppose that there exists a $\delta > 0$ such that $r(x) \geq \delta$ for all $x \in \mathcal{X}$. Then, in the case of space Y, one can choose r' in Theorem 1 to be positive. If the closure of $\mathcal{X}$ is contained in Ω, then the same is true in the case of space Z.*

Proof. Every neighborhood of r in Y contains a ball centered on r and with a sufficiently small radius $\epsilon > 0$. For $\epsilon < \delta$, this ball consists of functions that are positive on $\mathcal{X}$.

In the case of space Z and for $\overline{\mathcal{X}} \subset \Omega$, there exists an index m such that $\mathcal{X} \subset K_i$ for all $i \geq m$. Suppose that there exists a $\xi \in \mathcal{X}$ such that $r'(\xi) < 0$. Then

$$d(r, r') = \sum_{i=1}^{\infty} \frac{2^{-i} p_i(f-g)}{1 + p_i(f-g)} \geq \sum_{i=m}^{\infty} \frac{2^{-i} p_i(f-g)}{1 + p_i(f-g)} \geq \sum_{i=m}^{\infty} \frac{2^{-i}\delta}{1+\delta} \geq 2^{-(m-1)}\delta. \tag{A.5}$$

But such an r' does not belong to a ball centered on r and with a radius $\epsilon < 2^{-(m-1)}\delta$. This proves the theorem. $\square$

Appendix B

Two-species coexistence under smooth and kinked kernels

Let us consider two competing species in equilibrium, placed along a trait axis at trait values x_1 and x_2. We assume $x_2 > x_1$ without loss of generality. The equations read

$$\frac{\mathrm{d}n(x_1)}{\mathrm{d}t} = n(x_1)\Big(r_0(x_1) - a(x_1, x_1)n(x_1) - a(x_1, x_2)n(x_2)\Big), \tag{B.1}$$

$$\frac{\mathrm{d}n(x_2)}{\mathrm{d}t} = n(x_2)\Big(r_0(x_2) - a(x_2, x_2)n(x_2) - a(x_2, x_1)n(x_1)\Big). \tag{B.2}$$

If the two species are closely packed then the difference $\Delta x = x_2 - x_1$ between the strategies of the two species will be small. When this is so, several expansions become possible. First,

$$r_0(x_2) = r_0(x_1 + \Delta x) \approx \underbrace{r_0(x_1)}_{r_0} + \underbrace{\frac{\mathrm{d}r_0}{\mathrm{d}x}(x_1)}_{c}\,\Delta x = r_0 + c\Delta x, \tag{B.3}$$

where we introduced the notations r_0 and c for the value and the slope of the function $r_0(x)$ at $x = x_1$, respectively (we assume $r_0(x)$ is differentiable). Second, by introducing the function $A(x) = a(x, x)$, we get

$$a(x_2, x_2) = A(x_2) = A(x_1 + \Delta x) \approx \underbrace{A(x_1)}_{a_x} + \underbrace{\frac{\mathrm{d}A}{\mathrm{d}x}(x_1)}_{w}\,\Delta x = a_x + w\Delta x, \tag{B.4}$$

where $a_x = a(x_1, x_1)$ and w is the slope measuring the difference between the two intraspecific competition coefficients $a(x_1, x_1)$ and $a(x_2, x_2)$. Third, the interspecific competition coefficients are expanded as

$$\begin{aligned} a(x_1, x_2) = a(x_1, x_1 + \Delta x) &\approx a(x_1, x_1) + \underbrace{\partial_2 a(x_1, x_1^+)}_{-k_x} \Delta x + \frac{1}{2} \underbrace{\partial_2^2 a(x_1, x_1^+)}_{-d_x} \Delta x^2 \\ &= a_x - k_x \Delta x - \frac{d_x}{2} \Delta x^2 \end{aligned} \tag{B.5}$$

and

$$\begin{aligned} a(x_2, x_1) = a(x_2, x_2 - \Delta x) &\approx \underbrace{a(x_2, x_2)}_{a_y} - \underbrace{\partial_2 a(x_2, x_2^-)}_{k_y} \Delta x + \frac{1}{2} \underbrace{\partial_2^2 a(x_2, x_2^-)}_{-d_y} \Delta x^2 \\ &= a_y - k_y \Delta x - \frac{d_y}{2} \Delta x^2, \end{aligned} \tag{B.6}$$

where $\partial_k^n a(x, y)$ is the nth partial derivative of a with respect to the kth variable, evaluated at (x, y), and $\partial_k^n a(x, y^+)$ means the limit of the derivative as the second variable approaches y from values strictly higher than y itself. The derivatives in the expansions above are defined via the limiting procedure because in the kinked case the derivatives do not exist at zero trait difference. Moreover, even if the kernel is smooth, it might only be differentiable once and so its second derivative might only exist to the right and left of the maximum, not at the maximum itself. This procedure is justified since we assumed $x_2 > x_1$, therefore the competition coefficients $a(x_1, x_2)$ and $a(x_2, x_1)$ only need to be considered to the left and right of the kernel's maximum, respectively. Also, notice that the quantities r_0, a_x and a_y are positive due to the positivity of $r_0(x)$ and $a(x, y)$, and the positivity of k_x, k_y, d_x, and d_y is evident from the fact that the kernel is a decreasing function of $|x - y|$.

The dynamical equations may now be written as

$$\frac{\mathrm{d}n(x_1)}{\mathrm{d}t} = n(x_1) \left(r_0 - a_x n(x_1) - (a_x - k_x \Delta x - \frac{d_x}{2} \Delta x^2) n(x_2) \right), \tag{B.7}$$

$$\frac{\mathrm{d}n(x_2)}{\mathrm{d}t} = n(x_2) \left(r_0 + c \Delta x - a_y n(x_2) - (a_y - k_y \Delta x - \frac{d_y}{2} \Delta x^2) n(x_1) \right) \tag{B.8}$$

in this approximation.

The well-known inequalities expressing the necessary and sufficient conditions of stable coexistence under two-species Lotka–Volterra competition read

$$\frac{a_{12}}{a_{22}} < \frac{r_{01}}{r_{02}} < \frac{a_{11}}{a_{21}} \tag{B.9}$$

(e.g., Vandermeer 1975). In our notation, $a_{12} = a(x_1, x_2)$, $a_{21} = a(x_2, x_1)$, $a_{11} = a_x$, $a_{22} = a_y$, $r_{01} = r_0$, and $r_{02} = r_0 + c\Delta x$. Applying the criterion to these parameters,

$$\frac{a_x - k_x\Delta x - (d_x/2)\Delta x^2}{a_y} < \frac{r_0}{r_0 + c\Delta x} < \frac{a_x}{a_y - k_y\Delta x - (d_y/2)\Delta x^2} \tag{B.10}$$

must be true for coexistence to happen. Let us take the inverse of these conditions:

$$\frac{a_y}{a_x - k_x\Delta x - (d_x/2)\Delta x^2} > 1 + \frac{c}{r_0}\Delta x > \frac{a_y}{a_x} - \frac{k_y}{a_x}\Delta x - \frac{d_y}{2a_x}\Delta x^2. \tag{B.11}$$

At this point, we will consider the smooth and the kinked case separately. We start with the smooth case. If the kernel is smooth, it is differentiable at its maximum and the value of the derivative is zero — therefore $k_x = k_y = 0$ and the quadratic terms are the first nontrivial orders of expansion for the kernel. Then the above condition reduces to

$$\frac{a_y}{a_x - (d_x/2)\Delta x^2} > 1 + \frac{c}{r_0}\Delta x > \frac{a_y}{a_x} - \frac{d_y}{2a_x}\Delta x^2. \tag{B.12}$$

Multiplying by $a_x - (d_x/2)\Delta x^2$ and neglecting terms that are higher order than quadratic, we get

$$a_y > a_x + \frac{ca_x}{r_0}\Delta x - \frac{d_x}{2}\Delta x^2 > a_y - \left(\frac{d_x a_y}{2a_x} + \frac{d_y}{2}\right)\Delta x^2. \tag{B.13}$$

We subtract a_y and use $a_y = a_x + w\Delta x$ to obtain

$$0 > \left(\frac{ca_x}{r_0} - w\right)\Delta x - \frac{d_x}{2}\Delta x^2 > -\left(\frac{d_x a_y}{2a_x} + \frac{d_y}{2}\right)\Delta x^2, \tag{B.14}$$

or, after adding $(d_x/2)\Delta x^2$ and dividing by Δx,

$$\frac{d_x}{2}\Delta x > \frac{ca_x}{r_0} - w > \left(\frac{d_x}{2} - \frac{d_x a_y}{2a_x} - \frac{d_y}{2}\right)\Delta x. \tag{B.15}$$

If $ca_x/r_0 - w$ is positive, there will exist a Δx so small that the first inequality cannot be satisfied. The same is true for the second inequality when $ca_x/r_0 - w$ is negative. This puts a limit to the similarity of the two species: Δx must be large enough to satisfy both inequalities. Formally, the limit to the similarity of the species disappears when $ca_x/r_0 - w$ is zero, a nongeneric situation.

Having established the limits to the similarity of two competing species under smooth competition kernels, let us turn our attention to kinked ones. In this case the first-order expansion coefficients k_x and k_y are nonzero, rendering the second order negligible in comparison. Therefore in Eq. (B.11) we may neglect any terms that are quadratic or higher order. As a result, we get

$$\frac{a_y}{a_x - k_x\Delta x - (d_x/2)\Delta x^2} > 1 + \frac{c}{r_0}\Delta x > \frac{a_y}{a_x} - \frac{k_y}{a_x}\Delta x. \tag{B.16}$$

Multiplying by $a_x - k_x\Delta x - (d_x/2)\Delta x^2$ and neglecting all terms of quadratic or higher order leads to

$$a_y > a_x - k_x\Delta x + \frac{ca_x}{r_0}\Delta x > a_y - \left(\frac{k_x a_y}{a_x} + k_y\right)\Delta x. \tag{B.17}$$

Using $a_y = a_x + w\Delta x$, rearranging, and simplifying yields

$$0 > \frac{ca_x}{r_0} - k_x - w > -\frac{k_x a_y}{a_x} - k_y, \tag{B.18}$$

which is independent of Δx. The conclusion is that two species may be arbitrarily closely packed if the competition kernel is kinked, as long as these inequalities are satisfied.

Appendix C

Competition kernel as an overlap between sensitivities and impacts

Our purpose is to show that the competition kernel is always expressible as an overlap between two different functions called sensitivities and impacts (Meszéna et al. 2006). This expression does not depend on the assumptions that lead to the utilization overlap picture. The resource utilization overlap model turns out to be a special case of this general formalism where the sensitivity and impact functions are precisely proportional to one another.

As mentioned in the Introduction, species interactions are mediated through a number of regulating factors, i.e., variables that mediate the feedback loops between densities and growth rates. Familiar examples include resources, predators, pathogens, space, etc. We assume that there is a continuum of regulating entities in the system: $R(z)$ measures the quantity of the zth factor with $z \in [z_0, z_m] \subseteq \mathbb{R}$. Within this framework, the most general continuous time, continuous density model will read

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x)\, r\left(R(z,n), E\right), \tag{C.1}$$

where $n(x)$ is the density distribution along the trait axis, and E is the collection of all density-independent model parameters (they may depend on the trait values). Around a fixed point equilibrium with equilibrium distribution n^*, the linearization of the growth rates will read

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} \approx n(x)\Big(\underbrace{r(R(z,n^*),E)}_{0} + \delta r(R(z,n),E)\Big), \tag{C.2}$$

or

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} \approx n(x)\left(\int_{x_0}^{x_m} \frac{\delta r(x)}{\delta E(y)}\delta E(y)\,\mathrm{d}y + \int_{x_0}^{x_m}\int_{z_0}^{z_m} \frac{\delta r(x)}{\delta R(z)}\frac{\delta R(z)}{\delta n(y)}\delta n(y)\,\mathrm{d}z\,\mathrm{d}y\right), \tag{C.3}$$

where we used the chain rule of differentiation (see Section 2.2 for the meaning of the functional derivative); $r(x)$ is shorthand for $r\left(R(x, n(x)), E(x)\right)$. The factor in the second term of the expansion multiplying the perturbed densities $\delta n(y)$ consists of two parts. The first part,

$$S(x,z) = \frac{\delta r(x)}{\delta R(z)}, \tag{C.4}$$

is the *sensitivity* of the species with trait x to the zth regulating factor (Meszéna et al. 2006), since it measures how the growth rate of species x would change if the zth factor was slightly modified. The second part of the product,

$$I(y,z) = \frac{\delta R(z)}{\delta n(y)}, \tag{C.5}$$

is the *impact* of species with trait y on the zth regulating factor. It tells us how the factors regulating the populations are themselves affected by a change in species abundances. As before in Section 2.2, the full factor multiplying the perturbed densities $\delta n(y)$ in Eq. (C.3) is the competition kernel, which in our case is the overlap of the sensitivities and impacts:

$$a(x,y) = \int_{z_0}^{z_m} \frac{\delta r(x)}{\delta R(z)}\frac{\delta R(z)}{\delta n(y)}\,\mathrm{d}z = \frac{\delta r(x)}{\delta n(y)} = \int_{z_0}^{z_m} S(x,z)I(y,z)\,\mathrm{d}z. \tag{C.6}$$

Note that this formula applies to any ecological scenario near a fixed point, and as such, it is the proper generalization of the resource utilization overlap picture. The resource utilization function is a phenomenological construct that is intuitive and very useful, but not generalizable to arbitrary ecological situations. The sensitivities and impacts on the other hand are always well-defined, and the competition kernel is always obtained as their overlap integral. Indeed, the resource utilization model is simply the special case when the sensitivity and impact functions are strictly proportional to one another.

As an example, let us consider simple, linear resource competition, a continuous extension of MacArthur's (1970) model. The dynamics of the species densities is given by the equations

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x)\left(\int_{z_0}^{z_m} b(x,z)R(z)\,\mathrm{d}z - m(x)\right), \tag{C.7}$$

where $R(z)$ is the zth resource, $b(x,z)$ is the potential growth the xth population is able to achieve on a unit of the zth resource, and $m(x)$ is the density-independent mortality rate of species x. As we can see, the total birth rate is accumulated through the contribution of all the resources available to the species. The resources, in turn, have their own dynamics, which assumes logistic saturation in the absence of consumers and linear consumption in their presence:

$$\frac{\mathrm{d}R(z)}{\mathrm{d}t} = R(z)\left(R_0(z) - R(z) - \int_{x_0}^{x_m} f(y,z)n(y)\,\mathrm{d}y\right), \tag{C.8}$$

where $R_0(z)$ is the maximum (saturation) quantity of resource z, and $f(y,z)$ is the rate at which species y depletes resource z. Assuming that the dynamics of the resources is fast compared to that of the densities, it is always in its equilibrium state:

$$R(z) = R_0(z) - \int_{x_0}^{x_m} f(y,z)n(y)\,\mathrm{d}y. \tag{C.9}$$

Substituting Eq. (C.9) into Eq. (C.7) we obtain

$$\begin{aligned}\frac{\mathrm{d}n(x)}{\mathrm{d}t} &= n(x)\left(\int_{z_0}^{z_m} b(x,z)\left(R_0(z) - \int_{x_0}^{x_m} f(y,z)n(y)\,\mathrm{d}y\right)\mathrm{d}z - m(x)\right)\\ &= n(x)\Bigg(\underbrace{\int_{z_0}^{z_m} b(x,z)R_0(z)\,\mathrm{d}z - m(x)}_{r_0(x)}\\ &\quad - \int_{x_0}^{x_m} \underbrace{\left(\int_{z_0}^{z_m} b(x,z)f(y,z)\,\mathrm{d}z\right)}_{a(x,y)} n(y)\,\mathrm{d}y\Bigg).\end{aligned} \tag{C.10}$$

As we can see, the competition kernel is the overlap of the functions $b(x,y)$ and $-f(y,z)$. This suggests that these functions play the roles of sensitivities and impacts. Indeed, from their definitions we get

$$S(x,z) = \frac{\delta r(x)}{\delta R(z)} = \int_{z_0}^{z_m} b(x,z')\delta(z-z')\,\mathrm{d}z' = b(x,z) \tag{C.11}$$

and

$$I(y,z) = \frac{\delta R(z)}{\delta n(y)} = -\int_{x_0}^{x_m} f(y',z)\delta(y-y')\,\mathrm{d}y' = -f(y,z). \tag{C.12}$$

The original MacArthur resource utilization model is recovered when $b(x,z) = \alpha f(x,z)$ for some constant α. Since populations tend to influence those resources most that they depend upon the most, this assumption is reasonable — but it is neither ubiquitous nor necessary.

Appendix D

Generalization of the results of Section 2.5

Here we extend the results obtained in Section 2.5 from resource overlap to arbitrary models. The key to doing this is to write the competition kernel as the overlap of sensitivity and impact functions (see Appendix B); note that this is always possible and does not depend upon the specific assumptions of resource overlap models. The competition kernel is thus given by Eq. (C.6). Since we are interested in nondifferentiability at zero trait difference, we set $y = x$:

$$a(x, x) = \int_{z_0}^{z_m} S(x, z) I(x, z) \, \mathrm{d}z, \tag{D.1}$$

where $S(x, z)$ and $I(x, z)$ are the sensitivity and impact functions, respectively, assumed to be bounded. We now show that discontinuities in the sensitivities and impacts occurring at corresponding points between the two functions is sufficient to lead to kinked kernels. Let us consider functions that contain a jump for every possible trait value x:

$$S(x, z) = \alpha \Theta(x - z_1(x)) + \eta(x, z), \tag{D.2}$$

$$I(x, z) = \beta \Theta(x - z_2(x)) + \zeta(x, z), \tag{D.3}$$

where α and β are constants, η and ζ are continuous functions, Θ is the Heaviside unit step function and $z_1(x)$, $z_2(x)$ are curves along which the sensitivity and impact functions possess a discontinuity (they depend on x because we allow for the possibility of each species having their discontinuity at different points).

Similarly to the procedure in Section 2.5, our strategy for determining whether $a(x, x)$ is nondifferentiable will be to take the second derivative of the kernel with respect to the first variable and see whether the result obtained is infinitely large or not. The second derivative reads

$$\begin{aligned} \partial_1^2 a(x,x) &= \int_{z_0}^{z_m} \partial_1^2 S(x,z) I(x,z)\,\mathrm{d}z \\ &= \alpha \int_{z_0}^{z_m} \delta'(x - z_1(x)) I(x,z)\,\mathrm{d}z + \ldots, \end{aligned} \tag{D.4}$$

where $\partial_1^2 S(x,z)$ is the second partial derivative of S with respect to the first variable, evaluated at (x,z), δ' is the derivative of the Dirac delta function, and the ellipsis denotes all other terms the derivative produces that we have not written out, for the reason that those terms are necessarily finite and so they do not contribute to the nondifferentiability of the kernel. The integration can be performed with the help of the δ' function:

$$\partial_1^2 a(x,x) = -\alpha \partial_2 I(x, z_1(x)) + \ldots, \tag{D.5}$$

which is infinitely large if I is discontinuous along $z_1(x)$. This of course happens when $z_1(x) = z_2(x)$. Therefore, if $S(x, z_1(x))$ and $I(x, z_1(x))$ are both discontinuous along some curve $z_1(x)$, then the resulting competition kernel is kinked.

Appendix E

The Jacobian of the stroboscopic map

We want to obtain an expression for the derivative of the stroboscopic map Π_i with respect to the initial conditions x_j^0. According to the definition of Eq. (3.13),

$$\frac{\partial \Pi_i}{\partial x_j^0} = \left.\frac{\partial \varphi_i}{\partial x_j^0}\right|_{t=T} \tag{E.1}$$

with $x_i(t) = \varphi_i(x_1^0, \ldots, x_L^0, E, t)$ being the flow induced by the right hand side of Eq. (3.1) with initial conditions x_i^0. Now, let us calculate

$$\begin{aligned} \frac{\partial^2 \varphi_i}{\partial t\, \partial x_j^0} &= \frac{\partial}{\partial x_j^0}\left(\frac{\partial \varphi_i}{\partial t}\right) = \\ &= \frac{\partial}{\partial x_j^0} r_i(\mathbf{R}(x_1(t), \ldots, x_L(t)), E, t) = \\ &= \sum_{k=1}^{L} \frac{\partial r_i(t)}{\partial \mathbf{R}(t)} \frac{\partial \mathbf{R}(t)}{\partial x_k(t)} \frac{\partial \varphi_k}{\partial x_j^0}, \end{aligned} \tag{E.2}$$

where summation or integration for all indices of $\mathbf{R}$ is understood. The equation we have ended up with reads

$$\frac{\partial}{\partial t}\left(\frac{\partial \varphi_i}{\partial x_j^0}\right) = \sum_{k=1}^{L} \frac{\partial r_i(t)}{\partial \mathbf{R}(t)} \frac{\partial \mathbf{R}(t)}{\partial x_k(t)} \frac{\partial \varphi_k}{\partial x_j^0}, \tag{E.3}$$

where the derivative of r_i with respect to $\mathbf{R}$ and of $\mathbf{R}$ with respect to $x_k(t)$ are evaluated at the flow on the attractor. Since $\varphi_i(0) = x_i^0$ by definition, the initial condition to this equation is

$$\left.\frac{\partial \varphi_i}{\partial x_j^0}\right|_{t=0} = \delta_{ij}. \tag{E.4}$$

Let us introduce some simplifying notation, with $\Phi(t)$ being the derivative of the flow with respect to the initial conditions, and $a(t)$ being the time-dependent coefficient matrix multiplying $\Phi(t)$ on the right hand side of Eq. (E.3):

$$\Phi(t) = \frac{\partial \varphi_i}{\partial x_j^0} \tag{E.5}$$

and

$$a(t) = \frac{\partial r_i(t)}{\partial \mathbf{R}(t)} \frac{\partial \mathbf{R}(t)}{\partial x_k(t)}. \tag{E.6}$$

Eq. (E.3) can then be rewritten as

$$\frac{\mathrm{d}\Phi(t)}{\mathrm{d}t} = a(t) \cdot \Phi(t), \tag{E.7}$$

with the initial condition translating to $\Phi(0) = 1$.

The solution to the matrix differential equation (E.7) is nontrivial as the matrices $a(t_1)$ and $a(t_2)$ do not necessarily commute for $t_1 \neq t_2$. To handle the problem, we first define the matrix $\mathrm{Exp}(a)$, the exponential of the matrix a, by substituting a into the usual Taylor series of the exponential function. Note that $\mathrm{Exp}(a(t_1) + a(t_2)) \neq \mathrm{Exp}(a(t_1)) \cdot \mathrm{Exp}(a(t_2))$ except when the matrices $a(t_1)$ and $a(t_2)$ commute. The solution of Eq. (E.7) can now be written as an infinite product of matrix exponentials:

$$\begin{aligned} \Phi(t) &= \lim_{\Delta t \to 0} \mathrm{Exp}(a(t - \Delta t)\Delta t) \cdot \ldots \cdot \mathrm{Exp}(a(\Delta t)\Delta t) \cdot \mathrm{Exp}(a(0)\Delta t) = \\ &= \lim_{\Delta t \to 0} \prod_{\tau = N-1}^{0} \mathrm{Exp}\left(a(\tau \Delta t)\Delta t\right), \end{aligned} \tag{E.8}$$

where $N = t/\Delta t \to \infty$. It is easy to show that this is indeed the solution: for an infinitesimally small Δt, Eq. (E.7) can be written as

$$\begin{aligned} \Phi(t + \Delta t) &= \Phi(t) + a(t)\Phi(t)\Delta t = \\ &= (1 + a(t)\Delta t)\Phi(t) \approx \\ &\approx \mathrm{Exp}(a(t)\Delta t)\Phi(t), \end{aligned} \tag{E.9}$$

and applying this recursively from $t = 0$ to the final moment yields Eq. (E.8).

Note that the matrices within the product in Eq. (E.8) are ordered according to decreasing time. The expression can be made notationally more convenient by introducing the so-called time-ordering operator $\mathcal{T}$. By definition this operator rearranges a product of matrices to decreasing order in time:

$$\mathcal{T} a(t_1) \cdot a(t_2) = \mathcal{T} a(t_2) \cdot a(t_1) = \begin{cases} a(t_1) \cdot a(t_2) & \text{if } t_2 \leq t_1, \\ a(t_2) \cdot a(t_1) & \text{if } t_2 > t_1. \end{cases} \tag{E.10}$$

This somewhat obscure but very useful notation, widely used in quantum field theory (see, e.g., Weinberg 1995, p. 143), allows us to write Eq. (E.8) in the simple form

$$\Phi(t) = \mathcal{T}\mathrm{Exp}\left(\int_0^t a(\tau)\, \mathrm{d}\tau \right). \tag{E.11}$$

Substituting the definitions of $\Phi(t)$ and $a(t)$ from Eqs. (E.5) and (E.6), this solution actually reads

$$\frac{\partial \varphi_i}{\partial x_j^0} = \mathcal{T}\mathrm{Exp}\left(\int_0^t \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)}\, \mathrm{d}\tau \right), \tag{E.12}$$

and, using Eq. (E.1), the final expression for the Jacobian of the stroboscopic map is

$$\frac{\partial \Pi_i}{\partial x_j^0} = \mathcal{T}\mathrm{Exp}\left(\int_0^T \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)}\, \mathrm{d}\tau \right). \tag{E.13}$$

Though the result looks elegant, remember that the time-ordering operator is simply a convenient mnemotechnical symbol: its real content is expressed by the infinite matrix product in Eq. (E.8).

Appendix F

The criterion for robustness

Suppressing indices for better readability, Eq. (3.19) will read

$$\frac{\mathrm{d}x^*}{\mathrm{d}E} = -\Big(\mathcal{T}\mathrm{Exp}(A) - \delta\Big)^{-1} \frac{\partial \bar{r}}{\partial E}, \tag{F.1}$$

where x^* and $\bar{r}$ stand for the vectors x_i^* and $\bar{r}_j$, respectively, $A = \int_0^T a(\tau)\,\mathrm{d}\tau$ with $a(t) = \mathbf{S}_i(t)\,\mathbf{I}_j(t)$ as introduced in Section 3.4, and δ is the identity matrix.

Since the inverse of a matrix is proportional to the inverse of its determinant, and the determinant will be near zero if any of the eigenvalues approach zero, the left hand side of the equation (the response of the equilibrium densities) will become large, leading to the destabilization of the equilibrium point, if any one eigenvalue of $\mathcal{T}\mathrm{Exp}(A) - \delta$ approaches zero. Our intuition is that two species having similar temporal niche vectors will lead to one of the eigenvalues being almost zero, i.e., species that are too similar cannot coexist robustly.

First we prove that linear dependence of the temporal impact (sensitivity) niches makes the matrix $\mathcal{T}\mathrm{Exp}(A) - \delta$ degenarate, i.e., having an eigenvalue of 0. Linear dependence of the temporal impact vectors means that there exists a time-independent L-dimensional vector $\alpha = (\alpha_1, \alpha_2, \ldots, \alpha_L)$ such that $\sum_{j=1}^{L} \alpha_j \mathbf{I}_j(\tau) = 0$ for all $\tau \in [\,0, T)$. Then, for all τ, α is a right eigenvector of the matrix $a_{ij}(\tau) = \mathbf{S}_i(\tau)\mathbf{I}_j(\tau)$ with a corresponding eigenvalue of 0. Or, using Eq. (E.8), α is a right eigenvector of $\mathcal{T}\mathrm{Exp}(A)$ with an eigenvaue of 1. This means that $\mathcal{T}\mathrm{Exp}(A) - \delta$ has an eigenvalue of $1 - 1 = 0$, implying our proposition. The same argument applies for the sensitivities and the left eigenvectors. Then, since eigenvalues and eigenvectors depend on the matrix elements continuously, similarity (i.e., near linear dependence) of the temporal impact or sensitivity niches leads to having an eigenvalue that is nearly zero, leading to non-robust coexistence.

Next, we will show that the product of the volumes spanned by the temporal niche vectors ($\mathcal{V}_{\mathbf{S}}\mathcal{V}_{\mathbf{I}}$) is still the proper measure of robustness: the system gradually loses its stability as this number gets closer to zero. First we verify by direct calculation that the determinant of $\mathcal{T}\mathrm{Exp}(A)$ is insensitive to time-ordering. Using Eq. (E.8),

$$\begin{aligned}
\det\mathcal{T}\mathrm{Exp}(A) &= \det\mathcal{T}\mathrm{Exp}\left(\int_0^T a(\tau)\,\mathrm{d}\tau\right) = \\
&= \det \lim_{\Delta t\to 0} \mathrm{Exp}(a(T-\Delta t)\Delta t)\cdot\ldots\cdot\mathrm{Exp}(a(\Delta t)\Delta t)\cdot\mathrm{Exp}(a(0)\Delta t) = \\
&= \lim_{\Delta t\to 0} \mathrm{Exp}(\mathrm{Tr}\,a(T-\Delta t)\Delta t)\cdot\ldots\cdot\mathrm{Exp}(\mathrm{Tr}\,a(\Delta t)\Delta t)\cdot\mathrm{Exp}(\mathrm{Tr}\,a(0)\Delta t) = \\
&= \mathrm{Exp}\left(\int_0^T \mathrm{Tr}\,a(\tau)\,\mathrm{d}\tau\right) = \mathrm{Exp}\left(\mathrm{Tr}\,\int_0^T a(\tau)\,\mathrm{d}\tau\right) = \\
&= \det\,\mathrm{Exp}\left(\int_0^T a(\tau)\,\mathrm{d}\tau\right) = \det\,\mathrm{Exp}\,(A)\,,
\end{aligned} \tag{F.2}$$

where $\mathrm{Tr}\,a$ denotes the trace of the matrix a.

Note that these results imply that the determinant of $\mathcal{T}\mathrm{Exp}(A)-\delta$ will become zero precisely when $\det A$ does so. Indeed, what we have is just a trivial rescaling of A, an artefact of the conversion between discrete and continuous dynamics (in Eq. (3.19) the equilibrium densities x_i^* are quantities of the discrete dynamics, whilst everything else is derived from the continuous equations). So we may disregard this trivial rescaling and simply use $\det A$ as the measure of robustness. Furthermore, the inequality of Eq. (3.10) can be applied to the matrix A to yield $|\det A| \leq \mathcal{V}_{\mathbf{S}}\mathcal{V}_{\mathbf{I}}$, demonstrating that community robustness can be measured exactly like in the equilibium case, provided that we think of the full set of regulating factors as containing every regulating factor at every moment within the cycle as a separate factor. This also means that all the hassle of matrix exponentials and time-ordered products may be completely ignored when applying the formalism to specific models: all that matter are the temporal sensitivity and impact vectors and the volumes they span.

Appendix G

Model analysis using the framework of Chesson (1994)

Here we perform the analysis of the model defined by Eq. (3.27) in Section 3.5 using Chesson's formalism. For this model, Chesson's environmental and competition parameters can be chosen as

$$E_j = \cos(\omega t + \phi_j) \tag{G.1}$$

and

$$C_j = n_1 + n_2, \tag{G.2}$$

respectively. Note that $\overline{E}_j = 0$ and that the competition parameter C_j is the same for the two species. Chesson's theory applies for small fluctuations; this assumption can be implemented by choosing the parameters r_e and K_e small.

With this parametrization, the instantaneous growth rate $r_j = g_j\left(E_j(t), C_j(t)\right)$ of the model is

$$\begin{aligned} g_j\left(E_j(t), C_j(t)\right) &= \varrho_j(1 + r_\mathrm{e}E_j)\left(1 - \frac{C_j}{\kappa_j\left(1 + K_\mathrm{e}E_j\right)}\right) \approx \\ &\approx \varrho_j\left(1 + r_\mathrm{e}E_j\right) - \frac{\varrho_j}{\kappa_j}\Big(1 + (r_\mathrm{e} - K_\mathrm{e})E_j\Big)C_j = \\ &= \varrho_j\left(1 - \frac{C_j}{\kappa_j}\right) + \varrho_j r_\mathrm{e} E_j - \frac{\varrho_j}{\kappa_j}(r_\mathrm{e} - K_\mathrm{e})E_j C_j, \end{aligned} \tag{G.3}$$

where $\approx$ means the small fluctuation approximation. The natural reference points are $E_j^* = 0$ and $C_j^* = \kappa_j$, for which $g_j(E_j^*, C_j^*) = 0$ is satisfied, as required. Then the standardized parameters of Chesson are

$$\mathcal{E}_j = g_j(E_j, C_j^*) = \varrho_j K_\mathrm{e} E_j \tag{G.4}$$

and

$$\mathcal{C}_j = -g_j(E_j^*, C_j) = -\varrho_j \left(1 - \frac{C_j}{\kappa_j}\right). \tag{G.5}$$

Using these notations, the growth rate is

$$r_j \approx \mathcal{E}_j - \mathcal{C}_j + \gamma_j \mathcal{E}_j \mathcal{C}_j, \tag{G.6}$$

where

$$\gamma_j = -\frac{r_\mathrm{e} - K_\mathrm{e}}{K_\mathrm{e} \varrho_j} \tag{G.7}$$

is the measure of nonadditivity. Note that since r_e was greater than K_e in our simulations, the γ_j are negative, i.e., we have a subadditive situation.

Since the competition parameter C is a linear function of the competitive factors (the two densities in this case), this model does not produce relative nonlinearity. However, there is storage effect. Chesson's formula for the storage effect reads

$$\Delta I = \gamma_i \overline{\mathcal{E}_i \mathcal{C}_i^{-i}} - \sum_r q_{ir} \gamma_r \overline{\mathcal{E}_r \mathcal{C}_r^{-i}}, \tag{G.8}$$

where the overline denotes time-averaging, i is the invader index, r is the resident, the $-i$ superscript means that the given quantity is to be evaluated with species i at zero density and all other species at their equilibria, and

$$q_{ir} = \frac{\partial \mathcal{C}_i^{-i}}{\partial \mathcal{C}_r^{-i}} \tag{G.9}$$

are factors introduced into the theory so that all linear terms in the final expression for the coexistence-affecting mechanisms cancel (this does not play a great role in our case, but becomes crucial if the competitive factors are nonlinear functions of the densities, i.e., if relative nonlinearity is operating). Let us calculate ΔI in our model. The standardized competition parameter, as given by Eq. (G.5), is

$$\mathcal{C}_j = \frac{\varrho_j}{\kappa_j}(n_r + n_i) - \varrho_j \tag{G.10}$$

(j is a general species index which may refer to the resident or the invader), and so

$$C_j^{-i} = \frac{\varrho_j}{\kappa_j} n_r - \varrho_j. \tag{G.11}$$

The differential of this expression is

$$\mathrm{d}C_j^{-i} = \mathrm{d}\left(\frac{\varrho_j}{\kappa_j} n_r - \varrho_j\right) = \frac{\varrho_j}{\kappa_j} \mathrm{d}n_r, \tag{G.12}$$

therefore

$$q_{ir} = \frac{\partial C_i^{-i}}{\partial C_r^{-i}} = \frac{\varrho_i \kappa_r}{\varrho_r \kappa_i}. \tag{G.13}$$

Let us work a little more on the expression $\overline{\mathcal{E}_j C_k^{-i}}$, using the fact that $\mathcal{E}_j = \varrho_j K_e E_j$:

$$\begin{aligned} \overline{\mathcal{E}_j C_k^{-i}} &= \overline{\varrho_j K_e E_j \frac{\varrho_k}{\kappa_k}(n_r - \kappa_k)} = \\ &= \frac{\varrho_j \varrho_k K_e}{\kappa_k} \overline{E_j n_r} \end{aligned} \tag{G.14}$$

(the second term is zero, since $\overline{E}_j = 0$). Substituting all of this into Eq. (G.8) we get

$$\begin{aligned} \Delta I &= \gamma_i \overline{\mathcal{E}_i C_i^{-i}} - q_{ir} \gamma_r \overline{\mathcal{E}_r C_r^{-i}} = \\ &= \frac{K_e - r_e}{K_e \varrho_i} \frac{\varrho_i^2 K_e}{\kappa_i} \overline{E_i n_r} - \frac{\varrho_i \kappa_r}{\varrho_r \kappa_i} \frac{K_e - r_e}{K_e \varrho_r} \frac{\varrho_r^2 K_e}{\kappa_r} \overline{E_r n_r} = \\ &= \varrho_i \frac{K_e - r_e}{\kappa_i} \overline{E_i n_r} - \varrho_i \frac{K_e - r_e}{\kappa_i} \overline{E_r n_r} = \\ &= \varrho_i \frac{K_e - r_e}{\kappa_i} \left(\overline{E_i n_r} - \overline{E_r n_r}\right) = \\ &= \frac{\varrho_i}{\kappa_i} (r_e - K_e) \Big(\mathrm{Cov}(E_r n_r) - \mathrm{Cov}(E_i n_r)\Big), \end{aligned} \tag{G.15}$$

where we used Eq. (G.7) to evaluate γ_r. As mentioned before, $r_e - K_e$ is positive, and so is $\mathrm{Cov}(E_r n_r) - \mathrm{Cov}(E_i n_r)$, because the resident obviously correlates more strongly with its own E than that of the other species. It follows that $\Delta I > 0$ and so we have the storage effect.

Appendix H

Sensitivity analysis of forb-grass competition

Model description

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

$$N_1(t+1) = \left((1 - g_1(t))(1 - d_1) + \frac{\lambda_1(t) g_1(t)}{1 + g_1(t) N_1(t) + \alpha\, g_2(t) N_2(t)} \right) N_1(t), \tag{H.1}$$

$$N_2(t+1) = \left((1 - g_2(t))(1 - d_2) + \frac{\lambda_2(t) g_2(t)}{1 + g_1(t) N_1(t)/\alpha + g_2(t) N_2(t)} \right) N_2(t), \tag{H.2}$$

where $N_1(t)$ and $N_2(t)$ are the number of seeds of forb (species 1) and grass (species 2) in the seed bank in year t prior to germination, $g_1(t)$ and $g_2(t)$ are the the fraction of forb/grass seeds that germinate in year t, d_1 and d_2 are the death rates of ungerminated forb/grass seeds in the soil, $\lambda_1(t)$ and $\lambda_2(t)$ are the number of seeds in year t produced per individual of forb/grass that survive to the start of the growing season, and α is an interspecific competition parameter, assuming reciprocal competition: if the effect of grass on forb is α, then the effect of forb on grass is $1/\alpha$.

To analyze the model, we first choose the regulating factors. It is actually possible to choose a single regulating factor for this model:

$$\mathcal{R}(t) = \frac{g_1(t) N_1(t)}{\alpha} + g_2(t) N_2(t). \tag{H.3}$$

Using this, both model equations may be written in the form

$$N_i(t+1) = \left((1 - g_i(t))(1 - d_i) + \frac{\lambda_i(t) g_i(t)}{1 + \alpha_i \mathcal{R}(t)}\right) N_i(t), \tag{H.4}$$

where α_i is equal to α for $i = 1$ (forb) and to 1 for $i = 2$ (grass). The expression in parentheses is the annual geometric rate of growth; its natural log is the growth rate $r_i(t)$:

$$r_i(t) = \log\left((1 - g_i(t))(1 - d_i) + \frac{\lambda_i(t) g_i(t)}{1 + \alpha_i \mathcal{R}(t)}\right). \tag{H.5}$$

The meanings and numerical values of the parameters were summarized in Table 4.1.

The stationary state

As discussed in the main text, we assume the environment fluctuates periodically between good and bad years, i.e., we have a bad year whenever t is even and a good year whenever t is odd. This will generate a stationary two-cycle. If the model has a two-cycle, the twice-compounded model will have a fixed point. Moreover, it will have two possible solutions, corresponding to the two distinct points within the cycle. Using Eq. (H.4), the populations over two time steps remain constant:

$$1 = \left((1 - g_i(0))(1 - d_i) + \frac{\lambda_i(0) g_i(0)}{1 + \alpha_i \mathcal{R}(0)}\right)\left((1 - g_i(1))(1 - d_i) + \frac{\lambda_i(1) g_i(1)}{1 + \alpha_i \mathcal{R}(1)}\right). \tag{H.6}$$

We can write this as a function of the initial densities using Eq. (H.3):

$$\begin{aligned} 1 = &\left((1 - g_i(0))(1 - d_i) + \frac{\lambda_i(0) g_i(0)}{1 + \alpha_i \left(g_1(0) N_1(0)/\alpha + g_2(0) N_2(0)\right)}\right) \\ &\times \left((1 - g_i(1))(1 - d_i) + \frac{\lambda_i(1) g_i(1)}{1 + \alpha_i \left(g_1(1) N_1(1)/\alpha + g_2(1) N_2(1)\right)}\right), \end{aligned} \tag{H.7}$$

where $N_i(1)$ has to be expressed as a function of $N_i(0)$:

$$N_i(1) = \left((1 - g_i(0))(1 - d_i) + \frac{\lambda_i(0) g_i(0)}{1 + \alpha_i \left(g_1(0) N_1(0)/\alpha + g_2(0) N_2(0)\right)}\right) N_i(0). \tag{H.8}$$

For both $i = 1$ and $i = 2$, Eq. (H.7) constitutes an equation for the fixed point of the twice-compounded model (i.e., the limit cycle of the original one). With the parameters given in Table 4.1, the solution can be obtained numerically via any reputable algorithm for solving systems of nonlinear algebraic equations. The two pairs of solutions are

$$\begin{aligned}
&\Big(N_1(0) = 19.697; \quad N_2(0) = 4.329\Big), \\
&\Big(N_1(1) = 23.636; \quad N_2(1) = 10.044\Big).
\end{aligned} \tag{H.9}$$

Sensitivity of the two-cycle

The sensitivity of a discrete-time T-cycle to perturbing a model parameter $\mathbb{E}$ (Barabás et al. 2012a, Barabás and Ostling 2013) is given by the formula

$$\frac{\mathrm{d}N_i(0)}{\mathrm{d}\mathbb{E}} = -N_i(0) \sum_{j=1}^{S} (A^{-1})_{ij} z_j, \tag{H.10}$$

where $N_i(0)$ is the density of species i at the beginning of the cycle, S is the total number of species (2 in our case), the vector z_j is given by

$$z_j = \frac{\partial}{\partial \mathbb{E}} \sum_{t=0}^{T-1} r_j(t), \tag{H.11}$$

and the matrix A_{ij} is given as follows. Let us first define

$$a_{ij}(t) = \frac{\partial r_i(t)}{\partial \mathcal{R}(t)} \frac{\partial \mathcal{R}(t)}{\partial N_j(t)} N_j(t). \tag{H.12}$$

Then,

$$A_{ij} = -\delta_{ij} + \sum_{k_1} \sum_{k_2} \cdots \sum_{k_T} \left(\delta_{ik_1} + a_{ik_1}(T-1)\right) \left(\delta_{k_1 k_2} + a_{k_1 k_2}(T-2)\right) \cdots \Big(\delta_{k_T j} + a_{k_T j}(0)\Big) \tag{H.13}$$

(Barabás and Ostling 2013), where δ_{ij} is the Kronecker symbol, equal to 1 if $i = j$ and to 0 otherwise. We now calculate each of these components in turn.

First we obtain $a_{ij}(t)$. From Eq. (H.5), the derivative of $r_i(t)$ with respect to $\mathcal{R}(t)$ is

$$\frac{\partial r_i(t)}{\partial \mathcal{R}(t)} = \left((1 - g_i(t))(1 - d_i) + \frac{\lambda_i(t) g_i(t)}{1 + \alpha_i \mathcal{R}(t)} \right)^{-1} \frac{\alpha_i \lambda_i(t) g_i(t)}{(1 + \alpha_i \mathcal{R}(t))^2}, \tag{H.14}$$

and the derivative of $\mathcal{R}(t)$ with respect to $N_j(t)$ is, from Eq. (H.3),

$$\frac{\partial \mathcal{R}(t)}{\partial N_j(t)} = \frac{g_j(t)}{\alpha_j}. \tag{H.15}$$

By Eq. (H.12), the product of these two times $N_j(t)$ yields $a_{ij}(t)$:

$$a_{ij}(t) = \left((1 - g_i(t))(1 - d_i) + \frac{\lambda_i(t) g_i(t)}{1 + \alpha_i \mathcal{R}(t)}\right)^{-1} \frac{\alpha_i \lambda_i(t) g_i(t) g_j(t) N_j(t)}{\alpha_j \left(1 + \alpha_i \mathcal{R}(t)\right)^2}. \tag{H.16}$$

Using Table 4.1 and Eq. (H.9), $a_{ij}(0)$ and $a_{ij}(1)$ can be evaluated numerically:

$$a_{ij}(0) = -\begin{pmatrix} 0.473 & 0.267 \\ 0.577 & 0.326 \end{pmatrix}, \tag{H.17}$$

and

$$a_{ij}(1) = -\begin{pmatrix} 0.003 & 0.024 \\ 0.098 & 0.749 \end{pmatrix}. \tag{H.18}$$

We can now calculate A_{ij}. For a two-cycle, Eq. (H.13) reduces to

$$A_{ij} = -\delta_{ij} + \sum_k \Big(\delta_{ik} + a_{ik}(1)\Big)\Big(\delta_{kj} + a_{kj}(0)\Big). \tag{H.19}$$

Substituting in $a_{ij}(0)$, $a_{ij}(1)$, and the identity matrix for δ_{ij}, and performing the matrix operations leaves us with

$$A_{ij} = -\begin{pmatrix} 0.461 & 0.283 \\ 0.196 & 0.805 \end{pmatrix}. \tag{H.20}$$

The inverse of this matrix is then

$$(A^{-1})_{ij} = \begin{pmatrix} -2.549 & 0.894 \\ 0.621 & -1.460 \end{pmatrix}. \tag{H.21}$$

To obtain z_i from Eq. (H.11), we need the sum of the growth rates for the two points of the cycle. This we can get by taking the log of the right hand side of Eq. (H.7), using Eq. (H.8) to express $N_i(1)$. We then take the derivative of this expression with respect to any of the parameters and substitute in numerical values from Table 4.1 and Eq. (H.9) to obtain z_i. Table H.1 contains the results. The cycle's sensitivity to each parameter can now be obtained via Eq. (H.10), i.e., by multiplying these vectors with the matrix $(A^{-1})_{ij}$ and then multiplying the result by $-N_i(0)$.

These calculations assumed that the "first" moment within the cycle happened at $t = 0$. There is nothing special about this moment – indeed, we could treat $t = 1$ as the first moment in the cycle by simply relabeling the time tags ($t = 1$ becomes what

$\mathbb{E}$	z_1	z_2
α	-0.152	-0.134
d_1	-1.329	0.024
d_2	0.001	-0.243
$\lambda_1(0)$	0.026	-0.003
$\lambda_1(1)$	0.006	0
$\lambda_2(0)$	-0.001	0.008
$\lambda_2(1)$	0	0.186
$g_1(0)$	-0.298	-0.175
$g_1(1)$	-0.831	-0.980
$g_2(0)$	-0.311	0.181
$g_2(1)$	-0.026	-0.495

Table H.1: The two components of the vector z_i for each parameter.

used to be $t = 0$ and vice versa). This way the sensitivity of the second moment in the cycle can be calculated. Using Eq. (H.13) and the already calculated values for $a_{ij}(0)$ and $a_{ij}(1)$ (do not forget that the time labels have to be switched), we get

$$A_{ij} = -\begin{pmatrix} 0.449 & 0.079 \\ 0.641 & 0.818 \end{pmatrix}, \tag{H.22}$$

the inverse of which is

$$(A^{-1})_{ij} = \begin{pmatrix} -2.588 & 0.251 \\ 2.031 & -1.420 \end{pmatrix}. \tag{H.23}$$

The sensitivity of the second point in the cycle to a parameter is then calculated from Eq. (H.10), i.e., by multiplying the appropriate vector z_j with this matrix and then multiplying the result by the density of the ith population at the initial moment (which would have been at $t = 1$ and not $t = 0$ before relabeling time). These sensitivities were not shown in the main text, as they are very similar to the sensitivities at the other moment in the cycle.

Appendix I

The tolerance-fecundity tradeoff model

Model construction

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). The number of sites of stress level s_a is $c(s_a)$. Individuals produce seeds that disperse into all sites with a uniform probability distribution. Their fecundities are high enough so that no site ever remains empty after reproduction. Once a seed reaches a freshly vacated 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.

This model may be written as

$$\frac{\mathrm{d}N_{i,a}}{\mathrm{d}t} = f_i N_i Q_i(s_a) - m_i N_{i,a}, \tag{I.1}$$

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.,

$$N_i = \sum_{a=1}^{M} N_{i,a}. \tag{I.2}$$

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 a site of stress level s_a. This is given by

$$G(s_a) = \frac{c(s_a) - \sum_i N_{i,a}}{\sum_{b=1}^{M} c(s_b)}, \tag{I.3}$$

where the numerator expresses the number of sites of stress s_a that are not yet occupied (the summation runs over all the species), 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 6.3). 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 to 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 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

$$F(s_a) = \frac{\sum_k f_k N_k T_k(s_a)}{\sum_{b=1}^{M} c(s_b)}. \tag{I.4}$$

Therefore, $Q_i(s_a)$ may be written

$$Q_i(s_a) = G(s_a) T_i(s_a) \frac{1}{F(s_a)} = T_i(s_a) \frac{c(s_a) - \sum_i N_{i,a}}{\sum_k f_k N_k T_k(s_a)}. \tag{I.5}$$

Substituting this expression into Eq. (I.1) yields

$$\frac{\mathrm{d}N_{i,a}}{\mathrm{d}t} = f_i N_i T_i(s_a) \frac{c(s_a) - \sum_i N_{i,a}}{\sum_k f_k N_k T_k(s_a)} - m_i N_{i,a}. \tag{I.6}$$

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

$$\frac{\mathrm{d}N_{i,a}}{\mathrm{d}t} = \sum_{b=1}^{M} \left(f_i T_i(s_a) \frac{c(s_a) - \sum_i N_{i,a}}{\sum_k f_k N_k T_k(s_a)} - m_i \delta_{ab} \right) N_{i,b}, \tag{I.7}$$

where we used Eq. (I.2) in the first term on the right hand side; the δ_{ab} in the second term is the Kronecker symbol, equal to 1 if $a = b$ and to 0 otherwise (it therefore represents the identity matrix). The expression in the parentheses is the projection matrix $A_{i,ab}$ of species i, multiplying the stage distribution vector $N_{i,b}$:

$$A_{i,ab} = f_i T_i(s_a) \frac{c(s_a) - \sum_i N_{i,a}}{\sum_k f_k N_k T_k(s_a)} - m_i \delta_{ab}. \tag{I.8}$$

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.

Notice that the $A_{i,ab}$ depend on the densities only through the fraction in the first term of Eq. (I.8). Therefore, a natural choice for the regulating factors is

$$\mathcal{R}(s_a) = \frac{c(s_a) - \sum_i N_{i,a}}{\sum_k f_k N_k T_k(s_a)} = \frac{G(s_a)}{F(s_a)}, \tag{I.9}$$

which is the density-dependent factor in $Q_i(s_a)$. The model then reads

$$\frac{\mathrm{d}N_{i,a}}{\mathrm{d}t} = \sum_{b=1}^{M} \Big(f_i T_i(s_a) \mathcal{R}(s_a) - m_i \delta_{ab} \Big) N_{i,b}. \tag{I.10}$$

Sensitivities

As Eq. (I.10) is a model where each population is stage-structured, calculation of the sensitivities and impacts has to follow the formalism developed for this particular class of models (Szilágyi and Meszéna 2009a, Barabás et al. under review). The sensitivity of the ith species to the σth regulating factor reads

$$\mathcal{S}_{i,\sigma} = \sum_{a=1}^{M} \sum_{b=1}^{M} v_{i,a} \frac{\partial A_{i,ab}}{\partial \mathcal{R}(s_\sigma)} w_{i,b}, \tag{I.11}$$

where $v_{i,a}$ and $w_{i,a}$ are the ath component of the left and right leading eigenvectors of $A_{i,ab}$, respectively. For this formula to be true, the normalization conditions $\sum_{a=1}^{M} w_{i,a} = 1$ and $\sum_{a=1}^{M} v_{i,a} w_{i,a} = 1$ have to hold for all i. Biologically, since this formula is evaluated at equilibrium, the left leading eigenvector is the reproductive value vector while the right leading eigenvector is the stable stage distribution.

The derivative can be calculated directly:

$$\frac{\partial A_{i,ab}}{\partial \mathcal{R}(s_\sigma)} = \frac{\partial}{\partial \mathcal{R}(s_\sigma)}\Big(f_i T_i(s_a)\mathcal{R}(s_a) - m_i\delta_{ab}\Big) = f_i T_i(s_a)\delta_{a\sigma}. \tag{I.12}$$

To evaluate the eigenvectors of $A_{i,ab}$, notice first that the second term on the right hand side of Eq. (I.8) is proportional to the identity matrix and does not influence the eigenvectors. Therefore, only the first term (let us denote it by M_{ab}) needs to be considered for calculating eigenvectors. This first term can also be written $M_{ab} = g_a h_b$, where $g_a = f_i T_i(s_a)\mathcal{R}(s_a)$ and $h_b = 1$ (i.e., each component of h_b is equal to 1). Such a matrix has only one right and one corresponding left eigenvector, given by g_a and h_b themselves, with a nonzero corresponding eigenvalue. Indeed, for any vector x_a,

$$\sum_b M_{ab}x_b = \sum_b g_a h_b x_b = g_a\left(\sum_b h_b x_b\right), \tag{I.13}$$

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,

$$\sum_b x_b M_{ba} = \sum_b x_b g_b h_a = h_a\left(\sum_b g_b x_b\right). \tag{I.14}$$

From this it is also clear that the nonzero eigenvalue itself is given by $\sum_a g_a h_a$. 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 $g_a = f_i T_i(s_a)\mathcal{R}(s_a)$:

$$w_{i,a} = q_i f_i T_i(s_a)\mathcal{R}(s_a), \tag{I.15}$$

where

$$q_i = \left(\sum_{a=1}^{M} f_i T_i(s_a)\mathcal{R}(s_a)\right)^{-1}. \tag{I.16}$$

ensures proper normalization. Similarly, since $h_a = 1$, the properly normalized left eigenvector will be $v_{i,a} = 1$ for all species. The sensitivities can now be calculated:

$$\begin{aligned} \mathcal{S}_{i,\sigma} &= \sum_{a=1}^{M} \sum_{b=1}^{M} v_{i,a} \frac{\partial A_{i,ab}}{\partial \mathcal{R}(s_\sigma)} w_{i,b} = \sum_{a=1}^{M} \sum_{b=1}^{M} 1 \times f_i T_i(s_a) \delta_{a\sigma} q_i f_i T_i(s_b) \mathcal{R}(s_b) \\ &= \sum_{a=1}^{M} f_i T_i(s_a) \delta_{a\sigma} q_i \underbrace{\left(\sum_{b=1}^{M} f_i T_i(s_b) \mathcal{R}(s_b) \right)}_{1/q_i} = \sum_{a=1}^{M} f_i T_i(s_a) \delta_{a\sigma} = f_i T_i(s_\sigma). \end{aligned} \tag{I.17}$$

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

The volume spanned by the sensitivities

The area (two-dimensional volume) A spanned by two M-dimensional vectors x_a and y_a is given by the elementary formula

$$A = \sqrt{\left(\sum_{a=1}^{M} x_a^2 \right) \left(\sum_{a=1}^{M} y_a^2 \right) - \left(\sum_{a=1}^{M} x_a y_a \right)^2} \tag{I.18}$$

(Meszéna et al. 2006, Appendix C). We have determined above that the sensitivity of a species is given by $\mathcal{S}_{i,\sigma} = f_i T_i(s_\sigma)$. It is cleanest to assume here that there is no limit to how fine the various gradations of stress can be, and so the discrete sensitivity vector can be thought of as a continuous sensitivity function: $\mathcal{S}_i(\sigma) = f_i T_i(\sigma)$, where σ may take on any value between the minimum (s_{min}) and maximum (s_{max}) possible stress levels. Then, we have to use the generalization of Eq. (I.18) to two functions instead of two vectors:

$$\mathcal{V}_{\mathcal{S}} = \sqrt{\left(\int_{s_{\mathrm{min}}}^{s_{\mathrm{max}}} \mathcal{S}_1^2(\sigma)\, \mathrm{d}\sigma \right) \left(\int_{s_{\mathrm{min}}}^{s_{\mathrm{max}}} \mathcal{S}_2^2(\sigma)\, \mathrm{d}\sigma \right) - \left(\int_{s_{\mathrm{min}}}^{s_{\mathrm{max}}} \mathcal{S}_1(\sigma) \mathcal{S}_2(\sigma)\, \mathrm{d}\sigma \right)^2}. \tag{I.19}$$

This is the formula giving the area spanned by two functions, used to make Figure 6.4. The particular functional form we use for the tolerance function is

$$T_i(s) = \frac{\tanh\big(25(f_i - s)\big) + 1}{2}, \tag{I.20}$$

depicted on Figure 6.3.

Impacts

The formula for the impact of the jth species on the σth regulating factor in structured community models reads

$$\mathcal{I}_{j,\sigma} = \sum_{a=1}^{M} \frac{\partial \mathcal{R}(s_\sigma)}{\partial N_{j,a}} w_{j,a} \tag{I.21}$$

(Szilágyi and Meszéna 2009a, Barabás et al. under review). Using Eq. (I.15), this becomes

$$\mathcal{I}_{j,\sigma} = \sum_{a=1}^{M} \frac{\partial \mathcal{R}(s_\sigma)}{\partial N_{j,a}} q_j f_j T_j(s_a) \mathcal{R}(s_a). \tag{I.22}$$

We calculate the partial derivative:

$$\begin{aligned} \frac{\partial \mathcal{R}(s_\sigma)}{\partial N_{j,a}} &= -\frac{\delta_{a\sigma}}{\sum_k f_k N_k T_k(s_\sigma)} - \frac{c(s_\sigma) - \sum_i N_{i,\sigma}}{\left(\sum_k f_k N_k T_k(s_\sigma)\right)^2} \underbrace{\frac{\partial}{\partial N_{j,a}} \left(\sum_k f_k \left(\sum_{b=1}^{M} N_{k,b} \right) T_k(s_\sigma) \right)}_{f_j T_j(s_\sigma)} \\ &= -\frac{\delta_{a\sigma}}{\sum_k f_k N_k T_k(s_\sigma)} - \frac{c(s_\sigma) - \sum_i N_{i,\sigma}}{\left(\sum_k f_k N_k T_k(s_\sigma)\right)^2} f_j T_j(s_\sigma), \end{aligned} \tag{I.23}$$

or, using Eq. (I.9) in the second term,

$$\frac{\partial \mathcal{R}(s_\sigma)}{\partial N_{j,a}} = -\left(\frac{\delta_{a\sigma}}{\sum_k f_k N_k T_k(s_\sigma)} + \frac{f_j T_j(s_\sigma) \mathcal{R}(s_\sigma)}{\sum_k f_k N_k T_k(s_\sigma)} \right). \tag{I.24}$$

The impacts then read

$$\begin{aligned} \mathcal{I}_{j,\sigma} &= -\sum_{a=1}^{M} \left(\frac{\delta_{a\sigma}}{\sum_k f_k N_k T_k(s_\sigma)} + \frac{f_j T_j(s_\sigma) \mathcal{R}(s_\sigma)}{\sum_k f_k N_k T_k(s_\sigma)} \right) q_j f_j T_j(s_a) \mathcal{R}(s_a) \\ &= -\frac{q_j f_j T_j(s_\sigma) \mathcal{R}(s_\sigma)}{\sum_k f_k N_k T_k(s_\sigma)} - \frac{f_j T_j(s_\sigma) \mathcal{R}(s_\sigma)}{\sum_k f_k N_k T_k(s_\sigma)} q_j \sum_{a=1}^{M} f_j T_j(s_a) \mathcal{R}(s_a), \end{aligned} \tag{I.25}$$

and since the last sum is simply equal to $1/q_j$ due to Eq. (I.16), the impacts are given by

$$\mathcal{I}_{j,\sigma} = -\frac{(q_j + 1) f_j T_j(s_\sigma) \mathcal{R}(s_\sigma)}{\sum_k f_k N_k T_k(s_\sigma)}. \tag{I.26}$$

In this expression $T_j(s_\sigma)$ and $\mathcal{R}(s_\sigma)$ in the numerator are probabilities and so are between 0 and 1, and we have already made the assumption that the seed rain (the denominator) contains at least one seed per empty site and so 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; the q_j could in principle be made large, but that would require fine-tuning of parameters). This means that each component of all impact vectors are bounded in magnitude. Then, due to Eq. (I.18), the volume spanned by these vectors will also be bounded.

Since robustness is determined by $\mathcal{V}_\mathcal{S}\mathcal{V}_\mathcal{I}$, this observation means that whenever the sensitivity volume is small, robustness will also necessarily be small, because $\mathcal{V}_\mathcal{I}$ is bounded from above and so cannot compensate for a small $\mathcal{V}_\mathcal{S}$. Also, $\mathcal{I}_{j,\sigma}$ is proportional to $\mathcal{S}_{j,\sigma} = f_j T_j(s_\sigma)$, therefore one would expect $\mathcal{V}_\mathcal{I}$ to be large/small wherever $\mathcal{V}_\mathcal{S}$ is large/small. Therefore the sensitivity volumes are sufficient to determine the robustness of coexistence.

Appendix J

The Gross model

Model equations

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

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

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

$$\frac{1}{N_i} \frac{\mathrm{d}N_i}{\mathrm{d}t} = f_i(R) - m_i \tag{J.2}$$

for the species ($i = 1 \ldots S$), and

$$\frac{\mathrm{d}R}{\mathrm{d}t} = g(R) - \sum_{i=1}^{S} c_i f_i(R) N_i \tag{J.3}$$

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. (J.1), 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 hierarchical assumption

The form of the mortalities in Eq. (J.1) is fairly general. Kevin Gross 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:

$$m_i = m_i^0 - d_i \left(1 - \exp\left(-\theta \sum_{k<i} N_k \right) \right). \tag{J.4}$$

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.

The sensitivity and impact volumes

To analyze the robustness of coexistence, first we need to designate regulating factors. We choose $\mathcal{R}_{\mu=1} = R$ and $\mathcal{R}_{\mu>1} = \exp(-\theta \sum_{k<\mu} N_k)$. 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 $\mathcal{R}_{\mu>1} = N_\mu$. The final results are insensitive to our particular choice. 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 $\mathcal{R}_{\mu>1} = \exp(-\theta \sum_{k<\mu} N_k)$ lends itself to analytical treatment much better than the other choices.

The model equations, written in terms of the regulating factors, read

$$\begin{aligned} \frac{1}{N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} &= f_1(\mathcal{R}_1) - m_1^0, \\ \frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} &= f_i(\mathcal{R}_1) - m_i^0 + d_i - d_i\mathcal{R}_i \qquad (i = 2 \ldots S), \end{aligned} \tag{J.5}$$

where the regulating factors are governed by

$$\begin{aligned} \frac{\mathrm{d}\mathcal{R}_1}{\mathrm{d}t} &= g(\mathcal{R}) - \sum_{i=1}^{S} c_i f_i(\mathcal{R}_1) N_i, \\ \mathcal{R}_\mu &= \exp\left(-\theta \sum_{k<\mu} N_k\right) \qquad (\mu = 2\ldots S). \end{aligned} \tag{J.6}$$

We can now calculate the sensitivities $\mathcal{S}_{i,\mu}$ and impacts $\mathcal{I}_{j,\mu}$:

$$\mathcal{S}_{i,\mu} = \frac{\partial r_i}{\partial \mathcal{R}_\mu} = \left(\frac{\partial f_i}{\partial \mathcal{R}_1}, 0, \ldots, 0, \underbrace{-d_i}_{i\text{th}}, 0, \ldots, 0\right), \tag{J.7}$$

$$\mathcal{I}_{j,\mu} = \frac{\partial \mathcal{R}_\mu}{\partial N_j} = \left(\frac{\partial \mathcal{R}_1}{\partial N_j}, 0, \ldots, 0, \underbrace{-\theta \mathcal{R}_{j+1}}_{(j+1)\text{th}}, -\theta \mathcal{R}_{j+2}, \ldots, -\theta \mathcal{R}_S\right), \tag{J.8}$$

where $r_i = \mathrm{d}N_i/(N_i \mathrm{d}t)$ is the per capita growth rate of species i, and all quantities are evaluated at equilibrium.

The robustness of the system is governed by the determinant of the matrix $\partial r_i/\partial N_j$. In this model the determinant can be written

$$\det\left(\frac{\partial r_i}{\partial N_j}\right) = \det\left(\sum_{\mu=1}^{S} \frac{\partial r_i}{\partial \mathcal{R}_\mu} \frac{\partial \mathcal{R}_\mu}{\partial N_j}\right) = \det\left(\frac{\partial r_i}{\partial \mathcal{R}_\mu}\right) \det\left(\frac{\partial \mathcal{R}_\mu}{\partial N_j}\right) = \det\left(\mathcal{S}_{i,\mu}\right) \det\left(\mathcal{I}_{j,\mu}\right), \tag{J.9}$$

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

$$\left|\det\left(\mathcal{S}_{i,\mu}\right) \det\left(\mathcal{I}_{j,\mu}\right)\right| = \mathcal{V}_{\mathcal{S}} \mathcal{V}_{\mathcal{I}}, \tag{J.10}$$

i.e., the absolute values of the determinants measure the volumes spanned by their rows as vectors (or their columns as vectors: the volumes turn out to be the same either way).

We now explicitly calculate these two volumes. (This is where our particular choice for the regulating factors comes in handy – these volumes would be difficult or even impossible to determine using other choices.)

$$\mathcal{V}_\mathcal{S} = \left|\det\begin{pmatrix} \frac{\partial f_1}{\partial \mathcal{R}_1} & 0 & 0 & \cdots \\ \frac{\partial f_2}{\partial \mathcal{R}_1} & -d_2 & 0 & \cdots \\ \frac{\partial f_3}{\partial \mathcal{R}_1} & 0 & -d_3 & \cdots \\ \vdots & \vdots & \vdots & \ddots \end{pmatrix}\right| = \left|\frac{\partial f_1}{\partial \mathcal{R}_1}\right| \prod_{i=2}^{S} d_i, \tag{J.11}$$

$$\mathcal{V}_\mathcal{I} = \left|\det\begin{pmatrix} \frac{\partial \mathcal{R}_1}{\partial N_1} & -\theta\mathcal{R}_2 & -\theta\mathcal{R}_3 & \cdots \\ \frac{\partial \mathcal{R}_1}{\partial N_2} & 0 & -\theta\mathcal{R}_3 & \cdots \\ \frac{\partial \mathcal{R}_1}{\partial N_3} & 0 & 0 & \cdots \\ \vdots & \vdots & \vdots & \ddots \end{pmatrix}\right| = \left|\frac{\partial \mathcal{R}_1}{\partial N_S}\right| \theta^{S-1} \prod_{i=2}^{S} \mathcal{R}_i. \tag{J.12}$$

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

$$\begin{aligned} \mathcal{V}_\mathcal{S}\mathcal{V}_\mathcal{I} &= \left|\frac{\partial f_1}{\partial \mathcal{R}_1}\frac{\partial \mathcal{R}_1}{\partial N_S}\right| \theta^{S-1} \left(\prod_{i=2}^{S} d_i\right)\left(\prod_{i=2}^{S} \mathcal{R}_i\right) \\ &= \left|\frac{\partial f_1}{\partial \mathcal{R}_1}\frac{\partial \mathcal{R}_1}{\partial N_S}\right| \theta^{S-1} \left(\prod_{i=2}^{S} d_i\right) \mathrm{e}^{-\theta N_1}\mathrm{e}^{-\theta(N_1+N_2)}\cdots\mathrm{e}^{-\theta(N_1+\cdots+N_{S-1})} \\ &= \left|\frac{\partial f_1}{\partial \mathcal{R}_1}\frac{\partial \mathcal{R}_1}{\partial N_S}\right| \theta^{S-1} \left(\prod_{i=2}^{S} d_i\right) \mathrm{e}^{-\theta\left((S-1)N_1+(S-2)N_2+\cdots+N_{S-1}\right)}. \end{aligned} \tag{J.13}$$

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

$$\begin{aligned} \mathcal{V}_\mathcal{S}\mathcal{V}_\mathcal{I} &\leq \left|\frac{\partial f_1}{\partial \mathcal{R}_1}\frac{\partial \mathcal{R}_1}{\partial N_S}\right| \theta^{S-1} \left(\prod_{i=2}^{S} d_i\right) \mathrm{e}^{-\theta\left((S-1)N+(S-2)N+\cdots+N\right)} \\ &= \left|\frac{\partial f_1}{\partial \mathcal{R}_1}\frac{\partial \mathcal{R}_1}{\partial N_S}\right| \theta^{S-1} \left(\prod_{i=2}^{S} d_i\right) \mathrm{e}^{-\theta N S(S-1)/2}. \end{aligned} \tag{J.14}$$

This expression asymptotically depends on the number of species as $\exp(-\theta N S^2/2)$. It converges to zero faster than exponential as the number of species in the system increases (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 sensitivity and impact volumes must also converge to zero at least as fast as $\exp(-\theta N S^2/2)$.

Robustness of the system as a function of the number of species

If any one eigenvalue of the Jacobian matrix $\partial r_i/\partial N_j$ is very close to zero, the system will be unrobust. This is because in that case a very small perturbation of a model parameter could be enough to push that eigenvalue over to the right half of the complex plane, thus destabilizing the fixed point. We have shown above that in our model, the product of the sensitivity and impact volumes – and therefore, due to Eq. (J.9), the determinant of the Jacobian – converges to zero as S increases. An elementary theorem in linear algebra states that the determinant of a matrix is simply the product of its eigenvalues. Since this product then converges to zero, it is tempting to conclude that the infimum (greatest lower bound) of the eigenvalues themselves must also converge to zero. However, this claim is false, as it is trivial to construct a counterexample. Indeed, an $S \times S$ matrix with each of its S eigenvalues equal to $1/2$ has a determinant of 2^{-S}, which does approach zero az S increases – but, clearly, none of the eigenvalues get any closer to zero. Therefore, just the fact that the determinant shrinks does not guarantee the loss of robustness.

Instead, we should concentrate on the Sth root of the determinant – in other words, the geometric mean of the eigenvalues:

> *Proposition:* Consider an $S \times S$ matrix. Assume that the Sth root of its determinant (i.e., the geometric mean of its eigenvalues) approaches zero as S increases. Then, the infimum of its eigenvalues will also approach zero.

This proposition is true, because the geometric mean of a set of numbers must lie between the largest and smallest values. Therefore, if the geometric mean of the eigenvalues is ϵ, then at least one eigenvalue has to be less than or equal to ϵ. Thus, if ϵ approaches zero as S increases, this must mean that the greatest lower bound of the eigenvalues also approaches zero.

We need to add a quick remark that since the eigenvalues can be complex, it is not obvious what is meant by "larger" or "smaller". However, since the Jacobian has all real entries, its eigenvalues come in complex conjugate pairs. Their product will therefore reduce to the product of their magnitudes, since

$(a + \mathrm{i}b)(a - \mathrm{i}b) = a^2 + b^2 = (\text{length})^2$ for any complex conjugate pair. Therefore, "smaller" means "of smaller magnitude" in our case.

We have shown in the previous subsection that the determinant of the hierarchical facilitation model's Jacobian (which is the same as the product of the sensitivity and impact volumes) asymptotically approaches zero at least as fast as $\exp(-\theta N S^2/2)$. Denoting the determinant by Δ, we have

$$\Delta \sim \exp(-\theta N S^2/2) \to 0 \tag{J.15}$$

for large S. However, we would like the geometric mean and not just the simple product of the eigenvalues to approach zero: we would like $\sqrt[S]{\Delta} \to 0$. Taking the Sth root, we obtain, for large S,

$$\sqrt[S]{\Delta} \sim \sqrt[S]{\exp(-\theta N S^2/2)} = \exp\left(-\theta N S/2\right) \to 0. \tag{J.16}$$

This proves that robustness is indeed necessarily lost as more species are added into the system in the hierarchical facilitation model.

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