How competition leads to lumpy or uniform species distributions

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Abstract

A central model in theoretical ecology considers the competition of a range of species for a broad spectrum of resources. Recent studies have shown that essentially two different outcomes are possible. Either the species surviving competition are more or less uniformly distributed over the resource spectrum, or their distribution is 'lumped', consisting of clusters of species with similar resource use that are separated by gaps in resource space. Which of these outcomes will occur crucially depends on the 'competition kernel', which reflects the shape of the resource utilization pattern of the competing species. Most models considered in the literature assume a Gaussian (bell-shaped) competition kernel. This is unfortunate, since predictions based on such a Gaussian assumption are not robust. In fact, Gaussian kernels are a border case scenario of ecologically relevant kernels, and slight deviations from the Gaussian assumption can lead to either uniform or lumped species distributions. Here we illustrate the non-robustness of the Gaussian assumption by simulations of the standard competition model with constant carrying capacity and different competition kernels. In this scenario, lumped species distributions can come about by details of the numerical implementation of the model or by secondary ecological or evolutionary mechanisms.

Introduction

A central model behind the theoretical description of competition among dissimilar species is the model introduced by MacArthur and Levins (1967). In the model, species are characterized by their niche position x_i, which describes their utilization of a resource distributed as a function of x. The niche value x_i may represent body size of predators, where the resource is the size distribution of prey, or x_i could be beak size of birds, in which case the resource is the distribution of seed sizes. Mathematically this leads to a Lotka-Volterra type of competition equation, where the competition coefficients are a function of the distance between species on the niche axis x. This competition kernel is usually taken to be bell-shaped Gaussian function of the niche difference (also called normal curve). The implication of this choice of competition kernel is the central topic of this paper.

The model was originally proposed as part of the hypothesis of limiting similarity, namely that competing species can coexist only if they are sufficiently different from each other (MacArthur and Levins, 1967; Abrams, 1983). A mathematical analysis of the model revealed that arbitrarily similar species could in fact coexist in some cases. However adding further effects to the model, like noise (May and MacArthur (1972), but see Turelli (1978)) or extinction thresholds (Pigolotti et al., 2007), impose a limit to the similarity between species. This sensitivity to second order effects has led to the conclusion that the model, in its original form, is structurally unstable when used to predict limits of similarity (Meszéna et al., 2006). The competition model has also been applied to describe coevolving species (MacArthur and Levins, 1967; Case, 1981) and used in some formulations of the theory of island biogeography (Roughgarden, 1979). More recently the same type of model has been simulated numerically and used as a basis for dynamical models of sympatric speciation (Doebeli and Dieckmann, 2000), food web assembly and evolution (Loeuille and Loreau, 2005; Johansson and Ripa, 2006; Lewis and Law, 2007), elucidating the relation between competition and predator-prey interactions (Chesson and Kuang, 2008), and for explaining lumped size distributions of species (Scheffer and van Nes, 2006). For a more extensive review of the biological applications and the generalization of the model see (Szabò and Meszéna, 2006). Thus, the competition model has been fundamental for the development of basic principles in theoretical ecology, and it is still a core part of the vibrant topics of food web structure, assembly, and evolution though sympatric speciation. Therefore, it is relevant to achieve a full understanding also of the more technical aspects of the model.

In almost all applications of the model the chosen competition kernel is Gaussian. This choice facilitates mathematical analysis, and was justified because the exact shape of the kernel was thought to have no influence on the fundamental results of the model. However, recent work has shown that the equilibrium solution can be one of two fundamentally different types, depending on the form of the competition kernel (Pigolotti et al., 2007). One class of competition kernels preserves all species initially introduced in the system, with adjustments only in their relative abundance. The final equilibrium is a state with species closely spaced and with roughly similar abundances. Another class of competition kernels leads to the species being lumped in dense groups, separated by empty regions on the niche axis. Subsequent invasion of new species in these 'exclusion zones' is not possible due to competitive exclusion. The condition for uniform distribution of species is to have a *positive definite* competition kernel (see definition below). This criterion is automatically fulfilled when the kernel is constructed from the overlap of the species utilization of the resource (Roughgarden, 1979). If the kernel is not positive definite, a lumpy species distribution with exclusion zones emerges. The concern about this discovery is that, even though the Gaussian kernel is ecologically sound, it is exactly marginal between the two regimes. This indicates that numerical inaccuracies and/or secondary ecological effects may violate the positive definiteness of the competition kernel and cause a transition from a uniform to a lumpy species distribution.

The objective of this paper is to raise awareness in the theoretical ecology community of the potential pitfalls and subtleties associated with the use of Gaussian competition kernels or other marginal choices. Even though this functional form appears to be natural, in particular for analytical work, it may not be the most prudent choice for numerical exploration of competition models. To illustrate this, the consequences of the marginal nature of the Gaussian kernel in the competition model are explored. First, the sensitivity to numerical issues is demonstrated. Then, other ecologically relevant effects that may lead to lumpy distributions are examined.

Methods

The competition model considers n interacting populations, each utilizing a common distributed resource x according to a utilization function $u_i(x)$, $i = 1, ..., n$. The dynamics of the abundance of species i, N_i, is described by a Lotka-Volterra set of competition equations:

$$\dot{N}_i = N_i \left(1 - \frac{1}{K} \sum_{j=1}^{n} G_{ij} N_j \right), \quad i = 1, ..., n, \tag{1}$$

where the growth rate (considered to be the same for all species) is set to one for simplicity, and the carrying capacity K is uniform. Competition in (1) is described by competition coefficients G_{ij} which are constructed from the overlap of utilization functions of competing species (MacArthur and Levins, 1967; Roughgarden, 1979):

$$G_{ij} = \frac{\int u_i(x) u_j(x)\, dx}{\int u_i^2(x)\, dx}. \tag{2}$$

A justification of (2) rests upon considering the probability that consumer i meets consumer j (Levins, 1968; Roughgarden, 1979).

Often, utilization functions are ignored, and the competition coefficients are postulated directly. It is usually assumed that species i has an optimal exploitation of the resource at a value $x = x_i$, and the competition coefficients are taken to depend on the difference between the optimal resource values of two competing species, $y = |x_i - x_j|$, such that we can introduce the so-called competition kernel, $G_{ij} = G(y)$. Here we use a family of competition functions described by a parameter p:

$$G_{ij} = G(y) = e^{-|(x_i - x_j)/\sigma|^p}, \tag{3}$$

which contains the Gaussian kernel when $p = 2$, or the exponential one when $p = 1$. The width of the kernel σ gives the range of competition on the niche axis. Incidentally the Gaussian kernel is obtained from Eq. (2) when the utilization functions are also Gaussian and of the form $u_i = \exp(-((x - x_i)/s)^2)$ with $s^2 = \sigma^2/2$. When $p < 2$ the kernels are more peaked around $y \approx 0$ and for $p > 2$ they become more box-like (see Fig. 1).

Note that when competition coefficients are constructed by the formula (2), i.e. from the overlap of two utilization functions, they are always *positive definite*, meaning that $\sum_{ij} a_i G_{ij} a_j \geq 0$ for any set of numbers a_i (Roughgarden, 1979). This property holds for the family of kernels (3) for $p \leq 2$, but not for $p > 2$ (Fig. 1). The Gaussian kernel is therefore marginal in the sense that, corresponding to the limit case $p = 2$, even a very small perturbation may violate its positive definite character, generally believed to be an ecological requirement arising from expression (2).

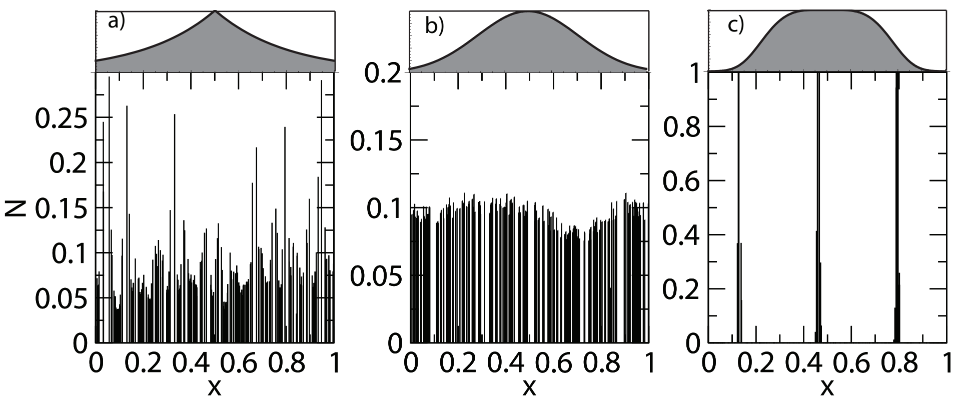

Figure 1: Three interaction kernels (top) and species distributions arising from simulation of the model after 1000 generations (bottom). a) Exponential competition ($p = 1$); b) Gaussian competition ($p = 2$); and c) box-like competition ($p = 4$). Simulations are initiated with 200 species randomly distributed, $K = 10$, and $\sigma = 0.3$.

An intuitive explanation for the appearance of the exclusion zones for $p > 2$ is the following. Interaction kernels with large p have a box-like shape. In these cases species compete very strongly with other species, roughly within a distance $\pm\sigma$ from their own niche value. Species with a niche x in that range will therefore not be able to invade the resident species, leading to the exclusion zones between them. When p is decreased, the resident species compete less and less with neighbouring species, until the exclusion zones disappear, leading to the possibility of continuous coexistence.

Understanding the fact that the transition occurs at $p = 2$, and also the coexistence of more than one species in each cluster, requires a mathematical stability analysis of the model. Consider the uniform solution with all species having the same abundance and perturb each population by a small quantity ΔN_i, which can be either positive or negative. If the competition kernel is not positive defined, there are sets of perturbations such that $\sum \Delta N_j G_{ij} \Delta N_i$ is less than zero. One can show that such perturbations are amplified by the dynamics, making the uniform solution unstable. The system will then evolve to a clustered state, where the distance between clusters is proportional to the interaction range σ.

We simulated the model (1) with competition kernel (3) for 1000 generations and 200 species initially at random niche positions. The width of the kernel is $\sigma = 0.3$ and the carrying capacity is $K = 10$. The niche range is taken to be $x \in [0,1]$. The standard mathematical way to avoid effects due to the borders of the niche space is to adopt periodic boundary conditions (e.g. Scheffer and van Nes (2006)). These are introduced for mathematical convenience and aim at modeling species far from endpoints in a large niche space. Adopting periodic boundary conditions means that when the interaction kernels extends beyond the left edge at $x = 0$, it enters back into right side at $x = 1$ and vice versa. Periodic boundaries therefore mimic an infinite system by considering the niche segment $[0,1]$ as embedded in an array of repeated copies of itself. Mathematically, this is properly implemented by making a 'kernel wrap', i.e. substitute $G(y)$ in (3) with $G_p(y) \equiv \sum_n G(y-n)$, where the sum runs from $n = 0, \pm 1, \pm 2, ... \pm \infty$.

Results

Simulations using the competition kernel (3) with $p = 1$ (exponential), 2 (Gaussian) and 4 (box-like) illustrate the uniform species distributions for $p = 1$ and $p = 2$, and the lumped species clusters for $p = 4$ (Fig. 1). The configurations in Fig. 1 are still transient states and at longer times configurations with $p \leq 2$ become more uniform, whereas the periodically spaced clusters of species for $p > 2$ become thinner until they contain only a single species. Transient states are more representative of states actually observed and facilitate comparison with previous works (Scheffer and van Nes, 2006). In any case, from the initial stages until the final equilibrium, the main difference between the dynamics for the two classes of competition kernel is unchanged: for $p \leq 2$ all initial species are preserved, leading to dense and evenly distributed configurations, whereas 'exclusion zones' develop for $p > 2$ leading to lumped species distributions.

Effects of numerical inaccuracies. The most obvious numerical simplification is to only partially implement the periodic boundary conditions, by omitting the kernel wrap around the niche interval, that is, using $G(y)$, with y being the minimum of the two possible distances among species i and j ($|x_i - x_j|$ and $1 - |x_i - x_j|$), instead of the periodic kernel $G_p(y)$. The resulting effective kernel is Gaussian but truncated at $|y| = 1/2$ making it no longer positive definite. Although the shapes of $G(y)$ and $G_p(y)$ are still very similar for the parameters used here ($\sigma = 0.3$), the change immediately leads to lumped species distributions (Fig. 2). In contrast, for $p = 1$ (or any other values of $p < 2$ which we have checked), changing $G_p(y)$ by $G(y)$ has no noticeable effect. Qualitatively, the dynamics for truncated Gaussian kernels resembles the outcome when the exponent of the competition kernel

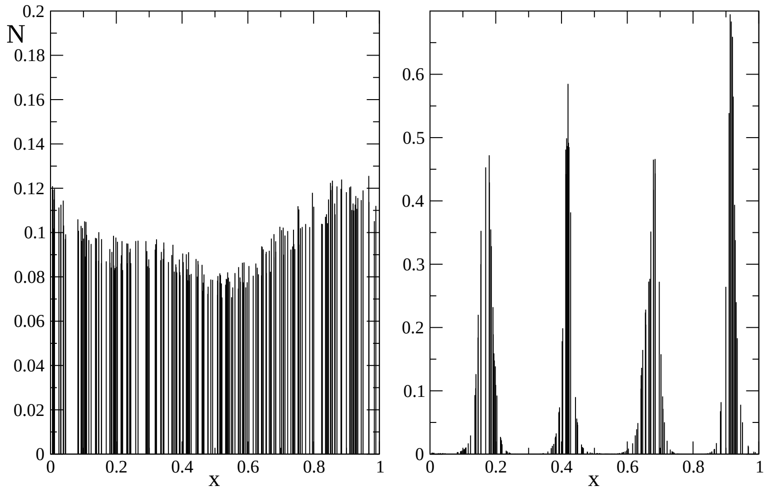

Figure 2: Populations of 200 species after 1000 generations with (left panel) Gaussian competition kernel with properly implemented boundary conditions, and (right panel) with truncated Gaussian competition kernel (see text). $K = 10$ and $\sigma = 0.3$.

is perturbed just slightly. E.g. using $p = 2.1$ instead of $p = 2$ also leads to lumped species distributions, even when periodic boundary conditions are correctly implemented (not shown).

Effects of secondary ecological processes. A natural question is whether the marginal nature of Gaussian competition has consequences exclusively for numerical aspects or if lumpy species distributions can also be brought on by secondary ecological effects. we have checked that adding a small immigration rate does not produce lumpy distributions. Adding noise or an extinction threshold (i.e. species are removed when their populations fall below a threshold) result in a limit to similarity between species (Pigolotti et al., 2007). This also happens in non marginal cases with $p < 2$, where the minimum distance between species is unrelated to the competition range σ.

Effect of species extinction and speciation was simulated by eliminating species below a given population threshold, and introducing invading species at a fixed rate. If they are introduced at random locations in niche space no patterns are observed. If invading species are introduced close to existing ones, the system ends with a lumped species distribution, even for $p = 2$ (Fig. 3). However, the same mechanism has no effect if an exponential competition kernel ($p = 1$) is chosen. It therefore seems as if evolutionary effects may favor lumpy species distributions, but only when the competition kernel is close to the Gaussian limiting case.

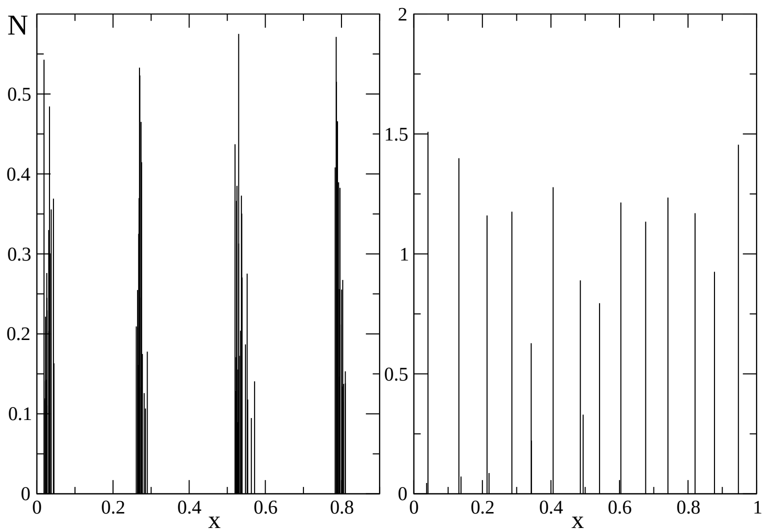

Figure 3: Final populations after 500 000 generations with speciation and extinction. Species whose population goes below 0.1 are removed from the system. Every 100 generations new species are introduced close to an existing one. The parent species is chosen with a probability proportional to its population; the distance of the new species to its parent is drawn from a Gaussian distribution of zero mean and spread $\sigma_p = 0.02$. The new species j is introduced with a population uniformly drawn from the interval $N \in [2, 3]$. (left panel) Gaussian kernel ($p = 2$) and (right panel) exponential kernel ($p = 1$). Simulations are performed under perfect periodic boundary conditions. $K = 10$ and $\sigma = 0.3$.

Finally, a possible generalization is to consider multi-dimensional niche spaces. This possibility would complicate the mathematical notation but would not introduce qualitative changes. This means that stability in a multi-dimensional niche space would still depend on the positive definiteness of the competition kernel. In particular, a multi-dimensional Gaussian competition kernel would still be marginal and the results of generalized models will also be sensitive to small numerical details and evolutionary effects considered above.

Discussion

The model (1)-(3) provides a very abstract representation of competition. Both empirical observations and theoretical approaches, based on explicit consideration of the coupled consumer-resource dynamics, lead to competition coefficients which are quite different from Gaussian, except in a few particular cases (Schoener, 1974; Wilson, 1975; Ackermann and Doebeli, 2004). Even so, the qualitative outcome of the model does not depend on the exact shape of the competition kernel, but only on it being positive definite. We have restricted our considerations primarily to the basic model (1) with 'bell shaped' interaction kernels since it is widely used for theoretical work and because it allowed us to illustrate the importance of G and the disadvantages of the choice of a Gaussian competition kernel.

The basic model with competition coefficients obtained from the overlap of utilization functions, which give always positive definite kernels, allows for dense species distributions with no limits to similarity. This fundamental solution may be changed by three different effects: 1) effects stemming from the competition kernel being no longer positive definite lead to lumpy species distributions. Clusters of species will appear, separated by exclusion zones in niche space with a spacing proportional to the width of the competition kernel σ; 2) second order ecological effects like noise, species heterogeneity or the introduction of an extinction threshold lead to a limit to the similarity with the spacing between species being independent of σ; 3) under a non constant carrying capacity, patterns of unevenly spaced species, lumpy or not, may appear. This lead Szabò and Meszéna (2006) to conclude that "the not-very-smooth nature of the carrying capacity seems to be essential for limiting similarity".

The first case arises when the competition kernel is not positive definite. This can be the result of a numerical approximation, such as truncating the tails of a Gaussian competition kernel. This effect is probably the underlying mechanism behind species clustering observed in recent numerical work (Scheffer and van Nes, 2006), which was used to explain observed lumpy distributions (May et al., 2007). These spurious effects can be avoided by paying attention to numerical details or by using a competition kernel which is not marginal, e.g. one with $p = 1.5$, which in practice is almost indistinguishable from the Gaussian one. It is worth mentioning that analytical (i.e. not numerical) results are not affected by the marginal nature of the Gaussian kernel, both in relation to limiting similarity (May and MacArthur, 1972), coevolution (Case, 1981) or criteria for sympatric speciation (Doebeli and Dieckmann, 2000). The marginal nature of Gaussian competition kernel may however affect numerical work on food web evolution and assembly (Doebeli and Dieckmann, 2000; Loeuille and Loreau, 2005; Lewis and Law, 2007). Beside numerical subtleties, we also demonstrated that a simple representation of evolutionary diffusion (Lawson and Jensen, 2007) may lead to lumpy species distributions, at least if the competition kernel is the marginal Gaussian. This effect is similar to that of evolutionary dynamics, where assortative mating is shown to lead to lumpy species distributions (Doebeli et al, 2007).

Since a non-positive definite competition kernel leads to lumpy species distributions a natural question is if simple ecological arguments could result in a non-positive definite kernel. This case is often neglected in the literature, since assuming Eq. (2) automatically leads to a positive definite competition kernel (Roughgarden, 1979). However, as emphasized in Meszéna et al. (2006) and references therein, under quite general assumptions one should introduce two different utilization-like functions: a *sensitivity* function $S_i(x)$, describing the effect of the resource at x on the growth of species i, and an *impact* function $D_i(x)$, describing the depletion of resources produced by i. Then, the competition coefficients depend on the overlap of these two quantities $\int S_i(x)D_j(x)dx$, and reduce to (2) only if the sensitivity and impact functions are proportional, with the constant of proportionality being the ecological efficiency. When the ecological efficiency is a function of x, and the sensitivity and impact functions are no longer proportional, the competition kernel ceases to be positive definite.

The third mechanism is that of a non-constant carrying capacity $K(x)$, which has been explored by Szabò and Meszéna (2006). They found that some choices of carrying capacity leads to an irregular species lumping. The effect of non-constant carrying capacity in conjunction with both positive and non-positive definite competition kernels was explored by Hernández-García et al (2008). The emerging picture is that the two mechanisms are independent. The cases in which a non-constant carrying capacity leads to uniform species distributions can also be destabilized by a non-positive defined kernel. This means that the mechanism explored here is not a particularity of constant carrying capacity but is present also in more general settings.

Having outlined the reasons that may cause the three different outcomes, the question arises if it is possible to infer whether one effect or the other is at play from the result of a numerical integration of the competition model. It can be difficult to distinguish between a uniform discrete species distribution and a lumpy one with very narrow and close lumps. Here, the fact that in the lumpy distribution the spacing of the lumps is proportional to the width of the competition kernel σ can be used. If changing σ results in a change in the distance between species proportional to σ, the effect is due to a non-positive definite competition kernel and vice versa. In the case where the effect is due to the carrying capacity being non-constant the spacing of species is usually more irregular (Szabò and Meszéna, 2006).

To summarize: in line with previous works we have found that the case of continuous coexistence (no limits to similarity) may be limited by a variety of effects, specially for the Gaussian kernel which has a marginal character. We have underlined that there are different ways to limit similarity, some leading to lumpy species distributions and others not. We hope that this article will increase the awareness in the theoretical ecological community of the potential pitfalls and subtleties associated with the use of the Gaussian competition kernel. Even though this functional form appears to be natural, in particular for analytical work, it may not be the most prudent choice for numerical exploration of the niche model.

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