Species packing in nonsmooth competition models

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Abstract

Despite the potential for competition to generate equilibrium coexistence of infinitely tightly packed species along a trait axis, prior work has shown that the classical expectation of system-specific limits to the similarity of stably coexisting species is sound. A key reason is that known instances of continuous coexistence are fragile, requiring fine-tuning of parameters: a small alteration of the parameters leads back to the classical limiting similarity predictions. Here we present, but then cast aside, a new theoretical challenge to the expectation of limiting similarity. Robust continuous coexistence can arise if competition between species is modeled as a nonsmooth function of their differences – specifically, if the competition kernel (differential response of species' growth rates to changes in the density of other species along the trait axis) has a nondifferentiable sharp peak at zero trait difference. We will say that these kernels possess a "kink". The difference in predicted behavior stems from the fact that smooth kernels do not change to a first order approximation around their maxima, creating strong competitive interactions between similar species. "Kinked" kernels, on the other hand, decrease linearly even for small species differences, reducing interspecific competition compared with intraspecific competition for arbitrarily small species differences. We investigate what mechanisms would lead to kinked kernels in the first place. It turns out that discontinuities in resource utilization generate them. We argue that such sudden jumps in the utilization of resources are unrealistic and therefore one should expect kernels to be smooth in reality.

Keywords: competition kernel; continuous coexistence; limiting similarity; trait axis

Note on Authorship: GB and RD'A contributed equally to the analysis; GB wrote the manuscript; AO supervised the project.

1 Introduction

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

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

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

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

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

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

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

Our article is structured as follows. After building the model framework and reviewing some of the better-known results emerging from it in Section 2, we go on to show examples of the model with kinked kernels (Section 3), which invariably produce robust continuous coexistence. Next, in Section 4 we give some mathematical arguments for why kinked kernels would have this property, but not smooth ones. Finally, in Section 5 we derive the conditions that lead to kinked kernels, and demonstrate that under realistic circumstances one should always expect kernels to be smooth.

2 Background

2.1 Models of competition around equilibria

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

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x)\, r(n, E). \tag{1}$$

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

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} \approx n(x)\Big(\underbrace{r(n^*, E)}_{0} + \delta r(n, E)\Big) = n(x)\left(\int_{x_0}^{x_m} \frac{\delta r(x)}{\delta E(y)}\delta E(y)\,\mathrm{d}y + \int_{x_0}^{x_m} \frac{\delta r(x)}{\delta n(y)}\delta n(y)\,\mathrm{d}y\right), \tag{2}$$

where $r(x)$ is shorthand for $r\left(n(x), E(x)\right)$ and the δ denotes functional differentiation (for those unfamiliar with functional derivatives, the expression $\delta r(x) = \int (\delta r(x)/\delta n(y))\delta n(y)\,\mathrm{d}y$, where x

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

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x) \left(c(x) - \int_{x_0}^{x_m} a(x,y) \delta n(y) \, \mathrm{d}y \right). \tag{3}$$

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

$$\begin{aligned}\frac{\mathrm{d}n(x)}{\mathrm{d}t} &= n(x) \left(c(x) - \int_{x_0}^{x_m} a(x,y) \Big(n(x) - n^*(x) \Big) \mathrm{d}y \right) \\ &= n(x) \left(\underbrace{c(x) + \int_{x_0}^{x_m} a(x,y) n^*(y) \, \mathrm{d}y}_{r_0(x)} - \int_{x_0}^{x_m} a(x,y) n(y) \, \mathrm{d}y \right),\end{aligned} \tag{4}$$

and so

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x) \left(r_0(x) - \int_{x_0}^{x_m} a(x,y) n(y) \, \mathrm{d}y \right), \tag{5}$$

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

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

2.2 The fragility of continuous coexistence solutions

As mentioned in the Introduction, the original idea of strict limits to similarity had to be abandoned when it was demonstrated that even in the original Lotka–Volterra model (where the idea was first proposed) it is possible to have the stable coexistence of a continuum of species (Roughgarden 1979). However, such coexistence is extremely sensitive to perturbations of model parameters and is therefore not expected to occur under realistic circumstances. Let us investigate the original example of Roughgarden and its behavior under model perturbations. From Eq. (5), the equilibrium condition reads

$$r_0(x) = \int_{x_0}^{x_m} a(x,y)n(y)\,\mathrm{d}y \tag{6}$$

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

$$r_0(x) = \exp\left(-\frac{(x-x^*)^2}{2w^2}\right), \tag{7}$$

$$a(x,y) = \exp\left(-\frac{(x-y)^2}{2\sigma^2}\right) \tag{8}$$

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

$$n(x) = \frac{w}{\sigma\sqrt{w^2-\sigma^2}} \exp\left(-\frac{(x-x^*)^2}{2(w^2-\sigma^2)}\right) \tag{9}$$

as long as $w > \sigma$.

This solution is structurally unstable, i.e. a perturbation of arbitrarily small amplitude may destroy it (Gyllenberg and Meszéna 2005). Fig. 1 shows an example where the continuous coexistence pattern collapses completely, even though the perturbation amplitude is small. Note that the spacing between surviving species is almost perfectly even, as expected in this model for the type of perturbation we employed (Barabás and Meszéna 2009).

It is instructive to look at these results in light of the Gyllenberg-Meszéna theorem (Gyllenberg and Meszéna 2005). As a matter of fact, this theorem is a collection of several related results. But, for our purposes, we only need to distinguish between two cases. The first one concerns the equilibrium condition Eq. (6) in its full generality. It first assumes that, given the continuous parameters $r_0(x)$ and $a(x,y)$, an equilibrium solution $n(x)$ is produced whose support (i.e. values of x for which $n(x)$ is nonzero) includes a domain of continuous coexistence. Then the theorem states that there exists a positive function $\eta(x)$ such that for an arbitrarily small ε, if one replaces $r_0(x)$ by $r_0(x) + \varepsilon\eta(x)$, the resulting perturbed solution $\hat{n}(x)$ will not have the same support as $n(x)$. In other words, some species are bound to go extinct, no matter how small the disturbance is: continuous coexistence is, in this sense, fragile. Notice that the theorem does *not* say that continuous coexistence *as a whole* is going to collapse, merely that certain species will go extinct. However, a stronger version of the theorem, guaranteeing that an arbitrarily small perturbation can break down all continuous coexistence and lead to strict spacing can be proven for the special case of $a(x,y) = a(x-y)$, where $a(x-y)$ and $r_0(x)$ are analytic functions of their arguments.

This second, stronger theorem applies to the example in Fig. 1, since the parameters are all analytic. Therefore it is no surprise that continuous coexistence is completely destroyed. The next section will explore what happens if the parameters are not chosen to be analytic. It will be shown that spacing is still expected for kernels that are *smooth*, i.e. differentiable at least once: though technically speaking the stronger version of the Gyllenberg-Meszéna theorem does not apply, the results look as if it did. However, when the kernel becomes nondifferentiable at zero trait difference, the situation changes drastically.

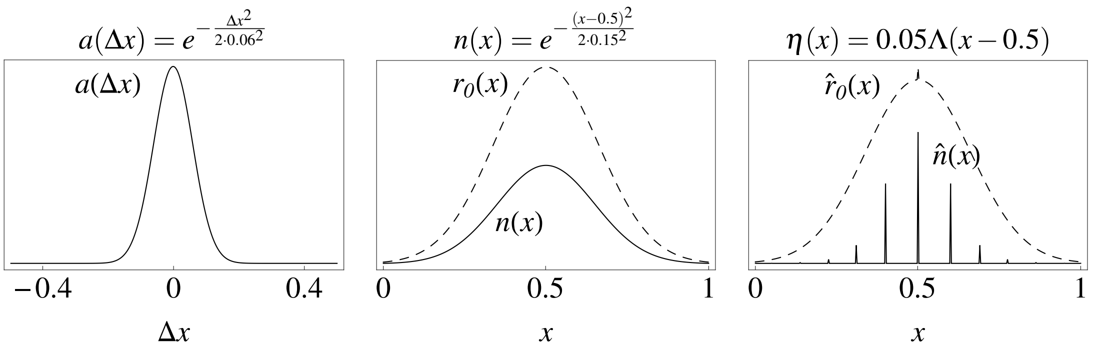


Figure 1: Equilibrium patterns produced by a Gaussian competition kernel. The first panel shows the equation and the graph of the competition kernel used; $\Delta x = x - y$. The second panel gives the formula for $n(x)$ and the curves of $n(x)$ and $r_0(x)$ (which can be obtained by substituting the given forms of $a(x-y)$ and $n(x)$ into Eq. (6) and performing the integration). The third panel presents what happens to the equilibrium state when $r_0(x)$ is perturbed. We obtained the perturbed equilibrium $\hat{n}(x)$ by first adding a small perturbing function $\eta(x)$ to the original $r_0(x)$ to obtain the perturbed intrinsic rates $\hat{r}_0(x) = r_0(x) + \eta(x)$, then simulating the dynamics via Eq. (5) until it reached its stable equilibrium. The function $\Lambda(x)$ involved in the perturbation in panel 3 is defined as $400(1-|x|)$ for $-1 < x < 1$ and zero otherwise. The argument is multiplied by 400 since this was the number of bins the trait axis was divided into in our simulations – this way the perturbation is effectively point-like, i.e. zero everywhere except at $x = 0.5$. In panels 2 and 3, $r_0(x)$ and $\hat{r}_0(x)$ have been scaled so they would fit on the same plot as the densities.

3 Demonstrating robust continuous coexistence under kinked kernels

Fig. 2 presents several examples of smooth nonanalytic kernels (column 1) that support continuous coexistence (column 2). Our method for generating these solutions was to first choose a positive $a(x,y)$ and $n(x)$ arbitrarily, then use the equilibium condition Eq. (6) to obtain the corresponding $r_0(x)$ by performing the integration. Then the function $r_0(x)$ was perturbed and we obtained the solution to the perturbed problem by numerically integrating Eq. (5) (column 3). The four examples presented differ in whether the kernel is a function of trait diference only ($a(x,y) = a(x-y)$, rows 1 and 2, or $a(x,y) \neq a(x-y)$, rows 3 and 4), and in whether the kernel is symmetric or not ($a(x,y) = a(y,x)$, rows 1 and 3, or $a(x,y) \neq a(y,x)$, rows 2 and 4).

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

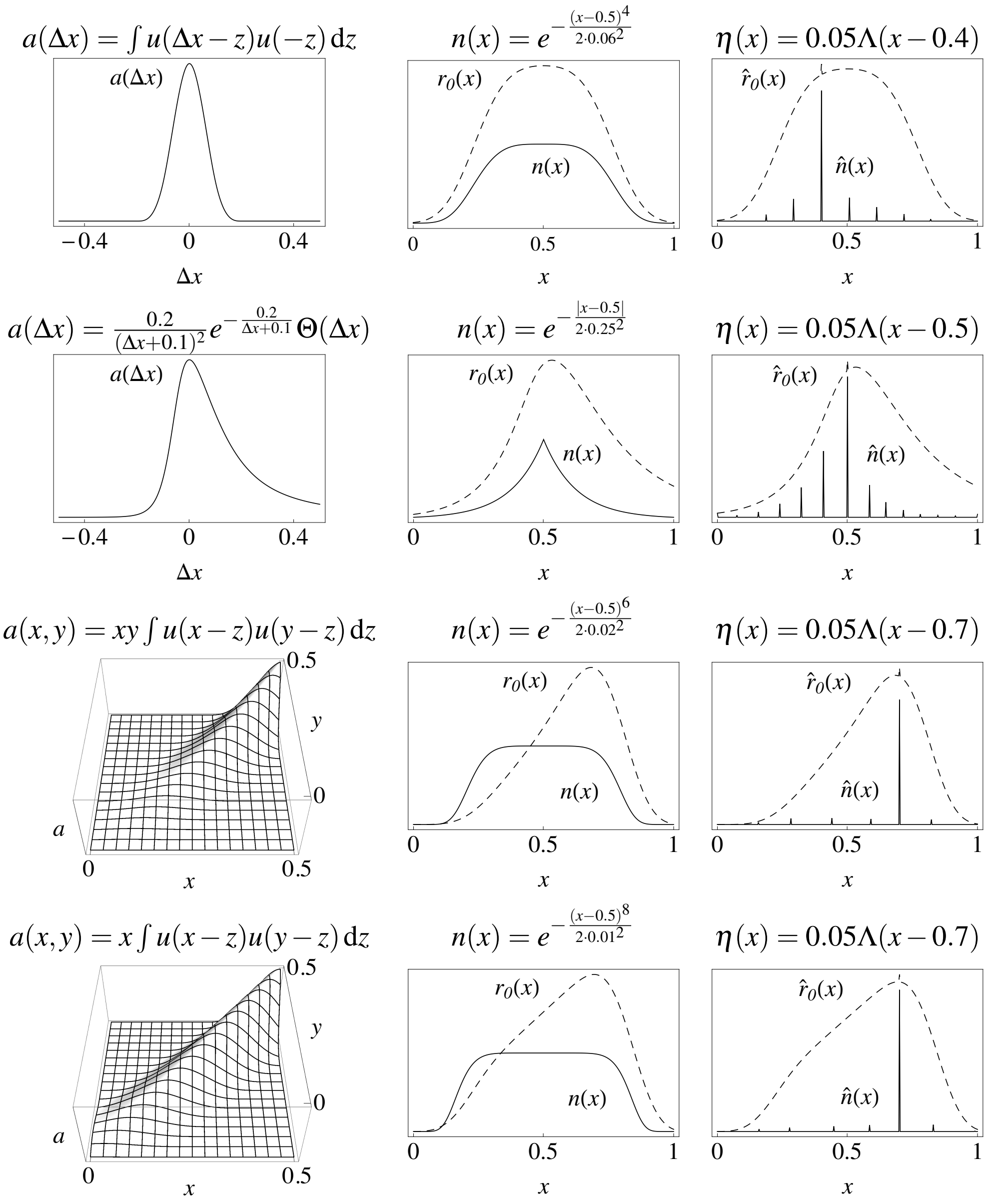


Figure 2: Equilibrium patterns produced by smooth nonanalytic competition kernels. Layout and notation and methods as in Fig. 1, with four rows instead of one; $u(x) = 1 - |x/0.1|$ if $|x| \leq 0.1$ and zero otherwise; $\Theta(x)$ is the Heaviside unit step function. The four rows present four different examples of continuous coexistence and the coexistence pattern obtained by slightly perturbing the intrinsic rates of growth. Continuous coexistence collapses in all cases following perturbation.

The situation is entirely different if the kernels are kinked (nondifferentiable at zero trait difference). Fig. 3 is analogous to Fig. 2, except that all kernels are kinked, which is evident from their graphs in column 1 (they all possess a sharp peak at each point where $x = y$). In these examples, though a few species do go extinct after perturbation, continuous coexistence itself is not eliminated: most regions on the trait axis still have arbitrarily similar species coexisting. This is exactly the situation we called robust continuous coexistence in the Introduction. Nondifferentiability at zero trait difference therefore has a tremendous impact on the robustness of the coexistence of similar species.

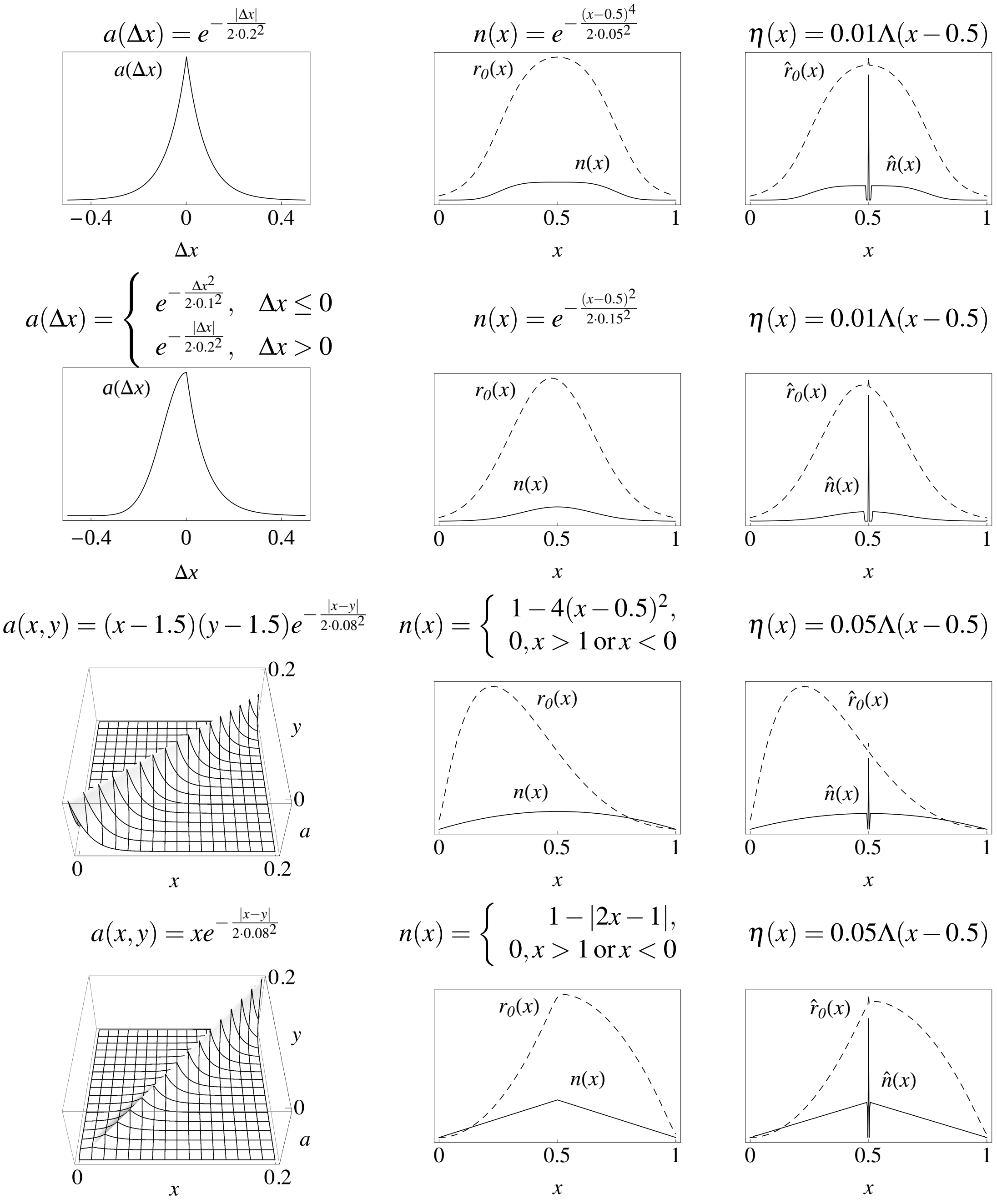
The perturbed densities in column 3 of Fig. 3 are not very different from their unperturbed counterparts (column 2), except in the direct vicinity of the perturbation. The effects of the perturbation therefore seem to be very local: beyond a certain distance, the coexistence pattern behaves as if no perturbation would have occurred at all. This distance depends on perturbation size, as Fig. 4 demonstrates: the larger the perturbation, the larger the exclusion zone in which species are driven extinct. Beyond that zone, however, coexistence is unaffected.

4 Kinked kernels and robust continuous coexistence

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

Consider two species that are extremely similar along the trait axis. The difference in their $r_0(x)$ values may then be expanded to linear order in the trait difference, neglecting higher order terms. If the competition kernel is smooth, then the smallest nontrivial order of expansion of the kernel around zero trait difference is quadratic, since the kernel has a maximum there. Hence, to first order, the competitive effect of one species on itself is equal to its effect on the other and vice versa. Competition is therefore not reduced between the species: coexistence will in general not be possible (MacArthur 1962, Metz et al. 2008). On the other hand, if the kernel is kinked, the linear-order decrease in competition is not zero anymore and so competition may immediately be reduced to tolerable levels where the two species can coexist, even for arbitrarily similar trait values. The abrupt decrease in competition in the case of kinked kernels brings about the possibility of the competitive coexistence of arbitrarily similar species. The precise, quantitative form of this argument is found in Appendix A.

Suggestive as it is, this result only applies for two competing species. We know and have seen in Sections 2 and 3 that smooth kernels do sometimes allow for continuous coexistence, so the limiting similarity condition obtained for the two-species case does not directly apply. However, the extreme fragility of such solutions signals that limiting similarity is still to be expected in all cases where the parameters have not been precisely fine-tuned. No such fine-tuning is required for retaining continuous coexistence in the case of kinked kernels. In the remainder of this section we demonstrate the extra fragility of continuous coexistence with smooth kernels via an argument based


$$a(\Delta x) = e^{-\frac{|\Delta x|}{2\cdot 0.2^2}} \qquad n(x) = e^{-\frac{(x-0.5)^4}{2\cdot 0.05^2}} \qquad \eta(x) = 0.01\Lambda(x-0.5)$$

$$a(\Delta x) = \begin{cases} e^{-\frac{\Delta x^2}{2\cdot 0.1^2}}, & \Delta x \leq 0 \\ e^{-\frac{|\Delta x|}{2\cdot 0.2^2}}, & \Delta x > 0 \end{cases} \qquad n(x) = e^{-\frac{(x-0.5)^2}{2\cdot 0.15^2}} \qquad \eta(x) = 0.01\Lambda(x-0.5)$$

$$a(x,y) = (x-1.5)(y-1.5)e^{-\frac{|x-y|}{2\cdot 0.08^2}} \qquad n(x) = \begin{cases} 1-4(x-0.5)^2, \\ 0, x > 1 \,\text{or}\, x < 0 \end{cases} \qquad \eta(x) = 0.05\Lambda(x-0.5)$$

$$a(x,y) = xe^{-\frac{|x-y|}{2\cdot 0.08^2}} \qquad n(x) = \begin{cases} 1-|2x-1|, \\ 0, x > 1 \,\text{or}\, x < 0 \end{cases} \qquad \eta(x) = 0.05\Lambda(x-0.5)$$

Figure 3: Equilibrium patterns produced by kinked competition kernels. Layout, methods, and notation as in Fig. 2. Though some species always go extinct after perturbation, continuous coexistence does not disappear.

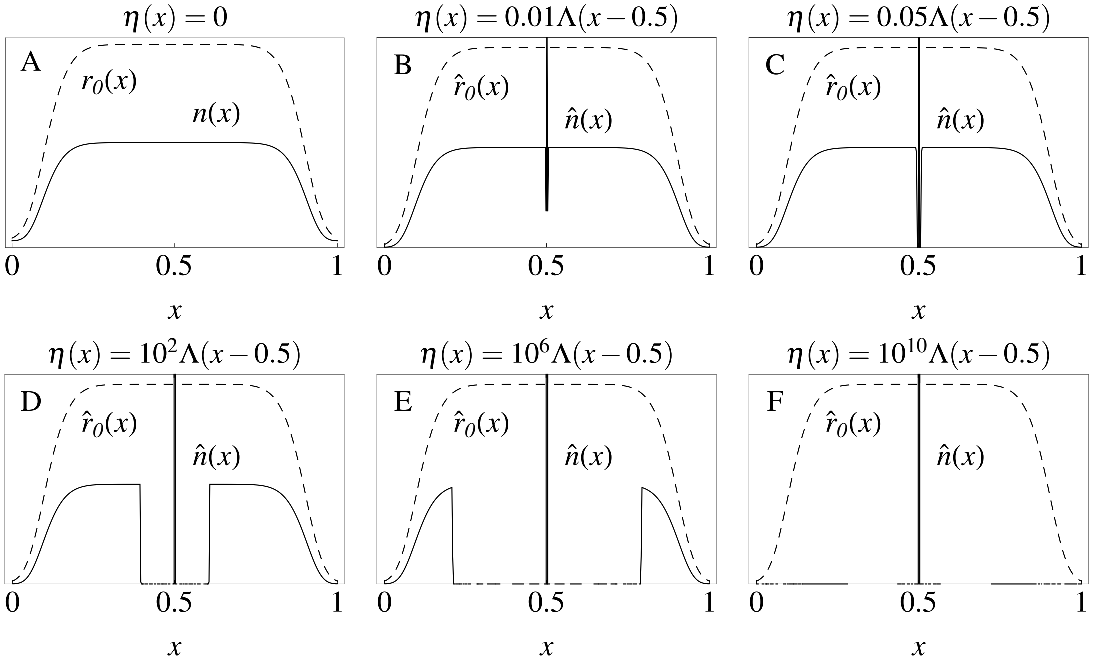


Figure 4: The effects of increasing perturbation size on a model with a kinked kernel. The kernel used is $a(\Delta x) = \exp(-|x|/(2 \cdot 0.1^2))$ (its general shape is given by the top left corner of Fig 3), and the unperturbed densities are $n(x) = \exp(-(x-1/2)^{10}/(2 \cdot 0.0083^2))$. Notation is as in the previous figures. Panel A depicts the unperturbed solution. For sufficiently small perturbations (panel B) the equilibrium abundances are altered but no extinctions occur. For larger perturbations (panels C, D and E), some species go extinct, but beyond a well-defined exclusion zone coexistence is just like it was without the perturbation. As the perturbation size increases, the exclusion zone progressively increases until all but one single species are excluded (panel F). Note that this happens when the perturbation size is approximately 10^{10} larger than the original function, i.e. the perturbation is astronomically large compared to the original $r_0(x)$.

on Fourier transforms. This comes at a price though: only the $a(x,y) = a(x-y)$ homogeneous case may be treated in this manner.

For the special case $a(x,y) = a(x-y)$, the equilibrium condition Eq. (6) reads

$$r_0(x) = \int_{-\infty}^{\infty} a(x-y)n(y)\,\mathrm{d}y, \tag{10}$$

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

$$r_0(x) + \varepsilon\eta(x) = \int_{-\infty}^{\infty} a(x-y)n(y)\,\mathrm{d}y. \tag{11}$$

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

$$\mathscr{F}(r_0) + \varepsilon\mathscr{F}(\eta) = \mathscr{F}(a)\mathscr{F}(n), \tag{12}$$

which yields the solution

$$n(x) = \mathscr{F}^{-1}\left(\frac{\mathscr{F}(r_0)}{\mathscr{F}(a)}\right) + \varepsilon\mathscr{F}^{-1}\left(\frac{\mathscr{F}(\eta)}{\mathscr{F}(a)}\right) = n_0(x) + \varepsilon\mathscr{F}^{-1}\left(\frac{\mathscr{F}(\eta)}{\mathscr{F}(a)}\right). \tag{13}$$

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

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

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

Returning to the ratio $\mathscr{F}(\eta)/\mathscr{F}(a)$: due to the above property of the Fourier transform, if the kernel is differentiable k times, then the perturbing function $\eta(x)$ has to be differentiable $j > k$ times, otherwise the perturbing term in Eq. (13) will grow arbitrarily large, irrespective of the value of ε.

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

$$\eta(x) = \int_{-\infty}^{\infty} \frac{u(x-z)u(-z)}{\int_{-\infty}^{\infty} u(y)u(y)\,\mathrm{d}y}\,\mathrm{d}z, \tag{14}$$

where $u(x) = 1 - |x/\sigma|$ for $|x| \leq \sigma$ and zero otherwise (the general shape of $u(x)$ is given in the top left corner of Fig. 2). It is easily seen that $\eta(x)$ is differentiable twice, therefore we expect its Fourier transform to decay asymptotically as ω^{-4}. This is indeed the case, since the transform of $\eta(x)$ is

$$\mathscr{F}(\eta) = \frac{3e^{-2i\omega\sigma}(e^{i\omega\sigma} - 1)^4}{2\sigma^3\omega^4}. \tag{15}$$

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

$$a(x-y) = \exp\left(-\frac{(x-y)^2}{2\sigma^2}\right). \tag{16}$$

Its Fourier transform is also Gaussian:

$$\mathscr{F}(a) = \sigma\sqrt{2\pi}\exp\left(-\frac{\omega^2\sigma^2}{2}\right). \tag{17}$$

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

$$\frac{\mathscr{F}(\eta)}{\mathscr{F}(a)} = e^{\frac{1}{2}\sigma^2\omega^2}\frac{3e^{-2i\omega\sigma}(e^{i\omega\sigma}-1)^4}{2\sqrt{2\pi}\sigma^4\omega^4}, \tag{18}$$

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

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

$$a(x-y) = \exp\left(-\frac{|x-y|}{\sigma}\right), \tag{19}$$

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

$$\mathscr{F}(a) = \frac{2\sigma}{1+\sigma^2\omega^2}, \tag{20}$$

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

$$\frac{\mathscr{F}(\eta)}{\mathscr{F}(a)} = \frac{3e^{-2i\omega\sigma}(e^{i\omega\sigma}-1)^4(1+\sigma^2\omega^2)}{4\sigma^4\omega^4}, \tag{21}$$

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

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

5 How do kinked competition kernels emerge?

5.1 Discontinuous utilization curves lead to kinked kernels

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

$$a(x,y) = \int_{z_0}^{z_m} u(x,z)u(y,z)\,\mathrm{d}z, \tag{22}$$

where z_0 and z_m are the maximum and minimum resource sizes, respectively (MacArthur and Levins 1967, MacArthur 1970, Chesson 1990). We also assume that the utilization function is bounded and only depends on the difference between resource type and trait: $u(x,z) = u(x-z)$. Then the competition kernel will also be a function of only the trait difference, since the amount of overlap depends only on how far the two traits are from each other, not on their absolute positions along the trait axis. (Appendix B generalizes the overlap picture to arbitrary ecological models, where it turns out that it is always possible to write the kernel as the overlap of two *different* functions, called the sensitivity and the impact; see also Meszéna et al. 2006, Barabás et al. 2011).

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

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

$$a''(x) = \int_{z_0}^{z_m} u''(x-z)u(-z)\,\mathrm{d}z, \tag{23}$$

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

$$a''(0) = \int_{z_0}^{z_m} u''(-z)u(-z)\,\mathrm{d}z = -\int_{z_0}^{z_m} u''(z)u(z)\,\mathrm{d}z \tag{24}$$

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

$$u(z) = \alpha\Theta(z-z^*) + \eta(z), \tag{25}$$

where Θ is the Heaviside unit step function, α is a constant and $\eta(z)$ is a continuous function. Substituting this form into Eq. (24) we get

$$a''(0) = -\alpha \int_{z_0}^{z_m} \delta'(z-z^*)u(z)\,\mathrm{d}z + \ldots, \tag{26}$$

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

$$a''(0) = -\alpha u'(z^*) + \ldots = -\alpha^2 \delta(0) + \ldots, \tag{27}$$

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

5.2 Mechanisms inhibiting discontinuous resource utilization

How is this result to be interpreted? A discontinuity in the resource utilization function means a species utilizing a certain resource is suddenly incapable of utilizing another, arbitrarily similar resource with similar efficiency. Expanding on the example of the competing bird species, one might imagine that each species has a box-like utilization curve: within a certain range σ of the beak size, all seeds are equally consumable, but outside of that limit, none at all ($u(x-z) = u_0$ if $|x-z| \leq \sigma$ and zero otherwise). Then, no matter how similar two species are, one will have access to seeds of certain sizes that the other does not, and vice versa (Fig. 5). Thinking of the various resources as the factors regulating the populations, this means that no matter how similar, the two species will still be independently regulated, which is the key to species coexistence in general (Levin 1970, Meszéna et al. 2006). It follows that two species very similar along the trait axis are not really similar in the relevant sense of the word: no matter how close they are in their traits, their way of relating to the available regulating factors will be different, meaning that they are ecologically differentiated and thus can coexist.

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

Natura non facit saltus – or does it? The question remains: what biological mechanisms would lead to sharp discontinuities in the resource utilization of species? Although one should not take the old Leibnitzian principle for granted (at least not in ecology), the question raised by Meszéna (2005) is still a serious challenge: what qualitative difference could there be between two bird species which only differ in that one has a beak 1μm larger than the other, when clearly no one would even

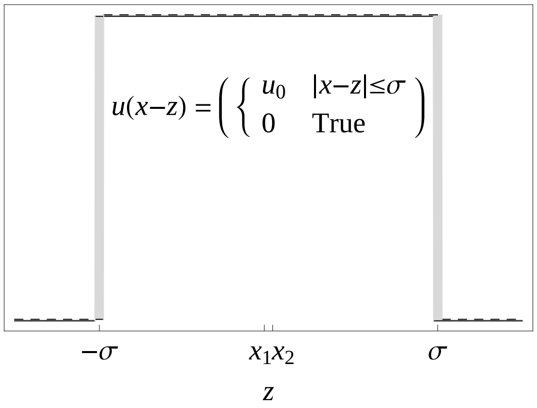


Figure 5: Utilization curves of two species with traits x_1 (solid line) and x_2 (dashed line), respectively. For the given box-like utilization function $u(x-z)$, no matter how similar the two species are, there will always be a range of resources (shaded in gray) that are utilized exclusively by only one of them. This leads to the independent regulation of the species and therefore to their coexistence, regardless of how close x_1 is to x_2.

notice that there are two separate species to begin with? The question may be analyzed more clearly if, instead of asking whether nature exhibits jumps, we ask whether the kinds of *models* we use would exhibit them. Here we give two arguments supporting the assertion that sudden jumps will in fact never occur in the kinds of deterministic competition models we have been considering.

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

$$u_s(\bar{x},z) = \int_{x_0}^{x_m} p(\bar{x},x)u(x-z)\,\mathrm{d}x. \tag{28}$$

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

$$p(\bar{x},x) = \frac{1}{\sqrt{2\pi\sigma^2(\bar{x})}} \exp\left(-\frac{(\bar{x}-x)^2}{2\sigma^2(\bar{x})}\right). \tag{29}$$

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

$$u_s(\bar{x}, z) = \int_{x_0}^{x_m} \frac{u(x-z)}{\sqrt{2\pi\sigma^2(\bar{x})}} \exp\left(-\frac{(\bar{x}-x)^2}{2\sigma^2(\bar{x})}\right) \mathrm{d}x, \tag{30}$$

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

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

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

6 Discussion

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

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

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

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

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

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

The concept that species with almost-equal intrinsic growth rates can coexist via relatively weak stabilization is surely uncontroversial. However, the situation is not that simple when the trait-dependence of the two terms is considered. We have seen in Section 4 (with the mathematical underpinning in Appendix A) that the equalizing term (difference in r_0) and the stabilizing, frequency dependent term do *not* approach zero at the same rate in general: the former is proportional to the difference in trait, while the latter is proportional to the square of the difference in trait. The stabilizing term is therefore incapable of overcoming differences in r_0 if the species are too similar – *except* when the competition kernel is kinked. For kinked kernels the stabilizing term changes linearly with trait difference, just like the equalizing term, and so it can compensate for differences in r_0. In conclusion, only models with kinked kernels can allow for the robust coexistence of similar species; for instance, in the work of Scheffer and van Nes (2006), only transient coexistence of similars was possible with a Gaussian competition kernel, but stable coexistence was observed when an extra term was added to the equations that rendered the kernel kinked.

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

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

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

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

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Appendix A: Two-species coexistence under smooth and kinked kernels

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

$$\frac{\mathrm{d}n(x_1)}{\mathrm{d}t} = n(x_1)\Big(r_0(x_1) - a(x_1,x_1)n(x_1) - a(x_1,x_2)n(x_2)\Big), \tag{31}$$

$$\frac{\mathrm{d}n(x_2)}{\mathrm{d}t} = n(x_2)\Big(r_0(x_2) - a(x_2,x_2)n(x_2) - a(x_2,x_1)n(x_1)\Big). \tag{32}$$

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

$$r_0(x_2) = r_0(x_1 + \Delta x) \approx \underbrace{r_0(x_1)}_{r_0} + \underbrace{\frac{\mathrm{d}r_0}{\mathrm{d}x}(x_1)}_{c}\Delta x = r_0 + c\Delta x, \tag{33}$$

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

$$a(x_2,x_2) = A(x_2) = A(x_1 + \Delta x) \approx \underbrace{A(x_1)}_{a_x} + \underbrace{\frac{\mathrm{d}A}{\mathrm{d}x}(x_1)}_{w}\Delta x = a_x + w\Delta x, \tag{34}$$

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

$$a(x_1, x_2) = a(x_1, x_1 + \Delta x) \approx a(x_1, x_1) + \underbrace{\partial_2 a(x_1, x_1^+)}_{-k_x} \Delta x + \frac{1}{2} \underbrace{\partial_2^2 a(x_1, x_1^+)}_{-d_x} \Delta x^2 = a_x - k_x \Delta x - \frac{d_x}{2} \Delta x^2 \tag{35}$$

and

$$a(x_2, x_1) = a(x_2, x_2 - \Delta x) \approx \underbrace{a(x_2, x_2)}_{a_y} - \underbrace{\partial_2 a(x_2, x_2^-)}_{k_y} \Delta x + \frac{1}{2} \underbrace{\partial_2^2 a(x_2, x_2^-)}_{-d_y} \Delta x^2 = a_y - k_y \Delta x - \frac{d_y}{2} \Delta x^2, \tag{36}$$

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

The dynamical equations may now be written as

$$\frac{\mathrm{d}n(x_1)}{\mathrm{d}t} = n(x_1) \left(r_0 - a_x n(x_1) - (a_x - k_x \Delta x - \frac{d_x}{2} \Delta x^2) n(x_2) \right), \tag{37}$$

$$\frac{\mathrm{d}n(x_2)}{\mathrm{d}t} = n(x_2) \left(r_0 + c\Delta x - a_y n(x_2) - (a_y - k_y \Delta x - \frac{d_y}{2} \Delta x^2) n(x_1) \right) \tag{38}$$

in this approximation.

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

$$\frac{a_{12}}{a_{22}} < \frac{r_{01}}{r_{02}} < \frac{a_{11}}{a_{21}} \tag{39}$$

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

$$\frac{a_x - k_x \Delta x - (d_x/2) \Delta x^2}{a_y} < \frac{r_0}{r_0 + c\Delta x} < \frac{a_x}{a_y - k_y \Delta x - (d_y/2) \Delta x^2} \tag{40}$$

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

$$\frac{a_y}{a_x - k_x\Delta x - (d_x/2)\Delta x^2} > 1 + \frac{c}{r_0}\Delta x > \frac{a_y}{a_x} - \frac{k_y}{a_x}\Delta x - \frac{d_y}{2a_x}\Delta x^2. \tag{41}$$

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

$$\frac{a_y}{a_x - (d_x/2)\Delta x^2} > 1 + \frac{c}{r_0}\Delta x > \frac{a_y}{a_x} - \frac{d_y}{2a_x}\Delta x^2. \tag{42}$$

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

$$a_y > a_x + \frac{ca_x}{r_0}\Delta x - \frac{d_x}{2}\Delta x^2 > a_y - \left(\frac{d_x a_y}{2a_x} + \frac{d_y}{2}\right)\Delta x^2. \tag{43}$$

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

$$0 > \left(\frac{ca_x}{r_0} - w\right)\Delta x - \frac{d_x}{2}\Delta x^2 > -\left(\frac{d_x a_y}{2a_x} + \frac{d_y}{2}\right)\Delta x^2, \tag{44}$$

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

$$\frac{d_x}{2}\Delta x > \frac{ca_x}{r_0} - w > \left(\frac{d_x}{2} - \frac{d_x a_y}{2a_x} - \frac{d_y}{2}\right)\Delta x. \tag{45}$$

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

Having established the limits to the similarity of two competing species under smooth competition kernels, let us turn our attention to kinked ones. In this case the first-order expansion coefficients k_x and k_y are nonzero, rendering the second order negligible in comparison. Therefore in Eq. (41) we may neglect any terms that are quadratic or higher order. As a result, we get

$$\frac{a_y}{a_x - k_x\Delta x - (d_x/2)\Delta x^2} > 1 + \frac{c}{r_0}\Delta x > \frac{a_y}{a_x} - \frac{k_y}{a_x}\Delta x. \tag{46}$$

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

$$a_y > a_x - k_x\Delta x + \frac{ca_x}{r_0}\Delta x > a_y - \left(\frac{k_x a_y}{a_x} + k_y\right)\Delta x. \tag{47}$$

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

$$0 > \frac{ca_x}{r_0} - k_x - w > -\frac{k_x a_y}{a_x} - k_y, \tag{48}$$

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

Appendix B: The competition kernel as an overlap between sensitivities and impacts

Our purpose is to show that the competition kernel is always expressible as an overlap between two different functions called sensitivities and impacts (Meszéna et al. 2006, Barabás et al. 2011). This expression does not depend on the assumptions that lead to the utilization overlap picture. The resource utilization overlap model turns out to be a special case of this general formalism where the sensitivity and impact functions are precisely proportional to one another.

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

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x)\, r\left(R(z,n),E\right), \tag{49}$$

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

$$\begin{aligned} \frac{\mathrm{d}n(x)}{\mathrm{d}t} &\approx n(x)\Big(\underbrace{r(R(z,n^*),E)}_{0} + \delta r(R(z,n),E)\Big) \\ &= n(x)\left(\int_{x_0}^{x_m} \frac{\delta r(x)}{\delta E(y)}\delta E(y)\,\mathrm{d}y + \int_{x_0}^{x_m}\int_{z_0}^{z_m} \frac{\delta r(x)}{\delta R(z)}\frac{\delta R(z)}{\delta n(y)}\delta n(y)\,\mathrm{d}z\,\mathrm{d}y\right), \end{aligned} \tag{50}$$

where we used the chain rule of differentiation (see Section 2 for the meaning of the functional derivative); $r(x)$ is shorthand for $r\left(R(x,n(x)),E(x)\right)$. The factor in the second term of the expansion multiplying the perturbed densities $\delta n(y)$ consists of two parts. The first part,

$$S(x,z) = \frac{\delta r(x)}{\delta R(z)}, \tag{51}$$

is called the *sensitivity* of the species with trait x to the zth regulating factor (Meszéna et al. 2006, Barabás et al. 2011), since it measures how the growth rate of species x would change if the zth factor was slightly modified. The second part of the product,

$$I(y,z) = \frac{\delta R(z)}{\delta n(y)}, \tag{52}$$

is the *impact* of species with trait y on the zth regulating factor. It tells us how the factors regulating the populations are themselves affected by a change in species abundances. As before in Section 2, the full factor multiplying the perturbed densities $\delta n(y)$ in Eq. (50) is the competition kernel, which in our case is the overlap of the sensitivities and impacts:

$$a(x,y) = \int_{z_0}^{z_m} \frac{\delta r(x)}{\delta R(z)} \frac{\delta R(z)}{\delta n(y)} \, \mathrm{d}z = \frac{\delta r(x)}{\delta n(y)} = \int_{z_0}^{z_m} S(x,z) I(y,z) \, \mathrm{d}z. \tag{53}$$

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

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

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = n(x) \left(\int_{z_0}^{z_m} b(x,z) R(z) \, \mathrm{d}z - m(x) \right), \tag{54}$$

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

$$\frac{\mathrm{d}R(z)}{\mathrm{d}t} = R(z) \left(R_0(z) - R(z) - \int_{x_0}^{x_m} f(y,z) n(y) \, \mathrm{d}y \right), \tag{55}$$

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

$$R(z) = R_0(z) - \int_{x_0}^{x_m} f(y,z) n(y) \, \mathrm{d}y. \tag{56}$$

Substituting Eq. (56) into Eq. (54) we obtain

$$\begin{aligned} \frac{\mathrm{d}n(x)}{\mathrm{d}t} &= n(x) \left(\int_{z_0}^{z_m} b(x,z) \left(R_0(z) - \int_{x_0}^{x_m} f(y,z) n(y) \, \mathrm{d}y \right) \mathrm{d}z - m(x) \right) \\ &= n(x) \left(\underbrace{\int_{z_0}^{z_m} b(x,z) R_0(z) \, \mathrm{d}z - m(x)}_{r_0(x)} - \int_{x_0}^{x_m} \underbrace{\left(\int_{z_0}^{z_m} b(x,z) f(y,z) \, \mathrm{d}z \right)}_{a(x,y)} n(y) \, \mathrm{d}y \right). \end{aligned} \tag{57}$$

As we can see, the competition kernel is the overlap of the functions $b(x,y)$ and $-f(y,z)$. This suggests that these functions play the roles of sensitivities and impacts. Indeed, from their definitions we get

$$S(x,z) = \frac{\delta r(x)}{\delta R(z)} = \int_{z_0}^{z_m} b(x,z')\delta(z-z')\,\mathrm{d}z' = b(x,z) \tag{58}$$

and

$$I(y,z) = \frac{\delta R(z)}{\delta n(y)} = -\int_{x_0}^{x_m} f(y',z)\delta(y-y')\,\mathrm{d}y' = -f(y,z). \tag{59}$$

The original MacArthur resource utilization model is recovered when $b(x,z) = \alpha f(x,z)$ for some constant α. Since populations tend to influence those resources most that they depend upon the most, this assumption is reasonable – but it is neither ubiquitous nor necessary.

Appendix C: Generalization of the results of Section 5

Here we extend the results obtained in Section 5 from resource overlap to arbitrary models. The key to doing this is to write the competition kernel as the overlap of sensitivity and impact functions (see Appendix B); note that this is always possible and does not depend upon the specific assumptions of resource overlap models. The competition kernel is thus given by Eq. (53). Since we are interested in nondifferentiability at zero trait difference, we set $y = x$:

$$a(x,x) = \int_{z_0}^{z_m} S(x,z)I(x,z)\,\mathrm{d}z, \tag{60}$$

where $S(x,z)$ and $I(x,z)$ are the sensitivity and impact functions, respectively, assumed to be bounded. We now show that discontinuities in the sensitivities and impacts occurring at corresponding points between the two functions is sufficient to lead to kinked kernels. Let us consider functions that contain a jump for every possible trait value x:

$$S(x,z) = \alpha\Theta(x - z_1(x)) + \eta(x,z), \tag{61}$$

$$I(x,z) = \beta\Theta(x - z_2(x)) + \zeta(x,z), \tag{62}$$

where α and β are constants, η and ζ are continuous functions, Θ is the Heaviside unit step function and $z_1(x)$, $z_2(x)$ are curves along which the sensitivity and impact functions possess a discontinuity (they depend on x because we allow for the possibility of each species having their discontinuity at different points).

Similarly to the procedure in Section 5, our strategy for determining whether $a(x,x)$ is nondifferentiable will be to take the second derivative of the kernel with respect to the first variable and see whether the result obtained is infinitely large or not. The second derivative reads

$$\partial_1^2 a(x,x) = \int_{z_0}^{z_m} \partial_1^2 S(x,z)I(x,z)\,\mathrm{d}z = \alpha \int_{z_0}^{z_m} \delta'(x - z_1(x))I(x,z)\,\mathrm{d}z + \ldots, \tag{63}$$

where $\partial_1^2 S(x,z)$ is the second partial derivative of S with respect to the first variable, evaluated at (x,z), δ' is the derivative of the Dirac delta function, and the ellipsis denotes all other terms the derivative produces that we have not written out, for the reason that those terms are necessarily finite and so they do not contribute to the nondifferentiability of the kernel. The integration can be performed with the help of the δ' function:

$$\partial_1^2 a(x,x) = -\alpha \partial_2 I(x, z_1(x)) + \ldots, \tag{64}$$

which is infinitely large if I is discontinuous along $z_1(x)$. This of course happens when $z_1(x) = z_2(x)$. Therefore, if $S(x, z_1(x))$ and $I(x, z_1(x))$ are both discontinuous along some curve $z_1(x)$, then the resulting competition kernel is kinked.

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