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Abstract

We study a model of competition for resource through a chemostat-type model where species consume the common resource that is constantly supplied. We assume that the species and resources are characterized by a continuous trait. As already proved, this model, although more complicated than the usual Lotka-Volterra direct competition model, describes competitive interactions leading to concentrated distributions of species in continuous trait space.

Here we assume a very fast dynamics for the supply of the resource and a fast dynamics for death and uptake rates. In this regime we show that factors that are independent of the resource competition become as important as the competition efficiency and that the direct competition model is a good approximation of the chemostat.

This is performed through asymptotic analysis, introducing different scales for the resource renewal rate and the uptake rate. The mathematical difficulty relies in a possible initial layer for the resource dynamics.

The chemostat model comes with a global convex Lyapunov functional. We show that the particular form of the competition kernel derived from the uptake kernel, satisfies a positivity property which is known to be necessary for the direct competition model to enjoy the related Lyapunov functional.

Key-Words: Ecological competition for resource; Direct competition; Multiscale analysis; Lyapunov functional, Adaptive dynamics.

Mathematics Subject Classification: 34E13, 35K57, 47G20, 92D15, 92D40

1 Introduction

Evolutionary origin of species diversity has been one of the most important problems in evolutionary ecology. Individuals with similar traits (e.g. body size or shape) face strong competition, which might lead to the adaptive radiation. As a model of such competition-driven speciation, several theoretical studies have shown that the species distribution in continuous trait space will often evolve toward single peak or multiple peaks that are distinct from each other (see [18, 10, 8, 17, 13, 16]). Although many

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previous results are derived from a simple model that assumes direct species competition of Lotka-Volterra type, competitive interaction among species generally occurs in competition for resource such as prey or nutrient. For example, birds with similar beak shapes are in competition because they utilize similar food resource. Another example is found in ecological stoichiometry where consumer species with similar C:N:P (carbon: nitrogen: phosphorus ratio) requirements experience competition for nutrient supply with their optimal C:N:P ratio (see [19]). Thus, the competitive interaction should be modeled not directly but implicitly through the resource.

Recently, we have proposed such a mechanistic model of species competition where species (with continuous trait) compete for common resource (which is characterized by another continuous trait) which is constantly supplied (chemostat-type model). We have shown that evolutionary branching, which is parallel to adaptive radiation, is possible in this chemostat-type model as well, supporting the results previously obtained by direct competition models.

In order to faithfully capture the dynamics of species competition, a detailed mechanism such as species-resource dynamics should be explicitly modeled. On the other hand, specifying a particular mechanism narrows the applicability of a model. This is why conceptual and simple Lotka-Volterra type models of direct competition are widely and intensively studied. Then a natural question arises: Can we reduce a species-resource dynamics model into a Lotka-Volterra model? If so, how are parameters (e.g., intrinsic growth rates, competition coefficients) determined by those of the original mechanistic model? The last question is interesting particularly when we think of a direct competition model in continuous trait space. If we naively assume a Gaussian function as competition kernel, then it promotes the coexistence of infinitely many species (continuous distribution over continuous trait axis). But as soon as the kernel deviates from Gaussian, the evolution toward single or multiple peaks occurs, which is parallel to the emergence of distinct species [12]. The importance of this established result would increase if the conversion of resource-consumption kernel into direct-competition kernel does not guarantee that a Gaussian function is converted into another Gaussian function.

This paper aims the reduction of a mechanistic model of species-resource dynamics to more conceptual model of direct species competition. In Section 2, we describe our chemostat model of species-resource dynamics and a brief summary of our reduction result. Section 3 is devoted to a rigorous description of this result and the proof. In section 4, we extend our result to include a system with mutation. In section 5, we study the Lyapunov functional property which is useful for evolutionary stability analysis. In section 6, we show some numerical examples to study how the reduced dynamics approximates the original dynamics.

2 Model and a brief summary of the results

In general, creatures require several different resource to survive and reproduce. Some resource might be in a strong competition with others, some resource might be sufficiently supplied, and some resource might not be in competition at all. In case of phytoplankton species, resources are light and nutrients. Although tremendous amount of light is supplied from the sun, the competition for light still exists. Nutrient supplied from the bottom is also a limiting resource, and this dynamics might have much slower timescale compared to the competition for light (but slower dynamics do not imply less importance). There might exist some features that determine growth or death rates independently of resource competition.

Inspired by such phytoplankton ecology, our mechanistic model for a chemostat with continuous resource supply and continuous consumer population trait is given by

$$\begin{cases} \frac{\partial}{\partial t} n(x,t) = n(x,t)\big[b(x) - d(x) + \int K(x,y)R(y,t)dy\big], \\ \frac{\partial}{\partial t} R(y,t) = m(y)\big[R_{\text{in}}(y) - R(y,t)\big] - R(y,t)\int K(x,y)n(x,t)dx, \end{cases} \tag{1}$$

where $n(x,t) \geq 0$ is consumer species density with trait $x \in \mathbb{R}$ and $R(y,t) \geq 0$ is the common resource density with trait $y \in \mathbb{R}$. We assume that a death rate $d(x)$ depends on species trait x. Reproduction rate consists of two parts: $b(x)$ denotes a basic reproduction rate independent of the competition for the common resource, and $\int K(x,y)R(y,t)dy$ denotes a reproduction rate coming from consuming the common resource R. The resource R is supplied into the system with a rate $m(y)$ so that $R(y,t)$ approaches $R_{\text{in}}(y) > 0$. These drive the system (a chemostat type model). Consumption for resource is denoted by a trait dependent uptake kernel $K(x,y) \geq 0$ that defines how species with trait x depends on resource with trait y.

All coefficients $(b(x), d(x), K(x,y), m(y), R_{\text{in}}(y)$; although they are functions of traits, we call them 'coefficients') can play an important role in the full system. Since we are interested in the reduction of this model to a direct-competition model, we hereafter consider some limiting situation. We assume that the dynamics has the following three different time scales.

- *Very fast dynamics for the common resource supply.* This imposes that, in the absence of consumer species, resource distribution R approaches R_{in}.
- *Fast dynamics for resource-consumption and the resulting reproduction and death.* This implies that competition for the common resource is a primary factor for the growth of consumer species population.
- *Slow dynamics.* Population dynamics of n is also affected by a basic reproduction rate $b(x)$ and a death rate $d_{\text{slow}}(x)$, both of which are independent of the common resource.

In order to include these assumptions in the equations, we scale accordingly the coefficients

- m is of order ε^{-2},
- K and d are of order ε^{-1},
- $d(x) = \frac{1}{\varepsilon}\int K(x,y)R_{\text{in}}(y,t)dy + d_{\text{slow}}(x)$,
- $a(x) = b(x) - d_{\text{slow}}(x)$.

A death rate must be sufficiently large to counterbalance fast growth based on resource-consumption (otherwise, the population will grow infinitely). For this purpose, in the third equation, we divide a death rate into two parts. The first term represents fast dynamics for death events that compensates fast resource-consumption. The second term, $d_{\text{slow}}(x)$, represents the remaining slow dynamics for death events independent of the competition for resource.

These result in a new formulation of (1) that is written as

$$\begin{cases} \frac{\partial}{\partial t} n_\varepsilon(x,t) = n_\varepsilon(x,t)\big[a(x) + \frac{1}{\varepsilon}\int K(x,y)\big(R_\varepsilon(y,t) - R_{\text{in}}\big)dy\big], \\ \frac{\partial}{\partial t} R_\varepsilon(y,t) = \frac{m(y)}{\varepsilon^2}\big[R_{\text{in}}(y) - R_\varepsilon(y,t)\big] - \frac{1}{\varepsilon}R_\varepsilon(y,t)\int K(x,y)n_\varepsilon(x,t)dx, \end{cases} \tag{2}$$

where new coefficients satisfy $m = O(1)$, $K = O(1)$, and $a = O(1)$.

We complement the system with initial data

$$n_\varepsilon(0,x) = n^0(x) \geq 0, \qquad R_\varepsilon(0,y) = R^0(y) \geq 0,$$

As the very fast and fast dynamics become infinitely fast, R should approach R_{in}, but it is not clear which distribution n should approach. When R is not close to R_{in}, the reproduction based on resource-consumption is dominant (fast dynamics with order ε^{-1}) so the dynamics of n is primarily determined by $R - R_{\text{in}}$. However, as $R - R_{\text{in}}$ approaches to zero, resource-dependent reproduction might become no longer dominant.

In this paper, we will show that an approximation of this dynamics is given by the direct competition model

$$\frac{\partial}{\partial t} n(x,t) = n(x,t)\big[a(x) - \int c(x,x')n(x',t)dx'\big], \tag{3}$$

where the binary competition kernel $c(x,x')$ is related to the coefficients in (2). We will show that it is given by

$$c(x,x') = \int K(x,y)\frac{R_{\text{in}}(y)}{m(y)}K(x',y)dy.$$

This equation can be seen as a conversion formula of kernels. The reduced competition-kernel $c(x,x')$ is very sensitive to $R_{\text{in}}(y)/m(y)$ as well as to resource-consumption kernel $K(x',y)$, but not to $R_{\text{in}}(y)$ or $m(y)$ separately. Note that this kernel is of order one (recall that resource-consumption kernel is of order ε^{-1} before rescaling) so the reduced direct competition model describes the slow dynamics of $n(x,t)$. We will later show that the inclusion of mutation in consumer species' trait does not essentially change the result.

One biologically interesting point of the equation (3) is that the growth rate of consumer species in the absence of competition for resource, which is described by $a(x)$, still has considerable effect on the long-term dynamics of consumer distribution n. This is because as R becomes very close to R_{in}, the dominant factor (fast dynamics) becomes weaker and a basic growth rate $a(x)$ becomes as important as the competition for resource. In this limit, we recover a Lotka-Volterra type competition dynamics from a mechanistic model of a chemostat type. It is natural that we do not have the reduced dynamics of the resource, R, because the reduction is possible when the detailed dynamics of the resource can be neglected and when the effects of competition for the resource can be put into the new competition coefficients in a Lotka-Volterra type system (i.e. $c(x,x')$).

Another question of our interest is whether a Gaussian uptake kernel $K(x,y)$ is converted to another Gaussian kernel of direct competition $c(x,x')$. This is not necessarily true. Take

$$K(x,y) = e^{-\alpha(x-y)^2}, \qquad R_{\text{in}}(y) = e^{-\beta y^2}, \qquad m(y) \equiv 1.$$

Then, choosing γ such that $\gamma(2\alpha+\beta) = \alpha^2$ so as to complete a square in the expression

$$\begin{aligned} c(x,x') &= e^{-[\alpha x^2 + \alpha(x')^2 - \gamma(x+x')^2]} \int e^{-[(2\alpha+\beta)y^2 - 2\alpha(x+x')y + \gamma(x+x')^2]}dy \\ &= e^{-[\alpha x^2 + \alpha(x')^2 - \gamma(x+x')^2]} \sqrt{\tfrac{\pi}{2\alpha+\beta}}, \end{aligned}$$

we find that $c(x,x')$ is not gaussian because it is proportional to

$$e^{-[\alpha x^2 + \alpha(x')^2 - \gamma(x+x')^2]} \neq e^{-(\alpha-\gamma)(x-x')^2} \qquad \text{when } \beta \neq 0.$$

Mathematically rigorous notations and results will follow in the next three sections. Section 3 is devoted to a rigorous derivation of this result. It goes through asymptotic analysis and compactness estimates that allow us to show that n_ε converges to n and thus n is the population density. In other words our theory is not a perturbation analysis on n_ε while it is on $R_\varepsilon \approx R_{\rm in}$. Mutations are not included in the model equations (1)–(3). In section 4, we show how to include them and which new rescaling this leads to perform. Another remarkable property of the chemostat is the Lyapunov functional property already used in [16]. The asymptotic form of this Lyapunov functional is related to that for the direct competition model in section 5 and in particular we explain why, in this context, the corresponding operator is always nonnegative.

3 Derivation of the direct competition

In order to state our result we need some assumptions

$$n^0,\ R^0,\ R_{\rm in} \in L^1\cap L^\infty(\mathbb{R}), \qquad \int |\frac{\partial}{\partial x} n^0|\,dx \le C_1, \tag{4}$$

$$a_M := \|a\|_\infty < \infty, \qquad \underline{m} = \min m > 0, \qquad \overline{m} = \max m < \infty, \tag{5}$$

$$K \in BUC(\mathbb{R}\times\mathbb{R})^1, \qquad K_M := \sup_{x,y} K(x,y) < \infty, \tag{6}$$

$$|\frac{\partial}{\partial x}K(x,y)| \le C_2, \qquad |\frac{\partial}{\partial x}a(x)| \le C_3. \tag{7}$$

With these in mind, we establish that the limiting problem for (2) is the direct competition model

Proposition 3.1 *As ε tends to 0 in (2), R_ε converges strongly to $R_{\rm in}$ in $L^1\big((0,T)\times\mathbb{R}\big)$ and n_ε converges strongly in $C\big(\mathbb{R}^+;L^1(\mathbb{R})\big)$ to n, the solution to (3) with the initial data n^0 and the competition kernel*

$$c(x,x') = \int K(x,y)\frac{R_{\rm in}(y)}{m(y)}K(x',y)dy. \tag{8}$$

It is more technical to improve the space-time convergence on R_ε. Indeed it leaves place for an initial layer which is needed because, in general, its limit $R_{\rm in}$ is incompatible with the initial data R^0_ε.

Proof. To begin with, we re-write the equation on R_ε in (2) as

$$R_\varepsilon(y,t) - R_{\rm in}(y) = -\varepsilon\frac{R_\varepsilon(y,t)}{m(y)}\int K(x,y)n_\varepsilon(x,t)dx \;-\; \frac{\varepsilon^2}{m(y)}\frac{\partial}{\partial t}R_\varepsilon(y,t).$$

We inject this to compute the growth rate for n_ε

$$\frac{1}{\varepsilon}\int K(x,y)\big(R_\varepsilon(y,t)-R_{\rm in}\big)dy = -\int K(x,y)\frac{R_{\rm in}(y,t)}{m(y)}\int K(x',y)n_\varepsilon(x',t)dx'dy + I_\varepsilon(x,t)$$

$$= -\int c(x,x')n_\varepsilon(x',t)dx' + I_\varepsilon(x,t),$$

as we use $c(x,x')$ as defined in (8) and with

$$I_\varepsilon(x,t) = -\varepsilon\frac{\partial}{\partial t}\int \frac{K(x,y)}{m(y)}R_\varepsilon(y,t)dy + \int K(x,y)\frac{R_{\rm in}(y)-R_\varepsilon(y,t)}{m(y)}\int K(x',y)n_\varepsilon(x',t)dx'dy.$$

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[1] Linear space of Bounded Uniformly Continuous functions

Therefore the equation on n_ε can also be written

$$\frac{\partial}{\partial t} n_\varepsilon(x,t) = n_\varepsilon(x,t)\Big[a(x) - \int c(x,x')n_\varepsilon(x',t)dx' + I_\varepsilon(x,t)\Big]. \tag{9}$$

Throwing away the terms in ε, we find formally (3).

To justify rigorously this limit, we need (i) estimates for compactness, (ii) explain how we can pass to the limit.

(i) Estimates. First notice that we have

$$0 \leq R_\varepsilon(y,t) \leq R_M(y) := \max(R^0, R_{\text{in}}) \in L^1 \cap L^\infty(\mathbb{R}).$$

Next, we define and write from the equation on R_ε in (2)

$$M_\varepsilon(t) := \int n_\varepsilon(x,t)dx, \qquad N_\varepsilon(t) := \int |R_\varepsilon(y,t) - R_{\text{in}}(y)|dy,$$

$$\frac{d}{dt}N_\varepsilon(t) + \frac{\underline{m}}{\varepsilon^2}N_\varepsilon(t) \leq \frac{\|R_M(\cdot)\|_\infty}{\varepsilon}K_M M_\varepsilon(t).$$

And from the equation on n_ε in (2), we deduce

$$|\frac{d}{dt}M_\varepsilon(t)| \leq a_M M_\varepsilon(t) + \frac{K_M}{\varepsilon}N_\varepsilon(t).$$

It follows from these two differential inequalities that $M_\varepsilon(t)$, $\varepsilon N_\varepsilon(t)$ and $\frac{1}{\varepsilon}\int_0^t N_\varepsilon(s)ds$ are uniformly bounded in ε on each time interval $[0,T]$ by a constant denoted by M_T. One step further, from the bound on M_ε and from the equation on N_ε, one also concludes that

$$\frac{N_\varepsilon(t)}{\varepsilon} \leq \frac{N(0)}{\varepsilon}e^{-\underline{m}t/\varepsilon^2} + \frac{\|R_M(\cdot)\|_\infty}{\underline{m}}K_M M_T, \qquad \forall t \in [0,T]. \tag{10}$$

(ii) Compactness in t. From this, and going back to the equation on n_ε, we conclude that, still for $t \in [0,T]$

$$\int \left|\frac{\partial n_\varepsilon(x,t)}{\partial t}\right| dx \leq a_M C(T) + K_M\frac{N(0)}{\varepsilon}e^{-\underline{m}t/\varepsilon^2} + K_M C(T). \tag{11}$$

This gives us that n_ε is uniformly equicontinuous in $C\big((0,T);L^1(\mathbb{R})\big)$.
(iii) Compactness in x. Dividing equation (2) by n_ε and differentiating in x, we find

$$\frac{\partial^2}{\partial x \partial t}\ln n_\varepsilon(x,t) = \frac{\partial}{\partial x}\,a(x) + \frac{1}{\varepsilon}\int \frac{\partial}{\partial x}\,K(x,y)\ \left(R_\varepsilon(y,t) - R_{\text{in}}(y)\right)dy.$$

From (7) and (10) we obtain that, for some constant D_1

$$|\frac{\partial^2}{\partial x \partial t}\ln n_\varepsilon(x,t)| \leq D_1.$$

It follows that

$$|\frac{\partial}{\partial x}\ln n_\varepsilon(x,t)| \leq |\frac{\partial}{\partial x}\ln n^0(x)| + D_1 t,$$

$$\int |\frac{\partial}{\partial x} n_\varepsilon(x,t)| dx \leq \int \frac{|\frac{\partial}{\partial x} n^0(x)|}{n^0(x)} n_\varepsilon(x,t)\, dx + D_1 t \int n_\varepsilon(x,t) dx.$$

Moreover, from the first equation of (2) and (10) we obtain that, for some constant D_2,

$$|\frac{\partial}{\partial t} \ln n_\varepsilon(x,t)| \leq D_2,$$

and thus: $\ln n_\varepsilon(x,t) \leq \ln n^0(x) + D_2 t$, which gives

$$\frac{n_\varepsilon(x,t)}{n^0(x)} \leq \exp(D_2 t).$$

Using the above arguments and (4), we conclude that, for some constant $D(T)$ and $0 \leq t \leq T$,

$$\int |\frac{\partial}{\partial x} n_\varepsilon(x,t)|\, dx \leq \exp(D_2 t) \int |\frac{\partial}{\partial x} n^0(x)|\, dx + D_1 t \int n_\varepsilon(x,t) dx \leq C_1 \exp(D_2 t) + D_1 t M_\varepsilon(t) \leq D(T).$$

Using this and step (ii) we conclude from the Arzela-Ascoli Theorem that, after extracting a subsequence, n_ε converges in $C\big((0,T); L^1(\mathbb{R})\big)$.

(iv) Passing to the limit. It remains to pass to the weak (distribution) limit in the equation on n_ε written as (9). Because of the strong convergence of n_ε and (10), the only difficulty is to pass to the limit in the term

$$\begin{aligned} \varepsilon n_\varepsilon(x,t) \frac{\partial}{\partial t} \int \frac{K(x,y)}{m(y)} R_\varepsilon(y,t) dy = {} & \varepsilon \frac{\partial}{\partial t} \big[n_\varepsilon(x,t) \int \frac{K(x,y)}{m(y)} R_\varepsilon(y,t) dy \big] \\ & - \varepsilon \int \frac{K(x,y)}{m(y)} R_\varepsilon(y,t) dy \frac{\partial}{\partial t} n_\varepsilon(x,t). \end{aligned}$$

The first term converges weakly to 0 (multiplying by a test function, after integration by parts all the terms are bounded and multiplied by ε). For the second term, we use the estimate (11) to reach the conclusion that it converges in L^1 to 0, thanks again to the multiplying factor ε.

Since uniqueness of weak solutions for the direct competition model is proved in [8], we conclude that the full family n_ε converges and not only subsequences. □

4 Mutations

In the present context of population equations structured by a physiological trait, there are several possibilities to represent mutations that have been widely used [3, 10, 8]. Integral oprators or diffusion operators can be derived from stochastic individual based models; see for instance [5, 6]. Mathematically they have many similar properties, in particular asymptotic analysis can be carried out using similar methods in the regime of small mutations for a long time of observation leading to speciation phenomena [2, 1, 14] although stochastic individual methods are also used for the same purpose [4, 7, 15].

Here, we restrict ourselves to representing the mutations by a diffusion operator with intensity μ^2, a very small rate. According to the mathematical theory in [10, 17], it is natural to rescale time so that the new timescale unit is $1/\mu$, very long timescale compared to the original 'generation' timescale. This leads to the competition model with mutations

$$\begin{cases} \mu \frac{\partial}{\partial t} n_\varepsilon(x,t) = n_\varepsilon(x,t)\big[a(x) + \frac{1}{\varepsilon}\int K(x,y)\big(R_\varepsilon(y,t) - R_{\text{in}}\big)dy\big] + \mu^2 \Delta n_\varepsilon, \\ \mu \frac{\partial}{\partial t} R_\varepsilon(y,t) = \frac{m(y)}{\varepsilon^2}\big[R_{\text{in}}(y) - R_\varepsilon(y,t)\big] - \frac{1}{\varepsilon} R_\varepsilon(y,t)\int K(x,y) n_\varepsilon(x,t)dx, \end{cases} \tag{12}$$

Because both the uptake rate ε and the mutation rate μ can be considered as small, it is interesting to see how the solutions behave in the different regimes of smallness.

We can formally follow the lines of the analysis in section 3 and find direct competition with mutations as the limit of infinitely fast uptake rate

$$\mu \frac{\partial}{\partial t} n(x,t) = n(x,t)\big[a(x) - \int c(x,x')n(x',t)dx'\big] + \mu^2 \Delta n. \tag{13}$$

One can also consider the small mutation rate and, assuming the initial data is well prepared, use the Hopf-Cole unknowns

$$u_\mu = \mu \ln(n_\varepsilon), \qquad u_\mu^0 = \mu \ln(n^0).$$

This leads now to study the equation on the limit $u_\varepsilon(x,t)$ of $u_\mu(x,t)$ and on the limit measure n_ε as $\mu \to 0$. Following [10, 17], one finds the constrained Hamilton-Jacobi equation

$$\begin{cases} \frac{\partial}{\partial t} u_\varepsilon = a(x) + \frac{1}{\varepsilon}\int K(x,y)\big(R_\varepsilon(y,t) - R_{\text{in}}\big)dy + |\frac{\partial u_\varepsilon}{\partial x}|^2, \qquad \max_{x\in\mathbb{R}} u_\varepsilon(x,t) = 0 \quad \forall t \geq 0, \\ \frac{m(y)}{\varepsilon^2}\big[R_{\text{in}}(y) - R_\varepsilon(y,t)\big] - \frac{1}{\varepsilon} R_\varepsilon(y,t)\int K(x,y)n_\varepsilon(x,t)dx = 0, \end{cases}$$

and n_ε is supported in the zeroes of u_ε (usually points).

This can be further analyzed in the regime ε small and leads to

$$\frac{\partial}{\partial t} u = a(x) + \int c(x,x')n(x',t)dx' + |\frac{\partial u}{\partial x}|^2, \qquad \max_{x\in\mathbb{R}} u(x,t) = 0 \quad \forall t \geq 0,$$

still with the information that the measure $n(t)$ is supported by the points where $u(t)$ vanishes. This is also the limit of (13) in the regime of small μ.

We can conclude that the analysis of small mutations, both for the chemostat model and the direct competiton model, is compatible with the multiscale analysis in section 3 that relates both models. This is the regime of interest that we choose later in section 6 for numerical illustration. In this regime, we recover also, at a populational level, the results of standard adpative dynamics [11, 9] and the references therein.

5 Lyapunov functionals for the two competition models

The large time behaviour of solutions to (2) has been studied in [16]. It is proved that steady states cannot be globally positive $(\overline{n}_\varepsilon, \overline{R}_\varepsilon)$ and they have to be either Dirac masses (speciation) or continuous with a support of n_ε that is small enough (except when the solution goes extinct that might happen if renewal/death rates are too high). When continuous, the steady state globally attracts all trajectories if they satisfy a particular sign property characterized the so-called *Evolutionary Stable Distribution*

(ESD in short), a notion that we recall below. The proof relies on a Lyapunov functional which has also been proved to exist for the direct competition model in [13] under the condition of positivity of a certain operator.

Our interest here is to understand the relation between the two Lyapunov functionals, for (2) and (3), and to understand why the operator positivity condition is important for Direct Competition but does not appear in the Competition for Resources.

We first recall that an ESD is defined as

Definition 5.1 (Evolutionary Stable Distribution for (3), **[13])** *A nonnegative bounded measure* $\overline{n}$ *is called an ESD for the direct competition equation* (3)

$$a(x) - \int c(x,x')\overline{n}(x')dx' = 0 \qquad \forall x \in \operatorname{Supp} \overline{n}, \tag{14}$$

$$a(x) - \int c(x,x')\overline{n}(x')dx' \le 0 \qquad \forall x \in \mathbb{R} \setminus \operatorname{Supp} \overline{n}. \tag{15}$$

Definition 5.2 (Evolutionary Stable Distribution for (2), **[13, 16])** *A state is* $(\overline{n}_\varepsilon, \overline{R}_\varepsilon)$ *is called an ESD for the competition for resources equation* (2) *if* $\overline{n}_\varepsilon$ *is a nonnegative bounded measure and*

$$a(x) + \frac{1}{\varepsilon}\int K(x,y)[\overline{R}_\varepsilon(y) - R_{\text{in}}]dy = 0 \qquad \forall x \in \operatorname{Supp} \overline{n}_\varepsilon, \tag{16}$$

$$a(x) + \frac{1}{\varepsilon}\int K(x,y)[\overline{R}_\varepsilon(y) - R_{\text{in}}]dy \le 0 \qquad \forall x \in \mathbb{R} \setminus \operatorname{Supp} \overline{n}_\varepsilon, \tag{17}$$

$$\frac{m(y)}{\varepsilon}[\overline{R}_\varepsilon(y) - R_{\text{in}}(y)] = \overline{R}_\varepsilon(y)\int K(x,y)\overline{n}_\varepsilon(x)dx \qquad \forall y \in \mathbb{R}. \tag{18}$$

For an ESD and following [16], we define the Lyapunov functional for the model of competition for resources as

$$S_{cr}(t) = -\int \overline{n}_\varepsilon(x)\ln n_\varepsilon(x,t)dx - \int \overline{R}_\varepsilon(y)\ln R_\varepsilon(y,t)dy + \int n_\varepsilon(x,t)dx + \int R_\varepsilon(y,t)dy.$$

The dissipation associated with this functional is given by the inequality

$$\begin{aligned} \frac{dS_{cr}}{dt}(t) := D_{cr}(t) = \; & -\int \frac{m(y)R_{\text{in}}(y)}{\varepsilon^2\overline{R}_\varepsilon(y)\;R_\varepsilon(y,t)}\left(\overline{R}_\varepsilon(y) - R_\varepsilon(y,t)\right)^2 dy \\ & + \int n_\varepsilon(x,t)\left(a(x) + \tfrac{1}{\varepsilon}\int K(x,y)[\overline{R}_\varepsilon(y) - R_{\text{in}}(y)]dy\right)dx \le 0. \end{aligned} \tag{19}$$

Because we expect that, according to the proof of Theorem 3.1, the expansion holds $R_\varepsilon(y,t) = R_{\text{in}}(y) + O(\varepsilon)$, the limiting Lyapunov functional is reduced (up to an additive constant) to

$$S_{dc}(t) = -\int \overline{n}(x)\ln n(x,t)dx + \int n(x,t)dx.$$

This is indeed the Lyapunov functional used in for direct competition but $\frac{d}{dt}S_{dc}(t)$ is negative only when a positivity condition holds true. This condition appears naturally in our framework because we can compute the dissipation associated with $S_{dc}(t)$

$$\frac{dS_{dc}}{dt}(t) := D_{dc}(t)$$

A direct computation of D_{dc} using (3) is of course also possible but is less instructive than an expansion in ε of D_{cr} that uses simply

$$\overline{R}_\varepsilon(y) = R_{\rm in}(y) - \frac{\varepsilon \overline{R}_\varepsilon(y)}{m(y)} \int K(x,y)\overline{n}_\varepsilon(x)dx.$$

In the limit $\varepsilon \to 0$, we obtain

$$\begin{aligned} D_{dc}(t) = \quad & -\int \tfrac{R_{\rm in}(y)}{m(y)} \left[\int K(x,y)\big(n(x,t)-\overline{n}(x)\big)\right]^2 dy \\ & + \int n(x,t) \Big(a(x) - \int K(x,y) \tfrac{R_{\rm in}(y)}{m(y)} \int K(x',y)\overline{n}(x')dx'dy \Big)\, dx. \end{aligned} \tag{20}$$

Using the expression of $c(x,x')$ in (8) yields the usual dissipation for the direct competition model

$$\begin{aligned} D_{dc}(t) = \quad & -\int\int c(x,x')\big(n(x,t)-\overline{n}(x)\big)\big(n(x',t)-\overline{n}(x')\big)dx\, dx' \\ & + \int n(x,t)\left(a(x) - \int c(x,x')\overline{n}(x')dx'\right) dx. \end{aligned}$$

The particular form of $c(\cdot,\cdot)$ in (8) makes that the integral with the quadratic term in $n - \overline{n}$ is always positive (we referred to that as operator positivity) and the definition of an ESS makes that the linear term also gives a nonpositive contribution.

6 Numerical illustration

How good is the approximation of competition through resources by direct competition? Beyond the pure theoretical statement in section 3, this can be illustrated thanks to some numerical simulations. We have performed such comparisons in the case with mutations given by (12). We assume that a resource uptake kernel and a distribution of resource supply are Gaussian. A trait-dependent (and competition-independent) growth rate takes the maximum at $x = 0$. We have used the coefficients given as follows

$$K(x,y) = \frac{1}{\sigma_K\sqrt{2\pi}} \exp(-\frac{(x-y)^2}{2\sigma_K^2}), \qquad R_{\rm in}(y) = \frac{M_{\rm in}}{\sigma_{\rm in}\sqrt{2\pi}} \exp(-\frac{y^2}{2\sigma_{\rm in}^2}), \qquad a(x) = 1 - x^2, \tag{21}$$

and $m(y)$ is taken as a constant. See section 2 for the converted kernel of direct competition. Throughout this section we have taken $\sigma_k = \sigma_{\rm in} = .5$, $\mu = 0.005$ and we vary ε, m and $M_{\rm in}$.

The initial data n^0 is a gaussian centered at -0.8, the mean variance is denoted by μ and R is initially chosen equal to $R_{\rm in}$. With all our choices of parameters, the solution is inititally monomorphic and undergoes a dimorphic branching. Then it stabilizes as depicted in Figure 1.

We first show how well approximated is the solution to (12) by that of (13). To do so, choose $m = M_{\rm in} = 1$ and choose two values of the parameter ε, namely $\varepsilon = .1$ and $\varepsilon = .001$. For $\varepsilon = .1$ equilibrium of resource $R \approx R_{\rm in}$ is not achieved since we obtained the relative error $\max \frac{|R-R_{\rm in}|}{R_{\rm in}} = .18$ but the case $\varepsilon = .001$ can be considered as the direct competition case since $\max \frac{|R-R_{\rm in}|}{R_{\rm in}} = .0018$. The population density are depicted in Figure 2 which show that the dimorphic situation is well kept in both solutions even though the total population is under estimated in the direct competition model

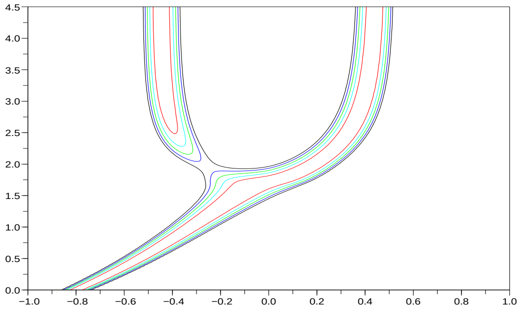

Figure 1: With our choice of parameters, the dynamics undergoes a branching from monomorphic to a dimorphic population. This figure depicts the typical isolines of the solution to (12) (horizontal axis is x, vertical axis is time).

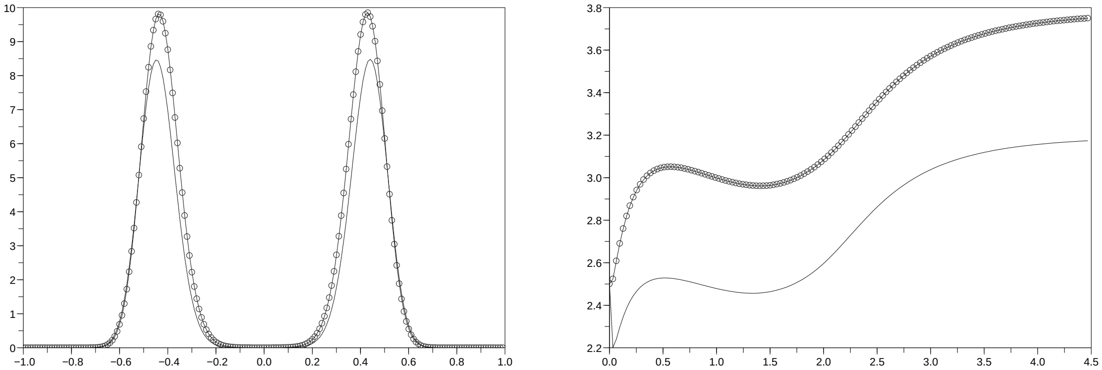

Figure 2: Comparisons between the model of competition for resources (dotted curve) and the direct competition model (continuous line). Left: the dimorphic population density as a function of the trait x for large times. Right: total population $\int n(x,t)dx$ as a function of time.

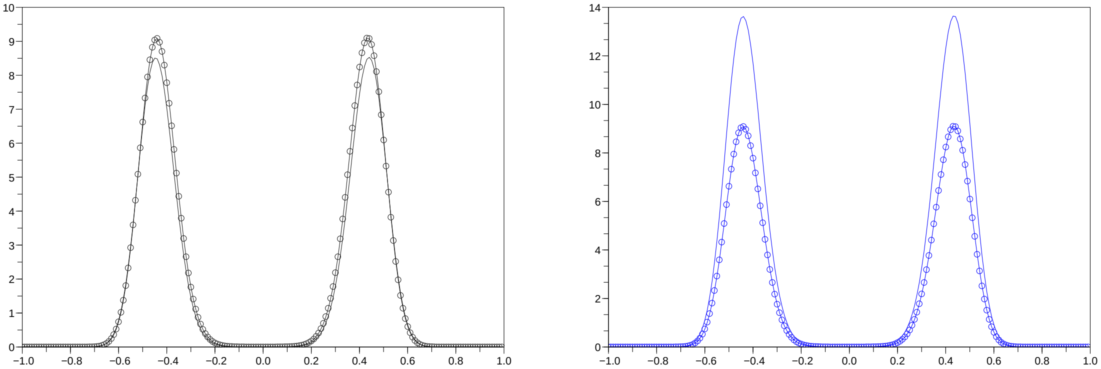

Figure 3: These figures illustrate that the direct competition kernel only depends upon on the ratio R_{in}/m and thus we can expect that the solutions to the model of competition for resource also does so. (Left) we compare for $\varepsilon = 0.05$, the population density solutions with $m = M_{\text{in}} = 1$ (dotted line) and with $m = M_{\text{in}} = 10$ (continuous line). (Right) we compare for $\varepsilon = 0.05$ the solutions with $m = M_{\text{in}} = 1$ (dotted line) and with $m = 1.5$, $M_{\text{in}} = 1$ (continous line). When the ratio is preserved (even though coefficients differ by a factor 10) the solutions are very close. But a small variation of the coefficients, that also changes the ratio, induces a visible difference on the solutions.

by a factor of approximately 25 percent.

The competition kernel (8) in the direct competition approximation has a remarkable property that it only depends upon the ratio R_{in}/m. Therefore we can expect that the solution to (12) depends only midly on this ratio. This is illustrated in Figure 3. We use the value $\varepsilon = 0.01$, and compare the solutions with two values of m and M_{in} and varying the ratio.

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