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On the impossibility of coexistence of infinitely many strategies

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Abstract. We investigate the possibility of coexistence of pure, inherited strategies belonging to a large set of potential strategies. We prove that under biologically relevant conditions every model allowing for coexistence of infinitely many strategies is structurally unstable. In particular, this is the case when the "interaction operator" which determines how the growth rate of a strategy depends on the strategy distribution of the population is compact. The interaction operator is not assumed to be linear. We investigate a Lotka-Volterra competition model with a linear interaction operator of convolution type separately because the convolution operator is not compact. For this model, we exclude the possibility of robust coexistence supported on the whole real line, or even on a set containing a limit point. Moreover, we exclude coexistence of an infinite set of equidistant strategies when the total population size is finite. On the other hand, for infinite populations it is possible to have robust coexistence in this case. These results are in line with the ecological concept of "limiting similarity" of coexisting species. We conclude that the mathematical structure of the ecological coexistence problem itself dictates the discreteness of the species.

1. Introduction

Competitive exclusion and limiting similarity are classical, but, still, controversial concepts of ecology. In the formulation of MacArthur and Levins [26], the principle of competitive exclusion states that the number of coexisting strategies cannot be larger than the number of limiting resources. Later Levin [24] extended the idea beyond the case of resource competition by introducing the notion of limiting factors. In the terminology of Diekmann et al. [10, 11] limiting factors are *environmental interaction variables* through which the self-regulating feedback of the ecosystem operates. Using the concept of environmental interaction variable Diekmann et al. [11] reformulated the principle of competitive exclusion for a large class of structured population models as follows: The dimension of the

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environmental interaction variable is an upper bound for the number of species that generically can coexist at steady state. The advantage of this formulation is its generality: the possible interpretation of the interaction variables as resource concentrations or other limiting factors is irrelevant.

Unfortunately, the existence of a finite number of clearly identifiable limiting factors is an exception rather than a rule in ecology. Often, the resources are not homogeneous in quality and one has to ask how resources should be counted [5]. For instance the biological interpretation of the Lotka-Volterra competition model used by MacArthur and Levins [27] implicitly assumes a continuous scale of resources, that is, an infinite number of limiting factors. The Lotka-Volterra model thus requires an infinite-dimensional interaction variable to be formulated properly. This raises the question whether it is possible for infinitely many species to coexist either in the Lotka-Volterra model, or in general.

The classical expectation is "limiting similarity": in order for two or more species to coexist, their resource usage should be "different enough" [27]. They are then said to live in different "niches". According to this concept, even a continuous scale of resources does not support coexistence of an unbounded number of species. Despite the lack of a clear mathematical basis, limiting similarity was verbally generalized beyond the Lotka-Volterra model, as "niche theory" [21] and has become one of the cornerstones of ecological thinking [23].

Coexistence of two, three or more strategies was investigated in several papers [7,27–29] with the general conclusion that coexistence of similar strategies are disfavoured. Later studies went beyond the Lotka-Volterra framework. However, no general results emerged and the hope to find a model-independent rule of how similar coexistent strategies may be faded away [1,3,4].

As a rather drastic stroke against the theory of limiting similarity, Roughgarden [35, p. 534–536] provided an example of coexistence of a *continuum* of strategies in the Lotka-Volterra competition model. While the example was intended to describe the phenotype distribution within a single species, it can be interpreted in the context of species coexistence, as well. It seems to violate the whole idea of limiting similarity as species with arbitrarily similar resource utilization strategies can coexist. As a matter of fact, coexistence of a continuum of species is possible even in the Lotka-Volterra model, which was the original example for limiting similarity.

The possibility of coexistence of a continuum of strategies was investigated by Sasaki & Ellner [37] in a model of adaptation to a fluctuating environment. They concluded that continuous coexistence is exceptional. Even if a specific choice of model ingredients would allow it, there exists an arbitrarily small perturbation of the ingredients, which makes coexistence impossible. It is easy to translate their argument to the equilibrium solution of the Lotka-Volterra model [33]. So, it is known that Roughgarden's example is nonrobust. A completely different, nonlinear model of seed-size evolution by Geritz [13] and Geritz et al. [18] showed a similar behaviour. In that model coexistence of a continuum of strategies was possible only for the extreme, singular form of asymmetric competition. Limiting similarity reappeared in the theory of adaptive dynamics [8, 15, 16, 33]: Two similar strategies cannot coexist except at the so-called singular strategy, where the local gradient of the fitness is zero.

Contrary to the general pessimism with respect to the generality of limiting similarity, these results on very different models seem to suggest a universal behaviour. The exceptionality of continuous coexistence is in line with a result of May [28,29] concerning the classical Lotka-Volterra competition model. It states that the range of parameters allowing two strategies to coexist shrinks to zero as the difference between the strategies goes to zero. The conclusion of May will be generalized for arbitrary, but finitely, many strategies in a model-independent way elsewhere [32]. Here, we concentrate on the question of infinitely many strategies. If the coexistence of similar strategies is constrained for a narrow range of parameters, coexistence of a continuous set of them, or a set of them containing a limit point, should be sensitive to an infinitesimally small perturbation. The purpose of the current paper is to state and prove this assertion in a model-independent way.

It was shown by McGehee and Armstrong [31] that the principle of competitive exclusion is valid only if a steady state is required for coexistence. Two species feeding on a single resource may very well coexist if the inherent population dynamics generates cyclic behaviour. In this paper we shall, however, stay within the realm of steady states. In this case the definition of coexistence that is most widely used in ecology is the one put forward by Armstrong and McGehee [6, p. 158]. According to it, for a model given by a system of differential equations, a finite number of species coexist at steady state if the system has an asymptotically stable equilibrium with the sizes of all species strictly positive.

In our investigation of the possibility of infinitely many coexisting species it is irrelevant whether the steady state is stable or not because we shall exclude coexistence by showing that a positive steady state is nonrobust in the sense that it will not survive arbitrarily small perturbations of the model ingredients. As a matter of fact, a perturbation of only the intrinsic growth rate suffices to destroy the steady state. To fix the terminology we distinguish between *coexistence* and *robust coexistence*. Two or more species (or strategies, see below) are said to coexist if there is a steady state of their combined population dynamics with the sizes of all species strictly positive. The coexistence is considered to be robust if it survives any small perturbation of the model ingredients.

We shall assume that the possible species are distinguished from each other by a (heritable) “strategy” value, which can be multi-dimensional. No specific biological interpretation of the strategy will be assumed.

One of our main theorems (Theorem 4) supposes that the feedback has a certain smoothening property called compactness. As we shall see, most biologically realistic models comply with this hypothesis. In this case we demonstrate the impossibility of robust coexistence of infinitely many strategies. As the assumption of compactness does not hold for Roughgarden’s example, in which the interaction is described by a convolution on the whole real line, we will discuss the case of convolution separately. For this class of models we demonstrate the impossibility of robust coexistence of any strategy set containing a limit point, that is when the strategy values are not well separated. In particular, a continuum of robustly coexisting strategies is excluded.

On the other hand, if the strategies are separated and thus “sufficiently different”, then an infinite number of robustly coexisting strategies would not immediately violate the principle of limiting similarity. In this case a new aspect enters the scene: the finiteness of the population. If the strategy set is the whole real line it makes sense to consider infinite populations (if there are infinitely many species present the whole *community* may be infinite although each of the species is finite). It turns out that for an infinity of discrete, equidistant strategies the distinction between finite and infinite populations is crucial: robust coexistence is excluded in the finite population case but possible in the infinite population case (Theorem 10).

Infinite populations and an infinite number of species are idealizations that are useful for mathematical analysis. But, after all, we live in a finite world. The biologically relevant distinction is therefore not so much between "finite" and "infinite" than between "few" and "many". In Section 4.1 we therefore investigate under what kind of interactions it is possible to give a finite upper bound for the number of robustly coexisting species. The obtained result is then interpreted in terms of the principle of competitive exclusion. Without any restrictions on the interaction, nothing decisive can be said.

It is important to stress that, in most of the paper, we investigate a purely ecological question rather than an evolutionary one. We consider a given set of coexisting strategies and ask whether the coexistence is robust. With the assumption of compactness we learn that the answer is in the negative for infinitely many strategies. In contrast, the evolutionary question would reverse the order, that is, ask whether there exists some infinite set of coexisting strategies for any parameter combination in a given (small) parameter set. In this paper we answer the latter, more difficult question, in the negative only in the convolution case with the additional condition on analyticity (Theorem 8).

Section 2 defines the general framework of the investigation. Section 3 introduces the concept of interaction operator and demonstrates that this operator is compact under mild conditions. Section 4 provides the basic results both for compact operators and for convolution operators. Section 5 discusses the Lotka-Volterra case and the seed-size model of Geritz [13] as examples. The general picture emerging from our investigation will be discussed in the last section.

2. The general setting

2.1. Steady states of a single physiologically structured population

We consider a population structured by some physiological features like size and age. The set of all admissible physiological states is denoted by Ω, which we shall assume to be a locally compact Hausdorff space. The population state space is the space $\mathcal{M}_+(\Omega)$ of all finite positive regular Borel measures on Ω. The σ-algebra of all Borel sets in Ω is denoted by $\mathcal{B}(\Omega)$.

The survival, development and reproductional behaviour of individuals are assumed to depend on the *environmental condition* I, which is represented by an element in a Banach space Z. If I is known as a function of time, then modelling the individual processes mentioned above leads to a linear time dependent dynamical system [10]. Assuming that individuals affect their environment we have a feedback mechanism eventually resulting in a nonlinear population model. Mathematically this means that there is a *feedback function* $H : \mathcal{M}(\Omega) \to Z$ mapping the present population state to the present environmental condition:

$$I = H(m), \quad m \in \mathcal{M}(\Omega). \tag{2.1}$$

Diekmann et al. [11] showed that the steady state conditions of such a model can be written as

$$\begin{cases} b = L(I)b, \\ I = G(I)b, \end{cases} \tag{2.2}$$

where the unknowns are the steady environmental condition $I \in Z$ and the vector b is the steady birth rate measure. The interpretation of this is that $b(\omega)$ is the rate at which individuals are born with state in the Borel set ω. The operator $L(I)$ is the *next-generation operator*: $L(I)b$ gives the expected state-at-birth-distribution of the offspring born to a set of individuals that were themselves born with state-at-birth-distribution b, given steady environmental conditions as specified by I. The *individual feedback operator* $G(I)$ takes on values in Z and gives the lifetime contribution to the environmental condition of individuals born with state-at-birth-distribution b, given steady environmental conditions as specified by I.

The first equation in (2.2) reflects the fact that at steady conditions the state-at-birth-distribution should remain the same from generation to generation. The latter equation in (2.2) follows from (2.1) by the observation that at steady conditions an individual is fully characterized by its state-at-birth and its age. As a consequence, the steady population state m can be expressed in terms of b and the submodels for individual development and survival. But these depend on the environmental condition I! Therefore m can be expressed in terms of b and I and we obtain the second equation in (2.2) (for details, see [11]).

The first equation in (2.2) is an eigenvalue problem. The biological interpretation requires $L(I)$ to be a positive operator, which we assume to be irreducible, and so Perron-Frobenius theory implies that there is a unique positive eigenvalue $R_0(I)$ (called the *basic reproduction ratio*) of $L(I)$ which is dominant. The first equation in (2.2) implies that if $b \neq 0$, that is, we have a nontrivial steady state, then

$$R_0(I) = 1. \tag{2.3}$$

Substituting (2.1) into (2.3) one obtains the following necessary condition for the measure m to be a nontrivial steady state:

$$R_0(H(m)) = 1. \tag{2.4}$$

We emphasize that for *structured* populations this is only a *necessary* condition for m to be a nontrivial steady population state: There may very well be a non-steady population state m that gives rise to an environment $I = H(m)$ for which $R_0(I) = 1$. To see this, consider an age-structured model with I being the total population size. Any measure concentrated on $[a, \infty)$ with $a > 0$ is clearly not steady, but it may well have a total size I such that $R_0(I) = 1$.

Unstructured models, in which Ω consists of only one point, are of course included in the general framework and for these models (2.4) is also sufficient: The basic reproduction ratio is

$$R_0(I) = \frac{\beta(I)}{\mu(I)}, \tag{2.5}$$

with β and μ being the per capita birth and death rates, respectively. Hence $R_0(I) = 1$ if and only if $\beta(I) = \mu(I)$, and thus any m (which in this case can be represented by a scalar) giving rise to an environment $I = H(m)$ is a steady state.

The equation (2.4) can of course be written as $r(m) = 0$, with $r(m) := R_0(H(m)) - 1$. A biologically more meaningul choice for r is the *Malthusian parameter*. In applications $R_0(I)$ is derived from more basic modelling ingredients describing individual behaviour and from these the Malthusian parameter (or per capita population growth rate) can be obtained by solving the so-called Euler-Lotka equation (see [9] for details). In any case, the necessary steady state condition can finally be brought into the form

$$r(m) = 0. \tag{2.6}$$

As pointed out above, this condition is also sufficient in the case of unstructured populations.

2.2. Strategy space and polymorphism

The purpose of this paper is to study the coexistence of different strategies. To this end we introduce the set $\mathcal{X}$ of all admissible strategies and we assume that $\mathcal{X}$ is equipped with a locally compact normal Hausdorff topology. For those readers uninterested in technical details suffice it to mention that all countable discrete spaces and all finite-dimensional Euclidean spaces (or, more generally, all finite Cartesian products of closed intervals) have these properties. Normality is a separation condition meaning that disjoint closed sets have disjoint neighbourhoods. It guarantees the existence of nonconstant continuous functions and is a necessary and sufficient condition for Tietze's extension theorem to hold: a continuous function defined on a closed subset can be continuously extended to the whole space [12, p. 149].

An individual is now characterized by its physiological state $y \in \Omega$ and its strategy $x \in \mathcal{X}$. A population is *polymorphic* if at least two different types (individuals playing different strategies) coexist. As pointed out by Diekmann et al. [10, 11], the general framework of physiologically structured populations includes the polymorphic situation of several interacting strategies; we simply have to take the population state space as $\mathcal{M}_+(\mathcal{X} \times \Omega)$. If the population is physiologically unstructured, then the population state space is $\mathcal{M}_+(\mathcal{X})$.

A basic assumption is that the reproduction is faithful with respect to strategy: an individual of a certain type can only beget offspring of the same type. This means that the next generation operator $L(I)$ acting on $\mathcal{M}(\mathcal{X}\times\Omega)$ has a "block-diagonal" form $(L(x, I))_{x\in\mathcal{X}}$. The necessary steady state condition (2.6) thus becomes

$$r(x, m) = 0 \tag{2.7}$$

for all strategies $x \in \mathcal{X}$ that are present in the population.

For the case of only finitely many strategies, it is clear what this last condition means, but for strategy sets having a limit point it needs a formal definition. We say that the strategies in the open set $E \subset \mathcal{X}$ are *not* present in the population described by the measure $m \in \mathcal{M}(\mathcal{X}\times\Omega)$ if $m(E\times\Omega) = 0$. We define the *set $\hat{\mathcal{X}}(m) \subset \mathcal{X}$ of all strategies present in the population* as the complement of the union of all open sets $E \subset \mathcal{X}$ of strategies not present. The set $\hat{\mathcal{X}}(m)$ is obviously closed. For unstructured populations $\hat{\mathcal{X}}(m)$ is simply the support $\operatorname{supp}(m)$ of $m \in \mathcal{M}_+(\mathcal{X})$.

In most cases it is natural to assume that the total number of individuals is finite and so far we have done so by taking the population state space as $\mathcal{M}_+(\mathcal{X}\times\Omega)$, the positive cone of the Banach lattice $\mathcal{M}(\mathcal{X}\times\Omega)$ of all *finite* signed Borel measures on $\mathcal{X}$ with the total variation norm. If the strategy space is noncompact, say the whole Euclidean space $\mathbf{R}^p$, then it makes sense to consider infinite communities even if each "local" subpopulation (the individuals with strategy in a compact set) is finite. Measures describing such communities are not finite. In order to still get a Banach space, we have to control the behaviour of the measures at infinity of the strategy space, that is, outside sufficiently large compact subsets of the strategy space. The easiest way out is to introduce a weight function. By a *weight function* on $\mathcal{X}$ we understand any continuous, strictly positive function w defined on $\mathcal{X}$. If w is a weight function, we denote by $\mathcal{M}(\mathcal{X}\times\Omega, w)$ the vector space of all regular signed Borel measures μ on $\mathcal{X}\times\Omega$ such that the signed measure

$$\omega \mapsto \int_\omega w(x)d\mu \tag{2.8}$$

is of bounded variation. The norm $\|\mu\|_w$ of μ in $\mathcal{M}(\mathcal{X}\times\Omega, w)$ is given by the total variation of the measure in (2.8) and makes $\mathcal{M}(\mathcal{X}\times\Omega, w)$ into a Banach space. Note that $\mathcal{M}(\mathcal{X}\times\Omega, 1) = \mathcal{M}(\mathcal{X}\times\Omega)$ and if $\mathcal{X}$ is compact, then $\mathcal{M}(\mathcal{X}\times\Omega, w) = \mathcal{M}(\mathcal{X}\times\Omega)$ so there is no need for a weight function. When $w = 1$ we omit the subscript from the norm.

3. Interaction operators

One can always formally rewrite the necessary steady state condition

$$r(x, m) = 0 \quad \text{for all} \quad x \in \hat{\mathcal{X}}(m) \tag{3.1}$$

as

$$(\mathbf{A}m)(x) = r_0(x) \quad \text{for all} \quad x \in \hat{\mathcal{X}}(m), \tag{3.2}$$

where r_0 is a function on $\mathcal{X}$ and

$$(\mathbf{A}m)(x) = r_0(x) - r(x, m). \tag{3.3}$$

However, in many applications the form (3.2) arises naturally from modelling with $r_0(x)$ being the density independent growth rate of strategy x and $(\mathbf{A}\nu)(x)$ describing how interaction affects the growth rate of strategy x. We assume that $r_0 \in C(\mathcal{X})$, the Banach space of all *bounded* continuous real valued functions on $\mathcal{X}$ equipped with the supremum norm, and that $\mathbf{A}$ maps $\mathcal{M}_+(\mathcal{X} \times \Omega, w)$ into $C(\mathcal{X})$.

In a virgin, that is, population free, environment there is no interaction. Therefore $\mathbf{A}(0)$ should equal 0, but this assumption is of no relevance for our analysis. In many cases it is natural to assume that $r_0(x)$ is positive for all x in $\mathcal{X}$ – a strategy with negative density independent growth rate cannot invade a virgin environment. But for instance when an Allee effect is present a strategy x may well be viable even if $r_0(x)$ is negative. We shall therefore not make any general assumptions concerning the sign of r_0 but state such assumptions later on when relevant.

The mapping $\mathbf{A} : \mathcal{M}_+(\mathcal{X} \times \Omega, w) \to C(\mathcal{X})$ will be referred to as the *interaction operator*. If all interaction is competitive, then $\mathbf{A}(\mu)(x)$ is positive for all x in $\mathcal{X}$, but we want to include the possibility of cooperation and therefore we do not make any assumptions concerning the sign of $\mathbf{A}(\mu)(x)$.

We stress that our treatment is not restricted to linear interaction operators. However, as pointed out by Diekmann et al. [10], in many population models the nonlinear feedback has a certain hierarchical structure in terms of linear operators, which we shall now briefly describe.

Let $Z_1, Z_2, \dots, Z_k$ and $\mathcal{M}$ be Banach spaces and assume that the mappings

$$L_1 : \mathcal{M} \to Z_1, \tag{3.4}$$

$$L_j : Z_1 \times Z_2 \times \cdots \times Z_{j-1} \times \mathcal{M} \to Z_j, \quad j = 1, 2, \dots k \tag{3.5}$$

are linear in their last argument. Define the mappings $H_j : \mathcal{M} \to Z_j$, $j = 1, 2, \dots, k$, recursively by

$$\begin{aligned} I_1 &= H_1(\nu) = L_1(\nu), \\ I_2 &= H_2(\nu) = L_2(I_1, \nu), \\ &\vdots \\ I_k &= H_k(\nu) = L_k(I_1, I_2, \dots, I_{k-1}, \nu). \end{aligned} \tag{3.6}$$

This construction yields a mapping $H : \mathcal{M} \to Z_1 \times Z_2 \times \cdots \times Z_k$ defined by $H(\nu) = (H_1(\nu), \dots, H_k(\nu))$ for $\nu \in \mathcal{M}$. With $\mathcal{M} = \mathcal{M}(\mathcal{X} \times \Omega, w)$ the nonlinear interaction operator is then defined as

$$\mathbf{A} = F \circ H \tag{3.7}$$

for some mapping $F : Z_1 \times Z_2 \times \cdots \times Z_k \to C(\mathcal{X})$.

One of our main theorems assumes that the interaction operator is compact. We therefore give an easily verifiable condition that guarantees that the interaction operator $\mathbf{A}$ obtained by the hierarchical setting (3.4) – (3.7) is compact. We start by a (provisional) definition.

Definition 1. *Let Y, $\mathcal{M}$ and Z be Banach spaces. A map T defined on the Cartesian product $Y \times \mathcal{M}$ with values in Z is called* skew-compact *if the closure of $T(U \times V)$ is a compact subset of Z whenever the closure of U is compact in Y and V is bounded in $\mathcal{M}$.*

Theorem 1. *Assume in the hierarchical setting of* (3.4) – (3.7) *that L_1 is compact and L_j is skew-compact in the sense of Definition 1 with $Y = Z_1 \times Z_2 \times \cdots \times Z_{j-1}$ for all $j = 2, 3, \ldots, k$ and that $F : Z_1 \times Z_2 \times \cdots \times Z_k \to C(\mathcal{X})$ is continuous. Then $\mathbf{A} = F \circ H$ is compact.*

Proof. Let $V \subset \mathcal{M}$ be bounded. We have to show that $\mathbf{A}(V)$ is precompact (that is, that it has compact closure). We first show that $H_j(V)$ is precompact in Z_j for all $j = 1, 2, \ldots, k$. Because L_1 is compact, $H_1(V)$ is precompact in Z_1. Assume that we have already shown that $H_{j-1}(V)$ is precompact. Then, by the definition of skew-compactness, $H_j(V) = L_j(H_{j-1}(V) \times V)$ is precompact in Z_j. Mathematical induction proves the claim.

Because the cartesian product of compact sets is compact, it follows that $\overline{H(V)}$ is compact and because continuous functions preserve compactness we have that $\overline{\mathbf{A}(V)} = \overline{F(H(V))} \subset \overline{F\left(\overline{H(V)}\right)} = F\left(\overline{H(V)}\right)$ is compact. This completes the proof. □

It is well known that continuous kernels on compact spaces generate compact linear integral operators. Next we prove that it follows from Theorem 1 that "powers" of linear integral operators are also compact. In applications to population dynamics we have to assume that both the strategy space $\mathcal{X}$ and the physiological state space Ω are compact. In the following theorems $\mathcal{Y}$ plays the role of $\mathcal{X} \times \Omega$

Theorem 2. *Suppose that $\mathcal{X}$ and $\mathcal{Y}$ are compact Hausdorff spaces. Let $L \geq 1$ be an integer and let $a : \mathcal{X} \times \mathcal{Y}^L \to \mathbf{R}$ be a continuous mapping. Then the operator $\mathbf{A} : \mathcal{M}(\mathcal{Y}) \to C(\mathcal{X})$ defined by*

$$(\mathbf{A}\nu)(x) = \int_{\mathcal{Y}^L} a(x, y_1, y_2, \ldots, y_L) \prod_{i=1}^{L} \nu(dy_i), \quad x \in \mathcal{X} \tag{3.8}$$

is compact and satisfies

$$\|\mathbf{A}\nu\|_\infty \leq \|a\|_\infty \|\nu\|^L \tag{3.9}$$

for all $\nu \in \mathcal{M}(\mathcal{Y})$.

Proof. The operator $\mathbf{A}$ is obtained through the hierarchical structure (3.4) – (3.7) by defining

$$\begin{aligned} I_1 &= L_1(\nu)(x, y_2, y_3, \ldots, y_L) = \int_{\mathcal{Y}} a(x, y_1, y_2, \ldots, y_L)\nu(dy_1), \\ I_2 &= L_2(I_1, \nu)(x, y_3, \ldots, y_L) = \int_{\mathcal{Y}} I_1(x, y_2, y_3, \ldots, y_L)\nu(dy_2), \\ &\vdots \\ I_L &= L_L(I_{L-1}, \nu)(x) = \int_{\mathcal{Y}} I_{L-1}(x, y_L)\nu(dy_L). \end{aligned} \tag{3.10}$$

Notice that the hierarchical structure is particularly simple in the present case, as each I_j depends only on the immediately preceding I_{j-1} and on ν. The compactness of L_1 is a classical application of Ascoli's theorem. The skew-compactness of L_j, $j = 2, 3, \dots, L$ follows in exactly the same way from (3.10). Theorem 1 now shows that $\mathbf{A} = \pi_k \circ H$ is compact (π_k is the projection onto Z_k). The estimate (3.9) follows from (3.10) by induction. □

In Section 5.2 we shall in connexion with a model of seed-size distribution encounter an interaction operator that could be called a "power series" of integral operators, that is, it is an infinite sum of operators of the type (3.8) with L ranging from 1 to infinity. Next we shall give a criterion for compactness of sums of general (nonlinear) interaction operators which immediately yields a corresponding criterion for the "power series".

Theorem 3. *Let $\mathcal{X}$ and $\mathcal{Y}$ be compact and $\mathbf{A}_L$, $L = 1, 2, 3, \dots$ a sequence of operators from $\mathcal{M}(\mathcal{Y})$ to $C(\mathcal{X})$ with the property that for every integer L there exist positive numbers d_L and l_L such that*

$$\|\mathbf{A}_L \nu\|_\infty \le d_L \|\nu\|^L \tag{3.11}$$

for every $\nu \in \mathcal{M}(\mathcal{Y})$ and if $\varepsilon > 0$, every $x \in \mathcal{X}$ has a neighbourhood V such that for all $y \in V$ and all $\nu \in \mathcal{M}(\mathcal{X})$

$$|\mathbf{A}_L(\nu)(x) - \mathbf{A}_L(\nu)(y)| \le \varepsilon l_L \|\nu\|. \tag{3.12}$$

If for some positive number M one has

$$\sum_{L=1}^{\infty} d_L M^L < \infty, \quad \sum_{L=1}^{\infty} l_L M^L < \infty, \tag{3.13}$$

then the series

$$\mathbf{A} = \sum_{L=1}^{\infty} \mathbf{A}_L \tag{3.14}$$

converges absolutely (that is, $\sum_{L=1}^{\infty} \|\mathbf{A}_L\|$ converges) and defines a compact operator $\mathbf{A}$ on the closed ball of radius M and center $0 \in \mathcal{M}(\mathcal{Y})$. In particular, if (3.13) holds for all $M > 0$, then $\mathbf{A}$ is compact on all of $\mathcal{M}(\mathcal{Y})$.

Proof. The estimate (3.11) together with the convergence condition (3.13) give absolute convergence of the series in (3.14) and boundedness of the image of the ball of radius M. Condition (3.12) yields equicontinuity and Ascoli's theorem completes the proof. □

Corollary 1. *Suppose that $\mathcal{X}$ and $\mathcal{Y}$ are compact. Let M be a nonnegative real number and let $a_L : \mathcal{X} \times \mathcal{Y}^L \to \mathbf{R}$ $(L \in \mathbf{N})$ be a sequence of continuous mappings with the following properties:*

(A) *For each* $L \in \mathbf{N}$ *there exists* $d_L \in \mathbf{R}$ *such that*

$$|a_L(x, y_1, y_2, \dots, y_L)| < d_L, \qquad x \in \mathcal{X},\ y_1, y_2, \dots, y_L \in \mathcal{Y}, \tag{3.15}$$

$$\sum_{L=1}^{\infty} d_L M^L < \infty. \tag{3.16}$$

(B) *For each* $L \in \mathbf{N}$ *there exists* $l_L \in \mathbf{R}$ *) such that for any* $\varepsilon > 0$ *and* $x \in \mathcal{X}$ *there exists a neighbourhood* V *of* x *such that for each* $z \in V$

$$|a_L(x, y_1, y_2, \dots, y_L) - a_L(z, y_1, y_2, \dots, y_L)| < \varepsilon l_L \tag{3.17}$$

for $y_1, y_2, \dots, y_L \in \mathcal{Y}$*, and*

$$\sum_{L=1}^{\infty} l_L M^L < \infty. \tag{3.18}$$

Then the series

$$\mathbf{A}(\nu)(x) = \sum_{L=1}^{\infty} \left(\int_{\mathcal{X}^L} a_L(x, y_1, y_2, \dots, y_L) \prod_{i=1}^{L} \nu(dy_i) \right). \tag{3.19}$$

is absolutely convergent for all $\nu \in \mathcal{M}(\mathcal{X})$ *with* $||\nu|| \leq M$ *and all* $x \in \mathcal{X}$ *and defines a compact operator* $\mathbf{A}$ *on the closed ball of radius* M *in* $\mathcal{M}(\mathcal{X})$ *with values in* $C(\mathcal{X})$*.*

Theorem 2 and Corollary 1 together establish that the interaction operator should be compact basically for any meaningful model provided that the strategy space itself is compact and the model is defined in a smooth way.

The case of Lotka-Volterra interaction mentioned in the introduction is of special historical importance. In this situation $\mathcal{Y} = \mathcal{X}$ and the interaction operator is linear:

$$\mathbf{A}(\nu)(x) = \int_{\mathcal{X}} a(x, y)\nu(dy) \tag{3.20}$$

As a special case of Theorem 2, this operator is compact, provided that the function a is continuous and $\mathcal{X}$ is compact. However, the Lotka-Volterra interaction operator defined by the *convolution*

$$\mathbf{A}(\nu)(x) = (a * \nu)(x) = \int_{\mathbf{R}} a(x - y)\nu(dy) \tag{3.21}$$

on the real line $\mathbf{R}$ is *not* compact. To see this, consider the set of absolutely continuous measures $\nu_i(dx) = n(x - i)dx$, $n \in L^1(\mathbf{R})$, $i \in \mathbf{N}$ and the corresponding functions g_i defined by $g_i(x) = \mathbf{A}(\nu_i)(x) = g(x - i)$. As the set $\{\nu_i : i \in \mathbf{N}\}$ is bounded in $\mathbf{R}$ by $\|n\|_1$, but the set $\{g_i : i \in \mathbf{N}\}$ is not relatively compact in $C(\mathbf{R})$, the operator $\mathbf{A}$ is not compact. This forces us to use different methods, viz. harmonic analysis, for Lotka-Volterra interaction operators of convolution type.

4. Results

4.1. Compact operators

Before we state the main theorem of this section, we introduce some notation. Let $\mathbf{A} : \mathcal{M}(\mathcal{X} \times \Omega) \to C(\mathcal{X})$ be the interaction operator introduced in Section 3. A measure ν on $\mathcal{X} \times \Omega$ induces in an obvious manner a measure $\hat{\nu}$ on $\hat{\mathcal{X}}(\nu) \times \Omega$. We define the operator $\hat{\mathbf{A}} : \mathcal{M}(\hat{\mathcal{X}}(\nu) \times \Omega) \to C(\hat{\mathcal{X}})$ by the formula

$$\left(\hat{\mathbf{A}}\hat{\nu}\right)(x) = (\mathbf{A}\nu)(x), \quad x \in \hat{\mathcal{X}}(\nu). \tag{4.1}$$

Theorem 4. *Suppose that the interaction operator* $\mathbf{A} : \mathcal{M}(\mathcal{X} \times \Omega) \to C(\mathcal{X})$ *is continuous and compact and that there exists a solution* ν^e *of* (3.2) *with an infinite number of strategies present (*$\hat{\mathcal{X}}(\nu^e)$ *an infinite set). Then for each* $\varepsilon > 0$ *there exists an* $r_0' \in C(\mathcal{X})$ *such that*

$$\|r_0 - r_0'\|_\infty < \varepsilon \tag{4.2}$$

and such that the equation (3.2) *with* r_0 *replaced by* r_0' *does not have a solution* ν *with* $\hat{\mathcal{X}}(\nu) = \hat{\mathcal{X}}(\nu^e)$*. If* $r_0(x) > \delta > 0$ *for all* $x \in \mathcal{X}$*, then* r_0' *can be chosen positive.*

Proof. Suppose that $\hat{\mathcal{X}}(\nu^e)$ is infinite. Then, $C(\hat{\mathcal{X}})$ is an infinite dimensional Banach space and hence not locally compact. Let U_t be the ball of radius t in $\mathcal{M}$. Because $\hat{\mathbf{A}}$ is compact, the interior of the closure of $\hat{\mathbf{A}}(U_t)$ is empty for all $t > 0$. It follows that the range of $\hat{\mathbf{A}}$ is of the first category and hence has empty interior by Baire's theorem. As $\hat{r}_0$ is an element of the range of $\hat{\mathbf{A}}$, there exists an $\hat{r_0'} \in C(\hat{\mathcal{X}})$ in an arbitrarily small neighbourhood of $\hat{r}_0$ such that $\hat{r_0'}$ is not in the range of $\hat{\mathbf{A}}$, that is, no solution of equation $\hat{\mathbf{A}}(\hat{\nu}) = \hat{r_0'}$ exists. Since $\mathcal{X}$ is normal, Tietze's extension theorem [12, p. 149] implies that there exists $\varphi \in C(\mathcal{X})$ such that $\varphi(x) = \hat{r_0'}(x) - \hat{r}_0(x)$ for $x \in \hat{\mathcal{X}}$. Tietze's theorem contains the statement that if the original function (in our case $\hat{r_0'}(x) - \hat{r}_0(x)$) has absolute value less than ε, then the extension φ can be chosen such that $|\phi(x)| < \varepsilon$ for all $x \in \mathcal{X}$. Therefore

$$r_0'(x) = r_0(x) + \varphi(x),\ x \in \mathcal{X}$$

constitutes the perturbed growth rate the existence of which was claimed.

Finally, if $r_0(x) > \delta > 0$ for all $x \in \mathcal{X}$, then we choose $\hat{r_0'}$ at most at a distance $\delta/2$ from r_0. This proves the last statement. □

A special class of compact operators is formed by operators, the range of which is a finite-dimensional manifold. If the interaction operator belongs to this class we can give an upper bound to the number of coexisting species.

Theorem 5. *Suppose that the range of the interaction operator* $\mathbf{A}$ *is a* p*-dimensional manifold in* $C(\mathcal{X})$*. Then no collection of* $L > p$ *strategies can coexist robustly at equilibrium.*

Proof. By assumption, **A** has the form

$$\mathbf{A}(\nu)(x) = \phi(I_1, I_2, \dots, I_p, x) = \phi(\lambda_1(\nu), \lambda_2(\nu), \dots, \lambda_p(\nu), x), \tag{4.3}$$

where ϕ is a continuous function from the Cartesian product of a subset of $\mathbf{R}^p$ and $\mathcal{X}$ into $\mathbf{R}$ and $I_j = \lambda_j(\nu)$ is a continuous real valued function for each $j = 1, 2, \dots, p$.

If $\hat{\mathcal{X}}(\nu)$ is finite: $\hat{\mathcal{X}}(\nu) = \{x_1, x_2, \dots, x_L\}$, then we obtain the following L equilibrium conditions:

$$\begin{aligned} \phi(I_1, I_2, \dots, I_p, x_1) &= r_0(x_1), \\ &\vdots \\ \phi(I_1, I_2, \dots, I_p, x_L) &= r_0(x_L). \end{aligned} \tag{4.4}$$

Being a system of L equations in p unknowns (4.4) does not have any solutions that survive arbitrarily small perturbations of r_0 if $L > p$. □

Theorem 5 is in fact nothing more than a reformulation of the principle of competitive exclusion with limiting factors I_j. In many models the I_j's can be interpreted as resource concentrations, whereas the function λ_j describes the strategy dependent utilization of the jth resource (often via time scaling arguments). Thus we are back to the resource competition interpretation of MacArthur & Levins [26]. However, as Diekmann et al. [11] did, we stress that the interpretation of the variables I_j is irrelevant for Theorem 5 to hold.

If the interaction operator has infinite-dimensional range, nothing can be said in general, not even if the interaction operator is linear. It is possible that at most one species can exist robustly and that an arbitrarily large (but finite) number of species can coexist robustly. The following examples (for unstructured populations) illustrate this.

Example 1. Let $\mathcal{X} = [0, 1]$ and consider the linear interaction operator $\mathbf{A} : \mathcal{M}[(0, 1)] \to C[0, 1]$ given by

$$(\mathbf{A}\nu)(x) = \int_0^1 a(x, y)\nu(dy) \quad x \in [0, 1] \tag{4.5}$$

for some continuous positive kernel a. Assume that *a cannot* be expanded as a finite sum $a(x, y) = \sum_{i=0}^{p} \alpha_i(x)\beta_i(y)$. Then **A** defined by (4.5) has infinite-dimensional range. Assume further that

$$a(x_2, y) > a(x_1, y) \quad \text{whenever} \quad x_2 > x_1 \tag{4.6}$$

and take $r_0(x) = 1$. Two competing strategies $x_1 < x_2$ lead to the equilibrium condition

$$\begin{aligned} a(x_1, x_1)n_1 + a(x_1, x_2)n_2 &= 1, \\ a(x_2, x_1)n_1 + a(x_2, x_2)n_2 &= 1 \end{aligned} \tag{4.7}$$

for the measure $\nu = n_1\delta_{x_1} + n_2\delta_{x_2}$. But the assumption (4.6) implies that the system (4.7) has no solution in the interior of $\mathbf{R}_+^2$. Hence two strategies cannot coexist.

This example is of course nothing else than the standard Lotka-Volterra model of competition between two species. Our condition (4.6) means that the species with the smaller strategy value is *dominant* and will outcompete the other species [20, p.56].

Example 2. Like in Example 1 we take a linear interaction operator of type (4.5) on $\mathcal{X} = [0, 1]$, but with a convolution kernel $a(x, y) = a(x - y)$ given by

$$a(x) = 1 - |x|. \tag{4.8}$$

As intrinsic growth rate we choose

$$r_0(x) = 1 - \left(x - \frac{1}{2}\right)^2. \tag{4.9}$$

Consider now $L + 1$ competing equidistant strategies $\{0, 1/L, 2/L, \dots, (L - 1)/L, 1\} \subset [0, 1]$. The equilibrium condition now becomes a system of linear equations conveniently written as

$$An = r, \tag{4.10}$$

where A is an $(L + 1) \times (L + 1)$ matrix with entries

$$a_{ij} = 1 - \left|\frac{i - j}{L}\right|, \quad i = 0, 1, \dots, L, \;\; j = 0, 1, \dots, L, \tag{4.11}$$

and r the vector with components

$$r_i = 1 - \left(\frac{i}{L} - \frac{1}{2}\right)^2, \quad i = 0, 1, \dots, L. \tag{4.12}$$

An easy computation shows that A is invertible for all L (in fact, $\det A = \frac{2^L}{L^L}$) and that the solution of (4.10) is the vector n with components

$$n_0 = n_L = \frac{L + 2}{4L}, \quad n_2 = n_3 = \cdots = n_{L-1} = \frac{1}{L}. \tag{4.13}$$

We have now shown, that for every L, the system (4.10) has a unique strictly positive solution. A sufficiently small perturbation of r_0 cannot destroy this. It follows that an arbitrary finite number of strategies can coexist robustly.

4.2. Convolution operators

As convolution defined on the whole real line is not compact, this case has to be discussed separately. From now onwards we shall exclusively consider unstructured populations. There will therefore be no need for the physiological state space Ω and individuals are fully characterized by their strategy $x \in \mathcal{X}$. The population state is now a measure ν on $\mathcal{X}$ and $\hat{\mathcal{X}}(\nu) = \operatorname{supp}(\nu)$.

We assume that a and r_0 are given real valued continuous functions defined on the whole real axis and consider the interaction operator defined by Eq. (3.21). For the strategy distribution $\nu \in \mathcal{M}_+(\mathbf{R}, w)$, the equilibrium condition reads

$$(a * \nu)(x) = r_0(x) \quad \text{for all} \quad x \in \operatorname{supp}(\nu). \tag{4.14}$$

We shall consider three special cases. In the first we assume that the equilibrium distribution ν has $\operatorname{supp}(\nu) = \mathbf{R}$. Then, we investigate the more general possibility that the support has a limit point. Finally, we consider measures concentrated on a discrete subgroup of $\mathbf{R}$, which we, without loss of generality, take as the group $\mathbf{Z}$ of integers.

As mentioned in Section 2.2 it makes sense to consider not necessarily finite measures when the strategy space is the whole real line. Because the assumptions on the ingredients are slightly different depending on whether we take the finite measures ($w = 1$) or a class of infinite measures as population state space, we shall treat these cases separately. As a matter of fact, also the results depend on the state space! It turns out that in the discrete case robust coexistence of infinitely many strategies is possible if we drop the requirement of finite populations.

In the first case the equilibrium condition (4.14) takes the form

$$(a * \nu)(x) = r_0(x) \quad \text{for all} \quad x \in \mathbf{R}. \tag{4.15}$$

We start by investing the case of finite measures. Intuitively, competition is weak between strategies that are far away from each other. Hence $a(x)$ should decrease to zero as $|x| \to \infty$. Therefore it makes sense to assume that $a \in L^1(\mathbf{R})$. Because the convolution of an L^1-function and a measure $\nu \in \mathcal{M}(\mathbf{R})$ is again an L^1-function, we see that (4.15) can hold only if r_0 is in $L^1(\mathbf{R})$ and we shall therefore make this assumption.

Next we prove a general result regarding Equation (4.15). The nonrobustness of a continuum of coexisting strategies will follow immediately.

Theorem 6. *Let r_0 and a be continuous real valued absolutely integrable functions on $\mathbf{R}$. If Equation* (4.15) *is satisfied by $\nu \in \mathcal{M}_+(\mathbf{R})$, then there exists an arbitrarily small (both in the supremum norm and in the L^1-norm) perturbation of r_0 such that Equation* (4.15) *has no solution in $\mathcal{M}_+(\mathbf{R})$. If r_0 is positive, then the perturbed growth rate r_0' can also be chosen positive.*

Proof. Taking the Fourier transformation of Equation (4.15) one obtains

$$\tilde{\nu}(z) = \frac{\tilde{r_0}(z)}{\tilde{a}(z)} \tag{4.16}$$

for all $z \in \mathbf{R}$ for which $\tilde{a}(z) \neq 0$. By the Riemann-Lebesgue lemma the Fourier transform $\tilde{a}$ is continuous on $\mathbf{R}$ and vanishes at infinity. We can therefore choose a sequence z_k of real numbers such that

$$\tilde{a}(z_k) \neq 0, \qquad \lim_{t \to \infty} \tilde{a}(z_k) = 0. \tag{4.17}$$

Define

$$r_0'(x) = r_0(x)\left(1 + \varepsilon' \cos z_k x\right) \tag{4.18}$$

where $\varepsilon' < \frac{\varepsilon}{2}\min\{1/\|r_0\|_1, 1/\|r_0\|_\infty\}$. Note that $||r_0' - r_0||_1 \le \varepsilon$, $||r_0' - r_0||_\infty \le \varepsilon$ and that r_0' is positive if r_0 is. The Fourier transform of r_0' is

$$\tilde{r_0'}(z) = \tilde{r_0}(z) + \varepsilon' \left(\tilde{r_0}(z - z_k) + \tilde{r_0}(z + z_k)\right). \tag{4.19}$$

If there exists a solution ν' of Equation (4.15) with r_0 replaced by r_0', then its Fourier transform satisfies

$$\tilde{\nu'}(z) = \frac{\tilde{r_0}(z) + \varepsilon' \left(\tilde{r_0}(z - z_k) + \tilde{r_0}(z + z_k)\right)}{\tilde{a}(z)}. \tag{4.20}$$

In particular,

$$\tilde{\nu'}(z_k) = \left(1 + \varepsilon' \frac{\tilde{r_0}(2z_k)}{\tilde{r_0}(z_k)}\right)\tilde{\nu}(z_k) + \varepsilon' \frac{\tilde{r_0}(0)}{\tilde{a}(z_k)}. \tag{4.21}$$

As $\tilde{r_0}(z_k) \to 0$ and $\tilde{a}(z_k) \to 0$ for $k \to \infty$ and $\tilde{\nu}$ is bounded, the absolute value of the right hand side of (4.21) can be made arbitrarily large at $z = z_k$ by choosing k large enough. On the other hand, it follows form (4.20) that

$$\tilde{\nu'}(0) \le \tilde{\nu}(0) + \frac{2\varepsilon}{|\tilde{a}(0)|} \tag{4.22}$$

independently of k. Consequently, for any ε, one can choose k to violate the inequality

$$|\tilde{\nu'}(z_k)| = \left|\int_{-\infty}^{\infty} e^{-ikx}\nu'(dx)\right| \le \int_{-\infty}^{\infty} |e^{-iz_k x}|\nu'(dx) = \int_{-\infty}^{\infty} \nu'(dx) = \tilde{\nu'}(0), \tag{4.23}$$

which holds for all $\nu' \in \mathcal{M}_+(\mathbf{R})$. □

We now turn to the case of not necessarily finite measures. To ensure that the convolution on the left hand side of (4.15) exists for all $x \in \mathbf{R}$ we must impose stronger conditions on the decay at infinity of the kernel a. A simple way out is to observe that if $\nu \in \mathcal{M}(\mathbf{R}, w)$ with $w(x) = (1 + x^2)^{-k}$ for some positive integer k, then ν is a tempered distribution and that the convolution of a rapidly decreasing function and a tempered distribution is a well defined continuous function (actually a C^∞-function). Recall that Roughgarden [35] used the Gaussian kernel which is indeed rapidly decreasing, so our treatment covers Roughgarden's example.

Theorem 7. *Let $a \neq 0$ be a rapidly decreasing function and r_0 a continuous function on $\mathbf{R}$. Assume that $\nu \in \mathcal{M}(\mathbf{R}, (1 + x^2)^{-k})_+$ for some positive integer k and that ν satisfies* (4.15)*. Then for every $\varepsilon > 0$ there exists a continuous function r_0' such that* $\sup\{|r_0(x) - r_0'| : x \in \mathbf{R}\} < \varepsilon$ *and such that Equation* (4.15) *with r_0 replaced by r_0' does not have a solution in $\mathcal{M}(\mathbf{R}, (1 + x^2)^{-k})_+$ for any positive integer k. If r_0 is positive, then the perturbed growth rate r_0' can also be chosen positive.*

Proof. Let ϕ be the "tent function" defined by $\phi(t) = 1 - |t|$ for $t \in [-1, 1]$ and $\phi(t) = 0$ outside that interval. The Fourier transform of ϕ is given by

$$\tilde{\phi}(z) = c\frac{1 - \cos z}{z^2}, \tag{4.24}$$

where c is a normalization constant. Assume that ν is a solution of

$$a * \nu = \phi. \tag{4.25}$$

Then its Fourier transform satisfies

$$z^2\tilde{a}(z)\tilde{\nu}(z) = c(1 - \cos z). \tag{4.26}$$

Because a is rapidly decreasing, the same is true of its Fourier transform $\tilde{a}$. It follows that the function $z \mapsto z^k\tilde{a}(z)$ is rapidly decreasing for all positive integers k, in particular for $k = 2$. Because the right hand side of (4.26) is not integrable, neither is the left hand side. Hence $\tilde{\nu}(z)$ does not define a linear functional on the rapidly decreasing functions, that is to say, $\tilde{\nu}$ is not a tempered distribution. As the Fourier transform of a tempered distribution is again a tempered distribution, it follows that ν is not tempered, hence does not belong to $\mathcal{M}(\mathbf{R}, (1 + x^2)^{-k})$ for any k.

We have now shown, that (4.25) does not have a solution in $\mathcal{M}(\mathbf{R}, (1 + x^2)^{-k})$ for any k. The theorem now follows by taking $r_0' = r_0 - \varepsilon\phi$. To see this just notice that if r_0 is positive, there exists an interval on which $r_0(x) > 2\varepsilon$ for some $\varepsilon > 0$. By suitable translation and scaling, this interval can be taken as $[0, 1]$. □

Theorems 6 and 7 immediately imply that if there exists an equilibrium measure (finite or not) supported on the whole real line, then there exists an arbitrarily small perturbation of the intrinsic growth rate leading to a situation in which no equilibrium supported on the whole real axis can exist. It is of course perfectly possible that the perturbed system has an equilibrium supported on some smaller subset of $\mathbf{R}$.

If we assume that kernel a and the intrinsic growth rate r_0 are *analytic* we obtain a much stronger result.

Theorem 8. *Assume that the functions a and r_0 of* Theorem 6 *are analytic, that is, can be extended to holomorphic functions in some open set of the complex plane containing the real axis. If there exists an equilibrium solution $\nu \in \mathcal{M}_+(\mathbf{R})$, the support of which has a limit point in $\mathbf{R}$, then there exists an arbitrarily small (both in the supremum norm and in the L^1-norm) perturbation of r_0 such that the perturbed system has no equilibrium with support having a limit point. In particular, no equilibrium of the perturbed system can have* $\mathrm{supp}(\nu)$ *as its support. If r_0 is positive, then the perturbed growth rate r_0' can also be chosen positive.*

Proof. Because Equation (4.14) holds for all $x \in \mathrm{supp}(\nu)$ and $\mathrm{supp}(\nu)$ has a limit point, it follows from the uniqueness theorem for analytic functions that both sides of the equation are equal for all $x \in \mathbf{R}$, that is, (4.15) holds. It now follows from the proof of Theorem 6 that we can find an arbitrarily small *analytic* perturbation $r_0'(x) = r_0(x)(1 + \varepsilon' \cos z_k x)$ of r_0, such that (4.15) does not hold for any $\nu' \in \mathcal{M}_+(\mathbf{R})$. Applying the uniqueness theorem once more we find that equality cannot hold in any subset having a limit point, in particular not in $\operatorname{supp}(\nu)$. □

Note that this Theorem, with its more restrictive conditions, says much more than the preceding results (Theorems 4, 6 and 7). While these theorems state the existence of a perturbation destroying coexistence of a pre-defined set of strategies, Theorem 8 demonstrates the non-coexistence of any set of strategies with a limit point.

We now turn to the case in which the support of ν is concentrated on $\mathbf{Z}$, that is, ν has the form

$$\nu = \sum_{j \in \mathbf{Z}} n_j \delta_j, \tag{4.27}$$

where δ_j is the Dirac measure (point mass) concentrated at the point $j \in \mathbf{Z}$. We start by considering the case of a finite total population, that is, the case in which $n = \{n_j\} \in \ell^1(\mathbf{Z})$. Define the sequences $a = \{a_j\}$ and $r = \{r_j\}$ in $\ell^1 = \ell^1(\mathbf{Z})$ by

$$a_j = a(j) \qquad \text{and} \qquad r_j = r_0(j). \tag{4.28}$$

The equilibrium condition (4.14) now takes the form of a convolution equation on ℓ^1:

$$a * n = r, \tag{4.29}$$

with the convolution in ℓ^1 defined by

$$(a * b)_i = \sum_{j \in \mathbf{Z}} a_{i-j} b_j. \tag{4.30}$$

Theorem 9. *Let $a \in \ell^1$, $a \geq 0$ and assume that a is not concentrated at a single point. Let $r \in \ell^1$ and assume that $n \in \ell^1$, $n > 0$ satisfies the equilibrium condition* (4.29). *Then to each $\varepsilon > 0$ there exists an $r' \in \ell^1$ with $\|r - r'\|_1 < \varepsilon$ such that the equation*

$$a * n' = r' \tag{4.31}$$

has no solution n' in ℓ^1 with $n' > 0$. If $r > 0$, then r' can be chosen such that $r' > 0$.

Proof. The Fourier transform of an element in ℓ^1 is a continuous function on the unit circle or, equivalently, a continuous 2π-periodic function. According to Wiener's lemma (see e.g. [12], Theorem 11.6) $a \in \ell^1$ is invertible in the convolution algebra ℓ^1 if and only if the Fourier transform $\tilde{a}(\theta)$ does not vanish for any $\theta \in [0, 2\pi]$. We therefore distinguish between two cases: (a) $\tilde{a}(\theta_0) = 0$ for some $\theta_0 \in [0, 2\pi]$ and (b) $\tilde{a}(\theta) \neq 0$ for all $\theta \in [0, 2\pi]$.

(a) Since a is not invertible in this case it is clear that there is an r' arbitrarily close to r such that Equation (4.31) has no solution $n' \in \ell^1$. That r' can be chosen positive if r is positive is also clear: Simply choose $r' = r + \varepsilon\delta_0$. Then $\tilde{r}'(\theta_0) = \varepsilon$ and the only candidate for a solution would have Fourier transform $\tilde{n}' = \tilde{r}'/\tilde{a}$. But this function has a singularity at θ_0 and hence cannot be the Fourier transform of an element of ℓ^1.

(b) In this case the Equation (4.31) has a unique solution $n' \in \ell^1$ for all $r' \in \ell^1$. We have to show that we can choose r' such that n' is not positive.

Let $\rho \in \ell^1$ be the unique solution of

$$a * \rho = \delta_0. \tag{4.32}$$

Because of the nonnegativity of a one has $|\tilde{a}(\theta)| \leq \tilde{a}(0)$ for all $\theta \in [0, 2\pi]$. Therefore

$$|\tilde{\rho}(\theta)| = \frac{1}{|\tilde{a}(\theta)|} \geq \frac{1}{\tilde{a}(0)} = \tilde{\rho}(0) \tag{4.33}$$

for all $\theta \in [0, 2\pi]$. If ρ is nonnegative, then (4.33) implies that

$$|\tilde{\rho}(\theta)| = \tilde{\rho}(0) \tag{4.34}$$

for all $\theta \in [0, 2\pi]$. We claim that (4.34) can hold only if ρ is a multiple of δ_k for some $k \in \mathbf{Z}$. To see this, assume without loss of generality that $\tilde{\rho}(0) = 1$ and notice that $\ell^2(\mathbf{Z}) \subset \ell^1(\mathbf{Z})$. Then, by Plancherel's theorem

$$\sum_{n\in\mathbf{Z}} \rho_n^2 = \frac{1}{2\pi}\int_0^{2\pi} |\tilde{\rho}(\theta)|^2 \, d\theta = 1 = \sum_{n\in\mathbf{Z}} \rho_n, \tag{4.35}$$

which is possible only if precisely one of the numbers ρ_n is equal to one and the rest are zero. This proves the claim which in turn by (4.32) implies that a is a multiple of δ_k for some $k \in \mathbf{Z}$. But this is excluded by the hypothesis. It follows that ρ has at least one negative component. It follows that the unique solution of (4.31) with $r' = r + \varepsilon\delta_k$, which is given by

$$n' = \rho * (r + \varepsilon\delta_k) = n + \varepsilon\rho * \delta_k \tag{4.36}$$

must have a negative component for k sufficiently large. □

Finally we consider the case of not necessarily finite measures concentrated on $\mathbf{Z}$. However, we restrict our investigation to measures that are representable by a sequence in ℓ^∞. As the convolution between an element in ℓ^1 and ℓ^∞ is in ℓ^∞ we shall assume that $r \in \ell^\infty$.

Theorem 10. *Assume that $a \in \ell^1$, $\tilde{a}(\theta) \neq 0$ for all $\theta \in [0, 2\pi]$, $r \in \ell^\infty$ and that $n \in \ell^\infty_+$ satisfies the discrete convolution equation* (4.29).

(a) *If $a \geq 0$, a is not concentrated in a single point and* $\inf n = 0$, *then for every $\varepsilon > 0$ there exists an $r' \in \ell^\infty$, $\|r - r'\|_\infty < \varepsilon$, such that* (4.29) *has no solution in ℓ^∞_+. If $r > 0$, then one can choose $r' > 0$.*

(b) *If* $\inf n > 0$, *then there exists an $\varepsilon > 0$ such that for all $r' \in \ell^\infty, r' > 0$ with $\|r - r'\|_\infty < \varepsilon$ the equation* (4.29) *with r replaced by r' has a unique solution $n' \in \ell^\infty$, $n' > 0$.*

Proof. (a) An inspection of the proof of Theorem 9 (b) shows that we only used that n had arbitrarily small components, that is, the assumptions of the present claim.

(b) Let $\rho \in \ell^1$ be the resolvent of a, that is, the unique solution of (4.32). Then $n = \rho * r$ and $n' = \rho * r'$ are the unique solutions of the convolution equation with growth rates r and r', respectively. The inequality

$$\|n - n'\|_\infty \leq \|\rho\|_1 \|r - r'\|_\infty \tag{4.37}$$

shows that the claim is valid with $\varepsilon = \inf\ n/\|\rho\|_1$. □

5. Examples

5.1. Lotka-Volterra model of competition

Roughgarden's example of continuous coexistence [35] fits into our framework of Section 4.2 if one chooses the Gaussian functions

$$r_0(x) = e^{-\frac{x^2}{2w^2}}, \quad x \in \mathbf{R}, \tag{5.1}$$

and

$$a(x) = e^{-\frac{x^2}{2\sigma^2}}, \quad x \in \mathbf{R}, \tag{5.2}$$

for the intrinsic growth rate and the convolution kernel, respectively.

The Gaussian measure $\nu(dx) = n(x)dx$ determined by the density

$$n(x) = \frac{w/\sigma}{\sqrt{2\pi(w^2 - \sigma^2)}}\, e^{-\frac{x^2}{2(w^2-\sigma^2)}} \tag{5.3}$$

is an equilibrium solution (Fig. 1a). This is an example of continuous coexistence. By Theorem 6 we know that it is nonrobust. It is, however, instructive to demonstrate this directly for this particular example.

Following the proof of Theorem 6, consider the cosine perturbation

$$r_0'(x) = r_0(x)\,(1 + \varepsilon \cos kx)\,, \tag{5.4}$$

where $1 > \varepsilon > 0$, $k > 0$ are reals numbers. (Note, that $r_0'(x) > 0$ for any $x \in \mathbf{R}$.) One can determine the equilibrium solution by deconvolution of r_0':

$$n'(x) = \frac{w/\sigma}{\sqrt{2\pi(w^2 - \sigma^2)}}\, e^{-\frac{x^2}{2(w^2-\sigma^2)}} \left[1 + \varepsilon\, e^{+\frac{w^2\sigma^2}{2(w^2-\sigma^2)}k^2} \cos\left(\frac{w^2}{w^2 - \sigma^2}kx\right)\right]. \tag{5.5}$$

Observe, that the perturbation of the density scales up exponentially with k^2. Figure 1b demonstrates this sensitivity of the density to the cosine perturbation of r_0. The condition of positivity of $n'(x)$ on the whole real line is clearly violated.

Fig. 1. Coexistence in the Lotka-Volterra competition model. Left plots: the intrinsic growth rate $r_0(x)$ (solid line) and the competition kernel $a(x)$ (dotted line). Right plots: the equilibrium population density, as calculated on the whole real line by de-convolution. Top row: Gaussian r_0. This is Roughgarden's example for continuous coexistence. Middle row: Periodic perturbation of r_0 according to equation (5.4). The equilibrium density experiences high perturbation and it is no longer positive on the whole real line. Bottom row: The intrinsic growth rate r_0 is perturbed by a small, narrow Gaussian according to equation (5.6). An equilibrium density function on the whole real line no longer exists.

It is interesting to consider another perturbation, too, which is biologically more meaningful. Perturb r_0 by a small, narrow Gaussian:

$$r_0''(x) = e^{-\frac{x^2}{2w^2}} + \varepsilon\, e^{-\frac{x^2}{2v^2}}. \tag{5.6}$$

For $\sigma > v$, no solution satisfying $r_0 = a * n$ exists, independently of the positivity condition.

The biological interpretation of this kind of perturbation is that a group of strategies earns some additional advantage relative to their original quality. Such an extra advantage destroys the continuous coexistence because the strategies gaining the advantage outcompete the other strategies in a *finite* range of strategies. The effect of an additional drawback of a group of strategies is similar.

Compare now the two kinds of perturbations from a mathematical point of view. The perturbation (5.4) demonstrated, that the positivity condition can be violated by an arbitrarily small perturbation because a small perturbation in r_0 can cause an arbitrarily large perturbation in n. On the other hand, the convolution operator is not invertible in L^1. The perturbation (5.6) demonstrates this noninvertibility.

5.2. Coexistence of different seed-sizes

5.2.1. Model definition

Evolution of seed-size of plants has been investigated by Geritz [13,14] and by Geritz et al. [17,18]. We present the model in a different notation consistent with the one used in the present paper. Competition between plant species with synchronous reproduction is considered. The inherited strategy x is interpreted as the size of the seeds. The environment consists of a large number of sites, each of them is able to support a single plant individual. The probability that a seed survives dispersal and the early seedling state is denoted by $f(x)$. Exactly one of the seedlings still present at a given site becomes established according to a size-dependent rule of competition. The total amount of per capita resource R available for seed production is fixed, so a plant with strategy x produces R/x number of seeds. The individual dies after seed production. Thus the strategy space is $\mathcal{X} = (0, R]$ and the effective number of seeds produced by a plant with strategy $x \in \mathcal{X}$ is $f(x)R/x$.

Two versions of the model have been presented in the literature. They differ only in the rules of competition. In the first version [13], the seedling with the largest seed-size always wins the competition within the site. This kind of competition is referred to as "extreme asymmetric competition" to recognize the fact that an arbitrarily small difference in seed-size decides the competition unequivocally.

In the second version of the model [18], the competitive ability of seed-size x is described by an increasing continuous function $c(x)$. The probability that a given seedling with seed-size x wins the competition for the site is

$$\frac{c(x)}{c(x) + \sum_{i=1}^{L} c(y_i)} \tag{5.7}$$

where $L \geq 0$ is the number of its competitors and $y_1, y_2, \ldots, y_L$ are the seed-sizes of the competitors. In this case of "nonextreme competition", the outcome of competition is random if the seed-size differences are small.

The first version of the model supports continuous coexistence [13], while the second one does not [18]. In the next subsection we show that, in accordance with the theory presented above, the interaction operator of the model is compact in the nonextreme asymmetric case but noncompact in the extreme asymmetric case.

5.2.2. Growth function of the model

Consider an arbitrary distribution of seed-sizes given by the measure $\nu \in \mathcal{M}_+(\mathcal{X})$. The number $\nu(\omega)$ is the expected number of seedlings in a specific germination site with size in the set $\omega \in \mathcal{B}(\mathcal{X})$. Then,

$$N = \int \nu(dx) = \nu(\mathcal{X}) \tag{5.8}$$

is the expected total number of seedlings and $\nu(\omega)/N$ is the probability that a given seedling belongs to the size class ω. (In (5.8) and in the rest of this subsection all integrals are taken over the whole strategy space $\mathcal{X} = (0, R]$). On the other hand,

$$P(L) = \frac{N^L}{L!} e^{-N} \tag{5.9}$$

is the probability of having exactly L number of seedlings in a site.

Suppose that the number of seedlings in a specific site is L and label the seedlings by the indices $1, 2, \ldots, L$. The probability that the $1^{\text{st}}, 2^{\text{nd}}, \ldots, L^{\text{th}}$ seedling belongs to the size classes $\omega_1, \omega_2, \ldots, \omega_L$, respectively, is

$$\frac{\nu(\omega_1)\, \nu(\omega_2) \cdots \nu(\omega_L)}{N^L}. \tag{5.10}$$

Denote the survival probability of a seedling of size x, provided that the site contains L number of further seedlings with sizes y_i $(i = 1, \ldots, L)$, by

$$b^L(x, y_1, y_2, \ldots, y_L). \tag{5.11}$$

Then the expected survival probability of a seedling of size x is

$$\int \cdots \int b^L(x, y_1, \ldots, y_L)\, \frac{\nu(dy_1) \cdots \nu(dy_L)}{N^L} \tag{5.12}$$

conditional that the number of seedlings other than the focal one is L. Taking into account distribution (5.9) and the other fitness components, the expected number of established offsprings per plant with seed-size x is

$$\lambda(x, \nu) = f(x) \frac{R}{x}\, e^{-N} \sum_{L=0}^{\infty} \frac{1}{L!} \int \cdots \int b^L(x, y_1, y_2, \ldots, y_L)\, \nu(dy_1) \cdots \nu(dy_L). \tag{5.13}$$

(By the nature of the Poisson distribution, the probability of having L *additional* seedlings is the same as having L of them in total.)

In the nonextreme asymmetric case, substitution of

$$b^L(x, y_1, y_2, \ldots, y_L) = \frac{c(x)}{c(x) + \sum_{i=1}^{L} c(y_i)} \tag{5.14}$$

into (5.13) leads to the growth function

$$\lambda(x, \nu) = f(x) \frac{R}{x}\, e^{-N} \sum_{L=0}^{\infty} \frac{1}{L!} \int \cdots \int \frac{c(x)}{c(x) + \sum_{i=1}^{L} c(y_i)}\, \nu(dy_1) \cdots \nu(y_L). \tag{5.15}$$

Note that substituting the discrete distribution

$$\nu = \sum_{i=1}^{M} n_i \delta_{x_i} \tag{5.16}$$

into (5.15) one obtains the formula

$$\lambda(x, \nu) = f(x) \frac{R}{x}\, e^{-N} \sum_{L=0}^{\infty} \sum_{\sum k_i = L} \frac{c(x)}{c(x) + \sum_{i=0}^{M} k_i c(x_i)}\, \frac{n_1^{k_1} \cdots n_M^{k_M}}{k_1! \cdots k_M!}, \tag{5.17}$$

which is Equation (7) of Geritz et al. [18]. Here, the multinomial coefficient

$$\frac{L!}{k_1! \cdot \cdots \cdot k_M!} \tag{5.18}$$

arises by matching the integration variables y_i ($i = 1, \ldots, L$) to the x_i ($i = 1, \ldots, K$) parameters of the Dirac measures in all possible ways during evaluation of the integrals.

5.2.3. *Compactness of the interaction operator*

We consider first the nonextreme asymmetric competition with growth function

$$\lambda(x, \nu) = f(x)\frac{R}{x} e^{-N} \sum_{L=0}^{\infty} \frac{1}{L!} \int \cdots \int \frac{c(x)}{c(x) + \sum_{i=1}^{L} c(y_i)} \nu(dy_1) \cdots \nu(y_L). \tag{5.19}$$

This expression is a product of two power series of type (3.19), as the factor $e^{-N} = e^{-\int n(dx)}$ itself can also be expressed in such a form. Both series are absolutely convergent. Consequently, the product can be re-expressed into a single series of type (3.19) by the Cauchy rearrangement. The continuity of the function $c(x)$ and the convergence ensured by the factors $1/L!$ makes sure that the conditions of Theorem 1 are met and the interaction operator of the nonextreme asymmetric model version is compact. This is consistent with the finding of [18] that the nonextreme asymmetric version of the model does not support continuous coexistence.

Otherwise, the interaction operator of the extreme asymmetric model is noncompact, as functions b^L are not continuous in this case. This is in line with the fact that a continuous set of strategies can (robustly) coexist in this version of the model [13]. Similarly to the case of Roughgarden's example, the noncompact interaction operator, which allows robust continuous coexistence, represents a biologically unfeasible assumption. In reality, one cannot expect that an arbitrarily small difference in seed-size decides the outcome of competition unequivocally.

6. Discussion

One of the most elementary facts of biology is that discreteness of the species is the rule and continuity between them is the exception. There are three potential explanations for this, none of them is sufficiently clear [30]:

1. Each species corresponds to a different peak of the fitness landscape.
2. Limiting similarity, that is, each species is adapted to a distinct ecological niche.
3. Separation between species is related to the genetics of sexual reproduction.

Maynard Smith & Szathmáry [30] disregard Explanation 2 because of Roughgarden's example of continuous coexistence. We have shown that this model is structurally unstable, so it is biologically irrelevant. We argue, that ecology itself dictates the discreteness of coexisting strategies.

In most biologically relevant cases, the strategy space is compact. This can be interpreted as the very extreme strategies being nonviable. Then, the principle of limiting similarity makes it plausible to suppose that only a finite number of strategies can coexist robustly because an infinite subset of a compact set necessarily has an accumulation point and hence there will be arbitrarily similar strategies present. Indeed, Theorem 4 guarantees just this.

The Lotka-Volterra competition model, defined on the whole real line via an interaction operator of convolution type, was discussed separately. We showed that coexistence is sensitive to perturbations oscillating with high frequency along the strategy axis. Consequently, coexistence of a continuum of strategies cannot be robust. Moreover, we showed that the existence of a limit point in the support of the strategy distribution is enough to destroy the possibility of robust coexistence. This latter conclusion is, again, in line with the concept of limiting similarity. In our last theorems, we studied coexistence of an infinite number of equidistant strategies on the real line. Because the strategies in this case are well separated the principle of limiting similarity does not exclude the possibility of an infinity of robustly coexisting species. Still, the coexistence of infinitely many strategies is sensitive to infinitesimal perturbation if the total population size is finite. The intuitive reason is that in this case the majority of the strategies are present in very small numbers. However, with the real line as strategy space it makes sense to consider infinite populations and for these the above intuitive argument does not apply. And indeed, we showed that robust coexistence of infinitely many discrete strategies is possible for infinite populations.

Beyond the ecological problem of limiting similarity and Roughgarden's counterexample, our investigation was motivated by the work of Sasaki & Ellner [37] and by the seed-size model of Geritz [13] and Geritz et al. [18]. Sasaki & Ellner [37] considered mixed strategies in a fluctuating environment. Their criterion for ESS mixing distribution is similar to the equilibrium condition (4.14), so their results are comparable to ours. Similarly to our Theorem 7, they used the uniqueness theorem of analytic functions to establish the discreteness of coexistence. The method of [37] was applied to investigate the spatial distribution of plants by Sasaki [36] and to establish the discreteness in a special form of Lotka-Volterra competition by Metz et al. [33]. While the nonlinear seed-size model is beyond the reach of the approach of [37], it behaves similarly: only a degenerate version of the model supports continuous coexistence. We provided the unifying view-point by requiring robustness of coexistence and extended the results of Sasaki & Ellner [37] to a much larger class of models, including models with nonlinear interaction operators.

Haccou and Iwasa [19] considered a model similar to the one of Sasaki & Ellner [37] and investigated the cases with continuous ESS strategy distribution. In response to the work of Sasaki & Ellner [37], they proved that the ESS distribution of the strategies changes continuously in the weak* sense with respect to the parameter changes. That is, despite the fact that the continuous distribution is nongeneric, it approximates meaningfully the discrete distributions appearing near to the continuous case. While we did not investigate this, it is natural to suppose that such kind of continuity generalizes to the nonlinear case, as well. On the other hand, as similar strategies can coexist only in a narrow rage of parameters, the gap between the coexisting strategies should increase with increasing perturbation of r_0.

The assumptions of a constant environment and a steady state of the population dynamics played a central role in our investigation. Armstrong & McGehee [6] and Abrams [2] emphasized the principle of competitive exclusion is violated if attractors other than steady states are allowed. On the other hand, Levins [25], Kisdi & Meszéna [22] generalized the concept of "limiting factors" to stationarily fluctuating environments by including the statistical moments into the consideration, so it is appealing to suppose that nongenericity of continuous coexistence generalizes also to stationarily fluctuating situations.

The current paper concentrates on the ecological side of the discreteness problem of a species. Undoubtedly, the full picture should include the genetical aspects, as well. In [34] A. Noest investigated the problem of a "sexual continuum", that is, whether coexistence of a continuum of genotypes is stable or not when partial reproductive isolation is supposed. We should warn that this model, which allows for continuous coexistence for asexual populations, is structurally unstable. The problem is worth being re-investigated.

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