Limiting similarity, species packing, and the shape of competition kernels

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ABSTRACT

A traditional question in community ecology is whether species' traits are distributed as more-or-less regularly spaced clusters. Interspecific competition has been suggested to play a role in such structuring of communities. The seminal theoretical work on limiting similarity and species packing, presented four decades ago by Robert MacArthur, Richard Levins and Robert May, has recently been extended. There is now a deeper understanding of how competitive interactions influence community structure, for instance, how the shape of competition kernels can determine the clustering of species' traits. Competition is typically weaker for greater phenotypic difference, and the shape of the dependence defines a competition kernel. The clustering tendencies of kernels interact with other effects, such as variation in resource availability along a niche axis, but the kernel shape can have a decisive influence on community structure. Here we review and further extend the recent developments and evaluate their importance.

1. Introduction

Throughout the history of evolutionary thinking, questions have been posed about the reason for species numbers and the distribution of their traits. When discussing evolutionary history, the point is often made that there have been transitional forms, appearing in a sequence from ancestral to derived, and that the transitional forms have gone extinct from competition with emerging forms. This observation suggests that competition is crucial for the distinctness of species.

Even though the clustering of species seems self-evident empirically, it has proven hard to understand theoretically. The basic issues were identified already in the pioneering studies on species packing into niche space. Over the years, a large body of work on the topic has appeared, and much of it can be portrayed in relation to the analyses of one of the founders of the discipline, Robert MacArthur. Discussing the utilization of a resource spectrum, MacArthur (1970) noted that: "Where the utilizations fall slightly below the production, a new species can enter if the addition of one pair (or propagule) will make the total utilization even closer to the available production. A small multiple of some appropriate species will always improve the fit somewhere so that some new species, in very small quantity,

could always invade." MacArthur's reasoning points to the theoretical possibility of an extremely close packing of species. In spite of this, he and his coworkers tended to side with the idea that there are limits to similarity (e.g., MacArthur and Levins, 1967). This tension in the field – a search for limits, while at the same time developing theories that suggest close packing – has added to its perceived difficulty.

In a critical approach, Abrams (1975, 1983) argued that the ecological relevance of theories of species packing depends on the realism of the underlying assumptions, and these can be questioned. Recent years have in fact seen a decisive broadening of the original analyses (Scheffer and van Nes, 2006; Pigolotti et al., 2007; Doebeli et al., 2007; Leimar et al., 2008; Abrams and Rueffler, 2009; Hernández-García et al., 2009; Ispolatov and Doebeli, 2009; Fort et al., 2009, 2010; Pigolotti et al., 2010). The new analyses relax some of the main presuppositions of the earlier work, potentially improving the ecological relevance of the predictions. It is our aim here to describe and further extend these developments.

The traditional theory of species packing and community structure appeared in a number of papers, of which those by MacArthur, Levins and May (MacArthur and Levins, 1967; MacArthur, 1969, 1970; May and MacArthur, 1972; May, 1974a,b) were especially influential. In these analyses, competition was modeled as an overlap of resource-utilization functions, implying that resources contributing to the growth of one species become unavailable to other species. This form of competition gives rise to competition kernels with special shapes, of which the Gaussian shape is one often used

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example. Based on their assumptions, May and MacArthur (1972) concluded that demographic stability (i.e., stability against small deviations in the densities of resident species) imposes no limit on species packing in a deterministic environment. An important aim of some of the recent work (Pigolotti et al., 2007, 2010; Leimar et al., 2008; Hernández-García et al., 2009) has been to investigate the consequences for species clustering of changing the idealized assumption that competition arises only from resource-utilization overlap. This is an important extension, not least because there are a number of well-established additional processes that cause effective competition in ways that need not follow the MacArthur-May assumptions, including interference competition and apparent

competition. A crucial insight from the new work, which considers competition kernels of general shape, is that this shape can have a decisive influence on species clustering (see Fig. 1 for an example).

In the following, we first explain the relation between competition kernel shape and clustering using Fourier analysis. This is a mathematical approach to the analysis of shape, and we attempt to provide an intuitive understanding of the method. We also discuss how competition kernels are determined by underlying ecological processes, and how they may depend on the within-population distribution of the mediating traits. Apart from competition kernel shape, heterogeneities in the distribution of resources can influence species clustering, and we give an overview of the state of knowledge of this phenomenon. We end by summing up the significance of the new developments.

2. Competition kernel shape

In modeling, species are often positioned along a niche axis or resource dimension (e.g., MacArthur and Levins, 1967; Scheffer and van Nes, 2006; Pigolotti et al., 2007), where a position can be described by the corresponding value x of a quantitative trait or phenotype best suited to the utilization of the resource. More generally, the individuals in a population can have different phenotypes. The effect of competition from individuals with phenotype x_k is to reduce the growth rate of a population with phenotype x_j. The reduction is quantified using a competition coefficient, which is often assumed to be a function of the phenotypic difference, expressed as $a(x_j-x_k)$. This function $a(x)$ is referred to as the competition kernel. The Lotka–Volterra competition equations describe the dynamics of the densities of the species in a community

$$\frac{dN_j}{dt} = N_j \left(K(x_j) - \sum_k a(x_j-x_k)N_k \right). \tag{1}$$

For simplicity, we can focus on the case where the maximum per capita growth rates and the carrying capacities $K(x_j)$ of the niche positions are equal to 1. To gain conceptual understanding, hypothetical communities where the species are placed either along an infinite niche axis or, for a finite numbers of species, along a circular niche space (e.g., May and MacArthur, 1972; May, 1974a,b) are sometimes studied.

2.1. Fourier analysis and demographic stability

The Fourier transform $\hat{a}(\phi)$ of a function $a(x)$ is defined as

$$\hat{a}(\phi) = \int a(x)\exp(-2\pi i\phi x)\,dx, \tag{2}$$

where ϕ can be regarded as a frequency, i is the imaginary unit, and integration extends over the real line. For a circular niche
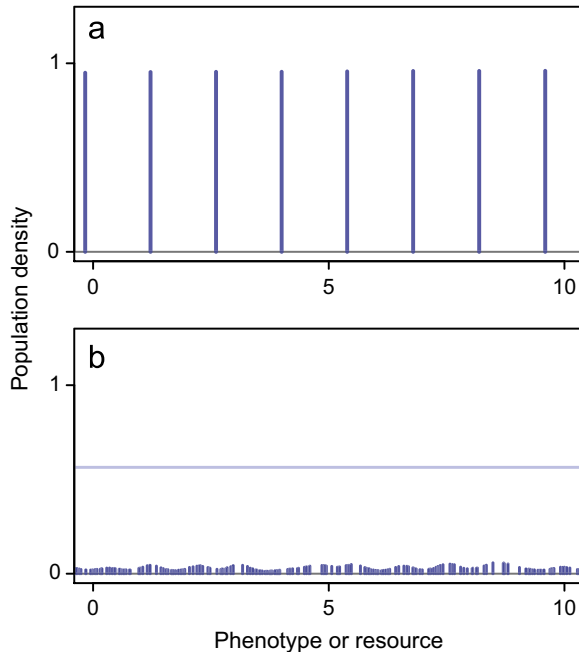

Fig. 1. Community simulations with competition kernels that either promote or counteract species clustering. In (a) the competition kernel is quartic, $a(x)=\exp(-x^4)$, which causes the species to cluster in phenotype space, with a gap size of about 1.37. At the depicted stable equilibrium, there is only one species per cluster, with population sizes given by the vertical lines. In (b) the competition kernel has a Gaussian shape, $a(x)=\exp(-x^2)$. There is no clustering and no limit to species packing. The vertical lines represent population sizes of individual species and the light blue line is a smoothed population density per unit phenotype. In the simulations, new species were first introduced intermittently at a density of 0.0001 at random positions along a circular niche space with period 100 (of which the range from 0 to 10 is shown). Species reaching densities below a threshold of 0.00008 were considered extinct. After a long period of species introduction and extinction, the introduction of new species was turned off and simulations were run for an additional long period to reach a stable equilibrium. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)
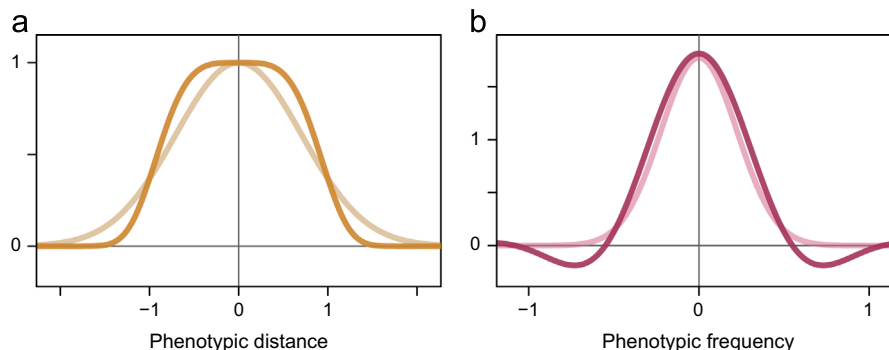

Fig. 2. (a) Quartic and Gaussian (pale curve) competition kernels and (b) their Fourier transforms.
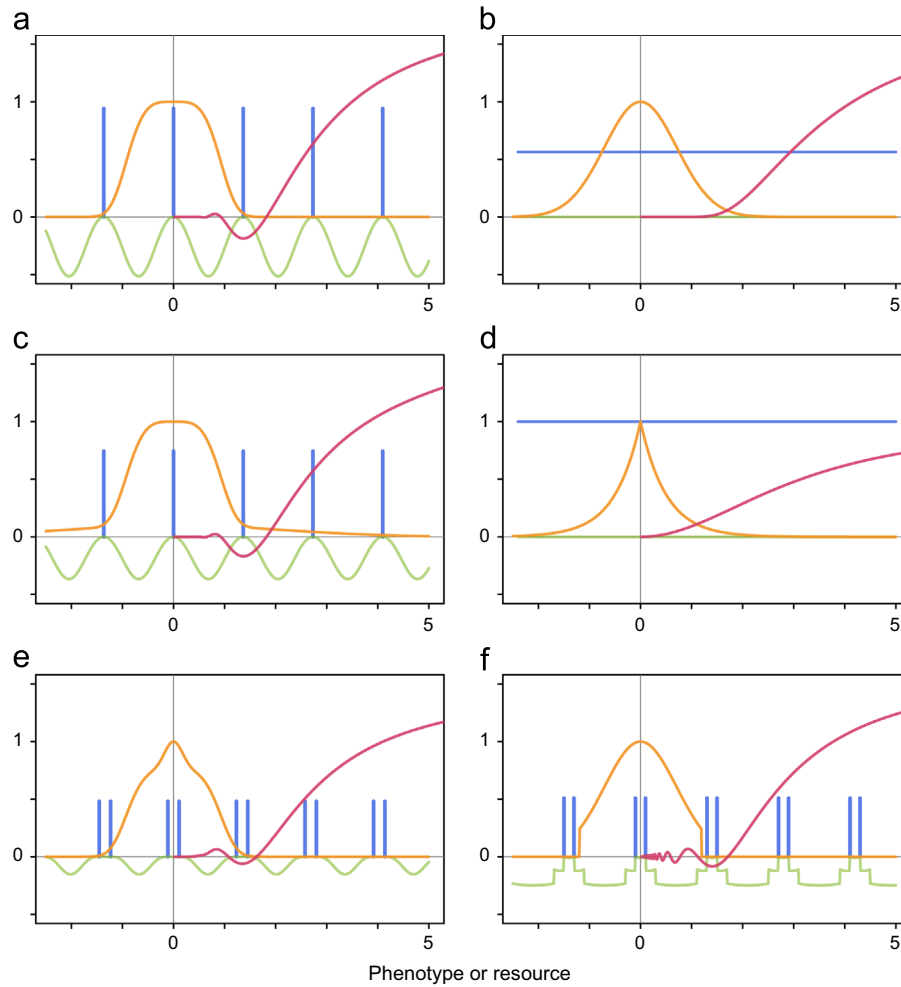
Fig. 3. The influence of competition kernel shape on clustering. Competition kernels $a(x)$ (orange), their Fourier transforms as functions of wavelength (red), demographically stable species distributions (blue), and fitness landscapes (green) are shown. Species are either clustered (blue vertical lines indicate population densities) or have continuous distributions (blue horizontal lines show population density per unit phenotype). Clustering occurs if the Fourier transform has a negative minimum. The wavelength at the minimum corresponds to the inter-cluster gap. (a) Quartic, $a(x) = \exp(-x^4)$; (b) Gaussian, $a(x) = \exp(-x^2)$; (c) quartic with extended tails: $a(x) = 0.9 \exp(-x^4) + 0.1 \exp(-x^2/9)$; (d) Laplacian: $a(x) = \exp(-2|x|)$; (e) quartic with central peak, $a(x) = 0.75 \exp(-x^4) + 0.25 \exp(-16x^2)$; (f) truncated Gaussian, $a(x) = \exp(-x^2)$ for $|x| < 1.2$ and $a(x) = 0$ otherwise. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

space, this means an infinite number of turns around the circle. If the function is symmetric, so that $a(-x) = a(x)$, the Fourier transform is real, but in general there are both real and imaginary parts. Fig. 2 shows two symmetric competition kernels, which were used for the results shown in Fig. 1, together with their Fourier transforms. We can express Fourier transforms as functions of a wavelength, given by $\lambda = 1/\phi$, which we write as $\tilde{a}(\lambda) = \hat{a}(1/\lambda)$ (the red curves in Fig. 3a,b show examples for quartic and Gaussian competition kernels).

Suppose there is an equilibrium community (i.e., densities such that the growth rates in Eq. (1) are all zero) in which the species are closely spaced along the niche axis, for instance, equidistantly. A perturbation of the density of one species can, because of competition, spread to neighboring species, and so on to more distant species, in this way influencing the whole community. If the perturbation is damped over time, the community is demographically stable, but if it is enhanced and causes extinction of some of the species, in this way increasing the gaps in the community, there is a clustering tendency.

The Fourier transform can be used to study these questions of demographic stability. In general, the purpose of Fourier analysis is to describe phenomena such as density perturbations in terms of components with different wavelengths; a typical application would be vibrations that are decomposed into individual frequency components. In the context of community ecology, one can examine whether a close-packed community would be stable. If it is not, one can find the most strongly destabilized wavelength. One can also examine the stability of equidistant communities (see below).

For a close-packed community, it is convenient to write the Lotka–Volterra dynamics in Eq. (1) as

$$\frac{\partial n(x)}{\partial t} = n(x)\left(1 - \int a(x-y)n(y)\,dy\right), \quad (3)$$

where $n(x)$ is the population density per unit phenotype along the niche axis. For species at discrete positions x_j, like in Eq. (1), $n(x)$ is a collection of delta peaks, $N_j\delta(x-x_j)$. For a close-packed community, we approximate $n(x)$ as a continuous function of x. One equilibrium solution to Eq. (3) is a constant density, $n^* = 1/\int a(y)\,dy$. We can determine the stability of this equilibrium by checking whether perturbations are damped or enhanced. Given a small perturbation $u(x)$, so that $n(x) = n^* + u(x)$, we can linearize the Lotka–Volterra dynamics in Eq. (3), obtaining

$$\frac{\partial u(x)}{\partial t} = -n^* \int a(x-y)n(y)\,dy. \quad (4)$$

The Fourier transform of the linearized equation is

$$\frac{\partial \tilde{u}(\lambda)}{\partial t} = -n^* \, \tilde{a}(\lambda)\tilde{u}(\lambda). \quad (5)$$

From this equation we conclude that a perturbation of wavelength λ is damped if the real part of the Fourier transform $\tilde{a}(\lambda)$ is positive, and is enhanced if the real part is negative (Pigolotti et al., 2007; Leimar et al., 2008).

If the Fourier transform of a symmetric competition kernel $a(x)$ is positive for a given wavelength, there is a damping of periodic density perturbations of that wavelength, as shown by Eq. (5). A symmetric competition kernel for which the Fourier transform is positive for all wavelengths causes damping of all small perturbations, and such a kernel is said to be positive definite. The terminology is standard and is formed in analogy with the concept of a symmetric positive definite matrix. If, on the other hand, the Fourier transform of a kernel is negative for some wavelength, perturbations for that wavelength can grow, breaking up a closely packed community. This then constitutes a clustering tendency of the kernel.

2.2. Symmetric competition

Most analyses of species clustering have assumed symmetric competition. In a successful transfer of approaches from physics to ecology, Pigolotti and co-workers were the first to establish the importance for clustering of the sign-structure of the Fourier transform of a symmetric competition kernel (Pigolotti et al., 2007, 2010; Hernández-García et al., 2009). The same approach was used to study clustering along an environmental gradient, involving both geographical and trait space, leading to similar conclusions about the role of competition kernel shape (Leimar et al., 2008). A range of examples of the relation between competition kernel shape and the equilibrium species distribution appears in Fig. 3. In each example, the Fourier transform (red) of the competition kernel (orange) explains the equilibrium patterning of species (blue). Positive definite competition kernels give rise to continuous (arbitrarily close-packed) species distributions (Fig. 3b,d), whereas kernels whose Fourier transforms take negative values lead to clustered distributions, with phenotype gap sizes that correspond to the wavelength of the minimum of the Fourier transform (Fig. 3a,c,e,f). The competition kernels in Fig. 3a, b were used in the simulations in Fig. 1 (Fig. 2b shows these Fourier transforms as functions of phenotypic frequency).

Kurtosis is a common measure of the peakedness of a distribution. Applied to competition kernel shapes, it can give useful guidance about clustering tendencies. Square or box-like kernels (Leimar et al., 2008; Pigolotti et al., 2010) are typically platykurtic and tend to promote clustering (Fig. 3a), whereas mesokurtic and leptokurtic kernels can be positive definite (Fig. 3b,d). The correspondence is not perfect, however, as seen in Fig. 3c, where the square central shape of the kernel dominates the clustering

tendency, giving rise to a Fourier transform with negative values, whereas the long tails of the kernel dominate kurtosis, making the kernel leptokurtic.

If the tails of a Gaussian are truncated, the resulting competition kernel becomes platykurtic and has negative Fourier transform values, resulting in species clustering (Fig. 3f). It has been argued that truncation of the competition kernel is a way to represent a finite niche space (Scheffer and van Nes, 2006; Fort et al., 2009, 2010). Alternatively, and preferably, a finite niche space can be modeled as the tapering off of a resource distribution at its limits (see Fig. 7 below). Note also that the equilibrium species distribution for the truncated Gaussian kernel consists of double peaks (Fig. 3f), with the gap between successive doubles corresponding to the wavelength at the minimum of the Fourier transform. Similar clustering patterns can occur for kernels that combine a platykurtic central part with a sharper peak (Hernández-García et al., 2009) (Fig. 3e).

2.3. Asymmetric competition

It is likely that many or even most instances of competitive interactions in nature are asymmetric, in the sense that, for two distinct trait values, one will have a competitive advantage over the other (Wilson, 1975) (for instance, the taller of two plants competing for light, Weiner, 1990). Theoretical studies of community evolution under asymmetric competition point to an important distinction compared with symmetric competition (Taper and Case, 1992; Law et al., 1997). Asymmetric competition can promote continual change in a community, for instance in the form of taxon cycles (Taper and Case, 1992; Dayan and Simberloff, 2005; Dieckmann et al., 2007). In spite of such basic differences between symmetric and asymmetric competition, questions of species clustering and typical sizes of gaps in species distributions may have similar answers for the two types of communities. For general competition kernel shapes, the real part of the Fourier transform of the kernel contains information about clustering, as shown by Eq. (5): if the real part is positive, a close-packed community will be stable, whereas negative values indicate a clustering tendency. Because the real part is equal to the Fourier transform of the symmetrized kernel, $a_s(x) = (a(x) + a(-x))/2$, one can use the shape of the symmetrized kernel as an intuitive guide to the properties of an asymmetric kernel. As an example, in Fig. 4a the asymmetric kernel is a shifted Gaussian, so the symmetrized kernel is a platykurtic mixture of Gaussians shifted left and right, whose Fourier transform takes negative values, promoting clustering. This can be compared with Fig. 4b, where the symmetrized kernel is a mixture of two Gaussians with equal
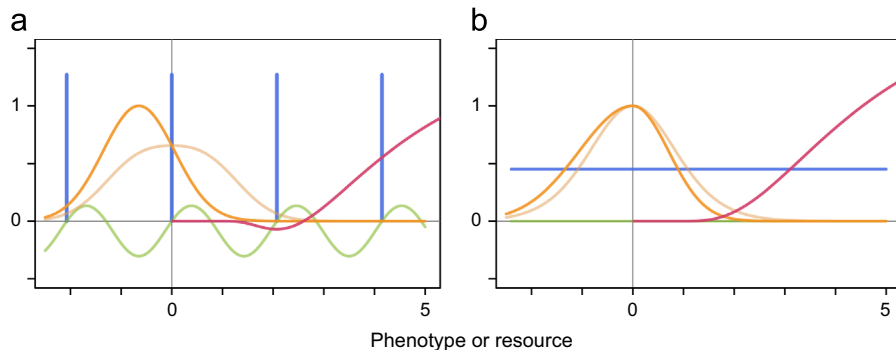

Fig. 4. The influence of asymmetric competition kernel shape on clustering. Competition kernels $a(x)$ (orange), symmetrized kernels (pale orange), the real part of their Fourier transforms as functions of wavelength (red), species distributions (blue), and fitness landscapes (green) are shown. (a) Asymmetric Gaussian, shifted left by 0.65: $a(x) = \exp(-[x + 0.65]^2)$; (b) asymmetric Gaussian for which the left half is 'stretched' by a factor of 1.5: $a(x) = \exp(-x^2)$ for $x \geq 0$ and $a(x) = \exp(-[x/1.5]^2)$ for $x < 0$. The community in (a) has a gap size of about 2.07, which is the position of the minimum of the real part of the Fourier transform, and it can be invaded to the right of the resident species. The community in (b) is demographically neutrally stable. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)
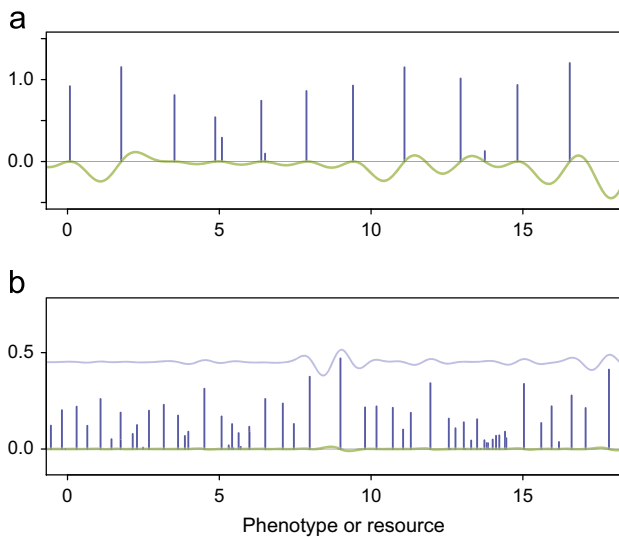
Fig. 5. Community simulations illustrating the influence of asymmetric competition kernel shape on clustering (using the same approach as in Fig. 1). (a) A 'typical snapshot' of a species distribution (blue verticals). The competition kernel is the one in Fig. 4a, for which the real part of the Fourier transform has a negative minimum. The fitness landscape at the time of the snapshot is shown in green, and indicates that the community can be invaded at several niche positions to the right of resident species. The average gap between species clusters is similar to but somewhat smaller than the gap size in Fig. 4a. (b) With the competition kernel in Fig. 4b, for which the real part of the Fourier transform is positive, a 'typical snapshot' shows a more closely packed community (blue) with a relatively flat fitness landscape (green). A smoothed species distribution (light blue curve) has approximately the same density per unit phenotype as in Fig. 4b. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

means, which becomes leptokurtic and is positive definite, potentially supporting a close-packed community.

While the species distributions in Fig. 4 are demographically stable, the fitness landscape in Fig. 4a shows that species from outside the community, with traits somewhat to the right of the resident species, could invade. As an illustration of how such invasions may influence species clustering, Fig. 5 shows the outcomes of community simulations (performed like those in Fig. 1) for the asymmetric kernels in Fig. 4. The simulations do not reach an equilibrium, but there is instead a turnover of species. Nevertheless, there is still a typical patterning of the species in Fig. 5a, with an approximate gap size that seems to be related to the gap in Fig. 4a, whereas there is closer packing in Fig. 5b. It thus seems that the Fourier transform of the kernel conveys important information about the distribution of traits in a community also for the case of asymmetric competition.

2.4. Demographic stability of equidistant communities

We have seen that Fourier analysis is helpful when examining questions of demographic stability of close-packed communities, as illustrated by Eq. (5). One can also apply Fourier analysis to equidistant communities. Thus, for symmetric competition kernels, an equidistant community with phenotypic gap size d is demographically stable if the inequality

$$\sum_j \hat{a}(1/\lambda + j/d) > 0 \qquad (6)$$

holds for all wavelengths λ, and it is unstable if the inequality is reversed for some λ (see Appendices A and B for a derivation of the corresponding result for general, possibly non-symmetric, competition kernels). For the case of a close-packed community, we recover our previous condition, because in the limit of d going to

zero, only the term for $j=0$ contributes to the sum on the left-hand side of (6), giving the condition $\hat{a}(1/\lambda) = \tilde{a}(\lambda) > 0$.

From condition (6) we see that equidistant communities with a positive definite competition kernel are always demographically stable, because each term in the sum is positive. Thus, while such kernels do not induce clustering, neither do they lead to demographic instability of equidistant communities (but they do allow invasions into the gaps of the community; see below). On the other hand, for a kernel whose Fourier transform changes sign, condition (6) entails that there is demographic stability only for certain values of the spacing d, such that the negative values are compensated by positive values in the sum. This compensation cannot occur for very small d, but is particularly likely when d is close to the wavelength at the minimum of the Fourier transform.

Condition (6) is related to and generalizes the classical results obtained by May (1974a,b), on the smallest rate of damping of density perturbations of equidistant communities. May (1974a,b) studied only positive definite competition kernels, without making use of Fourier analysis, and he emphasized that the smallest rate of damping can, for small d, be extremely close to zero, which he referred as an "essential singularity". In terms of condition (6), this can be understood as a very small value for the sum on the left-hand side, including for the term for $j=0$, when λ is small (see, e.g., the red curve in Fig. 3b; see also Appendix B).

2.5. Invasion into communities

An equilibrium community could be destabilized by the growth of a perturbation of the resident densities, but also by the introduction of new species with different traits. These two aspects of stability represent related investigations of a community dynamics such as the Lotka–Volterra equations. Both have been dealt with in analyses of limiting similarity, for instance, in three-species communities, where one can look for a stable coexistence of three species, as well as examine if a third species can invade into the gap between two resident species (e.g., MacArthur and Levins, 1967; May, 1974a,b; Roughgarden, 1974; Abrams, 1975). For equidistant communities along an infinite niche axis, or along a circular niche space, it seems that only the question of demographic stability has been examined using analytical methods (May, 1974a,b). Nevertheless, as it turns out, Fourier analysis can be applied to the question of invasion into the gaps of an equidistant community. As is suggested by the fitness landscapes (green curves) in Fig. 3, the analysis shows that the shape of competition kernels can have a decisive influence on whether new species can invade into the gaps.

Symmetric positive definite competition kernels have a positive Fourier transform, and from this one can show that invasion into the gaps of an equidistant community is always possible (Appendix C), but for close packing of the resident species, there is near-neutrality, with an essentially flat fitness landscape. Although not previously proven, this result has often been taken for granted, and it provides a motivation for the idea that positive definite competition kernels set no strict limit to similarity.

The situation is quite different for symmetric competition kernels whose Fourier transforms change sign (Appendix C). As illustrated by the fitness landscapes in Fig. 3, for these kernels there are values of the spacing d such that the gaps in the community are protected from invasion. This property, of disfavoring invading species at certain distances from the resident species, could represent an important influence of competition kernel shape on community structure. The influence is likely to be particularly strong for kernels with a pronounced negative minimum of the Fourier transform, because these kernels produce a strongly undulating fitness landscape (Appendix C, Fig. 3), with correspondingly robust consequences for community structure.

For asymmetric competition kernels, communities typically can be invaded at certain niche positions along a resource spectrum (Figs. 4 and 5). Even so, the competition kernel shape can influence the lengths of the intervals along a resource axis that are protected from invasion, as well as the gap sizes created when an invasion succeeds (Fig. 5). From the results shown here, it seems that the Fourier transform of a symmetrized competition kernel provides useful information about the clustering tendencies of the kernel.

3. Beyond idealized resource competition

The pioneering theoretical work on species packing assumed that competition was caused by an overlap of resource-utilization functions (MacArthur and Levins, 1967; MacArthur, 1969, 1970; May and MacArthur, 1972; May, 1974a,b). The concept of utilization overlap has been employed to also estimate competition coefficients from data (Levins, 1968; MacArthur, 1972; Roughgarden, 1974; Schoener, 1974; May, 1975; Wilson, 1975; Roughgarden, 1979; Case, 1981). In the most idealized case, in which the utilization functions of different species have identical shape and width, and resource availability along the niche axis is uniform, the resulting competition kernels are symmetric and positive definite (Appendix D), permitting a close packing of species. This holds not just for Gaussian utilization functions, but for arbitrary shapes, which means, for instance, that the work by Roughgarden (1974), investigating a family of utilization function shapes, remained within the confines of positive definite competition kernels.

It is of interest to go beyond this case, not least because one can doubt the general applicability of idealized resource competition (Abrams, 1975, 1983; Hernández-García et al., 2009). A common deviation could be related to inefficiency or wastefulness in competitive interactions, in the sense that the activity of members of one species reduce the availability of resources for another species, without fully utilizing these resources for their own population growth (Schoener, 1974; Hernández-García et al., 2009). Thus, only a part of the resources made unavailable to competitors by the activity of a species might contribute effectively to population growth, whereas the remainder might go to waste. Competition kernels for such situations are then given by the overlap of an effective utilization function of one species with a total utilization function of another species, and such kernels are in general not positive definite, but can instead promote clustering (Fig. 6, Appendix D). Among the reasons for waste in competition could be individuals that monopolize resources (interference competition), including resources they do not use. Waste could also be a side-effect of so-called trait-mediated interactions, in which individuals restrict their foraging in response to increased predation risk (Peckarsky et al., 2008; Preisser and Bolnick, 2008).

Furthermore, if competition is mediated by traits (such as body size) that influence the extent to which species share predators, which is referred to as apparent competition (Holt, 1977), one should not expect the resulting competition kernels to be positive definite. Species interactions through the sharing of predators could be either positive or negative (Abrams and Matsuda, 1996), although effects of trait-mediated interactions (Peckarsky et al., 2008; Preisser and Bolnick, 2008) will often be negative. It has been suggested that apparent competition is quite common in large and diverse groups of organisms, such as phytophagous insects (van Veen et al., 2006).

4. Within-population trait distributions

Individuals in a population vary in their traits, so the competitive effect of the population is a sum of effects of individual traits that have a distribution with a certain shape and width along the niche axis. The distribution of individual traits can depend, among other things, on whether selection is stabilizing or disruptive (Rueffler et al., 2006). Disruptive selection can broaden the distribution, which in turn acts to reduce disruptiveness, by flattening the fitness landscape. There can be different causes of within-population variation in resource-related traits, including developmental plasticity and genetic polymorphism, but a common pattern is that resource polymorphisms correspond to platykurtic or even bimodal trait distributions (Skúlason and Smith, 1995; Elmer et al., 2010). There is also empirical evidence that resource polymorphism is a response to strong within-population competition in combination with sufficient resource breadth (Martin and Pfennig, 2010).

If the within-population trait distribution becomes platykurtic, as a response to disruptive selection, the total competitive effect of the population is modified in the direction of a platykurtic competition kernel. Such self-organized platykurtosis could thus contribute to the clustering tendency of competition kernels (Sasaki and Dieckmann, 2011). Other causes of within-population trait variation will also influence the nature of the population's total competitive effect in a similar way. Populations are often structured into subsets having different trait means, such as age classes, or males and females. The influence of the population structure might typically be in the direction of a more platykurtic total competition kernel. For instance, for a population with sexual trait dimorphism, one should expect a platykurtic, and if the dimorphism is large enough, even bimodal total trait distribution, which can produce a clustering tendency of the resulting total competition kernel.

5. Niche-space heterogeneity

A simple explanation for patterns in the trait distributions of species is that they mirror patterns in the distribution of resources.
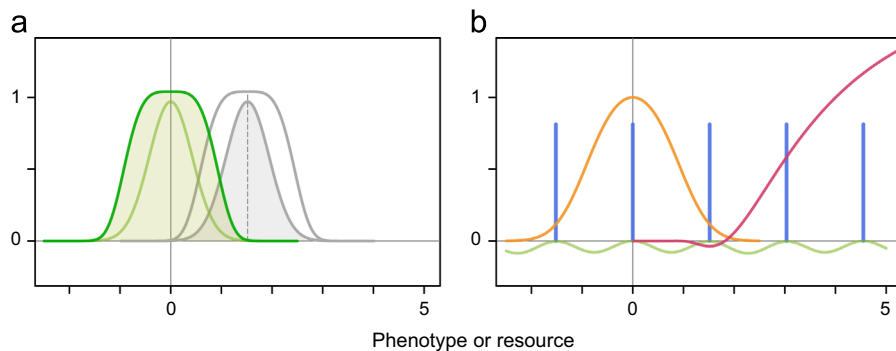

Fig. 6. (a) A total utilization function (shaded green) at niche position 0 overlaps with a narrower Gaussian effective utilization function (shaded gray) at niche position 1.52. (b) The resulting competition kernel (orange), together with its Fourier transform as a function of wavelength (red), a demographically stable species distribution (blue), and a fitness landscape (green). (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

Variation in the carrying capacities of species was an important issue already in the early treatments of species packing (May and MacArthur, 1972; May, 1974a,b; Abrams, 1975). An overall conclusion from that work is that closer packing of species increasingly restricts the range of carrying capacities permitting coexistence, which has been confirmed in recent theoretical analyses (Meszéna et al., 2006; Szabó and Meszéna, 2006; Barabás and Meszéna, 2009; Barabás et al., 2012a,b). It is also known that resource competition can strongly amplify resource heterogeneities, resulting in clumped distributions of population density (Sasaki, 1997).

There are different types of niche-space heterogeneity, for instance, small-scale variation in resource availability along a niche axis, or a unimodal resource distribution that defines a finite niche space (Fig. 7). In general, niche-space heterogeneity and competition kernel shape will jointly influence species distributions are determined by niche-space heterogeneity, but a few points can be mentioned.

First, for positive definite competition kernels, already a very small perturbation of a uniform resource availability (Sasaki, 1997) is enough to change the equilibrium species distribution from uniform to clustered (compare Figs. 7a,b and 1b), although for small perturbations, the selection promoting clustering will be weak. Second, according to the analysis by May on limiting similarity in stochastic environments (May, 1974a,b) (which assumes positive definite kernels and develops the idea of an "essential singularity"), gap sizes are expected to typically be larger than about 0.5 in Fig. 7a,b, and to become somewhat larger for increasing amplitudes of perturbation. There is indeed a reasonable agreement between these predictions and the species distributions in Fig. 7a,b. Third, for competition kernels that
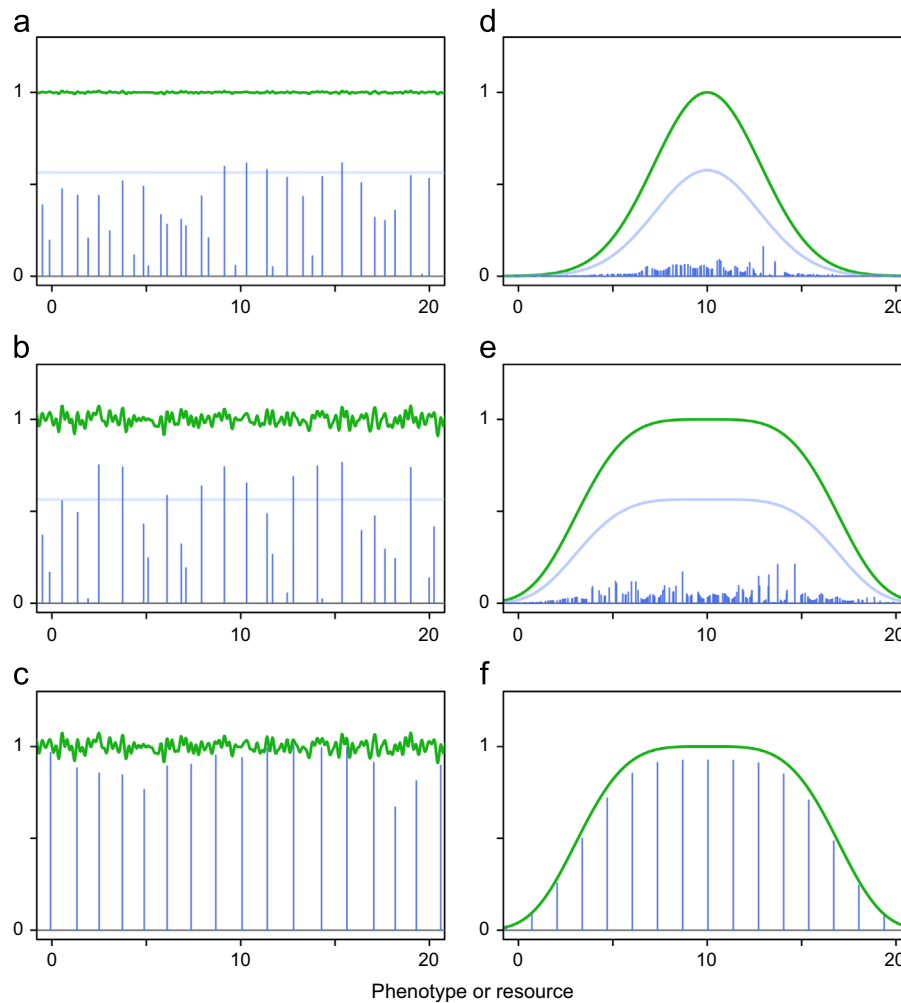

Fig. 7. Effects of competition kernel shape and resource heterogeneity on community simulations. (a) For a Gaussian kernel, $a(x) = \exp(-x^2)$, and a slightly perturbed $K(x)$ (see Eq. (1); green curve), there are fewer irregularly spaced species (blue verticals) compared with Fig. 1b. The light blue line gives the equilibrium population density per unit phenotype for $K(x) = 1$. (b) As in (a), but with a factor of 10 greater amplitude of perturbation of $K(x)$. (c) For a quartic kernel, $a(x) = \exp(-x^4)$, and the same perturbed $K(x)$ as in (b), the species distribution is similar to that in Fig. 1a, but has some variation in species densities and gap sizes. (d) For a Gaussian kernel and a Gaussian resource distribution $K(x) = \exp(-[(x-10)/4]^2)$, there is a very close-packed equilibrium species distribution. Smoothing this distribution (light blue curve) shows that the population density per unit phenotype is close to Gaussian. (e) As in (d), but with a resource distribution $K(x) = \exp(-[(x-10)/7.5]^4)$. (f) For a quartic kernel and the same $K(x)$ as in (e), the equilibrium species distribution has regular spacing. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

clustering (Fig. 7). In spite of considerable efforts (Sasaki, 1997; Ackermann and Doebeli, 2004; Meszéna et al., 2006; Szabó and Meszéna, 2006; Barabás and Meszéna, 2009; Hernández-García et al., 2009), there is currently no full understanding of how

promote clustering, like the quartic kernel, equilibrium species distributions are relatively robust to niche-space heterogeneities (Fig. 7c,f). The explanation for this robustness is the strong undulation of the fitness landscape for these kernels (green curves

in Fig. 3), in comparison with the fitness landscapes for positive definite kernels, which become very flat as soon as species distributions approach equilibrium.

In nature, the carrying capacity is likely to taper off at the edges of a niche range, which can be represented by a unimodal $K(x)$ along the niche axis (Fig. 7d–f). There is a well known theoretical result by Roughgarden (1979), that for a Gaussian competition kernel and a (wider) Gaussian $K(x)$, the equilibrium species distribution is also Gaussian, which in practice would correspond to a very close-packed distribution (Fig. 7d). Similar close-packed equilibrium species distributions can occur for other shapes of $K(x)$ (Fig. 7e), but if the shape is more narrow, or is perturbed by small-scale variation, the species distribution breaks up into a lower number of separated species (Sasaki, 1997; Meszéna et al., 2006; Szabó and Meszéna, 2006; Barabás and Meszéna, 2009). For competition kernels with a strong clustering tendency, the equilibrium species distribution is, however, relatively robust to niche-space heterogeneity (Fig. 7c,f). Finally, niche-space heterogeneity enters into the derivation of the competition coefficient from an underlying resource dynamics (Schoener, 1974), and the resulting competition kernels need not have the simple form $a(x_j − x_k)$, which by itself can promote clustering (Ackermann and Doebeli, 2004).

6. Discussion

The recent work on species packing, not least the approach of using Fourier analysis to characterize the effects of competition kernel shape on species clustering (Pigolotti et al., 2007, 2010; Leimar et al., 2008; Hernández-García et al., 2009), is a significant step forward, for instance, by overcoming assumptions of idealized resource competition. As shown here, the application of Fourier analysis can also move the theory beyond an assumption of symmetric competition, and thus beyond the domain of MacArthur's classical minimization principle (MacArthur, 1969, 1970).

There are of course additional directions in which the traditional theory of limiting similarity can usefully be extended, for instance, by studying cases where the community dynamics are not well approximated by the Lotka–Volterra competition equations. Depletion, or even extinction, of the resources in a niche interval is a possible consequence of resource utilization by competing consumers, leading to deviations from Lotka–Volterra dynamics, with implications for limiting similarity and the coexistence of consumer species (Abrams, 1998; Abrams et al., 2008; Abrams and Rueffler, 2009).

Apart from the extinction and invasion of species, there can be evolutionary changes of the traits in a community, for instance, in the form of character displacement (Dayan and Simberloff, 2005), and this topic has often been brought up in discussions of species packing. Concerning the effects of competition kernel shape on character displacement, one might expect that strong clustering tendencies of a kernel, in the sense of a pronounced minimum of its Fourier transform, select more strongly for divergence between species. The reason is that such kernels produce a strongly undulating fitness landscape. More generally, the ecological relevance of much recent work on species clustering, including the results presented here, to a large extent depends on whether competition in nature sometimes reasonably corresponds to competition kernels with strong clustering tendencies.

Going beyond the effects of competitive interactions per se, recent research has uncovered processes that promote clustering when acting in conjunction with competition, of which assortative mating in sexual organisms is a noteworthy example (Doebeli et al., 2007; Ispolatov and Doebeli, 2009). There are also theoretical arguments to the effect that clustering should be seen as a typical or generic outcome of competitive interactions. The idea

that continuous distributions in trait space or in physical space are fragile, lacking structural stability or otherwise readily disintegrating into discrete clusters, has gained support in recent theoretical work (Sasaki and Ellner, 1995; Sasaki, 1997; Gyllenberg and Meszéna, 2005; Meszéna et al., 2006; Pigolotti et al., 2010; Barábas, 2012a,b). The issue of continuous coexistence can thus be regarded as resolved, to the effect that continuous coexistence is an unlikely special case. Even so, interesting questions remain, such as the relation between niche-space heterogeneity and the resulting equilibrium species distributions. For instance, our examples in Fig. 7 suggest that large-scale, gradual variation of a carrying capacity along niche space does not in itself strongly influence smaller-scale species clustering (Fig. 7d,e,f), although more research is needed before definite conclusions can be drawn.

Scheffer and van Nes (2006) noted that body-size distributions across species are often composed of groups or clumps of similar-sized species, separated by gaps (see also Allen et al. (2006); Thibault et al. (2011) on the multimodality of body-size distributions), and argued that such distributions are the expected outcome of competitive interactions within a community (Scheffer and van Nes, 2006). Clumping of similar species, separated by gaps, can indeed be an equilibrium of the Lotka–Volterra competition equations for certain competition kernels (Pigolotti et al., 2007; Hernández-García et al., 2009, Fig. 3e,f). Another explanation is that there can be long-lasting transients during community assembly, in which clumps of similar species are slowly pruned down to singletons (Fort et al., 2009, 2010; Pigolotti et al., 2010). The swift manner in which this issue of species clumps has been clarified is a testament to the current vigor of research in this area.

While much work on species clustering remains to be done, the field is rapidly moving forward, indicating that its central position from the 1960s and 1970s could be regained. There is now a deeper understanding of the groundbreaking results by MacArthur, Levins and May, which has been achieved by placing the classical work into a wider context created by the recent theoretical progress. Even more, there is now a new set of ideas and theoretical results that might usefully interact with observations on the distribution of traits in communities.

Appendix A. The Poisson summation formula

The derivations in the Appendices B and C make use of the so-called Poisson summation formula for the Fourier transform $\hat{f}(\phi)$ of a function $f(x)$. The summation formula is given by

$$\sum_{j=-\infty}^{\infty} f(jd) = \frac{1}{d} \sum_{j=-\infty}^{\infty} \hat{f}(j/d), \tag{A.1}$$

where the Fourier transform is defined as in Eq. (2) and d is a positive real number. This is a well-known result and holds, for instance, if $f(x)$ is an integrable function of bounded variation (Benedetto and Zimmermann, 1997). The following two relations

are alternative versions of the summation formula:

$$\sum_{j=-\infty}^{\infty} f(jd) \exp(-i2\pi\phi_0 jd) = \frac{1}{d} \sum_{j=-\infty}^{\infty} \hat{f}(\phi_0 + j/d) \qquad (A.2)$$

and

$$\sum_{j=-\infty}^{\infty} f(jd + x_0) = \frac{1}{d} \sum_{j=-\infty}^{\infty} \hat{f}(j/d) \exp(i2\pi x_0 j/d). \qquad (A.3)$$

They follow because the transform of $g(x) = f(x) \exp(-i2\pi\phi_0 x)$ is given by $\hat{g}(\phi) = \hat{f}(\phi_0 + \phi)$ and the transform of $g(x) = f(x + x_0)$ is given by $\hat{g}(\phi) = \hat{f}(\phi) \exp(i2\pi x_0 \phi)$.

Appendix B. Demographic stability

This appendix contains a derivation of the following result: An equidistant community with competition kernel $a(x)$ and phenotypic gap size d is demographically stable if the inequality

$$\sum_{j=-\infty}^{\infty} \text{Re}[\hat{a}(1/\lambda + j/d)] > 0 \qquad (B.1)$$

holds for all wavelengths λ, and it is unstable if the inequality is reversed for some λ. The result in Eq. (6) in the main text is a special case of this condition, for symmetric kernels, for which the Fourier transform is real.

For the derivation it will be convenient to introduce the so-called discrete-time Fourier transform (the terminology "discrete-time" is traditional, but here the variable is not time, but niche position), which is defined as a transform $F(\phi)$ of the sampled values $f(x_j)$ of a function $f(x)$ at the equidistant niche positions $x_j = jd$, as follows:

$$F(\phi) = d \sum_{j=-\infty}^{\infty} f(jd) \exp(-i2\pi\phi jd). \qquad (B.2)$$

The discrete-time Fourier transform will be periodic, with period $1/d$, so that $F(\phi + 1/d) = F(\phi)$. We can find a relation between the discrete-time Fourier transform and the ordinary Fourier transform of $f(x)$, as follows:

$$F(\phi) = \sum_{j=-\infty}^{\infty} \hat{f}(\phi + j/d). \qquad (B.3)$$

This follows directly from the version of the Poisson summation formula in Eq. (A.2).

For an equidistant community, only the values $a(jd)$ of the competition kernel at the interspecific distances $x_j = jd$ can influence the community dynamics. It is then convenient to make use of the discrete-time Fourier transform $A(\phi)$ of the sampled competition kernel values $a(jd)$. Eq. (B.3) gives

$$A(\phi) = \sum_{j=-\infty}^{\infty} \hat{a}(\phi + j/d). \qquad (B.4)$$

We linearize Eq. (1), for the special case $K(x) = 1$, around the equilibrium

$$N^* = \frac{1}{\sum_{j=-\infty}^{\infty} a(jd)}. \qquad (B.5)$$

Writing $N_j = N^* + u_j$, we get the linearized dynamics

$$\frac{du_j}{dt} = -N^* \sum_{k=-\infty}^{\infty} a(jd - kd) u_k. \qquad (B.6)$$

Taking the discrete-time Fourier transform, as defined in Eq. (B.2), of the linearized dynamics in Eq. (B.6), we get

$$\frac{dU(\phi)}{dt} = -\frac{N^*}{d} d^2 \sum_j \sum_k a(jd - kd) u_k \exp(-i2\pi\phi jd)$$

$$= -\frac{N^*}{d} d \sum_k u_k \exp(-i2\pi\phi kd) \, d \sum_l a(ld) \exp(-i2\pi\phi ld)$$

$$= -\frac{N^*}{d} A(\phi) U(\phi), \qquad (B.7)$$

where ld was substituted for $jd - kd$ in the second line. From this equation we can conclude that the equilibrium is stable if the real part of the discrete-time Fourier transform $A(\phi)$ is positive, i.e. if $\text{Re}[A(\phi)] > 0$ holds for each ϕ, whereas the equilibrium is unstable if the inequality is reversed for some ϕ. From Eq. (B.4), and putting $\phi = 1/\lambda$, we see that this yields condition (B.1).

It is instructive to examine the special case of a close-packed community, for which d is small. In the limit of d going to zero, the discrete-time Fourier transform in Eq. (B.2) converges to the ordinary Fourier transform, and Eq. (B.7) converges to Eq. (5) in the main text.

For symmetric positive definite competition kernels, which were studied by May (1974a,b), we see from Eq. (B.7) that the smallest rate of damping of density perturbations is given by the minimum of $N^* A(\phi)/d$, which will typically occur for $\phi = 1/(2d)$. For small d, this minimum can be extremely close to zero, for instance, for a Gaussian kernel, resulting in effectively neutral demographic stability. May (1974a,b) referred to this phenomenon as an "essential singularity" of the community dynamics.

Appendix C. Invasion into gaps

Consider an equidistant community, with species at the niche positions $x_j = jd$, and a competition kernel $a(x)$. The equilibrium density in the community is given by Eq. (B.5). Using the Poisson summation formula in Eq. (A.1), we can write the equilibrium density as

$$N^* = \frac{d}{\sum_{j=-\infty}^{\infty} \hat{a}(j/d)}. \qquad (C.1)$$

For a potential invader species at x, having the low density u, the linearized dynamics is

$$\frac{du}{dt} = u\left(1 - N^* \sum_{j=-\infty}^{\infty} a(x - jd)\right), \qquad (C.2)$$

so that

$$F(x) = 1 - N^* \sum_{j=-\infty}^{\infty} a(x - jd) \qquad (C.3)$$

is a fitness landscape for invasion into the community (illustrated by the green curves in Figs. 3, 4 and 6b). Using the version of the summation formula from Eq. (A.3), we can express the fitness landscape in terms of the Fourier transform of the competition kernel as

$$F(x) = 1 - \frac{N^*}{d} \sum_{j=-\infty}^{\infty} \hat{a}(j/d) \exp(-i2\pi x j/d). \qquad (C.4)$$

Using Eq. (C.1), we can verify that $F(x) = 0$ at the positions $x = kd$ of the resident species. We can then write $F(x)$ as

$$F(x) = \frac{N^*}{d} \sum_{j=-\infty}^{\infty} \hat{a}(j/d)(1 - \exp(-i2\pi x j/d)). \qquad (C.5)$$

For a symmetric kernel, for which the Fourier transform is real and symmetric, the fitness landscape can be expressed as

$$F(x) = 2\frac{N^*}{d} \sum_{j=1}^{\infty} \hat{a}(j/d)(1 - \cos(2\pi x j/d)). \qquad (C.6)$$

It follows that $F(x) > 0$ for positions $x \neq kd$. Thus, for a symmetric positive definite kernel, invasion into the gaps of an equidistant

community is always possible. For small d, the values $\hat{a}(j/d)$ will be extremely small, making $F(x)$ small, so gap invaders are nearly neutral.

On the other hand, for a symmetric kernel whose Fourier transform changes sign, there can be gap sizes d such that $F(x) < 0$ in the gaps, preventing the growth of invading species (as illustrated in Fig. 3a,c,e,f). Examining the term for $j = 1$ of the sum in Eq. (C.6), which might represent an important contribution to the sum, such protection of the gaps in the community is likely to be strongest when d is close to the wavelength λ at which $\tilde{a}(\lambda) = \hat{a}(1/\lambda)$ has a minimum. Furthermore, a more negative value of $\tilde{a}(\lambda)$ typically results in stronger selection against invaders in the gaps of the community.

For asymmetric competition kernels, Eq. (C.5) seems not to provide a lot of insight into the shape of the fitness landscape. Perhaps the typical situation is that such communities can be invaded, resulting in a turnover or shifting of species, as illustrated in Figs. 4 and 5.

Appendix D. Competition kernels and waste in competition

A classical formulation for the competition coefficient is as the overlap $\int f_j(y)f_k(y)\,dy$ between the utilization functions $f_j(y)$ and $f_k(y)$ of two species j and k (May, 1974a,b). If all utilization functions have the same shape f, we can write the competition kernel as

$$a(x) = \int f(y-x)f(y)\,dy. \tag{D.1}$$

This kernel is symmetric, regardless of whether $f(y)$ is symmetric. Its Fourier transform is equal to the square of the transform of the utilization shape, $\tilde{a}(\lambda) = |\tilde{f}(\lambda)|^2$, so such a kernel is positive definite. If f instead is an effective utilization function, representing resources contributing to population growth, and g is a corresponding total utilization function, representing resources rendered unavailable to other species (Schoener, 1974; Hernández-García et al., 2009), including 'wasted resources', the competition kernel is given by

$$a(x) = \int f(y-x)g(y)\,dy. \tag{D.2}$$

This kernel need not be positive definite, as is illustrated by the example in Fig. 6.

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