A Kolmogorov-type Competition Model with Finitely Supported Allocation Profiles and its Applications to Plant Competition for Sunlight

Dedicated to Avner Friedman on the occasion of his 75th birthday

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Abstract

A Kolmogorov-type competition model featuring species allocation profiles, gain functions, and cost parameters is examined. For plant species that compete for sunlight according to the Canopy Partitioning Model (R.R. Vance and A.L. Nevai, J. Theor. Biol. 245 (2007) 210–219), the allocation profiles describe vertical leaf placement, the gain functions represent rates of leaf photosynthesis at different heights, and the cost parameters signify the energetic expense of maintaining tall stems necessary for gaining a competitive advantage in the light gradient. The allocation profiles studied here, being supported on three alternating intervals, determine an "interior" species and an "exterior" species. It is shown that when the allocation profile of the interior species is singular (*i.e.*, a Dirac-delta function) then either competitive exclusion or coexistence at a single globally attracting equilibrium point occurs. However, if the allocation profile of the interior species is piecewise continuous or multi-singular (*i.e.*, a weighted sum of Dirac-delta functions) then multiple coexistence states may also occur. These results have important implications for big-leaf plants that compete for sunlight.

Keywords: Kolmogorov-type competition model, canopy partitioning model, plant competition, light competition, phytoplankton competition, vertical leaf profile, allocation profile, gain function

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1 Introduction

Consider two species ($i = 1, 2$) that obey the Kolmogorov-type competition model [21, 32]

$$\frac{dx_i}{dt} = x_i\gamma_i \left(\int_0^\infty \phi_i\big(\sigma_1 \mathtt{S}_1(z)x_1 + \sigma_2 \mathtt{S}_2(z)x_2\big)\mathtt{s}_i(z)\, dz - C_i \right), \quad i = 1, 2, \tag{1.1}$$

where $x_i(t)$ denotes the population density of species i at time $t \geq 0$; the allocation profile $\mathtt{s}_i(z)$ is a fixed probability density function defined for $z \geq 0$ with complementary cumulative distribution function $\mathtt{S}_i(z) = \int_z^\infty \mathtt{s}_i(\zeta)\, d\zeta$; the gain function $\phi_i(x)$ is a positive, continuously differentiable, and strictly decreasing function of $x \geq 0$ which approaches zero as $x \to \infty$; and γ_i, σ_i, and C_i are positive constants.

The system (1.1) describes the interactions of two clonal plant species which compete for sunlight by placing their leaves at multiple heights [21, 32]. For species i, its total leaf area is denoted by x_i, the vertical position of its leaves (*i.e.*, its vertical leaf profile) is indicated by $\mathtt{s}_i(z)$, the rate of photosynthesis performed by its leaves when shaded from above by cumulative leaf area x is given by $\phi_i(x)$, its leaf light extinction coefficient is σ_i, its growth constant is γ_i, and the energetic cost of maintaining its leaves, stems, and roots is represented by C_i. The growth and cost parameters γ_i and C_i in turn depend on close to a dozen primary plant parameters such as tissue mass, mean stem height, and tissue metabolic rate. For a complete description of these parameters and functions see [32].

The application of (1.1) to light competition is not limited to terrestrial plants only. For example, Weissing and Huisman [34] proposed earlier a related system of equations to model phytoplankton that compete for sunlight in a lake. Both models are members of a more general class of systems

$$\frac{dx_i}{dt} = x_i f_i(x_1, x_2), \quad i = 1, 2, \tag{1.2}$$

first introduced in 1936 by Kolmogorov [20]. Previous research on (1.2) has centered primarily on Hardin's [8] competitive exclusion principle [2, 15, 26], establishing conditions under which all species can persist [3, 7, 12, 14, 16, 18, 29], and the influence of horizontal spatial heterogeneity [4, 5, 17]. However, it is difficult to apply many of these results directly to (1.1) because the allocation profiles and gain functions combine in a complicated way to form the per-capita growth rate functions f_i in (1.2).

Furthermore, it is usually of greatest interest to establish the *manner* in which the allocation profiles and gain functions influence the outcome of competition in (1.1). Toward this end, it is known that

(i) if two species have rectangular (*i.e.*, uniform) allocation profiles which are supported on non-overlapping intervals then either competitive exclusion or coexistence at a single globally attracting equilibrium point occurs [21];

(ii) if two species have rectangular allocation profiles which are supported on non-nested intervals, and the species share a common gain function, then either competitive exclusion or coexistence at a single globally attracting equilibrium point occurs [21];

(iii) there exist pairs of species possessing rectangular allocation profiles and distinct gain functions such that multiple non-trivial equilibrium points occur [19];

(iv) there exist pairs of species, one with a rectangular allocation profile surrounded by a bi-rectangular allocation profile belonging to the other, such that multiple non-trivial equilibrium points occur, even when the two species share the same gain function [19];

(v) if two species possess rectangular allocation profiles, they share a common gain function, *and* there exists some $\tau > 0$ such that $\mathtt{s}_2(z) = \mathtt{s}_1(z - \tau)$ and $C_2 = C_1 + b\tau$, then the competitive ability of species 2 diminishes from dominant to compatible to inferior as the allocation difference τ increases [22].

In this paper, we examine the outcome of competition for pairs of species in which one allocation profile is surrounded by the other and at least one has finite support.

1.1 Asymptotic behavior

Given any nonnegative initial condition, a solution to (1.1) exists for all time, it is unique, and it always approaches some finite equilibrium within the closed first quadrant as $t \to \infty$ [13] (pp. 144 and 250). Thus, to determine the asymptotic behavior of the dynamical system, it suffices to restrict our attention to nullclines and their intersections with each other and with the coordinate axes. In general, the (non-trivial) nullcline $\mathcal{N}_i$ for species i is the set of all (x_1, x_2) in the closed first quadrant that satisfy the equation

$$\int_0^\infty \phi_i\big(\sigma_1 \mathtt{S}_1(z)x_1 + \sigma_2 \mathtt{S}_2(z)x_2\big)\mathtt{s}_i(z)\,dz = C_i. \tag{1.3}$$

So that $\mathcal{N}_i$ exists non-trivially, the inequality $\phi_i(0) > C_i$ must be satisfied. When this condition holds, we will say that species i is *viable.* We define the *trivial equilibrium* to be the origin $(0, 0)$, a *semi-trivial equilibrium* to be a point $(x_1^\dagger, 0)$ which lies on $\mathcal{N}_1$ or a point $(0, x_2^\dagger)$ which lies on $\mathcal{N}_2$, and a *non-trivial equilibrium* to be a point (x_1^*, x_2^*) inside the open first quadrant which lies on both $\mathcal{N}_1$ and $\mathcal{N}_2$. It is not difficult to see from (1.1) and (1.3) that the trivial equilibrium always exists, and that two semi-trivial equilibrium points also exist whenever both species are viable. Thus, our main results focus on the number (and stability) of non-trivial equilibrium points, and we will often drop the qualifier *non-trivial.*

1.2 Preliminary definitions

So that we may state our results precisely, we must first make some preliminary definitions. As in [32], we define $\phi_i(x)$ to be a gain function if it satisfies the following properties:

(P_1) ϕ_i is a continuously differentiable function of $x \geq 0$;
(P_2) $\phi_i(x) > 0$ for $x \geq 0$;
(P_3) $\phi_i'(x) < 0$ for $x \geq 0$;
(P_4) $\phi_i(x) \to 0$ as $x \to \infty$.

To denote that ϕ_i is a gain function, we will write $\phi_i \in \Pi$. A special case arises when ϕ_1 and ϕ_2 both have the particular form

$$\phi_i(x) = \varphi_i \left[\frac{I_{\text{in}}}{I_{\text{in}} + J_i \exp(\pi_i x)}\right] \tag{1.4}$$

for some positive constants φ_i, I_{in} (independent of i), J_i, and π_i [32]. When this occurs, we say that ϕ_1 and ϕ_2 are *in parametric form* and we write $(\phi_1, \phi_2) \in \mathcal{R}$. For situations in which parameters such as I_{in}, J_1, and J_2 are fixed *a priori* we will write $(\phi_1, \phi_2) \in \mathcal{R}(I_{\text{in}}, J_1, J_2)$.

Let $\mathcal{A}$ denote the set of all allocation profiles, that is, $\mathtt{s}(z) \in \mathcal{A}$ if and only if $\mathtt{s}(z)$ is nonnegative for $z \geq 0$ and $\int_0^\infty \mathtt{s}(z)\,dz = 1$. Let $\Omega_{\mathtt{s}}$ denote the support of a given $\mathtt{s}(z) \in \mathcal{A}$. For $0 < a < c < \infty$, we define the following parameterized subsets of $\mathcal{A}$:

(a) $M(a,c) = \{\mathtt{s}(z) \in \mathcal{A} : \Omega_{\mathtt{s}} \subseteq (a,c)\}$,

(b) $C(a,c) = \{\mathtt{s}(z) \in M(a,c) : \mathtt{s}(z)$ is piecewise continuous and everywhere finite$\}$,

(c) $B(a) = \{\mathtt{s}(z) \in \mathcal{A} : \Omega_{\mathtt{s}} = \{a\}\}$,

(d) $B(a_1, a_2, \ldots, a_m) = \{\mathtt{s}(z) \in \mathcal{A} : \Omega_{\mathtt{s}} = \{a_1, a_2, \ldots, a_m\}\}$,

(e) $U(a) \oplus O(c) = \{\mathtt{s}(z) \in \mathcal{A} : \Omega_{\mathtt{s}} \subseteq (0,a) \cup (c,\infty)$, $\Omega_{\mathtt{s}} \not\subseteq (0,a)$, and $\Omega_{\mathtt{s}} \not\subseteq (c,\infty)\}$,

(f) $B(a) \oplus O(c) = \{\mathtt{s}(z) \in \mathcal{A} : \Omega_{\mathtt{s}} \subseteq \{a\} \cup (c,\infty)$, $\Omega_{\mathtt{s}} \not\subseteq \{a\}$, and $\Omega_{\mathtt{s}} \not\subseteq (c,\infty)\}$.

Some comments are in order. First, these definitions are not mutually exclusive. For example, $B(2), C(1,3) \subset M(1,3)$. Second, if $\mathtt{s}(z) \in C(a,c)$ and $\mathtt{S}(z) = \int_z^\infty \mathtt{s}(\zeta)\, d\zeta$ then

$$\int_0^\infty \psi(\mathtt{S}(z))\mathtt{s}(z)\, dz = \int_0^1 \psi(\alpha)\, d\alpha$$

whenever $\psi(x)$ is a continuous function of $x \geq 0$. Third, $B(a)$ consists of a single Dirac-delta function, $\mathtt{s}(z) = \delta(z-a)$, and we will refer to allocation profiles of this form as *singular*. Observe that in this case

$$\int_0^\infty \psi(\mathtt{S}(z))\mathtt{s}(z)\, dz = \psi(1)$$

is independent of a. Fourth, if $\mathtt{s}(z) \in B(a_1, a_2, \ldots, a_m)$ then $\mathtt{s}(z) = \sum_{i=1}^m \ell_i \delta(z - a_i)$ for some positive parameters $\ell_1, \ell_2, \ldots, \ell_m$ satisfying $\ell_1 + \ell_2 + \cdots + \ell_m = 1$. These *multi-singular* profiles satisfy, upon suitable relabeling of $a_1, a_2, \ldots, a_m$,

$$\int_0^\infty \psi(\mathtt{S}(z))\mathtt{s}(z)\, dz = \sum_{i=1}^m \ell_i \psi(L_i),$$

where $L_i = \ell_1 + \ell_2 + \cdots + \ell_i$. Finally, if $\mathtt{s}(z) \in U(a) \oplus O(c)$ or $\mathtt{s}(z) \in B(a) \oplus O(c)$ then the allocation profile of the species has two arbitrary but non-trivial portions, one supported in $(0,a)$ or on $\{a\}$ and one in (c,∞). In the former case, we can write

$$\int_0^\infty \psi(\mathtt{S}(z))\mathtt{s}(z)\, dz = \int_0^{a^-} \psi(\mathtt{S}(z))\mathtt{s}(z)\, dz + \int_{c^+}^\infty \psi(\mathtt{S}(z))\mathtt{s}(z)\, dz.$$

A similar equation applies for the latter case, but with the first integral on the right-hand side replaced by $\psi(1)$.

In applications of the model to plant competition for sunlight, allocation profiles in $B(a)$ and $B(a_1, a_2, \ldots, a_m)$ represent, respectively, the situation in which a plant species places its leaves exclusively at a single height or at m different heights. For allocation profiles in $U(a) \oplus O(c)$, the intervals $(0,a)$ and (c,∞) represent the understory (U) and overstory (O), respectively.

1.3 Statement of the main results

Below, we will usually assume that

(i) the supports of the two species allocation profiles do not overlap, and

(ii) the support of the allocation profile belonging to species 2 surrounds the support of the allocation profile belonging to species 1 on both sides.

This happens, for example, when $\mathtt{s}_1(z) = B(a)$ and $\mathtt{s}_2(z) = U(a) \oplus O(a)$. In naming the theorems, we will also use notation such as "U–B–O" to denote the form of the corresponding pair of allocation profiles.

Our first main result concerns a situation in which $\mathtt{s}_1(z)$ is singular and $\mathtt{s}_2(z)$ is arbitrary but subject to conditions (i) and (ii) above.

Theorem 1 (U–B–O)**.** *Suppose that $\mathtt{s}_1(z) \in B(a)$ and $\mathtt{s}_2(z) \in U(a) \oplus O(a)$ with $a > 0$, and let $\phi_1, \phi_2 \in \Pi$ and $\sigma_1, \sigma_2, C_1, C_2 > 0$ be given. Then at most one non-trivial equilibrium point exists, and when one does exist, it is always globally asymptotically stable with respect to the open first quadrant. This same result also holds for $\mathtt{s}_2(z) \in M(0, a)$ or $\mathtt{s}_2(z) \in M(a, \infty)$.*

Our second main result concerns the case in which $\mathtt{s}_1(z)$ is piecewise continuous and finite and $\mathtt{s}_2(z)$ is bi-singular.

Theorem 2 (B–C–B)**.** *Let $\mathtt{s}_1(z) \in C(a, c)$ and $\mathtt{s}_2(z) \in B(a, c)$ with $0 < a < c < \infty$, and let $\sigma_1, \sigma_2, C_1, C_2 > 0$ be given. Then there exist $\phi_1, \phi_2 \in \Pi$ such that infinitely many non-trivial equilibrium points exist. Examples exist where the two nullclines coincide on an interval with nonempty interior; there also exist examples with infinitely many locally asymptotically stable, and infinitely many unstable isolated equilibrium points. If $\mathtt{S}_2(c)C_1 < C_2 < C_1$ then all this can even be arranged so that $\phi_1 \equiv \phi_2$.*

The hypothesis of Theorem 2 excludes some pairs of profiles which are of type "B–M–B". The next result partially fills in this gap by addressing situations in which $\mathtt{s}_1(z)$ is multi-singular.

Theorem 3 (B–mB–B)**.** *Let $\mathtt{s}_1(z) \in B(z_1, z_2, \ldots, z_m)$ and $\mathtt{s}_2(z) \in B(a, c)$ with $0 < a < z_m < \cdots < z_1 < c < \infty$, and let $\sigma_1, \sigma_2, C_1, C_2 > 0$ be given.*

(a) *If $\mathtt{S}_1(z_1) < \mathtt{S}_2(c)$ then there exist $\phi_1, \phi_2 \in \Pi$ such that infinitely many non-trivial equilibrium points exist. Examples exist where the two nullclines coincide on an interval with nonempty interior; there also exist examples with infinitely many locally asymptotically stable, and infinitely many unstable isolated equilibrium points. If $\mathtt{S}_2(c)C_1 < C_2 < C_1$ then all this can even be arranged so that $\phi_1 \equiv \phi_2$.*

(b) *If $\mathtt{S}_1(z_1) \geq \mathtt{S}_2(c)$, then given any $\phi_1, \phi_2 \in \Pi$ at most one non-trivial equilibrium point exists, and when one does exist, it is always globally asymptotically stable with respect to the open first quadrant. This final result also holds for $\mathtt{s}_2(z) \in B(a) \oplus O(c)$.*

We remark that when $m = 1$, then the assumption in part (b) of Theorem 3 is always satisfied. In this case, the Theorem is simply a special case of Theorem 1.

The final result concerns a special case of the situation occurring in Theorem 3 in that it restricts attention to cases in which $\mathtt{s}_1(z)$ and $\mathtt{s}_2(z)$ are both bi-singular. However, its conclusion is different because of its restriction to gain functions in parametric form.

Theorem 4 (B–2B–B)**.** *Let $0 < a < z_2 < z_1 < c < \infty$ and $\sigma_1, \sigma_2, C_1 > 0$ be given. Then there exist $\mathtt{s}_1(z) \in B(z_1, z_2)$, $\mathtt{s}_2(z) \in B(a, c)$, $(\phi_1, \phi_2) \in \mathcal{R}$, and $C_2 > 0$, such that at least two non-trivial equilibrium points exist. In addition,*

(a) *ϕ_1 and ϕ_2 may be chosen so that $(\phi_1, \phi_2) \in \mathcal{R}(I_{\text{in}}, J_1, J_2)$ for any given $I_{\text{in}}, J_1, J_2 > 0$, even when $C_2 > 0$ is also given,*

(b) *ϕ_1 and ϕ_2 may be chosen so that $\phi_1 \equiv \phi_2$.*

Note that neither part (a) nor part (b) of Theorem 4 implies the other. If $(\phi_1, \phi_2) \in \mathcal{R}(I_{\text{in}}, J_1, J_2)$, then these functions may still differ in the parameters φ_i and π_i appearing in (1.4). Similarly, although the gain functions may be chosen to have the same parametric form, it may not be possible to specify values *a priori* for the parameters I_{in}, J_1, J_2, and C_2.

The biological implications of these results as they pertain to plants that compete for sunlight are outlined in the Discussion.

2 Proof of Theorem 1: (U–B–O)

In this section, we prove Theorem 1. Suppose first that $\mathtt{s}_1(z) \in B(a)$ and $\mathtt{s}_2(z) \in U(a) \oplus O(a)$ with $a > 0$, and let $\phi_1, \phi_2 \in \Pi$ and $\sigma_1, \sigma_2, C_1, C_2 > 0$ be given. Then the species 1 nullcline $\mathcal{N}_1 = (x_1, x_2^1)$ satisfies

$$\phi_1\big(\sigma_1 x_1 + \sigma_2 \mathtt{S}_2(a) x_2^1\big) = C_1, \tag{2.1}$$

and the species 2 nullcline $\mathcal{N}_2 = (x_1, x_2^2)$ satisfies

$$\int_0^{a^-} \phi_2\big(\sigma_1 x_1 + \sigma_2 \mathtt{S}_2(z) x_2^2\big) \mathtt{s}_2(z)\, dz + \int_{a^+}^{\infty} \phi_2\big(\sigma_2 \mathtt{S}_2(z) x_2^2\big) \mathtt{s}_2(z)\, dz = C_2. \tag{2.2}$$

Observe from (2.1) that $\mathcal{N}_1$ is a line with constant slope $\theta = -\sigma_1/\big[\sigma_2 \mathtt{S}_2(a)\big]$. We can show that at most one equilibrium point exists, and that when it does exist it is always globally asymptotically stable with respect to the open first quadrant, by demonstrating that the slope of $\mathcal{N}_2$ always exceeds θ. Implicit differentiation of (2.2) with respect to x_1 implies that

$$\frac{dx_2^2}{dx_1} = -\frac{\sigma_1 \int_0^{a^-} \phi_2'\big(\sigma_1 x_1 + \sigma_2 \mathtt{S}_2(z) x_2^2\big) \mathtt{s}_2(z)\, dz}{\sigma_2 \int_0^{a^-} \phi_2'\big(\sigma_1 x_1 + \sigma_2 \mathtt{S}_2(z) x_2^2\big) \mathtt{S}_2(z) \mathtt{s}_2(z)\, dz + \sigma_2 \int_{a^+}^{\infty} \phi_2'\big(\sigma_2 \mathtt{S}_2(z) x_2^2\big) \mathtt{S}_2(z) \mathtt{s}_2(z)\, dz}.$$

Since $\phi_2' < 0$, it follows that

$$\frac{dx_2^2}{dx_1} > -\frac{\sigma_1 \int_0^{a^-} \phi_2'\big(\sigma_1 x_1 + \sigma_2 \mathtt{S}_2(z) x_2^2\big) \mathtt{s}_2(z)\, dz}{\sigma_2 \int_0^{a^-} \phi_2'\big(\sigma_1 x_1 + \sigma_2 \mathtt{S}_2(z) x_2^2\big) \mathtt{S}_2(z) \mathtt{s}_2(z)\, dz} > -\frac{\sigma_1}{\sigma_2 \mathtt{S}_2(a)} = \theta.$$

The last inequality holds because $\mathtt{S}_2(0) = 1$, $\mathtt{S}_2(z)$ is a decreasing function, and $\mathtt{S}_2(a) \in (0,1)$. Therefore, the slope of $\mathcal{N}_2$ everywhere exceeds the slope of $\mathcal{N}_1$, and thus the two nullclines can coincide at most once. We conclude that at most one equilibrium point exists, and that when such a point does exist, it is always globally asymptotically stable with respect to the open first quadrant. (The stability of the equilibrium point is determined by the relative positions of the nullclines in state space, see Figure 4 (g) in [21]). For cases in which $\mathtt{s}_2(z) \in M(0,a)$ or $\mathtt{s}_2(z) \in M(a,\infty)$, then either $\mathcal{N}_1$ is vertical and $\mathcal{N}_2$ is strictly decreasing, or $\mathcal{N}_2$ is horizontal and $\mathcal{N}_1$ is strictly decreasing. In either case, the result is immediate. This completes the proof of Theorem 1.

3 Proof of Theorem 2: (B–C–B)

In this section, we prove Theorem 2. Suppose that $\mathtt{s}_1(z) \in C(a,c)$ and $\mathtt{s}_2(z) \in B(a,c)$ with $0 < a < c < \infty$, and let $\sigma_1, \sigma_2, C_1, C_2 > 0$ be given. We will construct $\phi_1, \phi_2 \in \Pi$ such that (1.1) has infinitely many equilibrium points.

Step 1. Getting started

Define $k = \mathtt{S}_2(c) \in (0,1)$.

(1a) Select $Y_1 > X_1 > X_0 > 0$.

(1b) Select $Y_0 > Y_1 + (\frac{1}{k} - 1)(X_1 - X_0)$.

(1c) Define $\omega_\ell = Y_\ell - X_\ell$ for $\ell \in \{0,1\}$.

(1d) Define $Z_\ell = \omega_\ell + (1/k) X_\ell$ for $\ell \in \{0,1\}$.

Observe from the construction above that

(i) $\omega_0 > \omega_1$.

(ii) $X_\ell < Y_\ell < Z_\ell$ for $\ell \in \{0, 1\}$.

(iii) $Z_0 > Z_1$.

For $\gamma \in [0, 1]$, define

(1e) $X(\gamma) = X_0 + \gamma(X_1 - X_0)$.

(1f) $Y(\gamma) = Y_0 + \gamma(Y_1 - Y_0)$.

(1g) $\omega(\gamma) = Y(\gamma) - X(\gamma)$.

(1h) $Z(\gamma) = \omega(\gamma) + (1/k)X(\gamma)$.

Observe that $X(\gamma)$, $Y(\gamma)$, $\omega(\gamma)$, and $Z(\gamma)$ are all linear and they satisfy $X(\gamma) \in [X_0, X_1]$, $Y(\gamma) \in [Y_1, Y_0]$, $\omega(\gamma) \in [\omega_1, \omega_0]$, and $Z(\gamma) \in [Z_1, Z_0]$ for $\gamma \in [0, 1]$.

Step 2. Select ϕ_1

We construct ϕ_1 as follows.

(2a) Define $\mathcal{I} = [X_0, Y_0]$.

(2b) Select $\phi_1(x) \in C^1(\mathcal{I})$ so that

(i) $\phi_1(x) > 0$ and $\phi_1'(x) < 0$ for $x \in \mathcal{I}$,

(ii) $\int_0^1 \phi_1(\alpha\omega(\gamma) + X(\gamma))\, d\alpha = C_1$ for $\gamma \in [0, 1]$.

(2c) Extend $\phi_1(x)$ elsewhere so that $\phi_1 \in \Pi$.

We remark that the operation in (2b) is well-defined. To see this, first select a function $\psi(x) \in C^1([X_0, X_1])$ which satisfies (a) $\frac{X_1 - X_0}{Y_1 - Y_0}\psi(X_0) + C_1 > 0$ and (b) $\psi(x) > 0$ and $\psi'(x) < 0$ for $x \in [X_0, X_1]$. Next, extend ψ to $[Y_1, Y_0]$ by setting $\psi(Y(\gamma)) = \frac{X_1 - X_0}{Y_1 - Y_0}\psi(X(\gamma))$ for $\gamma \in [0, 1]$. Extend ψ further to be a function in $C^1(\mathcal{I})$ which satisfies $\int_{X_1}^{Y_1} \psi(x)\, dx = 0$ and $\psi'(x) < 0$ for $x \in \mathcal{I}$. Finally, define $\phi_1(x) = \psi(x) + C_1$ for $x \in \mathcal{I}$. Observe from (1e) and (1f) that $\frac{d}{d\gamma}\int_{X(\gamma)}^{Y(\gamma)} \psi(x)\, dx = 0$ and therefore that $\int_{X(\gamma)}^{Y(\gamma)} \psi(x)\, dx = \int_{X_1}^{Y_1} \psi(x)\, dx = 0$ for $\gamma \in [0, 1]$. Since $\phi_1(Y_0) > 0$, and the integral in part (ii) represents the average value of ϕ_1 on $[X(\gamma), Y(\gamma)]$, it is straightforward to see that ϕ_1 satisfies the conditions in (2b).

Step 3. Select ϕ_2

We construct ϕ_2 as follows.

(3a) Select $\lambda_0 > \lambda_1 > \mu_1 > \mu_0 > 0$ so that $k\lambda_\ell + (1 - k)\mu_\ell = C_2$ for $\ell \in \{0, 1\}$.

(3b) Define $\phi_2(X(\gamma)) = (1 - \gamma)\lambda_0 + \gamma\lambda_1$ and $\phi_2(Z(\gamma)) = (1 - \gamma)\mu_0 + \gamma\mu_1$ for $\gamma \in [0, 1]$.

(3c) Extend $\phi_2(x)$ elsewhere so that $\phi_2 \in \Pi$.

It is straightforward to show that

(3d) $k\phi_2(X(\gamma)) + (1 - k)\phi_2(Z(\gamma)) = C_2$ for $\gamma \in [0, 1]$.

An interval of equilibrium points

Observe from steps 1 and 2 with $\gamma = 0$ that

$$\phi_1(0) = \int_0^1 \phi_1(0)\, d\alpha > \int_0^1 \phi_1(\alpha\omega_0 + X_0)\, d\alpha = C_1,$$

and from steps 1 and 3 with $\gamma = 0$ that

$$\phi_2(0) = k\phi_2(0) + (1-k)\phi_2(0) > k\phi_2(X_0) + (1-k)\phi_2(Z_0) = C_2.$$

Consequently, the species 1 nullcline $\mathcal{N}_1$ and the species 2 nullcline $\mathcal{N}_2$ both exist. Equations for these nullclines are obtained from (1.3) with $\mathtt{s}_1(z) \in C(a,c)$ and $\mathtt{s}_2(z) \in B(a,c)$. That is, $\mathcal{N}_1 = (x_1, x_2^1)$ satisfies

$$\int_0^1 \phi_1(\sigma_1\alpha x_1 + \sigma_2 k x_2^1)\, d\alpha = C_1 \tag{3.1}$$

and $\mathcal{N}_2 = (x_1, x_2^2)$ satisfies

$$k\phi_2(\sigma_2 k x_2^2) + (1-k)\phi_2(\sigma_1 x_1 + \sigma_2 x_2^2) = C_2. \tag{3.2}$$

In view of (2b), (3d), (3.1), (3.2), and (1h), let

$$u(\gamma) = \frac{\omega(\gamma)}{\sigma_1} \quad \text{and} \quad v(\gamma) = \frac{X(\gamma)}{\sigma_2 k}, \quad \text{for } \gamma \in [0,1].$$

Then $(u(\gamma), v(\gamma))$ is an equilibrium point within the interior of the first quadrant for every $\gamma \in [0,1]$. We conclude that the two nullclines coincide on an interval with nonempty interior.

Isolated equilibrium points

We now modify the construction above to get infinitely many locally asymptotically stable, and infinitely many unstable isolated equilibrium points. First, select an infinite sequence $\gamma_1, \gamma_2, \ldots$ satisfying $0 < \gamma_1 < \gamma_2 < \cdots < 1$. Then

$$\int_0^1 \phi_1(\alpha\omega(\gamma_j) + X(\gamma_j))\, d\alpha = C_1, \quad \text{for } j \geq 1,$$

and

$$k\phi_2(X(\gamma_j)) + (1-k)\phi_2(Z(\gamma_j)) = C_2, \quad \text{for } j \geq 1. \tag{3.3}$$

Next, let $u_j = u(\gamma_j)$ and $v_j = v(\gamma_j)$ for $j \geq 1$. Again, each of the infinitely many pairs (u_j, v_j) is an equilibrium point. Finally, we redefine ϕ_2 on the set $\mathcal{Z} = (Z_1, Z_0) \setminus \{Z(\gamma_j) : j \geq 1\}$ so that

$$k\phi_2(X(\gamma)) + (1-k)\phi_2(Z(\gamma)) \neq C_2, \quad \text{for } Z(\gamma) \in \mathcal{Z}, \tag{3.4}$$

and we do so without violating condition (3c). We have sufficient freedom here to choose ϕ_2 on $\mathcal{Z}$ so that $\mathcal{N}_2$ will cross $\mathcal{N}_1$ at (u_j, v_j) from below to above when j is even and from above to below when j is odd. To see that this can be done, note that the slope of $\mathcal{N}_2$ is given as

$$\frac{dx_2^2}{dx_1} = -\frac{\sigma_1(1-k)\phi_2'(Z(\gamma))}{\sigma_2 k^2 \phi_2'(X(\gamma)) + \sigma_2(1-k)\phi_2'(Z(\gamma))}, \quad \gamma \in [0,1]. \tag{3.5}$$

If ϕ_2 satisfies (3d), then (3.5) also gives the slope of $\mathcal{N}_1$ at $(u(\gamma), v(\gamma))$, since the two nullclines coincide on an interval. Now redefine ϕ_2 so that (3.3) and (3.4) are both satisfied and so that ϕ_2

is very close to horizontal or vertical in small neighborhoods around $Z(\gamma_j)$ when j is even or odd, respectively. Since this modification alters neither the slope of $\mathcal{N}_1$ nor the value of the first term in the denominator of (3.5), it follows that when j is even then the point (u_j, v_j) will be locally asymptotically stable and when j is odd the point will be unstable. In view of Figure 4 in [21], we will obtain infinitely many locally asymptotically stable, and infinitely many unstable isolated equilibrium points.

The same gain function

To complete the proof, it remains only to show that if $C_2 \in (kC_1, C_1)$ then we can modify the construction above so that $\phi_1 \equiv \phi_2$. Recall that ϕ_1 was subject to a certain integral condition on $[X_0, Y_0]$ in step 2 and that ϕ_2 was subject to a linear condition on $[X_0, X_1]$ and $[Z_1, Z_0]$ in step 3. Below, we arrange for the intervals $[X_0, Y_0]$ and $[Z_1, Z_0]$ to be disjoint so that we will have sufficient freedom to make $\phi_1 \equiv \phi_2$. First, we repeat step 1 but replace (1a) and (1b) with

(1a′) Select $Y_1 > X_1 > X_0 > 0$ so that $X_1 - X_0 < \left(\frac{1-k}{2}\right) X_1$.

(1b′) Select $\theta \in (1/k, 2/k)$ and define $Y_0 = Y_1 + \theta(X_1 - X_0)$.

These modifications allow us to directly compare Y_0 and Z_1:

$$\begin{aligned} Y_0 &= (Y_0 - Y_1) + (Y_1 - X_1) + X_1 \\ &= \theta(X_1 - X_0) + \omega_1 + X_1 \\ &< \frac{2}{k}\left(\frac{1-k}{2}\right) X_1 + \omega_1 + X_1 \\ &= \omega_1 + \frac{X_1}{k} \\ &= Z_1. \end{aligned}$$

We now obtain the following string of inequalities

$$X_0 < X_1 < Y_1 < Y_0 < Z_1 < Z_0. \tag{3.6}$$

In particular, the intervals $[X_0, Y_0]$ and $[Z_1, Z_0]$ are disjoint. Now we repeat (2a) and (2b), but we do so in such a way that the following two additional conditions are also satisfied in (2b):

(iii) $k\phi_1(X_0) < C_2$,

(iv) $k\phi_1(X_1) + (1-k)\phi_1(Y_0) > C_2$.

Since it is assumed that $C_2 \in (kC_1, C_1)$, all of this can be achieved if ϕ_1 is chosen to be sufficiently close to C_1 throughout the interval $[X_0, Y_0]$. Next, we define ϕ_1 on $[Z_1, Z_0]$ so that (3d) is satisfied, but with ϕ_1 in place of ϕ_2. Finally, we perform (2c). This modified construction again produces an interval of equilibrium points as argued earlier but with ϕ_1 in place of ϕ_2. Since $Z(\gamma_j)$ exceeds Y_0 for all $j \geq 1$, again the function ϕ_1 can be further modified on $\mathcal{Z}$ to alter $\mathcal{N}_2$ but not $\mathcal{N}_1$, and thus create infinitely many isolated equilibrium points as described earlier. The proof of Theorem 2 is complete.

4 Proof of Theorem 3: (B–mB–B)

In this section, we prove Theorem 3 using an approach which resembles the one used in the proof of Theorem 2. However, since both allocation profiles considered here are discrete, we will need notation and arguments that are very different.

Suppose that $\mathtt{s}_1(z) \in B(z_1, z_2, \ldots, z_m)$ and $\mathtt{s}_2(z) \in B(a, c)$ with $0 < a < z_m < \cdots < z_1 < c < \infty$, and let $\sigma_1, \sigma_2, C_1, C_2 > 0$ be given.

4.1 Proof of Theorem 3 part (a)

To prove part (a), we will again construct $\phi_1, \phi_2 \in \Pi$ such that (1.1) has infinitely many equilibrium points. Let $[m] = \{1, 2, \ldots, m\}$. Recall that $\mathtt{s}_1(z)$ has the form

$$\mathtt{s}_1(z) = \sum_{i=1}^{m} h_i \delta(z - z_i)$$

for some positive parameters $h_1, h_2, \ldots, h_m$ satisfying $h_1 + h_2 + \cdots + h_m = 1$. Define $H_i = h_1 + h_2 + \cdots + h_i$ for $i \in [m]$ and $k = \mathtt{S}_2(c) \in (0, 1)$, and let us suppose that $h_1 < k$ as the hypothesis of part (a) requires.

Step 1. Getting started

The construction begins as follows. First, select

(1a) $X_1^0 > X_0^0 > 0$.

(1b) $\omega_1 > 0$.

(1c) $\omega_0 \in \left(\omega_1 + \dfrac{X_1^0 - X_0^0}{\min\{k, h_1 + h_2\}},\ \omega_1 + \dfrac{X_1^0 - X_0^0}{h_1}\right)$.

Now, define

(1d) h^* so that $h^*\omega_0 + X_0^0 = h^*\omega_1 + X_1^0$.

(1e) $X^* = h^*\omega_0 + X_0^0 = h^*\omega_1 + X_1^0$.

(1f) $X_\ell^i = H_i\omega_\ell + X_\ell^0$ for $\ell \in \{0, 1\}$ and $i \in [m]$.

(1g) $\overline{X}_\ell = \omega_\ell + (1/k)X_\ell^0$ for $\ell \in \{0, 1\}$.

(1h) $\omega(\gamma) = (1 - \gamma)\omega_0 + \gamma\omega_1$ for $\gamma \in [0, 1]$.

(1i) $X^i(\gamma) = (1 - \gamma)X_0^i + \gamma X_1^i$ for $\gamma \in [0, 1]$ and $i \in \{0\} \cup [m]$.

(1j) $\overline{X}(\gamma) = (1 - \gamma)\overline{X}_0 + \gamma\overline{X}_1$ for $\gamma \in [0, 1]$.

It is straightforward to verify that (see Figure 1)

(i) $h_1 < h^* < \min\{k, h_1 + h_2\}$.

(ii) $X_\ell^0 < X_\ell^1 < X^* < X_\ell^2 < \cdots < X_\ell^m < \overline{X}_\ell$ for $\ell \in \{0, 1\}$.

(iii) $X_0^i < X_1^i$ for $i \in \{0, 1\}$.

(iv) $X_0^i > X_1^i$ for $i \in \{2, 3, \ldots, m\}$.

(v) $\overline{X}_0 > \overline{X}_1$.

(vi) $X^0(\gamma) < X^1(\gamma) < X^* < X^2(\gamma) < \cdots < X^m(\gamma) < \overline{X}(\gamma)$ for $\gamma \in [0,1]$.

(vii) $X^i(\gamma) = H_i\omega(\gamma) + X^0(\gamma)$ for $\gamma \in [0,1]$ and $i \in [m]$.

(viii) $\overline{X}(\gamma) = \omega(\gamma) + (1/k)X^0(\gamma)$ for $\gamma \in [0,1]$.

(ix) $X^* = h^*\omega(\gamma) + X^0(\gamma)$ for $\gamma \in [0,1]$.

We remark that (ix) is obtained from (1e), (1h), and (1i) in the following manner,

$$\begin{aligned} X^* &= (1-\gamma)X^* + \gamma X^* \\ &= (1-\gamma)(h^*\omega_0 + X_0^0) + \gamma(h^*\omega_1 + X_1^0) \\ &= h^*\big[(1-\gamma)\omega_0 + \gamma\omega_1\big] + \big[(1-\gamma)X_0^0 + \gamma X_1^0\big] \\ &= h^*\omega(\gamma) + X^0(\gamma). \end{aligned}$$

Step 2. Select ϕ_1

We now construct ϕ_1 as follows.

(2a) Define $\alpha = h_1(h_1 - h^*) < 0$ and $\beta = \sum_{i=2}^m h_i(H_i - h^*) > 0$.

(2b) Select $\epsilon > 0$ so that $(X^* - \epsilon, X^* + \epsilon) \subset (X_1^1, X_1^2)$.

(2c) For $\delta > 0$ define

$$\phi_1(x;\delta) = \begin{cases} (\delta/\alpha)(x - X^*) + C_1, & x \in [X_0^1, X^* - \epsilon], \\ (\delta/\beta)(X^* - x) + C_1, & x \in [X^* + \epsilon, X_0^m]. \end{cases}$$

(2d) Select $0 < \delta^* \ll 1$ so that $\phi_1(X_0^m, \delta^*) > 0$.

Since $\phi_1(X^* - \epsilon; \delta^*) > C_1 > \phi_1(X^* + \epsilon; \delta^*)$, we can

(2e) Extend $\phi_1(x;\delta^*)$ to a function $\phi_1 \in \Pi$ defined for $x \geq 0$.

This construction implies then that (with δ^* now omitted)

(x) $\sum_{i=1}^m h_i\phi_1(X^i(\gamma)) = C_1$ for $\gamma \in [0,1]$.

To see that (x) holds, apply (vii) and (ix) in step 1 and then (2c) and (2a) to get

$$\begin{aligned} \sum_{i=1}^m h_i\phi_1(X^i(\gamma)) &= \sum_{i=1}^m h_i\phi_1((H_i - h^*)\omega(\gamma) + X^*) \\ &= h_1\big[(\delta^*/\alpha)(h_1 - h^*)\omega(\gamma) + C_1\big] + \sum_{i=2}^m h_i\big[-(\delta^*/\beta)(H_i - h^*)\omega(\gamma) + C_1\big] \\ &= \delta^*\omega(\gamma)\left(\frac{h_1(h_1 - h^*)}{\alpha} - \frac{\sum_{i=2}^m h_i(H_i - h^*)}{\beta}\right) + C_1 \\ &= C_1. \end{aligned}$$

Step 3. Select ϕ_2

We construct ϕ_2 as follows.

(3a) Select $\lambda_0 > \lambda_1 > \overline{\lambda}_1 > \overline{\lambda}_0 > 0$ so that $k\lambda_\ell + (1-k)\overline{\lambda}_\ell = C_2$ for $\ell \in \{0,1\}$.

(3b) Define $\phi_2(X^0(\gamma)) = (1-\gamma)\lambda_0 + \gamma\lambda_1$ and $\phi_2(\overline{X}(\gamma)) = (1-\gamma)\overline{\lambda}_0 + \gamma\overline{\lambda}_1$ for $\gamma \in [0,1]$.

(3c) Extend $\phi_2(x)$ elsewhere so that $\phi_2 \in \Pi$.

It is straightforward to show that

(xi) $k\phi_2(X^0(\gamma)) + (1-k)\phi_2(\overline{X}(\gamma)) = C_2$ for $\gamma \in [0,1]$.

An interval of equilibrium points

Observe from steps 1 and 2 with $\gamma = 0$ that

$$\phi_1(0) = \sum_{i=1}^{m} h_i\phi_1(0) > \sum_{i=1}^{m} h_i\phi_1(X^i(0)) = C_1,$$

and from steps 1 and 3 with $\gamma = 0$ that

$$\phi_2(0) = k\phi_2(0) + (1-k)\phi_2(0) > k\phi_2(X^0(0)) + (1-k)\phi_2(\overline{X}(0)) = C_2.$$

Consequently, the species 1 nullcline $\mathcal{N}_1$ and the species 2 nullcline $\mathcal{N}_2$ both exist. Equations for these nullclines are obtained from (1.3) with $\mathtt{s}_1(z) \in B(z_1, z_2, \ldots, z_m)$ and $\mathtt{s}_2(z) \in B(a,c)$. That is, $\mathcal{N}_1 = (x_1, x_2^1)$ satisfies

$$\sum_{i=1}^{m} h_i\phi_1(\sigma_1 H_i x_1 + \sigma_2 k x_2^1) = C_1 \tag{4.1}$$

and $\mathcal{N}_2 = (x_1, x_2^2)$ satisfies

$$k\phi_2(\sigma_2 k x_2^2) + (1-k)\phi_2(\sigma_1 x_1 + \sigma_2 x_2^2) = C_2. \tag{4.2}$$

In view of (vii), (viii), (x) and (xi), let

$$u(\gamma) = \frac{\omega(\gamma)}{\sigma_1} \quad \text{and} \quad v(\gamma) = \frac{X^0(\gamma)}{\sigma_2 k}, \quad \text{for } \gamma \in [0,1].$$

Then $(u(\gamma), v(\gamma))$ is an equilibrium point within the interior of the first quadrant for every $\gamma \in [0,1]$. We conclude that the two nullclines coincide on an interval with nonempty interior.

Isolated equilibrium points

The procedure to obtain infinitely many locally asymptotically stable, and infinitely many unstable isolated equilibrium points is completely analogous to the construction given in the proof of Theorem 2. First, select an infinite sequence $\gamma_1, \gamma_2, \ldots$ satisfying $0 < \gamma_1 < \gamma_2 < \cdots < 1$. Then modify ϕ_2 on the interval $(\overline{X}_1, \overline{X}_0)$ so that $\mathcal{N}_2$ will cross $\mathcal{N}_1$ at $(u(\gamma_j), v(\gamma_j))$ from below to above when j is even and from above to below when j is odd. We omit the details.

The same gain function

To complete the proof of part (a), it remains only to show that if $C_2 \in (kC_1, C_1)$ then we can modify the construction above so that $\phi_1 \equiv \phi_2$. First, repeat step 1 but replace (1a) and (1b) with

(1a′) Select $X_1^0 > X_0^0 > 0$ so that $X_1^0 \left(\frac{1}{h_1} - \frac{1}{k}\right) < X_0^0 \left(\frac{1}{h_1} - 1\right)$.

(1b′) Select $\omega_1 > \frac{X_1^0 - X_0^0}{h_1}$.

It follows from (1c) and (1a′) that

$$\omega_0 < \omega_1 + \frac{X_1^0 - X_0^0}{h_1} < \omega_1 + \frac{X_1^0}{k} - X_0^0,$$

and therefore that $X_0^m = \omega_0 + X_0^0 < \omega_1 + (1/k)X_1^0 = \overline{X}_1$. In addition, it can be seen from (1b′), (1c), and (1f) that $X_1^0 < h_1\omega_1 + X_0^0 < h_1\omega_0 + X_0^0 = X_0^1$. Thus, we are assured that the interval $[X_0^1, X_0^m]$ where ϕ_1 was defined in step (2c) is disjoint from the intervals $[X_0^0, X_1^0]$ and $[\overline{X}_1, \overline{X}_0]$ on which ϕ_2 was defined in step (3b). Next, repeat step 2 and let ϕ be the restriction of ϕ_1 to the interval $[X_0^1, X_0^m]$. We now extend ϕ so that it belongs to Π and satisfies the following three conditions:

(A) $k\phi(X_0^1) = k\phi_1(X_0^1; \delta^*) < C_2$.

(B) $k\phi(X_0^1) + (1-k)\phi(X_0^m) = k\phi_1(X_0^1; \delta^*) + (1-k)\phi_1(X_0^m; \delta^*) > C_2$.

(C) $k\phi(X^0(\gamma)) + (1-k)\phi(\overline{X}(\gamma)) = C_2$ for $\gamma \in [0, 1]$.

Since $C_2 \in (kC_1, C_1)$, these conditions can easily be satisfied if δ^* is chosen to be sufficiently small in step (2d). As in the construction presented in the proof of Theorem 2, conditions (A) and (B) give us sufficient freedom to choose ϕ on the intervals $[X_0^0, X_1^0]$ and $[\overline{X}_1, \overline{X}_0]$ in such a way that the two nullclines coincide along an interval with nonempty interior, or meet at infinitely many locally asymptotically stable, and infinitely many unstable isolated equilibrium points. This completes the proof of part (a).

4.2 Proof of Theorem 3 part (b)

To prove part (b), let us assume that $\phi_1, \phi_2 \in \Pi$ are given. Using the same notation as in the proof of part (a), we need only to show that if $h_1 \geq k$ then at most one equilibrium point exists, and that when one does exist it is always globally asymptotically stable with respect to the open first quadrant. First, we argue by contradiction to show that the slope of $\mathcal{N}_1 = (x_1, x_2^1)$ cannot exceed $-(\sigma_1 h_1/\sigma_2 k)$. For suppose otherwise, *i.e.*, that $dx_2^1/dx_1 > -(\sigma_1 h_1/\sigma_2 k)$. It follows from implicit differentiation of (4.1) with respect to x_1 that

$$\sum_{i=1}^{m} h_i \phi_1'(\sigma_1 H_i x_1 + \sigma_2 k x_2^1) \left(\sigma_1 H_i + \sigma_2 k \frac{dx_2^1}{dx_1}\right) = 0. \tag{4.3}$$

Observe that $\phi_1' < 0$ and $\sigma_1 H_i + \sigma_2 k(dx_2^1/dx_1) > \sigma_1 H_i - \sigma_1 h_1 \geq 0$ for all $i \in [m]$. Thus, the left-hand side of (4.3) is negative, a contradiction. We conclude that the slope of $\mathcal{N}_1$ nowhere exceeds

$-(\sigma_1 h_1/\sigma_2 k)$. Next, we show that the slope of $\mathcal{N}_2 = (x_1, x_2^2)$ everywhere exceeds $-(\sigma_1/\sigma_2)$. Implicit differentiation of (4.2) with respect to x_1 implies that

$$\frac{dx_2^2}{dx_1} = -\frac{\sigma_1(1-k)\phi_2'(\sigma_1 x_1 + \sigma_2 x_2^2)}{\sigma_2 k^2 \phi_2'(\sigma_2 k x_2^2) + \sigma_2(1-k)\phi_2'(\sigma_1 x_1 + \sigma_2 x_2^2)}.$$

As $\phi_2' < 0$, we obtain $dx_2^2/dx_1 > -(\sigma_1/\sigma_2)$. Since $dx_2^1/dx_1 \le -(\sigma_1 h_1/\sigma_2 k) \le -(\sigma_1/\sigma_2) < dx_2^2/dx_1$, the two nullclines can coincide at most once. We conclude that at most one equilibrium point exists, and that when such a point does exist, it is always globally asymptotically stable with respect to the open first quadrant, as can be seen in Figure 4(g) in [14]. For the case $\mathtt{s}_2(z) \in B(a) \oplus O(c)$, a similar argument holds but with the first term in the denominator of dx_2^2/dx_1 replaced by $\sigma_2 \int_{c^+}^{\infty} \phi_2'\big(\sigma_2 \mathtt{S}_2(z) x_2^2\big) \mathtt{S}_2(z) \mathtt{s}_2(z)\, dz$. This completes the proof of Theorem 3.

5 Proof of Theorem 4: (B–2B–B)

In this section, we prove Theorem 4. Let $0 < a < z_2 < z_1 < c < \infty$ and $\sigma_1, \sigma_2, C_1 > 0$ be given.

5.1 Proof of Theorem 4 part (a)

To prove part (a), we fix C_2, I_{in}, J_1, $J_2 > 0$ and seek $\mathtt{s}_1(z) \in B(z_1, z_2)$, $\mathtt{s}_2(z) \in B(a, c)$, and $(\phi_1, \phi_2) \in \mathcal{R}(I_{\text{in}}, J_1, J_2)$ such that (1.1) has at least two equilibrium points.

Step 1. Select ϕ_1

To begin, let $0 < \epsilon \ll 1$ and define

$$X_1 = 1 + \epsilon^2, \quad Y_1 = 2\epsilon, \quad X_2 = 2, \quad \text{and} \quad Y_2 = \frac{1}{\epsilon} + \epsilon. \tag{5.1}$$

For $\nu > 1$ and $\gamma > 0$, also define

$$F(\epsilon, \nu, \gamma) = \epsilon^2 \left[\frac{1}{\theta + \nu^{\gamma z}}\right]_{z=Y_1}^{z=X_1} + (1-\epsilon^2)\left[\frac{1}{\theta + \nu^{\gamma z}}\right]_{z=Y_2}^{z=X_2}.$$

Here, θ is taken to be the positive constant I_{in}/J_1. Then

$$F(\epsilon, \nu, 1) = \epsilon^2 \left[\frac{1}{\theta + \nu^{z}}\right]_{Y_1}^{X_1} + (1-\epsilon^2)\left[\frac{1}{\theta + \nu^{z}}\right]_{Y_2}^{X_2} > 0,$$

because for sufficiently small ϵ we will have $F(\epsilon, \nu, \gamma) \approx (\theta + \nu^2)^{-1}$. In contrast,

$$F(\epsilon, \nu, 1/\epsilon) = \epsilon^2 \left[\frac{1}{\theta + \nu^{z/\epsilon}}\right]_{Y_1}^{X_1} + (1-\epsilon^2)\left[\frac{1}{\theta + \nu^{z/\epsilon}}\right]_{Y_2}^{X_2} < 0.$$

For the last inequality, we used the following facts:

(i) $\epsilon^2 \left[\theta + \nu^{z/\epsilon}\right]^{-1} \to 0$ as $\epsilon \to 0$ for $z = X_1$ and $z = Y_1$,

(ii) $(1-\epsilon^2)\left[\theta + \nu^{z/\epsilon}\right]^{-1} \to 0$ as $\epsilon \to 0$ for $z = X_2$ and $z = Y_2$,

(iii) $Y_1 \ll X_1$ and $X_2 \ll Y_2$,

(iv) $-\dfrac{\epsilon^2}{\theta + \nu^2} + \dfrac{1-\epsilon^2}{\theta + \nu^{2/\epsilon}} = \dfrac{-\epsilon^2 \nu^{2/\epsilon} + \theta(1-2\epsilon^2) + (1-\epsilon^2)\nu^2}{(\theta + \nu^2)(\theta + \nu^{2/\epsilon})}$,

(v) $\epsilon^2\nu^{2/\epsilon} = \epsilon^2 e^{(2/\epsilon)\ln\nu} = \sum_{k=0}^{\infty}(2\ln\nu)^k\epsilon^{2-k}/k! \to \infty$ as $\epsilon \to 0$.

Thus, there exists some $\gamma^* = \gamma^*(\epsilon,\nu) \in (1, 1/\epsilon)$ such that

$$F(\epsilon,\nu,\gamma^*) = \epsilon^2\left[\frac{1}{\theta+\nu^{\gamma^* z}}\right]_{Y_1}^{X_1} + (1-\epsilon^2)\left[\frac{1}{\theta+\nu^{\gamma^* z}}\right]_{Y_2}^{X_2} = 0.$$

This equation can be rewritten as

$$\frac{\epsilon^2}{\theta+\exp(\pi X_1)} + \frac{1-\epsilon^2}{\theta+\exp(\pi X_2)} = \frac{\epsilon^2}{\theta+\exp(\pi Y_1)} + \frac{1-\epsilon^2}{\theta+\exp(\pi Y_2)},$$

where $\pi(\epsilon,\nu) = \gamma^*(\epsilon,\nu)\ln\nu$. Letting $Q(\epsilon,\nu)$ denote the common value on both sides, define φ_1 so that $\varphi_1 \times Q(\epsilon,\nu) \times \theta = C_1$, and let

$$\phi_1(x) = \varphi_1\left[\frac{I_{\text{in}}}{I_{\text{in}} + J_1\exp(\pi x)}\right] \quad \text{for } x \geq 0. \tag{5.2}$$

Then by construction, $\phi_1 \in \Pi$ and (X_1, Y_1, X_2, Y_2) satisfies

$$\begin{aligned} \epsilon^2\phi_1(X_1) + (1-\epsilon^2)\phi_1(X_2) &= C_1, \\ \epsilon^2\phi_1(Y_1) + (1-\epsilon^2)\phi_1(Y_2) &= C_1. \end{aligned} \tag{5.3}$$

Step 2. Select ϕ_2

The argument to select ϕ_2 is similar to the one used to select ϕ_1, but it requires the use of different constants. With ϵ as above, let

$$X_0 = 1, \quad Y_0 = \epsilon, \quad X_3 = \frac{1}{2\epsilon} + 1, \quad \text{and} \quad Y_3 = \frac{1}{\epsilon} + \frac{1}{2}. \tag{5.4}$$

Also, for $\nu > 1$ and $\gamma > 0$ (not necessarily the same as before) define

$$K(\epsilon,\nu,\gamma) = 2\epsilon\left[\frac{1}{\theta+\nu^{\gamma z}}\right]_{z=Y_0}^{z=X_0} + (1-2\epsilon)\left[\frac{1}{\theta+\nu^{\gamma z}}\right]_{z=Y_3}^{z=X_3}.$$

This time θ is taken to be the positive constant I_{in}/J_2. Observe that

$$K(\epsilon,\nu,\epsilon) = 2\epsilon\left[\frac{1}{\theta+\nu^{\epsilon z}}\right]_{Y_0}^{X_0} + (1-2\epsilon)\left[\frac{1}{\theta+\nu^{\epsilon z}}\right]_{Y_3}^{X_3} > 0$$

due to the estimate $K(\epsilon,\nu,\epsilon) \approx (\theta+\nu^{1/2})^{-1} - (\theta+\nu)^{-1}$. On the other hand,

$$K(\epsilon,\nu,1/\epsilon) = 2\epsilon\left[\frac{1}{\theta+\nu^{z/\epsilon}}\right]_{Y_0}^{X_0} + (1-2\epsilon)\left[\frac{1}{\theta+\nu^{z/\epsilon}}\right]_{Y_3}^{X_3} < 0.$$

For the last inequality, we used the following facts:

(i) $2\epsilon\left[\theta+\nu^{z/\epsilon}\right]^{-1} \to 0$ as $\epsilon \to 0$ for $z = X_0$ and $z = Y_0$,

(ii) $(1-2\epsilon)\left[\theta+\nu^{z/\epsilon}\right]^{-1} \to 0$ as $\epsilon \to 0$ for $z = X_3$ and $z = Y_3$,

(iii) $Y_0 \ll X_0$ and $X_3 \ll Y_3$,

(iv) $-\dfrac{2\epsilon}{\theta+\nu}+\dfrac{1-2\epsilon}{\theta+\nu^{X_3/\epsilon}}=\dfrac{-2\epsilon\nu^{X_3/\epsilon}+\theta(1-4\epsilon)+(1-2\epsilon)\nu}{(\theta+\nu)(\theta+\nu^{X_3/\epsilon})}$,

(v) $\epsilon\nu^{X_3/\epsilon}=\epsilon e^{(X_3/\epsilon)\ln\nu}=\epsilon\sum_{k=0}^{\infty}\left[(X_3/\epsilon)\ln\nu\right]^k/k!\to\infty$ as $\epsilon\to 0$.

Thus, there exists some $\gamma^{**}=\gamma^{**}(\epsilon,\nu)\in(\epsilon,1/\epsilon)$ such that

$$K(\epsilon,\nu,\gamma^{**})=2\epsilon\left[\frac{1}{\theta+\nu^{\gamma^{**}z}}\right]_{Y_0}^{X_0}+(1-2\epsilon)\left[\frac{1}{\theta+\nu^{\gamma^{**}z}}\right]_{Y_3}^{X_3}=0.$$

We can rewrite this equation as

$$\frac{2\epsilon}{\theta+\exp(\tau X_0)}+\frac{1-2\epsilon}{\theta+\exp(\tau X_3)}=\frac{2\epsilon}{\theta+\exp(\tau Y_0)}+\frac{1-2\epsilon}{\theta+\exp(\tau Y_3)},$$

where $\tau(\epsilon,\nu)=\gamma^{**}(\epsilon,\nu)\ln\nu$. Letting $Q(\epsilon,\nu)$ denote the common value on both sides, define φ_2 so that $\varphi_2\times Q(\epsilon,\nu)\times\theta=C_2$, and let

$$\phi_2(x)=\varphi_2\left[\frac{I_{\text{in}}}{I_{\text{in}}+J_2\exp(\tau x)}\right]\quad\text{for } x\geq 0. \tag{5.5}$$

Then by construction, $\phi_2\in\Pi$ and (X_0,Y_0,X_3,Y_3) satisfies

$$\begin{aligned}2\epsilon\phi_2(X_0)+(1-2\epsilon)\phi_2(X_3)&=C_2,\\ 2\epsilon\phi_2(Y_0)+(1-2\epsilon)\phi_2(Y_3)&=C_2.\end{aligned} \tag{5.6}$$

Furthermore, it is clear from (5.2), (5.5), and (1.4) that $(\phi_1,\phi_2)\in\mathcal{R}(I_{\text{in}},J_1,J_2)$.

Multiple equilibrium points

Let

$$\begin{aligned}\mathtt{s}_1(z)&=\epsilon^2\delta(z-z_1)+(1-\epsilon^2)\delta(z-z_2)\\ \mathtt{s}_2(z)&=2\epsilon\delta(z-c)+(1-2\epsilon)\delta(z-a).\end{aligned}$$

Then $\mathtt{s}_1(z)\in B(z_1,z_2)$ and $\mathtt{s}_2(z)\in B(a,c)$, and equations for the species nullclines $\mathcal{N}_1$ and $\mathcal{N}_2$ can be obtained from (1.3), That is, $\mathcal{N}_1=(x_1,x_2^1)$ satisfies

$$\epsilon^2\phi_1(\epsilon^2\sigma_1x_1+2\epsilon\sigma_2x_2^1)+(1-\epsilon^2)\phi_1(\sigma_1x_1+2\epsilon\sigma_2x_2^1)=C_1 \tag{5.7}$$

and $\mathcal{N}_2=(x_1,x_2^2)$ satisfies

$$2\epsilon\phi_2(2\epsilon\sigma_2x_2^2)+(1-2\epsilon)\phi_2(\sigma_1x_1+\sigma_2x_2^2)=C_2. \tag{5.8}$$

In view of (5.1), (5.3), (5.4), and (5.6), let

$$u_1=\frac{1}{\sigma_1},\quad u_2=\frac{1}{\epsilon\sigma_1},\quad v_1=\frac{1}{2\epsilon\sigma_2},\quad\text{and}\quad v_2=\frac{1}{2\sigma_2}.$$

Then the two species coexist at the two equilibrium points (u_1,v_1) and (u_2,v_2) within the interior of the first quadrant. Other equilibrium points may also exist. This completes the proof of part (a).

5.2 Proof of Theorem 4 part (b)

To prove part (b), we will select $\mathtt{s}_1(z) \in B(z_1, z_2)$, $\mathtt{s}_2(z) \in B(a, c)$, $(\phi_1, \phi_2) \in \mathcal{R}$, and $C_2 > 0$ such that $\phi_1 \equiv \phi_2$ and at least two equilibrium points exist. Although the following argument uses similar notation as in the proof of part (a), it relies on a different set of techniques.

Select ϕ_1, ϕ_2, and C_2

For $\zeta \in [-\frac{1}{12}, \frac{1}{12}]$ and $0 < \epsilon \ll 1$, define

$$\begin{aligned} X_0 &= 1, & Y_0 &= \epsilon^2, \\ X_1 &= \frac{5}{2} - 3\zeta, & Y_1 &= (1-2\zeta)\frac{2-\epsilon}{1-\epsilon} + \epsilon^2, \\ X_2 &= 4, & Y_2 &= 2 + \frac{2}{1-\epsilon} + \epsilon^2, \\ X_3 &= 3 + \frac{1}{1-\epsilon}, & Y_3 &= 2 + \frac{2+\epsilon^2}{1-\epsilon}. \end{aligned} \tag{5.9}$$

Since $0 < \epsilon \ll 1$, we have

(i) $X_3 \approx 4$, $Y_0 \approx 0$, $Y_1 \approx 2 - 4\zeta$, $Y_2 \approx 4$, and $Y_3 = Y_2 + \frac{\epsilon^3}{1-\epsilon} \approx 4$,

(ii) $Y_0 < X_0 < X_3 < Y_3$,

(iii) $Y_1 < X_1 < X_2 < Y_2$,

(iv) $X_0 - Y_0 = 1 - \epsilon^2$,

(v) $X_1 - Y_1 \approx \frac{1}{2} + \zeta$,

(vi) $Y_2 - X_2 = \dfrac{2\epsilon}{1-\epsilon} + \epsilon^2 \approx 2\epsilon$,

(vii) $Y_3 - X_3 = \dfrac{\epsilon + \epsilon^2}{1-\epsilon} \approx \epsilon$.

For $\gamma > 0$ and $\theta > 0$, let

$$F(\epsilon, \gamma, \zeta, \theta) = \left(\tfrac{1}{2} - \zeta\right) \left[\frac{1}{\theta + e^{\gamma z}}\right]_{z=Y_1}^{z=X_1} + \left(\tfrac{1}{2} + \zeta\right) \left[\frac{1}{\theta + e^{\gamma z}}\right]_{z=Y_2}^{z=X_2} \tag{5.10}$$

and

$$K(\epsilon, \gamma, \theta) = (1-\epsilon) \left[\frac{1}{\theta + e^{\gamma z}}\right]_{z=Y_0}^{z=X_0} + \epsilon \left[\frac{1}{\theta + e^{\gamma z}}\right]_{z=Y_3}^{z=X_3}. \tag{5.11}$$

In view of the estimate

$$\frac{1}{\theta + A} - \frac{1}{\theta + B} = \frac{B - A}{(\theta + A)(\theta + B)} \approx \frac{B - A}{\theta^2} \quad \text{for} \quad \theta \gg 1,$$

let us define

$$M(\epsilon, \gamma, \zeta) = \left(\tfrac{1}{2} - \zeta\right)(e^{\gamma Y_1} - e^{\gamma X_1}) + \left(\tfrac{1}{2} + \zeta\right)(e^{\gamma Y_2} - e^{\gamma X_2})$$

and

$$N(\epsilon, \gamma) = (1-\epsilon)(e^{\gamma Y_0} - e^{\gamma X_0}) + \epsilon(e^{\gamma Y_3} - e^{\gamma X_3}).$$

We remark that if ϵ, γ, and ζ are fixed so that $M(\epsilon,\gamma,\zeta)$ is nonzero, then the pair of functions $M(\epsilon,\gamma,\zeta)$ and $F(\epsilon,\gamma,\zeta,\theta)$ have the same sign when θ is sufficiently large, and that a similar relationship holds between $N(\epsilon,\gamma)$ and $K(\epsilon,\gamma,\theta)$.

We now show that there exists some $\hat{\gamma}(\epsilon)>0$ such that $N(\epsilon,\hat{\gamma}(\epsilon))=0$. For the moment, fix $0<\delta\ll 1$, let $\overline{\gamma}=-(\frac{2}{3}+\delta)\ln\epsilon$, and let ϵ tend to zero. Then $\epsilon\ln\epsilon\approx 0$, and the estimates

$$(1-\epsilon)(e^{\overline{\gamma}Y_0}-e^{\overline{\gamma}X_0})=(1-\epsilon)(e^{-(2/3+\delta)\epsilon^2\ln\epsilon}-e^{-(2/3+\delta)\ln\epsilon})\approx 1-\epsilon^{-2/3-\delta}\approx -\epsilon^{-2/3-\delta}$$

and

$$\epsilon(e^{\overline{\gamma}Y_3}-e^{\overline{\gamma}X_3})=\epsilon e^{\overline{\gamma}Y_3}\big(1-e^{\overline{\gamma}(X_3-Y_3)}\big)\approx\epsilon^{-5/3-4\delta}\overline{\gamma}(Y_3-X_3)\approx\overline{\gamma}\epsilon^{-2/3-4\delta}$$

imply that

$$N(\epsilon,\overline{\gamma})\approx\epsilon^{-2/3-\delta}\big(\overline{\gamma}\epsilon^{-3\delta}-1\big)>0.$$

By repeating the same procedure with $\underline{\gamma}=-\big(\frac{2}{3}-\delta\big)\ln\epsilon$, we conclude that

$$N(\epsilon,\underline{\gamma})\approx\epsilon^{-2/3+\delta}\big(\underline{\gamma}\epsilon^{3\delta}-1\big)<0.$$

It follows that for sufficiently large θ we also have $K(\epsilon,\overline{\gamma},\theta)>0$ and $K(\epsilon,\underline{\gamma},\theta)<0$. Since $K(\epsilon,\gamma,\theta)$ is a continuous function of γ, there exists some $\hat{\gamma}(\epsilon)\in(\underline{\gamma},\overline{\gamma})$ such that $K(\epsilon,\hat{\gamma}(\epsilon),\theta)=0$. In addition, $\hat{\gamma}(\epsilon)=-\big(\frac{2}{3}+\mathrm{o}(1)\big)\ln\epsilon$.

We now turn to the pair of functions $M(\epsilon,\gamma,\zeta)$ and $F(\epsilon,\gamma,\zeta,\theta)$. Recall that

$$M(\epsilon,\hat{\gamma},\zeta)=\big(\tfrac{1}{2}-\zeta\big)\left(e^{\hat{\gamma}Y_1}-e^{\hat{\gamma}X_1}\right)+\big(\tfrac{1}{2}+\zeta\big)\left(e^{\hat{\gamma}Y_2}-e^{\hat{\gamma}X_2}\right)\tag{5.12}$$

and that $\zeta\in[-\frac{1}{12},\frac{1}{12}]$. First, when $\zeta=-\frac{1}{12}$ we have the estimate

$$e^{\hat{\gamma}Y_1}-e^{\hat{\gamma}X_1}=e^{\hat{\gamma}X_1}\big(e^{\hat{\gamma}(Y_1-X_1)}-1\big)\approx -e^{(11/4)\hat{\gamma}}=-\epsilon^{-11/6+\mathrm{o}(1)}\tag{5.13}$$

and when $\zeta=\frac{1}{12}$ we have

$$e^{\hat{\gamma}Y_1}-e^{\hat{\gamma}X_1}=e^{\hat{\gamma}X_1}\big(e^{\hat{\gamma}(Y_1-X_1)}-1\big)\approx -e^{(9/4)\hat{\gamma}}=-\epsilon^{-3/2+\mathrm{o}(1)}.\tag{5.14}$$

Next, we note that $\hat{\gamma}(X_2-Y_2)\approx(\frac{4}{3}+\mathrm{o}(1))\epsilon\ln\epsilon\approx 0$ and $\hat{\gamma}(X_3-Y_3)\approx(\frac{2}{3}+\mathrm{o}(1))\epsilon\ln\epsilon\approx 0$. Also, recall that $Y_3=Y_2+\frac{\epsilon^3}{1-\epsilon}$. Thus, we can estimate

$$\frac{e^{\hat{\gamma}Y_2}-e^{\hat{\gamma}X_2}}{e^{\hat{\gamma}Y_3}-e^{\hat{\gamma}X_3}}=\frac{1}{e^{\hat{\gamma}\epsilon^3/(1-\epsilon)}}\times\frac{1-e^{\hat{\gamma}(X_2-Y_2)}}{1-e^{\hat{\gamma}(X_3-Y_3)}}\approx\frac{Y_2-X_2}{Y_3-X_3}\approx 2.$$

Also,

$$e^{\hat{\gamma}Y_3}-e^{\hat{\gamma}X_3}=e^{\hat{\gamma}Y_3}\big(1-e^{\hat{\gamma}(X_3-Y_3)}\big)\approx e^{\hat{\gamma}Y_3}\hat{\gamma}(Y_3-X_3)\approx\hat{\gamma}\epsilon^{-5/3+\mathrm{o}(1)}.$$

Therefore,

$$e^{\hat{\gamma}Y_2}-e^{\hat{\gamma}X_2}\approx 2\hat{\gamma}\epsilon^{-5/3+\mathrm{o}(1)}.\tag{5.15}$$

It follows from (5.12)–(5.15) that for sufficiently small ϵ we have both $M(\epsilon,\hat{\gamma}(\epsilon),-\frac{1}{12})<0$ and $M(\epsilon,\hat{\gamma}(\epsilon),\frac{1}{12})>0$. Hence, for sufficiently large θ we also have $F(\epsilon,\hat{\gamma}(\epsilon),-\frac{1}{12},\theta)<0$ and $F(\epsilon,\hat{\gamma}(\epsilon),\frac{1}{12},\theta)>0$. Since $F(\epsilon,\hat{\gamma}(\epsilon),\zeta,\theta)$ depends continuously on ζ, there exists some $\hat{\zeta}(\epsilon)\in(-\frac{1}{12},\frac{1}{12})$ such that $F(\epsilon,\hat{\gamma}(\epsilon),\hat{\zeta}(\epsilon),\theta)=0$. Thus, we have shown that there exist ϵ, $\hat{\gamma}(\epsilon)$, and $\hat{\zeta}(\epsilon)$ such that

$$F(\epsilon,\hat{\gamma}(\epsilon),\hat{\zeta}(\epsilon),\theta)=K(\epsilon,\hat{\gamma}(\epsilon),\theta)=0.\tag{5.16}$$

Finally, with $\psi(x)=(\theta+e^{\hat{\gamma}x})^{-1}$, we observe from (5.10) and (5.16) that

$$\big(\tfrac{1}{2}-\hat{\zeta}\big)\psi(X_1)+\big(\tfrac{1}{2}+\hat{\zeta}\big)\psi(X_2)=\big(\tfrac{1}{2}-\hat{\zeta}\big)\psi(Y_1)+\big(\tfrac{1}{2}+\hat{\zeta}\big)\psi(Y_2).\tag{5.17}$$

Now let Q denote the common value on both sides, define φ such that $\varphi \times Q \times \theta = C_1$, and let

$$\phi(x) = \varphi\left[\frac{I_{\text{in}}}{I_{\text{in}} + J\exp(\pi x)}\right] \quad \text{for } x \geq 0. \tag{5.18}$$

Here, we require that $I_{\text{in}}/J = \theta$ and $\pi = \hat{\gamma}(\epsilon)$. Then (5.17) implies that

$$\begin{aligned} \left(\tfrac{1}{2} - \hat{\zeta}\right)\phi(X_1) + \left(\tfrac{1}{2} + \hat{\zeta}\right)\phi(X_2) &= C_1 \\ \left(\tfrac{1}{2} - \hat{\zeta}\right)\phi(Y_1) + \left(\tfrac{1}{2} + \hat{\zeta}\right)\phi(Y_2) &= C_1. \end{aligned} \tag{5.19}$$

A similar argument involving (5.11) and (5.16) shows that, for the same function ϕ and some positive constant C_2,

$$\begin{aligned} (1-\epsilon)\phi(X_0) + \epsilon\phi(X_3) &= C_2 \\ (1-\epsilon)\phi(Y_0) + \epsilon\phi(Y_3) &= C_2. \end{aligned} \tag{5.20}$$

Define $\phi_1, \phi_2 \equiv \phi$. Then $(\phi_1, \phi_2) \in \mathcal{R}$.

Multiple equilibrium points

Let

$$\begin{aligned} \mathtt{s}_1(z) &= \left(\tfrac{1}{2} - \hat{\zeta}\right)\delta(z - z_1) + \left(\tfrac{1}{2} + \hat{\zeta}\right)\delta(z - z_2) \\ \mathtt{s}_2(z) &= (1-\epsilon)\delta(z - c) + \epsilon\delta(z - a). \end{aligned}$$

Then $\mathtt{s}_1(z) \in B(z_1, z_2)$ and $\mathtt{s}_2(z) \in B(a, c)$, and equations for the species nullclines $\mathcal{N}_1$ and $\mathcal{N}_2$ can be obtained from (1.3). That is, $\mathcal{N}_1 = (x_1, x_2^1)$ satisfies

$$\left(\tfrac{1}{2} - \hat{\zeta}\right)\phi_1\left(\left(\tfrac{1}{2} - \hat{\zeta}\right)\sigma_1 x_1 + (1-\epsilon)\sigma_2 x_2^1\right) + \left(\tfrac{1}{2} + \hat{\zeta}\right)\phi_1\left(\sigma_1 x_1 + (1-\epsilon)\sigma_2 x_2^1\right) = C_1 \tag{5.21}$$

and $\mathcal{N}_2 = (x_1, x_2^2)$ satisfies

$$(1-\epsilon)\phi_2\left((1-\epsilon)\sigma_2 x_2^2\right) + \epsilon\phi_2(\sigma_1 x_1 + \sigma_2 x_2^2) = C_2. \tag{5.22}$$

In view of (5.9), (5.19), and (5.20) with $\phi_1, \phi_2 \equiv \phi$, let

$$u_1 = \frac{3}{\sigma_1}, \quad u_2 = \frac{2 + \frac{2}{1-\epsilon}}{\sigma_1}, \quad v_1 = \frac{1}{(1-\epsilon)\sigma_2}, \quad \text{and} \quad v_2 = \frac{\epsilon^2}{(1-\epsilon)\sigma_2}.$$

Then the two species coexist at the two equilibrium points (u_1, v_1) and (u_2, v_2) within the interior of the first quadrant. Other equilibrium points may also exist. This completes the proof of Theorem 4.

6 Discussion

In analytical studies of terrestrial plant competition, it is usually assumed that model species place their leaves at a single height (*e.g.*, [23, 25, 27, 35, 36]) or, if a coarse distinction between sun leaves and shade leaves is to be made, then at two heights (see [6, 30]). Such simplified approaches involving *big-leaf* species are appropriate when studying multiple factors in combination that together influence plant competition (*e.g.*, light-limitation, nutrient-limitation, and dispersal) because they can make otherwise intractable problems more amenable to mathematical methods. Yet, there remain situations in which sunlight appears to be *the* limiting resource for plants in competition [10, 11, 28, 33, 34]. In such cases, we consider it appropriate to include a fuller account

of the competitors' vertical leaf profiles (or VLPs) because higher leaves everywhere receive more sunlight energy than lower leaves and therefore can perform photosynthesis at higher rates [1, 9, 11]. Furthermore, higher leaves must be supported by taller stems, which are energetically more expensive to construct and to maintain than shorter stems [24].

Enter the mechanistic Canopy Partitioning Model [21, 32], which can be used to predict the outcome of competition between two plant species with fixed VLPs that occupy a relatively constant environment. Its defining feature is that it accommodates arbitrary shapes for the competitors' VLPs and can therefore capture in real time subtle and usually nonlinear changes in leaf photosynthesis rates at different heights which result when plant populations change in leaf area over time. Although initial applications of the model focused on species possessing VLPs which are constant functions over a height interval (*rectangular profiles*) or a pair of disjoint height intervals (*bi-rectangular profiles*) [19, 21, 22], it can equally well accommodate species with big-leaves positioned at multiple discrete heights in a canopy. The purpose of this paper is to examine this latter situation.

In general, a central problem is to determine how many non-trivial equilibrium points the Kolmogorov-type competition model (1.1) can have as well as to establish their stability. Early work by Nevai and Vance [21, 22] delineated conditions under which at most one such equilibrium can exist and demonstrated that if this unique equilibrium exists for rectangular VLPs, it must globally attract the interior of the first quadrant when the species share the same photosynthesis gain function. In [19] it was shown that there exist pairs of species with rectangular VLPs and distinct gain functions for which any finite number of stable and unstable equilibrium points are possible. It was also shown that at least two equilibrium points are possible even if the species share the same gain function, provided that one of their VLPs is bi-rectangular and surrounds the other. However, no non-trivial examples of plant species pairs that obey (1.1) and admit infinitely many equilibrium points were previously known; neither were there known examples of such systems with multiple equilibrium points in which both gain functions are in parametric form (1.4).

All of our theorems here concern cases in which at least one species has a VLP composed of one or more big-leaves (*i.e.*, with finite support) and the canopy is partitioned into three height zones: an upperstory consisting only of leaves belonging to species 2, a middlestory consisting only of leaves belonging to species 1, and an understory consisting only of leaves belonging to species 2. Thus, we may refer to species 1 as the *interior* species and to species 2 as the *exterior* species. We would like to point out that this framework applies equally well to phytoplankton that compete for sunlight in lakes according to the well-known model of Weissing and Huisman [34].

We show in Theorem 1 that when the interior species has a single big-leaf and it is surrounded from below and above by an arbitrary VLP belonging to the exterior species, then there are only two long-term possibilities: either competitive exclusion results with the identity of the surviving species depending only on parameter values but not on initial plant population abundances, or else competitive coexistence occurs at a single globally attracting equilibrium point. Below, we will refer to either of these competitive outcomes as being of "type I." We remark that type I outcomes do not admit the possibility of competitive exclusion due to founder control. These same comments also apply when one species has a single big-leaf lying entirely above or below an arbitrary VLP belonging to the other, which complements a similar result obtained in [21] for two species with uniform but non-overlapping VLPs.

The situation changes dramatically when the VLP of the interior species consists of multiple big-leaves situated at different heights.

Theorem 2 shows that there exist many pairs of model species which can experience both type I competitive outcomes and also coexistence at any one of infinitely many equilibrium points ("type II"). In particular, one may specify *a priori* a VLP for the interior species which is not

concentrated at any single point, a VLP for the exterior species which consists of two big-leaves (one lying in the overstory and one in the understory), and arbitrary cost parameters. Then corresponding species can be found whose nullclines coincide at infinitely many points. This remarkable conclusion continues to hold even when it is required that both species share the same photosynthesis gain function. The actual construction of this gain function is performed in the proof of Theorem 2. The numerous basins of attraction which are possible in Theorem 2 constitute a form of founder control in which different initial species abundances lead to different equilibrium abundances without necessarily resulting in competitive exclusion for either species.

Theorem 3 concerns canopies in which the interior species has an arbitrary but finite number of big-leaves and the exterior species still has a single big-leaf in both the overstory and understory. Again, there exist pairs of species for which type II competitive outcomes occur. However, in these cases, the uppermost leaf belonging to the interior species must bear a smaller fraction of the plant's total leaf area than the highest leaf of the exterior species does relative to its own total leaf area. If not, then we can deduce from Theorem 3 (b) that no combination of parameters and functions exist for which two species can coexist at multiple equilibrium points and the competitive outcome will always be of type I. The distinction which arises between the results in parts (a) and (b) warrants corroboration by empirical results.

Finally, Theorem 4 implies that if the interior species has exactly two big-leaves and they are surrounded on either side by single big-leaves belonging to the exterior species, then *parametric* photosynthesis gain functions can be chosen which produce coexistence at multiple equilibrium points. The shared parameter I_{in} represents the constant irradiance striking the upper surface of the canopy and J_1 and J_2 are the species half-saturation constants [31]. The proof of Theorem 4 uses the Intermediate Value Theorem in both parts. In the proof of part (a), we carefully choose constants and functions so that the two gain functions are in parametric form for specified values of I_{in}, J_1, and J_2. Our construction involves two species which allocate small fractions (ϵ^2 and 2ϵ) of their total leaf area to their upper leaves. When ϵ is very small, these two upper leaves each carry very low leaf areas. Thus, the lower leaf of the interior species experiences nearly full sunlight and is capable of casting substantial shade on the understory leaf belonging to the exterior species. In the proof of part (b), we have more freedom to obtain the parameters and functions in our construction, but we need to ensure that the two gain functions coincide. We accomplish this by letting the interior species be fairly balanced in its allocation of leaf area to its two leaves and then letting the proportion of leaf area in the overstory (which belongs to the exterior species) tend to one.

Our results open up several new avenues for future research. In particular, it is an open question to determine which of our results have analogues for competitive systems in which both VLPs are continuous on their supports. For example, if the VLP for the interior species is rectangular and the VLP for the exterior species is bi-rectangular and surrounds the first, then can there be infinitely many equilibrium points? Can one obtain multiple equilibrium points for any non-trivial pair of VLPs, continuous on their supports, when both photosynthesis gain functions are required to be in parametric form?

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References

[1] N.P.R. Anten and T. Hirose: Limitations on photosynthesis of competing individuals in stands and the consequences for canopy structure. Oecologia 129 (2001) 186–196.

[2] R.A. Armstrong and R. McGehee: Competitive exclusion. Am. Nat. 115 (1980) 151–170.

[3] G.J. Butler, H.I. Freedman, and P. Waltman: Uniformly persistent systems. Proc. Amer. Math. Soc. 96 (1986) 425–430.

[4] R.S. Cantrell, C. Cosner, and V. Hutson: Permanence in ecological systems with spatial heterogeneity. Proc. Royal Soc. Edinburgh 123A (1993) 533–559.

[5] R.S. Cantrell, C. Cosner, and V. Hutson: Ecological models, permanence and spatial heterogeneity. Rocky Mountain J. Math. 26 (1996) 1–35.

[6] D.G.G. De Pury and G.D. Farquhar. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell Env. 20 (1997) 537–557.

[7] H.I. Freedman and S.G. Ruan: Uniform persistence in functional differential equations. J. Diff. Eqns. 115 (1995) 173–192.

[8] G. Hardin: The competitive exclusion principle. Science 131 (1960) 1292–1297.

[9] K. Hikosaka, S. Sudoh, and T. Hirose: Light acquisition and use by individuals competing in a dense stand of an annual herb, *Xanthium canadense*. Oecologia 118 (1999) 388–396.

[10] T. Hirose: Development of the Monsi-Saeki theory on canopy structure and function. Ann. Bot. 95 (2005) 483–494.

[11] T. Hirose and M.J.A. Werger: Canopy structure and photon flux partitioning among species in a herbaceous plant community. Ecology 76 (1995) 466–474.

[12] M.W. Hirsch: Systems of differential equations which are competitive or cooperative. III. Competing species. Nonlinearity 1 (1988) 51-71.

[13] M.W. Hirsch, S. Smale, and R.L. Devaney: Differential equations, dynamical systems, and an introduction to chaos. Academic Press, San Diego, CA, USA, 2004.

[14] J. Hofbauer and B. Garay: Robust permanence for ecological differential equations, minimax, and discretizations. SIAM J. Math. Anal. 34 (2003) 1007–1039.

[15] F. Hofbauer, J. Hofbauer, P. Raith, and T. Steinberger: Intermingled basins in a two species system. J. Math. Biol. 49 (2004) 293–309.

[16] J. Hofbauer and S.J. Schreiber: To persist or not to persist? Nonlinearity 17 (2004) 1393–1406.

[17] V. Hutson, Y. Lou, and K. Mischaikow: Convergence in competition models with small diffusion coefficients. J. Diff. Eqns. 211 (2005) 135–161.

[18] V. Hutson and K. Schmitt: Permanence and the dynamics of biological systems. Math. Biosci. 111 (1992) 1–71.

[19] W. Just and A.L. Nevai: A Kolmogorov-type competition model with multiple coexistence states and its applications to plant competition for sunlight. In review.

[20] A. Kolmogorov: Sulla teoria di Volterra della lotta per l'esistenza. Gi. Inst. Ital. Attuari 7 (1936) 74–80.

[21] A.L. Nevai and R.R. Vance: Plant interspecies competition for sunlight: a mathematical model of canopy partitioning. J. Math. Biol. 55 (2007) 105–145.

[22] A.L. Nevai and R.R. Vance: The role of leaf height in plant interspecies competition for sunlight: analysis of a canopy partitioning model. Math. Biosci. Engin. (2008) In press.

[23] L.G. Perry, C. Neuhauser, and S.M. Galatowitsch: Founder control and coexistence in a simple model of asymmetric competition for light. J. Theor. Biol. 222 (2003) 425–436.

[24] T.E. Pronk, F. Schieving, N.P.R. Anten and M.J.A. Werger: Plants that differ in height investment can coexist if they are distributing non-uniformly within an area. Ecol. Complexity 4 (2007) 182–191.

[25] M. Rees and J. Bergelson: Asymmetric light competition and founder control in plant communities. J. Theor. Biol. 184 (1997) 353–358.

[26] A. Rescigno and I.W. Richardson: The struggle for life. I. Two species. Bull. Math. Biophys. 29 (1967) 377–88.

[27] H.L. Reynolds and S.W. Pacala: An analytical treatment of root-to-shoot ratio and plant competition for soil nutrient and light. Am. Nat. 141 (1993) 51–70.

[28] T. Takada and Y. Iwasa: Size distribution dynamics of plants with interaction by shading. Ecol. Mod. 33 (1986) 173–184.

[29] B. Tang and Y. Kuang: Permanence in Kolmogorov-type systems of nonautonomous functional-differential equations. J. Math. Anal. Appl. 197 (1996) 427–447.

[30] J.H.M. Thornley: Instantaneous canopy photosynthesis: analytical expressions for sun and shade leaves based on exponential light decay down the canopy and an acclimated non-rectangular hyperbola for leaf photosynthesis. Ann. Bot. 89 (2002) 451–458.

[31] J.H.M. Thornley and I. Johnson: Plant and crop modelling – a mathematical approach to plant and crop physiology, Clarendon Press, Oxford, UK, 1990.

[32] R.R. Vance and A.L. Nevai: Plant population growth and competition in a light gradient: a mathematical model of canopy partitioning. J. Theor. Biol. 245 (2007) 210–219.

[33] P.E. Weihe and R.K. Neely: The effects of shading on competition between purple loosestrife and broad-leaved cattail. Aquat. Bot. 59 (1997) 127–138.

[34] F. Weissing and J. Huisman: Growth and competition in a light gradient. J. Theor. Biol. 168 (1994) 323–336.

[35] S. Xiao, S.-Y. Chen, and G. Wang: An ESS for the height of a plant population, or an optimal height for an individual? – Rethinking game-theoretic models for plant height. Bull. Math. Biol. 68 (2006) 957–967

[36] M.A. Zavalaa and R. Bravo de la Parra: A mechanistic model of tree competition and facilitation for Mediterranean forests: scaling from leaf physiology to stand dynamics. Ecol. Mod. 188 (2005) 76–92.

Figure

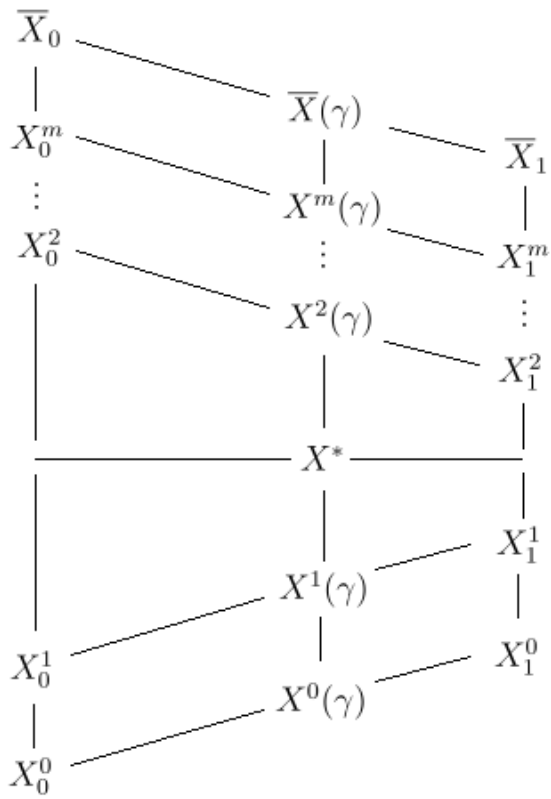

Figure 1: The relative magnitudes of certain quantities appearing in the proof of Theorem 3. Some but not all quantities can be directly compared. Quantities appearing higher are provably larger than quantities that appear lower when they are path-connected by upward lines or ellipses. For example, X_1^2 is greater than X^* and any quantity on the bottom two diagonals but less than any other quantity on the upper m diagonals. However, the relative position of $X^2(\gamma)$ with respect to the quantities in the column above X_1^2 is unknown.