International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

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György Barabás
Simone Pigolotti
Mats Gyllenberg
Ulf Dieckmann (dieckmann@iiasa.ac.at)
Géza Meszéna

Approved by

Pavel Kabat
Director General and Chief Executive Officer

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

György Barabás[1], Simone Pigolotti[2], Mats Gyllenberg[3],
Ulf Dieckmann[4] and Géza Meszéna[5]

[1]*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, USA,*
[2]*Department of Physics and Nuclear Engineering, Polytechnic University of Catalonia, Barcelona, Spain,*
[3]*Department of Mathematics and Statistics, University of Helsinki, Helsinki, Finland,*
[4]*International Institute for Applied Systems Analysis, Evolution and Ecology Program, Laxenburg, Austria*
and [5]*Department of Biological Physics, Eötvös Loránd University, Budapest, Hungary*

ABSTRACT

Question: Is the coexistence of a continuum of species or ecological types possible in real-world communities? Or should one expect distinctly different species?

Mathematical methods: We study whether the coexistence of species in a continuum of ecological types is (a) dynamically stable (against changes in population densities) and (b) structurally robust (against changes in population dynamics). Since most of the reviewed investigations are based on Lotka-Volterra models, we carefully explain which of the presented conclusions are model-independent.

Mathematical conclusions: Seemingly plausible models with dynamically stable continuous-coexistence solutions do exist. However, these models either depend on biologically unrealistic mathematical assumptions (e.g. non-differentiable ingredient functions) or are structurally unstable (i.e. destroyable by arbitrarily small modifications to those ingredient functions). The dynamical stability of a continuous-coexistence solution, if it exists, requires positive definiteness of the model's competition kernel.

Biological conclusions: While the classical expectation of fixed limits to similarity is mathematically naive, the fundamental discreteness of species is a natural consequence of the basic structure of ecological interactions.

Keywords: competition kernel, dynamical stability, kinked kernel, limiting similarity, Lotka-Volterra models, niche axis, structural robustness, structural stability.

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

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Correspondence: G. Barabás, Department of Ecology and Evolutionary Biology, University of Michigan, 830 North University, Ann Arbor, MI 48109-1048, USA. e-mail: dysordys@umich.edu

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.

MacArthur and Levins’s (1967) seminal work initiated investigations of coexistence along a niche axis. They examined a Lotka-Volterra model with the assumption that the strength of competition decreased with increasing 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 (May, 1973, Ch. 6; Abrams, 1975, 1983), 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 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 behaviour relative to the Lotka-Volterra model (e.g. Abrams, 1980a, 1980b, 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. Armstrong and McGehee (1976) coined the term ‘coexistence bandwidth’ for the parameter range allowing coexistence. 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 modelling 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, several authors have reinvestigated Lotka-Volterra models 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 article 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, the Appendix 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.

2. PRELIMINARIES

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 non-equilibrium 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 non-trivial 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 modeller 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 modeller 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 neighbourhood 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 neighbourhood 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 article 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 article.

Figure 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 Fig. 1) and the fact that a dynamically stable fixed point is not necessarily all-positive (left and middle columns of Fig. 1).

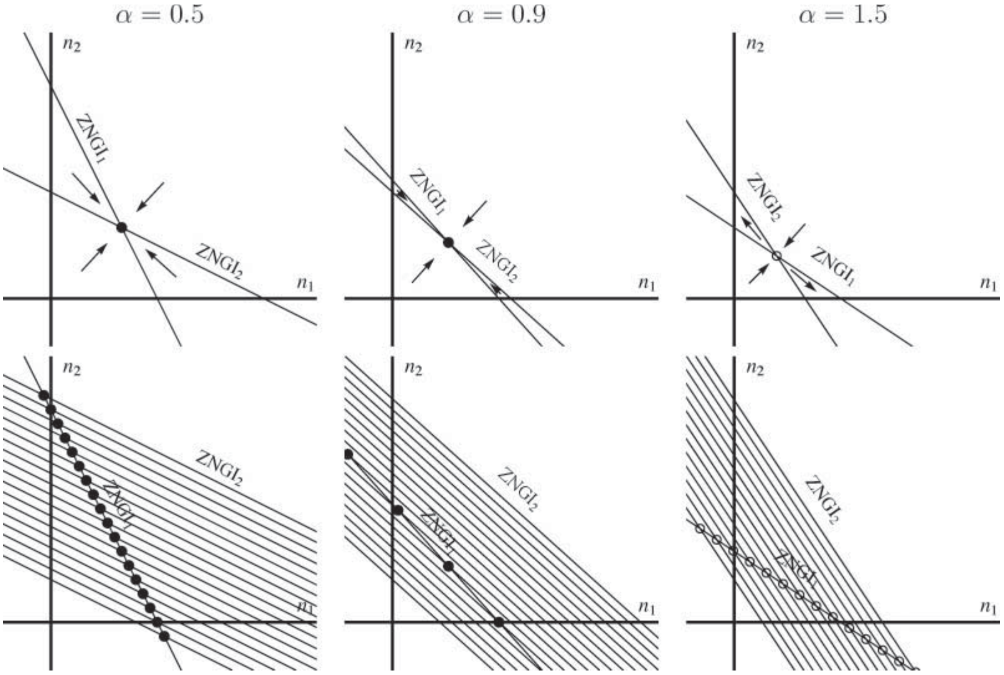

Fig. 1. Dynamical stability (top row) and structural robustness (bottom row) of coexistence for the two-species competitive Lotka-Volterra model described in Box 1 [see also figure 12.3 in Krebs (2001)]. In each panel, the population densities n_1 and n_2 of Species 1 and 2, respectively, vary along 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 solid (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. Note 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 advantages/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.

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 Fig. 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:

$$\boldsymbol{f} = \boldsymbol{r} - \boldsymbol{an}.$$

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

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

where adj($\boldsymbol{a}$) is the adjoint of the matrix $\boldsymbol{a}$ and det($\boldsymbol{a}$) is its determinant (Cramer's rule). Note that $\det(\boldsymbol{a}) = 0$ 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 $\boldsymbol{n}$ is $\det(\boldsymbol{a}) \neq 0$. As the determinant appears in the denominator, the fixed point becomes sensitive to changes in $\boldsymbol{r}$ for small det($\boldsymbol{a}$). 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, $\boldsymbol{n} > 0$. Therefore, structurally robust existence of the positive solution requires det($\boldsymbol{a}$) to be not only non-zero, but *significantly* different from zero. For $\det(\boldsymbol{a}) = 0$, 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 $\boldsymbol{n}$ is $\boldsymbol{A} = (A_{ij})$ 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 1 if $i = j$ and 0 otherwise. Note that the term $f_i\delta_{ij}$ vanishes, since the partial derivatives comprising $\boldsymbol{A}$ have to be taken at the fixed point $\boldsymbol{n}$, where $f_i = 0$. The two eigenvalues of $\boldsymbol{A}$ 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 $\boldsymbol{A}$ are negative. Equivalently, the eigenvalues of $\boldsymbol{a}$ must be positive for dynamical stability.

As the determinant is the product of the eigenvalues, dynamical stability requires det($\boldsymbol{a}$) to be positive. When det($\boldsymbol{a}$) 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 $\det(\boldsymbol{a}) = 0$ 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 Fig. 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 the matrix $\boldsymbol{a}$ are $\lambda_\pm = 1 \pm \alpha$, while the determinant is $\det(\boldsymbol{a}) = 1 - \alpha^2 = \lambda_+\lambda_-$. 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 two species. Increasing species similarity invariably leads to diminished structural robustness and weakened dynamical stability.

Figure 1 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 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 behaviour of losing robustness with similarity for several species in a model-independent way, beyond the Lotka-Volterra model.

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

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 were questioned in light of more mechanistic models. Here we argue that Lotka-Volterra models, when considered with proper care, may be used to tease 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) [for technical details, see, for example, Barabás *et al.* (2012a)]. 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 non-linear and intricate ways, this dependence reduces to a simple linear relationship near any fixed point [for the special role of Lotka-Volterra models in evolutionary analyses, see Durinx *et al.* (2008)]. 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, the traditional way of studying a Lotka-Volterra model is to define it using 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 through 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 that 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 [for a detailed analysis, see Meszéna *et al.* (2006)].

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, 2009). 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 remain 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 behaviour. Indeed, experience shows that models of competition along single niche axes often converge to fixed points and do not exhibit complex dynamics. MacArthur (1970) has shown this for Lotka-Volterra models with symmetric interactions among species. Beyond this, different models of competition–colonization trade-offs (Kinzig *et al.*, 1999; Adler and Mosquera, 2000; Parvinen and Meszéna, 2009), tolerance–fecundity trade-offs (Muller-Landau, 2010; D'Andrea *et al.*, in press), 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 behaviour 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; Hofbauer and Schreiber, 2010; Szilágyi and Meszéna, 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 behaviour, since on the longer timescale the time-averaged model is an accurate representation of the original one [for the case of cyclic oscillations, see Barabás *et al.* (2012b), and for random-noise fluctuations, see Szilágyi and Meszéna (2010)]. Note, however, that we do not claim that the effects 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 (Barabás *et al.*, 2012b), leading out of our assumption of a single regulating continuum. We will therefore not consider models exhibiting complex dynamics in this article.

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 the Appendix, on the other hand, is a more general result pertaining to structural stability, and it does not rely on Lotka-Volterra approximations at all.

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 equations:

$$\frac{\mathrm{d}n(x,t)}{\mathrm{d}t} = n(x,t)\left(r(x) - \int_{x_\mathrm{A}}^{x_\mathrm{B}} a(x,y)n(y,t)\,\mathrm{d}y\right), \tag{1}$$

for all $x_\mathrm{A} \le x \le x_\mathrm{B}$. 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 non-negative, i.e. $a(x, y) \ge 0$ 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

$$r(x) = \int_{x_\mathrm{A}}^{x_\mathrm{B}} a(x,y)n(y)\mathrm{d}y \qquad \text{for all } x \text{ with } n(x) > 0. \tag{2}$$

It is worthwhile stressing the mathematical non-triviality 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 equation (1) the left-hand side will be zero for a given x either if equation (2) holds for x or if $n(x) = 0$. If we assume that all possible species are present with positive population density, then condition (2) yields an equation for each possible x. Hernandez-Garcia *et al.* (2009) call the solution to the resultant set of equations the 'natural' solution. However, after finding a solution to equation (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 $n(x) \le 0$ 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 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, analysing 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, 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. $x_A = -\infty$ and $x_B = \infty$. The competition kernel is chosen to be homogeneous, symmetric, and Gaussian, with variance σ^2,

$$a(x, y) = \exp\left(-\frac{(x-y)^2}{2\sigma^2}\right), \tag{3a}$$

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

$$r(x) = \exp\left(-\frac{x^2}{2\omega^2}\right). \tag{3b}$$

For $\omega > \sigma$, the equilibrium density distribution satisfying equation (2) is

$$n(x) = \frac{\omega/\sigma}{\sqrt{2\pi(\omega^2 - \sigma^2)}} \exp\left(-\frac{x^2}{2(\omega^2 - \sigma^2)}\right). \tag{3c}$$

This continuous-coexistence solution exists only when the distribution of intrinsic growth rates is wider than the competition kernel. For $\omega \le \sigma$, 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 equation (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.

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 equation (2) has been found.

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. In this context, 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 non-linear 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.

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 $\tilde{f}(z) = \int_{-\infty}^{\infty} f(x)e^{-2\pi ixz}\,\mathrm{d}x$, 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 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 equation (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 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 added to the original function. Note how the frequency of the induced oscillation corresponds to the frequency with which we perturbed the Fourier transform.

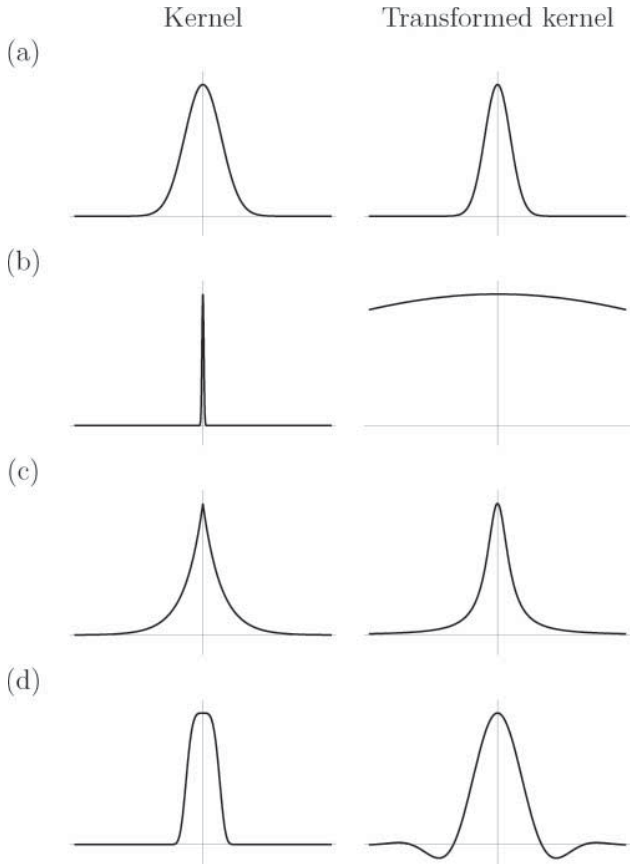

Fig. 2. Examples of different homogeneous competition kernels a (left column) and their Fourier transforms $\tilde{a}$ (right column). The examples shown focus on symmetric kernels, whose Fourier transforms are symmetric functions with real values. Interpretation of the values $\tilde{a}(z)$ for continuous z is analogous to that of the eigenvalues of the Jacobian matrix $\boldsymbol{A}$ 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: because $\tilde{a}(z) > 0$ 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.

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 $\boldsymbol{A}$ in Box 1 is the competition kernel itself, the eigenvectors in Box 1 correspond to sine

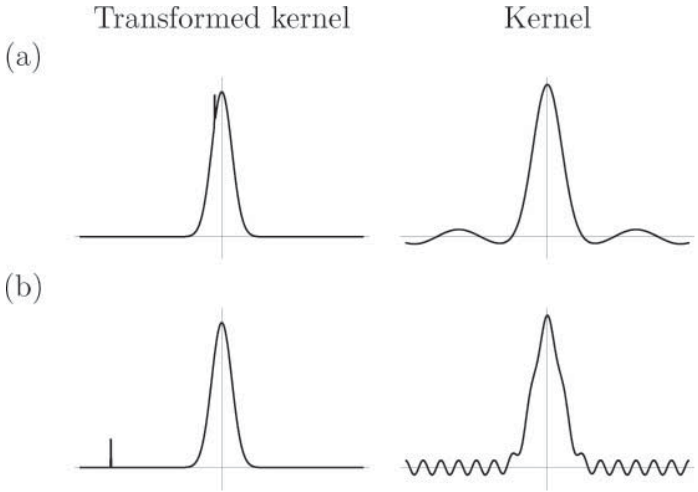

Fig. 3. The effects of small- versus high-frequency perturbations in the Fourier transform on the original function. The left-hand column contains the Fourier transforms: a Gaussian (whose backtransform is also a Gaussian; see Fig. 2) and an extra, very narrow Gaussian added on top of it. Due to the 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 behaviour on top of the original Gaussian shape. (b) When the perturbing frequency is larger, the kernel exhibits much more rapid oscillations.

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.

3.3. Marginal stability

All Fourier transforms in Fig. 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, for example, Bochner and Chandrasekharan, 1949)]. This means that the high-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 (3a) of Roughgarden's model as an example (Fig. 2a). We know that the corresponding natural solution (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, 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 (Fig. 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 (i.e. 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 non-singular (Geritz *et al.*, 1999; Adler and Mosquera, 2000; Rueffler *et al.*, 2007; Barabás *et al.*, 2012a) (see the section 'Kinked kernels' below, which argues that any non-smooth competition kernel is in fact biologically unrealistic). Therefore, dynamical stability is marginal at best for any realistic example of continuous coexistence.

3.4. Non-differentiable positive-definite kernels

To move beyond the realm of Gaussian functions, the following property of Fourier transforms is helpful. As mentioned before, all non-singular 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) and Barabás *et al.* (2012a) analysed kernels that are non-differentiable at $x = 0$ (i.e. at the point of self-competition; these have been dubbed 'kinked' kernels). See Fig. 2c for an example. By comparing Fig. 2c with Fig. 2a, it is evident that the Fourier transform of such kinked kernels approaches zero much more slowly than that of Gaussian kernels of similar width. This means that the continuous-coexistence solution has non-marginal stability for a much wider range of frequencies, and therefore for a much wider class of perturbations.

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 (Fig. 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, for example, 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 latter two sources and by Meszéna *et al.* (2006), analysing 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.

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 Fig. 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.

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. $\iint f(x)a(x,y)f(y)\,\mathrm{d}x\,\mathrm{d}y$ 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.

4. STRUCTURAL ROBUSTNESS

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

4.1. Two aspects of structural robustness

The Lotka-Volterra models in equation (1) have two ingredient functions: the competition kernel a and the distribution r of intrinsic growth rates. Structural stability and robustness therefore need to be analysed 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 article 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 $[x_\mathrm{A}, x_\mathrm{B}]$ 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 modifies 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.

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 a way that the perturbed model no longer allows for the coexistence of any infinite set of species. Gyllenberg and Meszéna (2005) proved this theorem 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 the Appendix, here we provide a model-independent generalization of this theorem.

Figure 4 provides an example. The kernel is homogeneous, but that is just for the sake of easier presentation: non-homogeneous 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

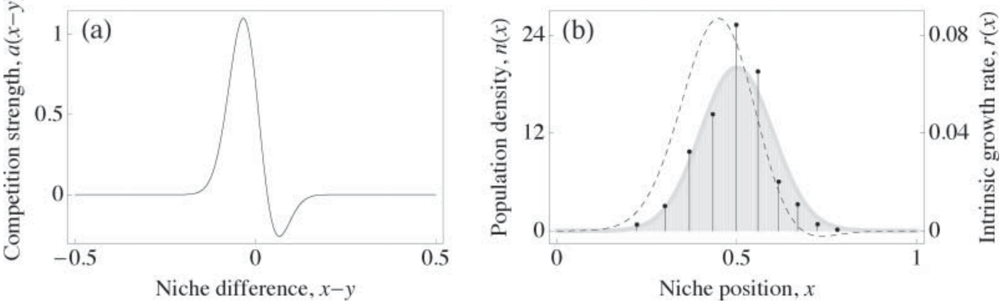

Fig. 4. Coexistence under an analytic competition kernel. (a) The competition kernel a is obtained as $a(x-y) = e^{-225(x-y)^2}(1\text{–}30(x-y))/\sqrt{2}$. One can show that this kernel is positive definite. Note that the kernel does not attain its maximum at zero niche difference, and that the species 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 $n(x) = \exp(-(x-0.5)^2/0.02)$ (grey curve and area) in conjunction with this particular competition kernel. This is achieved by inserting the kernel and the desired continuous-coexistence solution into equation (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 equation (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).

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 the Appendix 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 neighbours is proportional to $((2\sigma)^{-1} - \beta \ln \varepsilon)^{-1}$, 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 equation 3b). This expression predicts that for small σ, the average nearest-neighbour niche distance rises very steeply with ε, towards an intermediate plateau at 2σ (the spacing exactly equals 2σ for $\varepsilon = 1$). For example, for $\sigma = 0.01$, a spacing of 90% of 2σ is reached already for perturbation amplitudes as small as $\varepsilon \approx 0.4\%$. For very small values of ε, species packing can be very tight. As $\varepsilon \to 0$, 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 question remaining is what happens when the intrinsic rates $r(x)$ are perturbed and the competition kernel is not analytic.

4.3. Smooth non-analytic 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'. (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.) While there are no such powerful theorems as in the case of analytic kernels to rule out structurally robust continuous coexistence, smooth non-analytic kernels are visually similar to analytic ones and there is no obvious argument to discard them *a priori* as being biologically unrealistic.

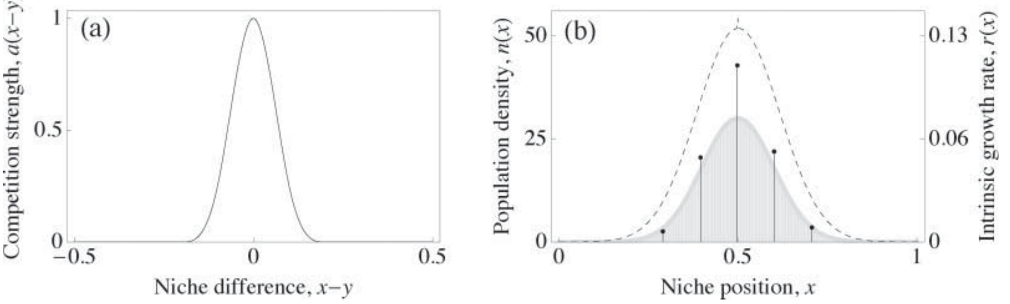

Fig. 5. Coexistence under a smooth non-analytic competition kernel. (a) The competition kernel a is obtained as $a(x-y) = \int u(x-z)u(y-z)\,\mathrm{d}z$ with a resource-utilization function u that equals $u(x) = 1 - |10x|$ for $x \leq 1/10$ and zero otherwise. The construction of this kernel as an overlap 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 $n(x) = \exp(-(x-0.5)^2/0.02)$ (grey curve and area) in conjunction with this particular competition kernel, just as in Fig. 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 equation (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 neighbouring surviving species roughly equals twice the standard deviation of the competition kernel.

Barabás *et al.* (2012a) have performed extensive numerical analyses to clarify what kinds of coexistence patterns are to be expected under such conditions: they chose smooth non-analytic kernels a and intrinsic rate distributions $r(x)$ that produced continuous-coexistence solutions, and then numerically solved equation (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 means that the model behaved in every way as if the competition kernel were analytic [Fig. 5; see also figure 2 in Barabás *et al.* (2012a)].

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

4.4. Kinked kernels

As stated earlier, we refer to a competition kernel as being 'kinked' if it is non-differentiable at the point of self-competition (kernels possessing non-differentiabilities 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. Barabás *et al.* (2012a) numerically analysed many instances of Lotka-Volterra models with kinked kernels, the result invariably being that continuous coexistence turned out to be structurally robust [Fig. 6; see also figure 3 in Barabás *et al.* (2012a)]. 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

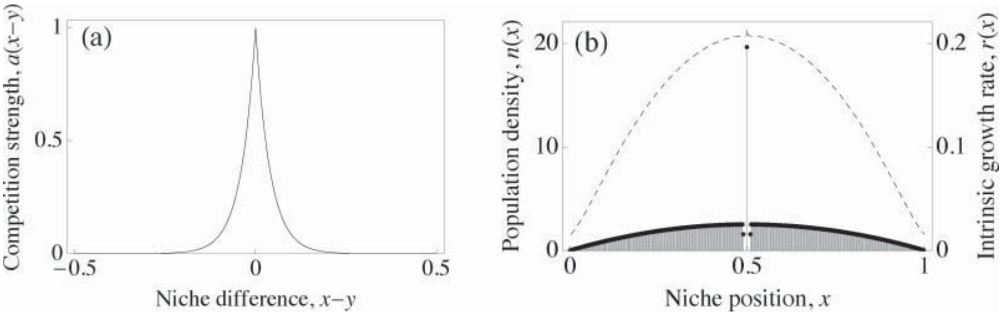

Fig. 6. Coexistence under a kinked competition kernel. (a) The competition kernel a is given by $a(x-y) = \exp(-|x-y|/0.04)$. This kernel is kinked (not differentiable at $x = 0$). (b) The distribution r of intrinsic growth rates (dashed curve) is constructed so as to yield the continuous-coexistence 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 equation (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.

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 non-negligible role in reducing interspecific competition. In contrast, if the kernel is kinked, 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 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 (Barabás *et al.*, 2012a) 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 non-differentiabilities 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, such as the hierarchical competition–colonization and competition–mortality trade-off models [(Kinzig *et al.*, 1999; Adler and Mosquera, 2000); in these models, competition kernels are discontinuous, making structurally robust continuous coexistence even easier than in models in which competition kernels are merely kinked], the tolerance–fecundity trade-off 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 behaviour. For instance, D'Andrea *et al.* (in press) have investigated the tolerance–fecundity and competition–colonization trade-off 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 non-smooth 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). Adler and Mosquera (2000) obtained very similar results for the competition–mortality trade-off model, and 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.

The importance of the shape of the competition kernel has already been emphasized by Abrams (1975), whose 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 (Barabás *et al.*, 2012a) 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.

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 occur 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 (Fig. 7). These findings are compatible with the interpretation that local dynamics along the trait axis are

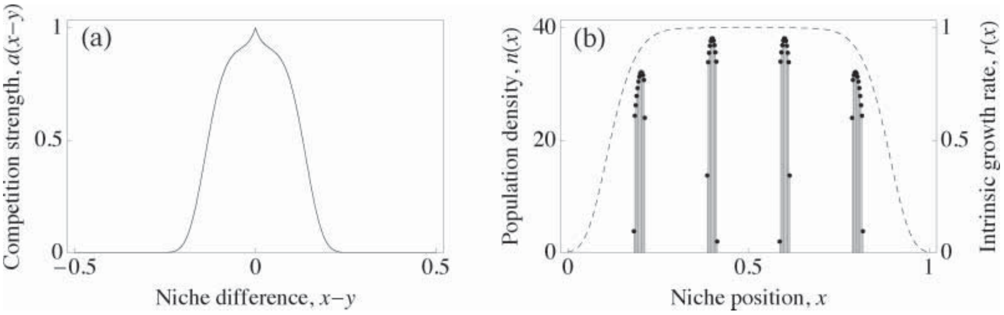

Fig. 7. Coexistence under a kinked non-positive-definite competition kernel. (a) The competition kernel a is given by $a(x-y) = 0.9\ \exp(-(x-y)^4/0.15^4) + 0.1\ \exp(-|x-y|/0.02)$. This kernel is kinked (not differentiable at $x = 0$), and its Fourier transform is negative for some frequencies. (b) 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 equation (1), approximated by 400 equidistant species, until equilibrium is reached, from a uniform initial condition. This perturbation 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.

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.

The relevance of these findings is not just in future research: kinked non-positive-definite kernels have already been used in the literature, leading to the patterns described in the preceding paragraph (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 highlighted earlier 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 (Fig. 7). To appreciate the connection, note 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 this article, we claimed that a Dirac delta might be thought of as a Gaussian with an infinitely narrow variance. There is no contradiction: the two 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 are 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.

4.6. Summary

Analytic competition kernels never allow for structurally stable continuous coexistence, as is proved in the Appendix. Smooth non-analytic kernels seem to behave exactly like their analytic cousins, though the evidence so far is purely numerical (see, for example, Fig. 5). While kinked kernels do lead to the robust possibility of many arbitrarily similar coexisting species, such kernels are biologically unrealistic, thus 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.

5. DISCUSSION

In this article, 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 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 the Appendix). We also find that smooth non-analytic 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 all point in this direction. Finally, competition kernels that are 'kinked' (i.e. are non-differentiable 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 things motivated 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 behaviours 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 – and the stabilizing effect (Chesson, 2000) 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 decrease significantly for large enough niche differences. The distance over which this 'significant decrease' occurs 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 the Appendix) 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, including: 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 article 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 influences 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 has not only motivated the notion of limiting similarity, but has also been 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 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.

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APPENDIX: 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 non-linear) operator describing population interactions is compact in the sense defined below. This assumption is valid if, for example, the trait values in niche space are constrained to a finite volume (like $[x_\mathbf{A}, x_\mathbf{B}]$ 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 by Barabás *et al.* (2012a), the assumption of analyticity is an important prerequisite for this theorem, as kinked kernels (which are non-analytic) 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 values 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 equation (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 and 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

$$d(f, g) = \sum_{i=1}^{\infty} \frac{2^{-i} p_i(f-g)}{1 + p_i(f-g)}, \tag{4}$$

where

$$p_i(f) = \sup \{ |f(z)| : z \in K_i \}, \tag{5}$$

with $K_1 \subset K_2 \subset \cdots$ being a sequence of non-empty 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 (non-linear) 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*

$$r(x) = A(n)(x) \qquad \text{for all } x \in \operatorname{supp}(n), \tag{6}$$

the support of which has a limit point in Ω, then in every neighbourhood of r there exists an r' such that equation (6) *with r replaced by r' does not have any solution with a support with a limit point in* Ω.

Proof. Suppose equation (6) holds and $\operatorname{supp}(n)$ has a limit point in Ω. Then, because of analyticity,

$$r(x) = A(n)(x) \qquad \text{for all } x \in \Omega. \tag{7}$$

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 neighbourhood of r such that r' is not in the range of A, i.e. no solution of (7) 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 neighbourhood of r in Y contains a ball centred on r and with a sufficiently small radius $\varepsilon > 0$. For $\varepsilon < \delta$, this ball consists of functions that are positive on $\mathcal{X}$.

In the case of space Z and for $\bar{\mathcal{X}} \subset \Omega$, 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,

$$d(r, r') = \sum_{i=1}^{\infty} \frac{2^{-i} p_i(f-g)}{1 + p_i(f-g)} \geq \sum_{i=m}^{\infty} \frac{2^{-i} p_i(f-g)}{1 + p_i(f-g)} \geq \sum_{i=m}^{\infty} \frac{2^{-i}\delta}{1+\delta} \geq 2^{-(m-1)}\,\delta. \tag{8}$$

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