A Kolmogorov-type Competition Model with Multiple Coexistence States and its Applications to Plant Competition for Sunlight

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Abstract

It is demonstrated that a Kolmogorov-type competition model featuring species allocation and gain functions can possess multiple coexistence states. Two examples are constructed: one in which the two competing species possess rectangular allocation functions but distinct gain functions, and the other in which one species has a rectangular allocation function, the second species has a bi-rectangular allocation function, and the two species share a common gain function. In both examples, it is shown that the species nullclines may intersect multiple times within the interior of the first quadrant, thus creating both locally stable and unstable equilibrium points. These results have important applications in the study of plant competition for sunlight, in which the allocation functions describe the vertical placement of leaves for two competing species, and the gain functions represent rates of photosynthesis performed by leaves at different heights when shaded by overlying leaves belonging to either species.

Keywords: Kolmogorov-type competition model, canopy partitioning model, plant competition, light competition, nullcline endpoint analysis

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1 Introduction

Consider two species ($i = 1, 2$) that obey the Kolmogorov-type competition model [10, 15]

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

where x_i denotes the population density of species i at time $t \geq 0$; the gain function $\phi_i(x)$ is a positive, strictly decreasing, and continuously differentiable function of $x \geq 0$ with $\phi_i(x) \to 0$ as $x \to \infty$; the allocation function $\mathtt{s}_i(z)$ is defined for $z \geq 0$, it is a probability density function, and its complementary cumulative distribution function $\mathtt{S}_i(z)$ is given by $\int_z^\infty \mathtt{s}_i(\zeta)\, d\zeta$; and γ_i and C_i are positive constants. The roles of the gain and allocation functions in determining the outcome of competition in (1.1) are almost completely unknown, although some progress has been made in special cases as described below [10, 11].

The system (1.1) arises in a recent study of plant competition for sunlight [10, 15]. It describes the interactions of two competing plant species whose leaves are positioned at different heights within a light gradient. With x_i the total leaf area of species i, the allocation functions $\mathtt{s}_i(z)$ describe the vertical placement of each species' leaves, and the gain functions $\phi_i(x)$ represent rates of photosynthesis performed by leaves at different heights z when shaded by overlying leaves belonging to either species. The resulting canopy partitioning model has been used to predict that the competitive exclusion principle [6] may not apply to some plants that compete for sunlight [10].

The system (1.1) is a member of a more general class of equations

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

first introduced in 1936 by Kolmogorov [9]. Despite the progress made in studying (1.2) by [1]–[5], [7], [8], [12]–[14] and many others, it still remains a difficult problem to establish the roles of the gain and allocation functions on the outcome of competition in (1.1) because f_i is a complicated functional of each, especially when the supports of $\mathtt{s}_1(z)$ and $\mathtt{s}_2(z)$ overlap on an interval or alternate on intervals.

We say that $\phi(x)$ is a *gain function* if it belongs to $\Pi = \{\varphi(x) : \varphi(x)$ is a positive, strictly decreasing, and continuously differentiable function of $x \geq 0$ with $\varphi(x) \to 0$ as $x \to \infty\}$. We say that $\mathtt{s}(z)$ is a *rectangular allocation function* if it belongs to $\Sigma_{\mathrm{r}} = \{\sigma(z) : \sigma(z)$ is a uniform probability density function on an interval $[a, b]$ with $0 \leq a < b\}$ and that $\mathtt{s}(z)$ is a *bi-rectangular allocation function* if it belongs to $\Sigma_{\mathrm{b}} = \{\sigma(z) : \sigma(z)$ is a probability density function that takes positive constant values on two intervals $[a, b]$ and $[c, d]$ with $0 \leq a < b < c < d$ and is zero elsewhere$\}$.

Let K denote the interior of the first quadrant. The species nullclines of (1.1) satisfy

$$\int_0^\infty \phi_i\big(\mathtt{S}_1(z)x_1 + \mathtt{S}_2(z)x_2\big)\mathtt{s}_i(z)\, dz = C_i, \quad i = 1, 2. \tag{1.3}$$

These implicit curves intersect K in the phase plane if and only if $\phi_i(0) > C_i$ for $i = 1, 2$. In [10] it is shown that if

(a) $\phi_1(x), \phi_2(x) \in \Pi$,

(b) $\phi_1(x) = \phi_2(x)$ for $x \geq 0$, and

(c) $\mathtt{s}_1(z), \mathtt{s}_2(z) \in \Sigma_{\mathrm{r}}$,

then the nullclines coincide at most once within the closed first quadrant (we disregard the exceptional case in which the species share the same rectangular allocation function $\mathtt{s}_i(z)$ and the same cost parameter C_i, as then the nullclines would coincide everywhere.) In some cases, the nullclines coincide exactly once, and they can do so in such a way that the resulting equilibrium point lies within K and the nullclines cross there. When it exists, the equilibrium point is always stable and globally attracts K. Thus, if two species have the same gain function and they each have a rectangular allocation function, then stable coexistence may occur (and if so only at a single point) but unstable coexistence cannot. These results continue to hold even if two species obeying conditions (a), (b), and (c) differ only in that $\mathtt{s}_2(z) = \mathtt{s}_1(z - \tau)$ and $C_2 = C_1 + b\tau$ for some $\tau, b > 0$ [11].

In this paper, we show that multiple equilibrium points can occur within K for species whose gain functions do not satisfy (b) or whose allocation functions do not satisfy (c). More precisely, we show in Section 2 that if condition (b) does not hold then the number of stable and unstable equilibrium points lying within K may exceed any given finite integer:

Theorem 1 *Let ℓ be any positive integer. There exist species 1 $(\phi_1, \mathtt{s}_1, C_1, \gamma_1)$ and species 2 $(\phi_2, \mathtt{s}_2, C_2, \gamma_2)$ satisfying* (1.1) *with $\phi_1(x), \phi_2(x) \in \Pi$ and $\mathtt{s}_1(z), \mathtt{s}_2(z) \in \Sigma_{\mathrm{r}}$ and with the property that K contains at least $\ell + 1$ stable equilibrium points and at least ℓ unstable equilibrium points.*

In Section 3, we show that if condition (c) does not hold then K may again possess multiple equilibrium points:

Theorem 2 *There exist species 1 $(\phi_1, \mathtt{s}_1, C_1, \gamma_1)$ and species 2 $(\phi_2, \mathtt{s}_2, C_2, \gamma_2)$ satisfying* (1.1) *with $\phi_1(x), \phi_2(x) \in \Pi$, $\phi_1(x) = \phi_2(x)$ for $x \geq 0$, $\mathtt{s}_1(z) \in \Sigma_{\mathrm{r}}$, and $\mathtt{s}_2(z) \in \Sigma_{\mathrm{b}}$ and with the property that K contains at least one stable equilibrium point and at least one unstable equilibrium point.*

The biological implication of these results is that both locally stable and unstable coexistence may occur for the same parameter values if two species possess different gain functions or one species has a non-rectangular allocation function.

2 Distinct Gain Functions

In this section we prove the following result.

Lemma 1 *Suppose that species 1 $(\phi_1, \mathtt{s}_1, C_1, \gamma_1)$ and species 2 $(\phi_2, \mathtt{s}_2, C_2, \gamma_2)$ satisfy* (1.1) *with $\phi_1(x), \phi_2(x) \in \Pi$; $\mathtt{s}_1(z), \mathtt{s}_2(z) \in \Sigma_{\mathrm{r}}$ with $\mathrm{supp}(\mathtt{s}_1) = [a, b]$, $\mathrm{supp}(\mathtt{s}_2) = [a, c]$, and $0 \leq a < b < c$; $0 < C_1 < \phi_1(0)$; and $0 < C_2 < \phi_2(0)$. Suppose also that a stable equilibrium point (x_1^*, x_2^*) exists in K, and that no other equilibrium point exists within the closure of K. Let $\bar{x}_1 \in (0, x_1^*)$ and let ℓ be any positive integer.*

(a) *Then one can remove species 1 and replace it with a mutant species 3 $(\phi_3, \mathtt{s}_1, C_3, \gamma_1)$ with $\phi_3(x) \in \Pi$ and whose nullcline coincides with the species 2 nullcline in at least $2\ell + 1$ points within K.*

(b) *Species 3 can be chosen so that at least $\ell + 1$ of the equilibrium points in K are stable and at least ℓ are unstable; all original nullcline endpoints are preserved, the original points on the species 1 nullcline with x_1-coordinate lying within the interval $[0, \bar{x}_1]$ are preserved; the original equilibrium point (x_1^*, x_2^*) remains on both nullclines; and (x_1^*, x_2^*) is now unstable.*

A sufficient condition for the assumed equilibrium point (x_1^*, x_2^*) in Lemma 1 to exist, and for it to be unique, is if $\phi_1(x) = \phi_2(x)$ for $x \geq 0$ and if (a, b, c, C_1, C_2) are chosen appropriately ([10], Thms 2.5 and 3.3). Thus, all of the assumptions of Lemma 1 can be satisfied. Since species 1 and the mutant species 3 share the same allocation function, Theorem 1 follows directly from Lemma 1 but with species 3 relabeled as species 1.

To prove Lemma 1, we will construct the mutant species 3 in four stages.

Stage 1: Getting started

Consider two species ($i = 1, 2$) that satisfy (1.1). To start our construction, we assume that the two species have rectangular allocation functions given by

$$\mathtt{s}_1(z) = \begin{cases} \dfrac{1}{b-a}, & z \in [a, b], \\ 0, & \text{otherwise}, \end{cases} \tag{2.1a}$$

and

$$\mathtt{s}_2(z) = \begin{cases} \dfrac{1}{c-a}, & z \in [a, c], \\ 0, & \text{otherwise}, \end{cases} \tag{2.1b}$$

with $0 \leq a < b < c$. Let

$$k = \mathtt{S}_2(b) = \int_b^\infty \mathtt{s}_2(\zeta)\, d\zeta = \frac{c-b}{c-a}, \tag{2.2}$$

and observe that $k \in (0, 1)$. We also assume that the gain functions ϕ_1 and ϕ_2 are in Π, i.e., they satisfy the following properties:

(P_1) ϕ_i is a continuously differentiable function of $x \geq 0$;

(P_2) $\phi_i > 0$ for $x \geq 0$;

(P_3) $\phi_i' < 0$ for $x \geq 0$;

(P_4) $\phi_i \to 0$ as $x \to \infty$.

It follows from (1.3), (2.1), (2.2), and the change of variable $\alpha = \mathtt{S}_1(z)$ that the equation for the species 1 nullcline is given by

$$\Psi_1(x_1, x_2) \stackrel{\text{def}}{=} \int_0^1 \phi_1(\alpha x_1 + \mathtt{r}_1(\alpha) x_2)\, d\alpha = C_1, \tag{2.3a}$$

where

$$\mathtt{r}_1(\alpha) = (1-k)\alpha + k. \tag{2.3b}$$

Similarly, but with the change of variable $\alpha = \mathtt{S}_2(z)$, the equation for the species 2 nullcline is given by

$$\Psi_2(x_1, x_2) \stackrel{\text{def}}{=} \int_0^1 \phi_2(\mathtt{r}_2(\alpha) x_1 + \alpha x_2)\, d\alpha = C_2, \tag{2.4a}$$

where

$$\mathtt{r}_2(\alpha) = \max\left\{\frac{\alpha - k}{1-k}, 0\right\}. \tag{2.4b}$$

The properties of $\phi_1(x)$, $\phi_2(x)$, $\mathtt{r}_1(\alpha)$, and $\mathtt{r}_2(\alpha)$ imply that Ψ_1 and Ψ_2 are both continuous and strictly decreasing functions of $x_1 \geq 0$ and $x_2 \geq 0$. We assume that $0 < C_i < \phi_i(0)$ for $i = 1, 2$, so that both nullclines exist in the first quadrant.

Let us now suppose that the nullcline system possesses a single equilibrium point (x_1^*, x_2^*) lying within the closure of K, that $(x_1^*, x_2^*) \in K$, that (x_1^*, x_2^*) is stable, and that the nullclines cross there. We allow for the possibility that the two nullclines are tangent at (x_1^*, x_2^*) as long as they cross there. This initial configuration is illustrated in Figure 1. We remark that this arrangement of the nullclines can always be achieved for some parameter combinations (k, C_1, C_2) if we assume that $\phi_1(x) = \phi_2(x)$ for $x \geq 0$ ([10], Thms 2.5 and 3.3), but we will not assume in what follows that this additional restriction on ϕ_1 and ϕ_2 holds.

By definition, the equilibrium point (x_1^*, x_2^*) satisfies the equations

$$\Psi_1(x_1^*, x_2^*) = C_1 \quad \text{and} \quad \Psi_2(x_1^*, x_2^*) = C_2. \tag{2.5}$$

To simplify notation, we sometimes write $\Psi_i^* = \Psi_i(x_1^*, x_2^*)$ and $\partial\Psi_i^*/\partial x_j = \partial\Psi_i/\partial x_j(x_1^*, x_2^*)$ for $1 \leq i, j \leq 2$.

When they exist, let $(x_1^\dagger, 0)$ and $(0, x_2^\ddagger)$ denote the endpoints of the species 1 nullcline, and let $(x_1^\ddagger, 0)$ and $(0, x_2^\dagger)$ denote the endpoints of the species 2 nullcline (see Figure 1). These nullcline endpoints (which we identify with their non-zero coordinates) are defined by the relations

$$\begin{aligned} \Psi_1(x_1^\dagger, 0) &= C_1, \qquad \Psi_2(x_1^\ddagger, 0) = C_2, \\ \Psi_1(0, x_2^\ddagger) &= C_1, \qquad \Psi_2(0, x_2^\dagger) = C_2. \end{aligned} \tag{2.6}$$

In the biological interpretation of the model, $x_i^\dagger$ denotes the equilibrium population density for species i when living alone (i.e., when the other species is absent) and $x_i^\ddagger$ denotes the minimum population density for which species i living alone cannot be invaded by the other species. According to ([10], Thms 2.1 and 2.2), three of these endpoints ($x_1^\dagger$, $x_2^\ddagger$, and $x_2^\dagger$) are guaranteed to be positive and finite, whereas the fourth endpoint ($x_1^\ddagger$) may be either positive and finite or undefined. If undefined, we will set $x_1^\ddagger = \infty$ to denote the fact that the species 2 nullcline is defined for all $x_1 \geq 0$. The stability of the equilibrium point (x_1^*, x_2^*), and the fact that the nullclines can coincide at most once within the closed first quadrant, together imply that

$$0 < x_1^* < x_1^\dagger < x_1^\ddagger \quad \text{and} \quad 0 < x_2^* < x_2^\dagger < x_2^\ddagger \tag{2.7}$$

(see Figure 1).

Stage 2: Desired properties of the mutant species 3

We now describe a process that transforms a stable equilibrium point into an unstable equilibrium point, and also produces two nearby locally stable equilibrium points. This process can be repeated as many times as desired to create an arbitrary number of additional locally stable and unstable equilibrium points. At each step of the iteration, we select a stable equilibrium point within K, and we label it (x_1^*, x_2^*). This point should be rightmost, in the sense that no other stable equilibrium point has x_1-coordinate lying within the interval $(x_1^*, x_1^\dagger)$. By compactness of the species 1 nullcline in the closed first quadrant and the fact that $x_1^\dagger < x_1^\ddagger$, such a rightmost stable equilibrium point must always exist.

In general, the point (x_1^*, x_2^*) will belong to an interval $\mathcal{I}$ of equilibrium points. We remark that x_1^* will be positive. If $\mathcal{I}$ is a singleton, then we say that the nullclines *cross* at (x_1^*, x_2^*),

otherwise, we say that the nullclines *diverge* there. In any case, the point (x_1^*, x_2^*) satisfies (2.5) and (2.7).

Fix a point $(\bar{x}_1, \bar{x}_2)$ on the species 1 nullcline with $\bar{x}_1 \in (0, x_1^*)$ and $\bar{x}_2 \in (x_2^*, x_2^\ddagger)$. At later iterations of our construction we will want to preserve finitely many equilibrium points with x_1-coordinates less than x_1^*. The point $(\bar{x}_1, \bar{x}_2)$ should be chosen so that $\bar{x}_1$ exceeds the x_1-coordinates of all these equilibrium points. Now let

$$\Gamma = \{(x_1, x_2) \in [0, \bar{x}_1] \times [\bar{x}_2, x_2^\ddagger] : \Psi_1(x_1, x_2) = C_1\} \tag{2.8}$$

be the portion of the graph of the species 1 nullcline which extends from $(0, x_2^\ddagger)$ to $(\bar{x}_1, \bar{x}_2)$ (see Figure 1). It follows from ([10], Thms 2.1 and 2.2) that the slopes of the species nullclines both lie strictly between -1 and 0 everywhere. Therefore, if $(x_1, x_2) \in \Gamma$ then $x_2^\ddagger \le x_1 + x_2 \le \bar{x}_1 + \bar{x}_2$ (with equality achieved only at the endpoints of Γ).

Let m_i^* be the slope of the species i nullcline at (x_1^*, x_2^*) with respect to x_1. We obtain an equation for m_i^* by implicitly differentiating (2.5) with respect to x_1,

$$\frac{\partial \Psi_i^*}{\partial x_1} + m_i^* \frac{\partial \Psi_i^*}{\partial x_2} = 0. \tag{2.9}$$

As mentioned before, $m_i^* \in (-1, 0)$ for $i = 1, 2$, and thus

$$x_2^\ddagger < \bar{x}_1 + \bar{x}_2 < x_1^* + x_2^* < x_1^\dagger \tag{2.10}$$

(see Figure 1). Since we assumed that (x_1^*, x_2^*) is a stable equilibrium point, it also follows that $m_1^* \le m_2^*$ (see Figure 1).

Let

$$D_i^*(m) = \frac{\partial \Psi_i^*}{\partial x_1} + m \frac{\partial \Psi_i^*}{\partial x_2}, \quad m \in (-\infty, \infty), \tag{2.11}$$

be the directional derivative of Ψ_i at (x_1^*, x_2^*) in the direction of the vector $(1, m)$. Observe from (2.9) and the sign of $\partial \Psi_i^* / \partial x_2$ that

$$\begin{aligned} D_i^*(m) &> 0, \quad \text{for } m < m_i^*, \\ D_i^*(m) &= 0, \quad \text{for } m = m_i^*, \\ D_i^*(m) &< 0, \quad \text{for } m > m_i^*. \end{aligned} \tag{2.12}$$

Thus, if $m < m_1^*$ then $D_i^*(m) > 0$ for $i = 1, 2$; if $m \in (m_1^*, m_2^*)$ then $D_1^*(m) < 0 < D_2^*(m)$, and if $m > m_2^*$ then $D_i^*(m) < 0$ for $i = 1, 2$.

We will ultimately remove species 1 (ϕ_1, C_1) and replace it with a mutant species 3 (ϕ_3, C_3) that is identical to species 1 in all ways except that ϕ_1 and C_1 are replaced by ϕ_3 and C_3, respectively. Since species 1 and species 3 have the same allocation function, the equation for the species 3 nullcline will be given by

$$\Psi_3(x_1, x_2) \stackrel{\text{def}}{=} \int_0^1 \phi_3(\alpha x_1 + \mathtt{r}_1(\alpha) x_2)\, d\alpha = C_3. \tag{2.13}$$

Let us define m_3^* by the relation

$$\frac{\partial \Psi_3^*}{\partial x_1} + m_3^* \frac{\partial \Psi_3^*}{\partial x_2} = 0.$$

Since removing species 1 and replacing it with the mutant species 3 will have no effect on ϕ_2, C_2, or k, it follows from (2.4) that the species 2 nullcline is unchanged. Thus, it still passes

through the points $(0, x_2^\dagger)$, (x_1^*, x_2^*), and $(x_1^\ddagger, 0)$, and it still has slope m_2^* at the point (x_1^*, x_2^*). We will select ϕ_3 and C_3 so that the species 3 nullcline passes through the points $(0, x_2^\ddagger)$, $(\bar{x}_1, \bar{x}_2)$, (x_1^*, x_2^*), and $(x_1^\dagger, 0)$, and so that it coincides with the species 1 nullcline along Γ, but that its slope m_3^* at the point (x_1^*, x_2^*) now exceeds m_2^*. That is, we want

(A_1) ϕ_3 satisfies (P_1)-(P_4);

(A_2) $\Psi_3(x_1, x_2) = C_3$ for $(x_1, x_2) \in \Gamma$;

(A_3) $\Psi_3(x_1^*, x_2^*) = C_3$;

(A_4) $\Psi_3(x_1^\dagger, 0) = C_3$;

(A_5) $m_3^* > m_2^*$.

If we succeed, then (x_1^*, x_2^*) will again be an equilibrium point within K at which the nullclines cross. Furthermore, the continuity of the species nullclines implies that there exist two additional equilibrium points: (x_1^{**}, x_2^{**}) with $x_1^{**} \in (\bar{x}_1, x_1^*)$ and $x_2^{**} \in (x_2^*, \bar{x}_2)$, and (x_1^{***}, x_2^{***}) with $x_1^{***} \in (x_1^*, x_1^\dagger)$ and $x_2^{***} \in (0, x_2^*)$, which can be chosen to be locally stable (although they may not necessarily be locally asymptotically stable). It remains only to show that we can achieve (A_1)-(A_5).

Stage 3 - The intermediate mutant species 4

In this third stage, we find an intermediate mutant (ϕ_4, C_1), which we call species 4, for which

(B_1) ϕ_4 satisfies (P_1) and (P_3);

(B_2) $\phi_4 \to -L$ as $x \to \infty$, for some $L \geq 0$;

(B_3) $\Psi_4(x_1, x_2) = C_1$ for $(x_1, x_2) \in \Gamma$;

(B_4) $\Psi_4(x_1^*, x_2^*) = C_1$;

(B_5) $\Psi_4(x_1^\dagger, 0) = C_1$;

(B_6) $m_4^* > m_2^*$,

where

$$\Psi_4(x_1, x_2) = \int_0^1 \phi_4(\alpha x_1 + \mathtt{r}_1(\alpha) x_2)\, d\alpha \tag{2.14}$$

and m_4^* satisfies

$$\frac{\partial \Psi_4^*}{\partial x_1} + m_4^* \frac{\partial \Psi_4^*}{\partial x_2} = 0.$$

Observe that if $L = 0$ in (B_2) then species 3 can be taken to be species 4 because its strategy $(\phi_3, C_3) = (\phi_4, C_1)$ satisfies (A_1)-(A_5) with $m_3^* = m_4^*$. But if $L > 0$, then we will need to proceed to stage 4 to discover the identity of species 3.

The species 4 nullcline is defined analogously to the species 1 nullcline,

$$\Psi_4(x_1, x_2) = C_1. \tag{2.15}$$

Observe from (2.3a) that if $\phi_4(x) = \phi_1(x)$ for $x \geq 0$ in (2.14), then (2.15) coincides exactly with (2.3a). Let $m \in (m_2^*, 0)$ and define

$$M = -\frac{1}{m}\frac{\partial \Psi_1^*}{\partial x_1}. \tag{2.16}$$

Observe that $M < 0$.

The change of variable $x = \alpha x_1 + \mathtt{r}_1(\alpha)x_2$ in (2.3a) and (2.14) produces

$$\Psi_i(x_1, x_2) = \frac{1}{x_1 + (1-k)x_2}\int_{kx_2}^{x_1+x_2} \phi_i(x)\,dx, \quad i = 1, 4, \tag{2.17}$$

where we have used (2.3b). It follows that

$$\frac{\partial \Psi_i}{\partial x_1} = \frac{\phi_i(x_1+x_2) - \Psi_i(x_1, x_2)}{x_1 + (1-k)x_2}, \quad i = 1, 4, \tag{2.18a}$$

and

$$\frac{\partial \Psi_i}{\partial x_2} = \frac{\phi_i(x_1+x_2) - k\phi_i(kx_2) - (1-k)\Psi_i(x_1, x_2)}{x_1 + (1-k)x_2}, \quad i = 1, 4. \tag{2.18b}$$

Eqs. (2.18) imply that

(i) $\partial\Psi_4^*/\partial x_1$ depends only on the values of three expressions: $x_1^* + (1-k)x_2^*$, $\phi_4(x_1^* + x_2^*)$ and Ψ_4^*; and

(ii) there exists $N > 0$ such that if $\phi_4(x_1^* + x_2^*) = \phi_1(x_1^* + x_2^*)$, $\Psi_4^* = \Psi_1^*$, and $\phi_4(kx_2^*) > N$, then $\partial\Psi_4^*/\partial x_1 = \partial\Psi_1^*/\partial x_1$ and $\partial\Psi_4^*/\partial x_2 < M$.

Let

$$Q = \max\{N+1, \phi_1(0)\} - \phi_1(kx_2^*), \tag{2.19}$$

which we note to be a positive constant.

It follows from (2.7) and (2.10), together with the definition of $(\bar{x}_1, \bar{x}_2)$, that

$$0 < kx_2^* < k\bar{x}_2 < kx_2^\ddagger < x_2^\ddagger < \bar{x}_1 + \bar{x}_2 < x_1^* + x_2^* < x_1^\dagger. \tag{2.20}$$

We will construct several functions (see Figure 2) which satisfy important integral relations along intervals defined by the inequalities in (2.20). We then exploit these integral relations to construct our function ϕ_4. To begin, there exists a function $\psi_1(x)$ defined on $[\bar{x}_1 + \bar{x}_2, x_1^* + x_2^*]$ such that:

(a) $\psi_1(\bar{x}_1 + \bar{x}_2) = \psi_1'(\bar{x}_1 + \bar{x}_2) = \psi_1(x_1^* + x_2^*) = \psi_1'(x_1^* + x_2^*) = 0$;

(b) $\psi_1(x) < 0$ on $(\bar{x}_1 + \bar{x}_2, x_1^* + x_2^*)$;

(c) $(k\bar{x}_2 - kx_2^*)Q + \int_{\bar{x}_1+\bar{x}_2}^{x_1^*+x_2^*} \psi_1(x)\,dx > 0$;

(d) $\phi_1(x) + \psi_1(x)$ satisfies (P_1) and (P_3) on $[\bar{x}_1 + \bar{x}_2, x_1^* + x_2^*]$.

Part (d) can be achieved because $\phi'(x)$ is uniformly bounded from above by a negative constant on $[\bar{x}_1 + \bar{x}_2, x_1^* + x_2^*]$. There exists a second function $\psi_2(x)$ defined on $[kx_2^*, k\bar{x}_2]$ such that:

(e) $\psi_2(kx_2^*) = Q$ and $\psi_2'(kx_2^*) = \psi_2(k\bar{x}_2) = \psi_2'(k\bar{x}_2) = 0$;

(f) $\psi_2(x) > 0$ on $(kx_2^*, k\bar{x}_2)$;

(g) $\int_{kx_2^*}^{k\bar{x}_2} \psi_2(x)\,dx + \int_{\bar{x}_1+\bar{x}_2}^{x_1^*+x_2^*} \psi_1(x)\,dx = 0$;

(h) $\phi_1(x) + \psi_2(x)$ satisfies (P_1) and (P_3) on $[kx_2^*, k\bar{x}_2]$.

Part (g) can be obtained because part (c) is assumed to hold, and part (h) will follow if we insist that $\psi_2(x)$ be continuously differentiable and strictly decreasing on $[kx_2^*, k\bar{x}_2]$. Next, there exists a third function $\psi_3(x)$ defined on $[x_1^* + x_2^*, x_1^\dagger]$ such that:

(i) $\psi_3(x_1^* + x_2^*) = \psi_3'(x_1^* + x_2^*) = 0$, $\psi_3(x_1^\dagger) < 0$, and $\psi_3'(x_1^\dagger) = 0$;

(j) $\psi_3(x) < 0$ on $(x_1^* + x_2^*, x_1^\dagger)$;

(k) $Q(kx_2^*) + \int_{x_1^*+x_2^*}^{x_1^\dagger} \psi_3(x)\,dx = 0$;

(l) $\phi_1(x) + \psi_3(x)$ satisfies (P_1) and (P_3) on $[x_1^* + x_2^*, x_1^\dagger]$.

Again, part (l) will follow if we insist that $\psi_3(x)$ be continuously differentiable and strictly decreasing on $[x_1^* + x_2^*, x_1^\dagger]$. Now let

$$\phi_4(x) = \begin{cases} \phi_1(x) + Q, & x \in [0, kx_2^*], \\ \phi_1(x) + \psi_2(x), & x \in [kx_2^*, k\bar{x}_2], \\ \phi_1(x), & x \in [k\bar{x}_2, \bar{x}_1 + \bar{x}_2], \\ \phi_1(x) + \psi_1(x), & x \in [\bar{x}_1 + \bar{x}_2, x_1^* + x_2^*], \\ \phi_1(x) + \psi_3(x), & x \in [x_1^* + x_2^*, x_1^\dagger]. \end{cases} \tag{2.21}$$

Define $\phi_4(x)$ for $x > x_1^\dagger$ so that (P_1), (P_3), and (B_2) are satisfied for $x \geq 0$. Then ϕ_4 globally satisfies (B_1) and (B_2). Furthermore, the fact that $\phi_4(0) > \phi_1(0) > C_1$ implies that the species 4 nullcline exists in the first quadrant. Recall that if $(x_1, x_2) \in \Gamma$ then $kx_2 \in [k\bar{x}_2, kx_2^\ddagger]$ and $x_1 + x_2 \in [x_2^\ddagger, \bar{x}_1 + \bar{x}_2]$. This fact, together with the definition of ϕ_4 on $[k\bar{x}_2, \bar{x}_1 + \bar{x}_2]$, implies that

$$\int_{kx_2}^{x_1+x_2} \phi_4(x)\,dx = \int_{kx_2}^{x_1+x_2} \phi_1(x)\,dx, \quad (x_1, x_2) \in \Gamma. \tag{2.22}$$

Eq. (2.22) with $(x_1, x_2) = (\bar{x}_1, \bar{x}_2)$, the definition of ϕ_4 on $[kx_2^*, x_1^* + x_2^*]$, and part (g) imply that

$$\int_{kx_2^*}^{x_1^*+x_2^*} \phi_4(x)\,dx = \int_{kx_2^*}^{x_1^*+x_2^*} \phi_1(x)\,dx. \tag{2.23}$$

We conclude from (2.23), the definition of ϕ_4 on $[0, x_1^\dagger]$, and part (k) that

$$\int_0^{x_1^\dagger} \phi_4(x)\,dx = \int_0^{x_1^\dagger} \phi_1(x)\,dx. \tag{2.24}$$

We are now in a position to verify that (B_3)-(B_6) are satisfied. It follows from (2.17), (2.22), and (2.8) that if $(x_1, x_2) \in \Gamma$ then

$$\begin{aligned} \Psi_4(x_1, x_2) &= \frac{1}{x_1 + (1-k)x_2} \int_{kx_2}^{x_1+x_2} \phi_4(x)\,dx \\ &= \frac{1}{x_1 + (1-k)x_2} \int_{kx_2}^{x_1+x_2} \phi_1(x)\,dx \end{aligned}$$

$$= \Psi_1(x_1, x_2)$$
$$= C_1.$$

Thus, condition (B_3) holds. Conditions (B_4) and (B_5) follow from similar calculations but make use of (2.23) or (2.24) instead of (2.22), and (2.5) or (2.6) instead of (2.8). Finally, the fact that $\phi_4(x_1^* + x_2^*) = \phi_1(x_1^* + x_2^*)$ in (2.21), $\Psi_4^* = \Psi_1^*$, and $\phi_4(kx_2^*) > N$ implies that $\partial\Psi_4^*/\partial x_1 = \partial\Psi_1^*/\partial x_1$ and $\partial\Psi_4^*/\partial x_2 < M$. It follows from (2.16) and (2.11) that $D_4^*(m) > 0$. Eq. (2.12) implies that $m \in (m_2^*, m_4^*)$, i.e., condition (B_6) holds. Thus, the intermediate mutant species 4 (ϕ_4, C_1) satisfies conditions (B_1)-(B_6).

Stage 4 - The mutant species 3

As mentioned earlier, if $L = 0$ in (B_2) then species 3 can be taken to be species 4 because its strategy $(\phi_3, C_3) = (\phi_4, C_1)$ satisfies (A_1)-(A_5) with $m_3^* = m_4^*$. If this is the case, then we are done with this step of the iteration.

We now suppose that $L > 0$, so that (P_1), (P_3), and (B_2) are satisfied but (P_2) and (P_4) are not. Define $\phi_3(x) = \phi_4(x) + L$ and $C_3 = C_1 + L$. These "liftings" ensure that

(i) ϕ_3 satisfies (P_1)-(P_4), and

(ii) the species 3 nullcline is identical to the species 4 nullcline.

To see (ii), observe from (2.13) and (2.14) that if $\Psi_4(x_1, x_2) = C_1$ then

$$\begin{aligned}
\Psi_3(x_1, x_2) &= \int_0^1 \phi_3(\alpha x_1 + \mathtt{r}_1(\alpha)x_2)\, d\alpha \\
&= \int_0^1 \left[\phi_4(\alpha x_1 + \mathtt{r}_1(\alpha)x_2) + L\right] d\alpha \\
&= \int_0^1 \phi_4(\alpha x_1 + \mathtt{r}_1(\alpha)x_2)\, d\alpha + L \\
&= \Psi_4(x_1, x_2) + L \\
&= C_1 + L \\
&= C_3.
\end{aligned}$$

Similarly, if $\Psi_3(x_1, x_2) = C_3$ then $\Psi_4(x_1, x_2) = C_1$. It follows that the species 3 nullcline is the same as the species 4 nullcline. Thus, (A_1)-(A_5) are satisfied with $m_3^* = m_4^*$.

More equilibrium points

By iterating this construction, we can obtain an arbitrarily large (but perhaps only finite) number of locally stable and unstable equilibrium points. After each step, we will have transformed the rightmost stable equilibrium point (x_1^*, x_2^*) into an unstable equilibrium point at which the nullclines cross. We will also have created at least two new equilibrium points: (x_1^{**}, x_2^{**}) with $x_1^{**} \in (\bar{x}_1, x_1^*)$ and $x_2^{**} \in (x_2^*, \bar{x}_2)$, and (x_1^{***}, x_2^{***}) with $x_1^{***} \in (x_1^*, x_1^\dagger)$ and $x_2^{***} \in (0, x_2^*)$. These two equilibrium points can be chosen to be locally stable (although they may not necessarily be locally asymptotically stable), and either may itself lie on an interval of equilibrium points which does not include (x_1^*, x_2^*). We now relabel species 3 as species 1 and we relabel x_1^* as x_1^{***}. We reset (x_1^*, x_2^*) to be the rightmost stable equilibrium point. As remarked earlier, such a point must always exist. It follows then that $x_1^* \in (x_1^{***}, x_1^\dagger)$ and $m_1^* \leq m_2^*$. The construction then proceeds

verbatim as in stage 2, beginning with the selection of $(\bar{x}_1, \bar{x}_2)$ on the species 1 nullcline with $\bar{x}_1 \in (x_1^{***}, x_1^*)$ and $\bar{x}_2 \in (x_2^*, x_2^{***})$. After ℓ steps, we will have at least $2\ell + 1$ equilibrium points, for any given positive integer ℓ. Because each step preserves the ever increasing graph of Γ along the species 1 nullcline, the stability of the equilibrium points on Γ will also be preserved at every step.

3 A Non-Rectangular Allocation Function

In this section we will prove Theorem 2. We will construct the species so that $\mathrm{supp}(\mathtt{s}_1) = [b_1, b_2]$ and $\mathrm{supp}(\mathtt{s}_2) = [a_1, a_2] \cup [c_1, c_2]$ for some $0 \le a_1 < a_2 \le b_1 < b_2 \le c_1 < c_2$.

3.1 The construction

We first construct the species in two stages, and then we will confirm that their nullclines do actually coincide at least twice within K.

Stage 1: Preliminaries

Consider two species ($i = 1, 2$) that satisfy (1.1). We assume that species 1 has a rectangular allocation function given by

$$\mathtt{s}_1(z) = \begin{cases} \dfrac{1}{b_2 - b_1}, & z \in [b_1, b_2], \\ 0, & \text{otherwise}, \end{cases} \tag{3.1a}$$

and that species 2 has a bi-rectangular allocation function given by

$$\mathtt{s}_2(z) = \begin{cases} \dfrac{1}{(a_2 - a_1) + (c_2 - c_1)}, & z \in [a_1, a_2] \cup [c_1, c_2], \\ 0, & \text{otherwise}, \end{cases} \tag{3.1b}$$

with $0 \le a_1 < a_2 \le b_1 < b_2 \le c_1 < c_2$. Thus $\mathtt{s}_2(z)$ is supported on either side of $\mathtt{s}_1(z)$ without overlapping on an interval. Let

$$k = \mathtt{S}_2(c_1) = \int_{c_1}^{\infty} \mathtt{s}_2(\zeta)\, d\zeta = \frac{c_2 - c_1}{(a_2 - a_1) + (c_2 - c_1)}, \tag{3.2}$$

and observe that $k \in (0, 1)$. The gain function ϕ is assumed to be the same for both species and to have the following properties,

(P_1) ϕ is a continuously differentiable function of $x \ge 0$;

(P_2) $\phi > 0$ for $x \ge 0$;

(P_3) $\phi' < 0$ for $x \ge 0$;

(P_4) $\phi \to 0$ as $x \to \infty$.

It follows from (1.3), (3.1), (3.2), and the change of variable $\alpha = \mathtt{S}_1(z)$ that the equation for the species 1 nullcline is given by

$$\Psi_1(x_1, x_2) \stackrel{\text{def}}{=} \int_0^1 \phi(\alpha x_1 + k x_2)\, d\alpha = C_1. \tag{3.3}$$

Similarly, but with the change of variable $\alpha = \mathtt{S}_2(z)$, the equation for the species 2 nullcline is given by

$$\Psi_2(x_1, x_2) \stackrel{\text{def}}{=} \int_0^k \phi(\alpha x_2)\, d\alpha + \int_k^1 \phi(x_1 + \alpha x_2)\, d\alpha = C_2. \tag{3.4}$$

The species nullclines are thus defined solely by the four quantities ϕ, C_1, C_2, and k. We again assume that $0 < C_i < \phi(0)$ for $i = 1, 2$, so that both nullclines exist in the first quadrant.

As before, let $(x_1^\dagger, 0)$ and $(0, x_2^\ddagger)$ denote the endpoints of the species 1 nullcline, and $(x_1^\ddagger, 0)$ and $(0, x_2^\dagger)$ denote the endpoints of the species 2 nullcline, when they exist. These nullcline endpoints again satisfy (2.6) but with Ψ_1 and Ψ_2 now defined as above. In view of (3.3) and (3.4), we obtain

$$\begin{aligned} \int_0^1 \phi(\alpha x_1^\dagger)\, d\alpha = C_1, \qquad & k\phi(0) + (1-k)\phi(x_1^\ddagger) = C_2, \\ \phi(k x_2^\ddagger) = C_1, \qquad & \int_0^1 \phi(\alpha x_2^\dagger)\, d\alpha = C_2. \end{aligned} \tag{3.5}$$

Observe that $x_1^\dagger = x_1^\dagger(\phi, C_1)$, $x_2^\ddagger = x_2^\ddagger(\phi, k, C_1)$, $x_1^\ddagger = x_1^\ddagger(\phi, k, C_2)$, and $x_2^\dagger = x_2^\dagger(\phi, C_2)$. The properties of ϕ guarantee that three of these endpoints ($x_1^\dagger$, $x_2^\ddagger$, and $x_2^\dagger$) are positive and finite, whereas the remaining endpoint ($x_1^\ddagger$) may be either positive and finite or otherwise undefined. If undefined, we again set $x_1^\ddagger = \infty$.

The fact that Ψ_i is a positive, continuous, and strictly decreasing function of $x_1 \geq 0$ and $x_2 \geq 0$ for $i = 1, 2$ allows us to make some additional observations. Since we will conceptualize the nullclines differently here than in Section 2, we will also use different notation to represent them.

Eq. (3.3) defines x_1 as an implicit function of x_2, and so there exists a function θ for which

$$\int_0^1 \phi(\alpha\theta(x_2) + k x_2)\, d\alpha = C_1. \tag{3.6}$$

The defining equations for $x_1^\dagger$ and $x_2^\ddagger$ in (3.5) and the properties of ϕ imply that $\theta(0) = x_1^\dagger$, that θ is a nonnegative, continuous, and strictly decreasing function of $x_2 \in [0, x_2^\ddagger]$, and that $\theta(x_2^\ddagger) = 0$. Thus, the nullcline for species 1, which can be described by the graph

$$\{\big(\theta(x_2), x_2\big) : 0 \leq x_2 \leq x_2^\ddagger\},$$

lies entirely within the closed first quadrant. Finally, $\theta(x_2)$ in (3.6) is a continuous and strictly decreasing function of $k \in (0, 1)$ for fixed $x_2 > 0$; we sometimes emphasize this k-dependence by writing $\theta(x_2, k)$.

Similar remarks apply to the species 2 nullcline. Eq. (3.4) defines x_2 as an implicit function of x_1, and so there exists a function π for which

$$\int_0^k \phi(\alpha\pi(x_1))\, d\alpha + \int_k^1 \phi(x_1 + \alpha\pi(x_1))\, d\alpha = C_2. \tag{3.7}$$

The defining equation for $x_2^\dagger$ in (3.5) and the properties of ϕ imply that $\pi(0) = x_2^\dagger$. Moreover, if $x_1^\ddagger \in (0, \infty)$ then π is a nonnegative, continuous, and strictly decreasing function of $x_1 \in [0, x_1^\ddagger]$ with $\pi(x_1^\ddagger) = 0$; but if $x_1^\ddagger = \infty$ then π is a positive, continuous, and strictly decreasing function of $x_1 \in [0, \infty)$. In either case, the nullcline for species 2, which can be described by the graph

$$\{\big(x_1, \pi(x_1)\big) : 0 \leq x_1 \leq x_1^\ddagger \text{ and } x_1 < \infty\},$$

lies entirely within the closed first quadrant. Finally, $\pi(x_1)$ in (3.7) is a continuous and strictly increasing function of $k \in (0,1)$ for fixed $x_1 > 0$; we sometimes emphasize this k-dependence by writing $\pi(x_1, k)$. We remark that the monotone dependence of π on k follows from the implicit function theorem, which allows us to implicitly differentiate (3.7) with respect to k, and property (P_3).

An important distinction between this problem and the one considered in Section 2 is that since the species 2 allocation function is supported on either side of the species 1 allocation function, it is no longer true that the slopes of both nullclines always lie within the interval $(-1, 0)$. However, it is still true that the slopes of these nullclines are negative everywhere.

In the next stage, we will define a gain function ϕ and a set of parameters $\{C_1, C_2, k\}$ that satisfy certain properties. We then demonstrate that species 1 can invade an environment in which species 2 is at equilibrium ($x_2^\ddagger > x_2^\dagger$). Next, we show that an equilibrium point (x_1^*, x_2^*) exists within K (a so-called *interior equilibrium point*), and that the nullclines cross (or at least diverge) there. The leftmost such equilibrium point must be stable. Finally, we show that species 2 cannot invade an environment in which species 1 is at equilibrium ($x_1^\ddagger < x_1^\dagger$). These intermediate results will immediately imply that a second interior equilibrium point (x_1^{**}, x_2^{**}) also exists but with $x_1^{**} \in (x_1^*, x_1^\ddagger)$ and $x_2^{**} \in (0, x_2^*)$ (see Figure 3). For at least one such point the nullclines must cross (or diverge) in such a way that the equilibrium point (x_1^{**}, x_2^{**}) is unstable.

For ease of reference, we will label some assumptions in this section as (D_j), and some results as (E_j), where j is a positive integer.

Stage 2: Selection of ϕ, C_1, C_2, and k

Let $C_1 \in (0, \infty)$, $\lambda \in (0,1)$, and $\mu \in (\lambda, 1) \cap (\frac{1}{2}, 1)$. Define

(D_1) $C_2 = \left(\dfrac{1+\lambda}{1+\mu}\right) C_1.$

Let $\xi \in (0, \infty)$, $\gamma \in (0, \xi)$, and $\nu \in (4, \infty)$. Choose a function ϕ satisfying (P_1)-(P_4) and in addition

(D_2) $\phi(0) = (1+\lambda)C_1$;

(D_3) $\phi(\xi) = C_1$;

(D_4) ϕ is linear on the interval $[\xi - \gamma, \xi + \gamma]$;

(D_5) $\int_0^1 \phi(\alpha\nu\xi)\, d\alpha = \frac{1}{\nu\xi} \int_0^{\nu\xi} \phi(x)\, dx > C_1$.

We remark that the centered interval in (D_4) on which ϕ is linear will be small if γ is also small, and (D_5) can be achieved simply by letting ϕ decrease slowly between $\xi+\gamma$ and $\nu\xi$ for γ sufficiently small relative to λ and C_1.

We may also assume, without loss of generality, that

(D_6) $\phi(\nu\xi) \le (1-\mu)C_2$.

For suppose that (D_6) does not hold, i.e., $\phi(\nu\xi) > (1-\mu)C_2$. We describe a procedure for replacing (ν, ϕ) with a pair $(\hat{\nu}, \hat{\phi})$ such that $\hat{\nu} \in (4, \infty)$ and $\hat{\phi}$ satisfies (P_1)-(P_4) and (D_2)-(D_6) with $\hat{\nu}$ in place of ν. Observe that conditions (D_2)-(D_5) place restrictions on ϕ only within the interval

$[0, \nu\xi]$. Thus, if $\hat{\phi}$ satisfies (P_1)-(P_4) and $\hat{\phi}(x) = \phi(x)$ for $x \in [0, \nu\xi]$, then $\hat{\phi}$ satisfies (D_2)-(D_5). Define

$$\psi(x) = \begin{cases} \phi(x), & x \in [0, \nu\xi], \\ (1-\mu)C_2 e^{\nu\xi - x}, & x \in (\nu\xi, \infty). \end{cases}$$

Then ψ satisfies (P_2), (P_4), and (D_2)-(D_5). Furthermore, ψ is a strictly decreasing function of $x \geq 0$, with a jump discontinuity at $x = \nu\xi$. Observe that

$$G(\sigma) = \int_0^1 \psi(\alpha\sigma\xi)\, d\alpha$$

is a well-defined, continuous, and strictly decreasing function of $\sigma \geq 0$. The definition of ψ and assumption (D_5) imply that

$$G(\nu) = \int_0^1 \psi(\alpha\nu\xi)\, d\alpha = \int_0^1 \phi(\alpha\nu\xi)\, d\alpha > C_1.$$

It follows from the continuity of G that we can find $\hat{\nu} \in (\nu, \infty) \subset (4, \infty)$ such that $G(\hat{\nu}) > C_1$. We may also choose $\hat{\nu}$ so that $\psi(x) < \phi(x)$ for all $x \in (\nu\xi, \hat{\nu}\xi]$. Next, there exists a function $\beta(x)$ such that

(1) β is a continuously differentiable function of $x \in [\nu\xi, \hat{\nu}\xi]$;

(2) $\beta(\nu\xi) = \phi(\nu\xi)$ and $\beta'(\nu\xi) = \phi'(\nu\xi)$;

(3) $\psi(x) \leq \beta(x) \leq \phi(x)$ and $\beta'(x) < 0$ for $x \in [\nu\xi, \hat{\nu}\xi]$; and

(4) $\beta(\hat{\nu}\xi) = \psi(\hat{\nu}\xi)$ and $\beta'(\hat{\nu}\xi) = \psi'(\hat{\nu}\xi)$.

Finally, define

$$\hat{\phi}(x) = \begin{cases} \phi(x), & x \in [0, \nu\xi], \\ \beta(x), & x \in (\nu\xi, \hat{\nu}\xi), \\ \psi(x), & x \in [\hat{\nu}\xi, \infty). \end{cases}$$

Observe that $\hat{\phi}(\hat{\nu}\xi) = \psi(\hat{\nu}\xi) < \psi(\nu\xi) = (1-\mu)C_2$. Let us now relabel the pair $(\hat{\nu}, \hat{\phi})$ as (ν, ϕ). Then $\nu \in (4, \infty)$ and ϕ satisfies (P_1)-(P_4) and (D_2)-(D_6). Thus, we may assume that (D_6) holds and that ϕ is now a fixed function.

Now, consider the positive, continuous, and strictly decreasing function

$$F(\sigma) = \int_0^1 \phi(\alpha\sigma\xi)\, d\alpha = \frac{1}{\sigma}\int_0^\sigma \phi(\tilde{\alpha}\xi)\, d\tilde{\alpha}$$

for $\sigma > 0$. It follows from (D_5) that $F(\nu) > C_1$, from (D_1) that $C_1 > C_2$, and from L'Hospital's rule and (P_4) that $F(\sigma) \to 0$ as $\sigma \to \infty$. Thus, there exists some $\tau \in (\nu, \infty)$ such that $F(\tau) = C_1$, and some $\kappa \in (\tau, \infty)$ such that $F(\kappa) = C_2$. The relation

$$0 < \phi(\tau\xi) < \phi(\nu\xi) \leq (1-\mu)C_2$$

implies that $\phi(\tau\xi) = \eta C_2$ for some $\eta \in (0, 1-\mu)$. The definition of F and the defining equations for $x_1^\dagger$ and $x_2^\dagger$ in (3.5) imply that

$$x_1^\dagger = \tau\xi \quad \text{and} \quad x_2^\dagger = \kappa\xi. \tag{3.8}$$

To summarize, the endpoints $x_1^\dagger$ and $x_2^\dagger$, which are now fixed, satisfy

(E$_1$) $\phi(x_1^\dagger) = \eta C_2$ for some $\eta \in (0, 1-\mu)$;

(E$_2$) $0 < x_1^\dagger < x_2^\dagger < \infty$.

It remains only to select k. We emphasize that $x_2^\dagger$ is now fixed and does not depend on k. Define $\hat{k}$ by

$$\hat{k} x_2^\dagger = \xi - \gamma.$$

Observe from (3.8) that $\hat{k} \in (0, s)$ where $s = 1/\kappa$. It follows from the relation $\pi(0, \hat{k}) = x_2^\dagger$, the continuity of $\pi(x_1, \hat{k})$ as a function of x_1, and (E$_2$) that for sufficiently small $\zeta > 0$, we have $\pi(x_1, \hat{k}) > x_1^\dagger$ for $x_1 \in (0, \zeta)$. Fix some such $\zeta \in (0, x_1^\ddagger)$. Define $k^* = k^*(\epsilon^*)$ by

$$k^* x_2^\dagger = \xi - \epsilon^*$$

for $\epsilon^* \in [0, \gamma]$. Observe that k^* is a positive, continuous, and decreasing function of $\epsilon^* \in [0, \gamma]$, that $k^* = s$ when $\epsilon^* = 0$, and that $k^* = \hat{k}$ when $\epsilon^* = \gamma$. Furthermore, $\pi(x_1, k^*) \geq \pi(x_1, \hat{k}) > x_1^\dagger$ for $\epsilon^* \in [0, \gamma]$ and $x_1 \in (0, \zeta)$.

Since $\tilde{\theta} \stackrel{\text{def}}{=} \theta(x_2^\dagger, s)$ satisfies (3.6) with $x_2 = x_2^\dagger$ and $k = s$, it follows from (D$_3$), (3.8), and the relation $s = 1/\kappa$ that

$$\int_0^1 \phi(\alpha\tilde{\theta} + s x_2^\dagger)\, d\alpha = C_1 = \phi(\xi) = \phi(s x_2^\dagger).$$

The properties of ϕ imply that $\tilde{\theta} = 0$. Since $\theta(x_2^\dagger - \delta^*, k^*) = \tilde{\theta} = 0$ when $\delta^* = \epsilon^* = 0$, and $\theta(x_2^\dagger - \delta^*, k^*)$ is a continuous and increasing function of $\delta^* \in [0, x_2^\dagger]$ and $\epsilon^* \in [0, \gamma]$, it follows that $\theta(x_2^\dagger - \delta^*, k^*) \in (0, \zeta)$ whenever $0 < \delta^* \ll x_2^\dagger$ and $0 < \epsilon^* \ll \gamma$.

Observe from the inequality $2\left(1 + \frac{\mu}{1-\eta}\right) < 4 < \tau$ that the relation

$$2\left(1 + \frac{\mu}{1-\eta}\right)\left(\epsilon^* + \frac{\delta^*}{\tau}\right) < \delta^* < \left[\frac{\gamma - \epsilon^*}{\xi - \epsilon^*}\right] x_2^\dagger \tag{3.9}$$

is always satisfied for sufficiently small values of ϵ^* whenever $\delta^* < (\gamma/\xi) x_2^\dagger$. We now fix some such δ^* and ϵ^* with $0 < \delta^* \ll (\gamma/\xi) x_2^\dagger$ and $0 < \epsilon^* \ll \gamma$ so that $\theta(x_2^\dagger - \delta^*, k^*) \in (0, \zeta)$ and (3.9) holds. Now, let $\delta = \delta^*$, $\epsilon = \epsilon^*$, and $k = k^*$. It follows from the argument above that

(E$_3$) $\delta \in (0, x_2^\dagger)$;

(E$_4$) $\epsilon \in (0, \gamma)$;

(E$_5$) $k x_2^\dagger = \xi - \epsilon$;

(E$_6$) $\pi(x_1, k) > x_1^\dagger$ for $x_1 \in (0, \zeta)$;

(E$_7$) $\theta(x_2^\dagger - \delta, k) \in (0, \zeta)$;

(E$_8$) $2\left(1 + \dfrac{\mu}{1-\eta}\right)\left(\epsilon + \dfrac{\delta}{\tau}\right) < \delta < \left[\dfrac{\gamma - \epsilon}{\xi - \epsilon}\right] x_2^\dagger$.

Furthermore, as we have now fixed ϕ, C_1, C_2, and k, we have also fixed the nullcline functions $\theta(x_2) = \theta(x_2, k)$ and $\pi(x_1) = \pi(x_1, k)$, as well as the remaining endpoints $x_1^\ddagger$ and $x_2^\ddagger$ in (3.5). This finishes our construction.

3.2 Species 1 can invade when species 2 is alone and at equilibrium

We now show that $x_2^\ddagger > x_2^\dagger$. The defining equation for $x_2^\ddagger$ in (3.5) and (D_3) imply that $kx_2^\ddagger = \xi$. Eq. (3.6) with $x_2 = x_2^\dagger$, (D_3), (P_3), and (E_5) imply that

$$\int_0^1 \phi(\alpha\theta(x_2^\dagger) + kx_2^\dagger)\, d\alpha = C_1 = \phi(\xi) < \phi(\xi - \epsilon) = \phi(kx_2^\dagger). \tag{3.10}$$

It follows from (3.10) and the properties of ϕ that

(E_9) $\theta(x_2^\dagger) > 0$.

Since $\theta(x_2^\ddagger) = 0$, and θ is a strictly decreasing function of x_2, we conclude that $x_2^\ddagger > x_2^\dagger$.

3.3 The first interior equilibrium point

We now demonstrate the existence of an interior equilibrium point at which the nullclines cross (or diverge). Observe from (D_1) and (D_2) that

(E_{10}) $\phi(0) = (1+\mu)C_2$.

It follows from (E_5) and (E_8) that

$$k(x_2^\dagger - \delta) = kx_2^\dagger - k\delta = \xi - \epsilon - k\delta \in (\xi - \gamma, \xi - \epsilon),$$

and therefore

(E_{11}) $k(x_2^\dagger - \delta) \in (\xi - \gamma, \xi)$.

Let $f(\omega) = x_2^\dagger - \omega$ and $g(\omega) = \theta(f(\omega))$. Observe that f and g are continuous functions of $\omega \in [0, x_2^\dagger]$. Moreover, f decreases from $x_2^\dagger$ to 0, and g increases from $\theta(x_2^\dagger)$ to $x_1^\dagger$, as ω increases from 0 to $x_2^\dagger$. Result (E_3) implies that δ is in the domain of f and that $f(\delta) \in (0, x_2^\dagger)$. Furthermore, ($E_9$) implies that $g(\delta) \in (0, x_1^\dagger)$. By definition, the expression $g(\delta)$ satisfies (3.6) with $f(\delta)$ in place of x_2,

$$\int_0^1 \phi(\alpha g(\delta) + kf(\delta))\, d\alpha = C_1,$$

which implies that

$$\frac{1}{g(\delta)} \int_{kf(\delta)}^{kf(\delta)+g(\delta)} \phi(x)\, dx = C_1.$$

The left-hand side represents an average value. The lower limit of the integral exceeds $\xi - \gamma$ by (E_{11}). It follows from (D_4), (P_3), and the relation $\phi(\xi) = C_1$ that

$$kf(\delta) + g(\delta) - \xi = \xi - kf(\delta).$$

We conclude from this relation, (E_5), and

$$k < s = 1/\kappa < 1/\tau \tag{3.11}$$

that

$$g(\delta) = 2\big[\xi - kf(\delta)\big] = 2\big[\xi - k(x_2^\dagger - \delta)\big] = 2(\epsilon + k\delta) < 2(\epsilon + \delta/\tau).$$

That is,

(E_{12}) $g(\delta) < 2(\epsilon + \delta/\tau)$.

Next, let $h(\omega) = \pi(g(\omega))$. Observe from ($E_9$), the properties of g, and (E_7) that

$$0 < \theta(x_2^\dagger) = g(0) < g(\delta) = \theta(x_2^\dagger - \delta) < \zeta < x_1^\ddagger.$$

It follows that $g(\omega) \in (0, x_1^\ddagger)$ for all $\omega \in [0, \delta]$. Thus h is a well-defined function of $\omega \in [0, \delta]$. By the properties of π, we obtain that h is a positive, continuous, and strictly decreasing function of $\omega \in [0, \delta]$. Moreover, since π is strictly decreasing, it must be that $h(0) = \pi(g(0)) < \pi(0) = x_2^\dagger = f(0)$. That is,

(E_{13}) $h(0) < f(0)$.

We now show that $h(\delta) > f(\delta)$. Results (E_6) and (E_7) imply that

(E_{14}) $h(\delta) > x_1^\dagger$.

By definition, the expression $h(\delta)$ satisfies (3.7) with $g(\delta)$ in place of x_1,

$$\int_0^k \phi(\alpha h(\delta))\, d\alpha + \int_k^1 \phi(g(\delta) + \alpha h(\delta))\, d\alpha = C_2.$$

Since the argument of ϕ is nonnegative for all values of $\alpha \in [0, 1]$, the left-hand side is well-defined. A change of variable produces

$$\frac{1}{h(\delta)} \left[\int_0^{kh(\delta)} \phi(x)\, dx + \int_{g(\delta)+kh(\delta)}^{g(\delta)+h(\delta)} \phi(x)\, dx \right] = C_2.$$

This equation can be rewritten as

$$\int_0^{x_2^\dagger} \phi(x)\, dx - \int_{g(\delta)+h(\delta)}^{x_2^\dagger} \phi(x)\, dx - \int_{kh(\delta)}^{kh(\delta)+g(\delta)} \phi(x)\, dx = C_2 h(\delta),$$

independently of the relative magnitude of $x_2^\dagger$ and $g(\delta) + h(\delta)$. The definition of $x_2^\dagger$ in (3.5) together with the change of variable $x = \alpha x_2^\dagger$ implies that the first integral is simply $C_2 x_2^\dagger$. Thus, we have

$$C_2\big[x_2^\dagger - h(\delta)\big] = \int_{g(\delta)+h(\delta)}^{x_2^\dagger} \phi(x)\, dx + \int_{kh(\delta)}^{kh(\delta)+g(\delta)} \phi(x)\, dx.$$

It follows from (P_3), (E_{14}), and (E_1) that $\phi(g(\delta)+h(\delta)) < \phi(h(\delta)) < \phi(x_1^\dagger) = \eta C_2$, and from ($E_2$) and ($E_1$) that $\phi(x_2^\dagger) < \phi(x_1^\dagger) = \eta C_2$. Therefore,

$$C_2\big[x_2^\dagger - h(\delta)\big] < \big[x_2^\dagger - g(\delta) - h(\delta)\big]\eta C_2 + g(\delta)\phi(0).$$

We rearrange to get

$$(1-\eta)C_2\big[x_2^\dagger - h(\delta)\big] < g(\delta)\big[\phi(0) - \eta C_2\big].$$

Now, (E_{12}) and (E_{10}) imply that

$$(1-\eta)C_2\big[x_2^\dagger - h(\delta)\big] < 2(\epsilon + \delta/\tau)(1 + \mu - \eta)C_2,$$

or

$$x_2^\dagger - h(\delta) < 2\left(1 + \frac{\mu}{1-\eta}\right)\left(\epsilon + \frac{\delta}{\tau}\right).$$

Finally, (E_8) implies that

$$h(\delta) > x_2^\dagger - \delta = f(\delta).$$

In view of this result, (E_{13}), and the continuity of f and h on $[0, \delta]$, there exists some $\delta^{**} \in (0, \delta)$ such that

(i) $h(\delta^{**}) = f(\delta^{**})$ and

(ii) $h(\omega) > f(\omega)$ for $\omega \in (\delta^{**}, \delta]$.

We conclude that $(x_1^*, x_2^*) = (g(\delta^{**}), f(\delta^{**}))$ is an equilibrium point because $\theta(f(\delta^{**})) = g(\delta^{**})$ and $\pi(g(\delta^{**})) = h(\delta^{**}) = f(\delta^{**})$, and that it lies within K because $g(\delta^{**}) > 0$ and $f(\delta^{**}) > 0$.

To summarize, let $y_1 = f(\delta)$ and $\rho = \theta(y_1) = \theta(f(\delta))$. Then (ρ, y_1) lies on the species 1 nullcline. As the species 1 nullcline is strictly decreasing, and it passes through the points $(0, x_2^\ddagger)$ and $(x_1^\dagger, 0)$, it follows that $\rho \in (0, x_1^\dagger)$ and $y_1 \in (0, x_2^\ddagger)$. Let (ρ, y_2) be the corresponding point on the species 2 nullcline. Then by a similar argument $\rho \in (0, x_1^\ddagger)$ and $y_2 \in (0, x_2^\dagger)$. Furthermore, $y_2 = \pi(\rho) = \pi(\theta(f(\delta)) = h(\delta) > f(\delta) = y_1$. Since $x_2^\ddagger > x_2^\dagger$, we conclude that there exists an equilibrium point (x_1^*, x_2^*) with $x_1^* \in (0, \rho)$ and $x_2^* \in (0, x_2^\dagger)$ at which the nullclines cross (or diverge) in such a way that the point is stable (see Figure 3).

3.4 Species 2 cannot invade when species 1 is alone and at equilibrium

Finally, we show that $x_1^\ddagger < x_1^\dagger$. We argue by contradiction. Suppose that $x_1^\ddagger \geq x_1^\dagger$. Then $\pi(x_1^\dagger) \geq \pi(x_1^\ddagger) = 0$. By definition, $\pi(x_1^\dagger)$ satisfies (3.7) with $x_1^\dagger$ in place of x_1, i.e.,

$$\int_0^k \phi(\alpha\pi(x_1^\dagger))\, d\alpha + \int_k^1 \phi(x_1^\dagger + \alpha\pi(x_1^\dagger))\, d\alpha = C_2.$$

The first integral is bounded from above by $k\phi(0)$, which is less than $(1/\tau)(1+\mu)C_2$ by (3.11) and (E_{10}). The second integral is bounded from above by $(1-k)\phi(x_1^\dagger)$, which is itself less than $\phi(x_1^\dagger)$. By (E_1), the sum of these bounds is $\big[(1/\tau)(1+\mu)+\eta\big]C_2$, which is less than C_2 because $\tau > 4$, $\mu \in (\frac{1}{2}, 1)$, and $\eta < 1-\mu$. This is a contradiction. We conclude that $x_1^\ddagger < x_1^\dagger$.

As mentioned before, there must exist a second interior equilibrium point (x_1^{**}, x_2^{**}), with $x_1^{**} \in (x_1^*, x_1^\ddagger)$ and $x_2^{**} \in (0, x_2^*)$, at which the nullclines cross (or diverge) in such a way that the equilibrium is unstable (see Figure 3).

4 Summary and Discussion

It was shown in [10] that if two species obeying the canopy partitioning model (1.1) share a common gain function, and each species possesses a rectangular allocation function, then at most one equilibrium point can exist within the interior of the first quadrant K, and when it exists, this equilibrium point globally attracts K. Here, we show that neither of these assumptions can be dropped.

Our first theorem states that if two species with rectangular allocation functions have distinct gain functions then their nullclines may intersect an arbitrary number of times within K. In the proof, we begin with two species whose allocation functions $\mathtt{s}_1(z)$ and $\mathtt{s}_2(z)$ are both rectangular and satisfy $\text{supp}(\mathtt{s}_1) = [a, b]$ and $\text{supp}(\mathtt{s}_2) = [a, c]$ with $0 \leq a < b < c$. We assume that a single equilibrium point exists in the closed first quadrant, and that this point is actually in K and that it is stable. (As mentioned in the body of the paper, this arrangement of the nullclines can

always be arranged for certain parameter combinations if the two species share the same gain function.) We then modify the gain function and cost parameter of species 1 in such a way that the new nullcline system possesses at least $\ell+1$ stable, and at least ℓ unstable, equilibrium points in K for any given positive integer ℓ. Furthermore, we preserve many properties of the original nullcline system in our construction, including all nullcline endpoints, the original equilibrium point (which will now be unstable), and the portion of the species 1 nullcline adjacent to its left endpoint $(0, x_2^{\ddagger})$.

Our second theorem states that if two species share a common gain function, but one species has a non-rectangular allocation function, then their nullclines may again intersect multiple times within K. In the proof, we construct two species (one of which has a rectangular allocation function and the other of which has a bi-rectangular allocation function supported on either side of the first) whose nullcline system has at least one stable and one unstable equilibrium point in K.

Our results demonstrate that unstable coexistence can occur for hypothetical plant species that compete for sunlight when their gain functions are distinct or if one species has a non-rectangular allocation function. As we showed in proving our second theorem, it may, in principle, be sufficient for one species to possess an allocation function which is supported on either side of the other species' allocation function. This occurs, for example, when one species places all of its leaves between two layers of its competitors' leaves.

Our results open several avenues of future research.

First, since the nullcline system for two species sharing a common gain function and possessing rectangular allocation functions can have at most one equilibrium point in K, it would be interesting to determine under what conditions this uniqueness result will generalize. Of course, our second theorem shows that the assumption of rectangular allocation functions cannot be completely dropped, but can it be meaningfully weakened? If two species share a common gain function, and this function has the biologically realistic form described in [15], then can one obtain multiple equilibrium points in K if either species has a bi-rectangular (or fully non-rectangular) allocation function? Similarly, if two species have distinct gain functions and each has a rectangular allocation functions, then under what conditions can one prove uniqueness of the equilibrium point in K? Or, if the gain functions have the biological form described in [15], can one then obtain more than one equilibrium point? Can one prove an analogue of our lemma in Section 2 but with species 3 now a mutation of species 2 rather than species 1?

Second, in situations where uniqueness of an equilibrium point in K cannot be proved, we may ask how many equilibrium points are possible. Even for rectangular allocation functions, we were able to show that the number of equilibrium points may exceed any given positive integer. When can we find infinitely many, or even uncountably many equilibrium points? Notice that it is not in general clear that our construction in Section 2 can be iterated infinitely often, since the number Q may increase at each step of the construction, and this increase needs to be bounded by the sum of a convergent series if we are to iterate our construction infinitely often. If Q can be kept below an upper bound, then it should be possible to construct a countably infinite set of equilibrium points. The construction of a pair of two species whose nullcline system possesses an uncountable set of equilibrium points whose x_1-coordinates resemble the Cantor set might also be possible in this case, provided that we can also preserve a given portion $\tilde{\Gamma}$ of the species 1 nullcline that is adjacent to its right endpoint $(x_1^{\dagger}, 0)$ (see Figure 4). However, preserving $\tilde{\Gamma}$ appears to require certain assumptions about the second derivative of the original nullcline which may not in general be satisfied.

Finally, we showed in Section 3 that at least two distinct equilibrium points in K are possible

if the gain functions are the same and only one species has a rectangular allocation function, with the other species having a bi-rectangular allocation function. Is two the maximum number of possible equilibrium points in K for this situation? If so, can one prove a more general theorem about the relationship between the shape of the allocation functions and the number of possible equilibrium points in K under the assumption that the gain functions are the same? If not in general, what additional properties on the common gain function would be sufficient for such a theorem? In particular, if the common gain function has the particular form described in [15], what is the maximum number of equilibrium points for species with two given types of allocation functions?

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Figures

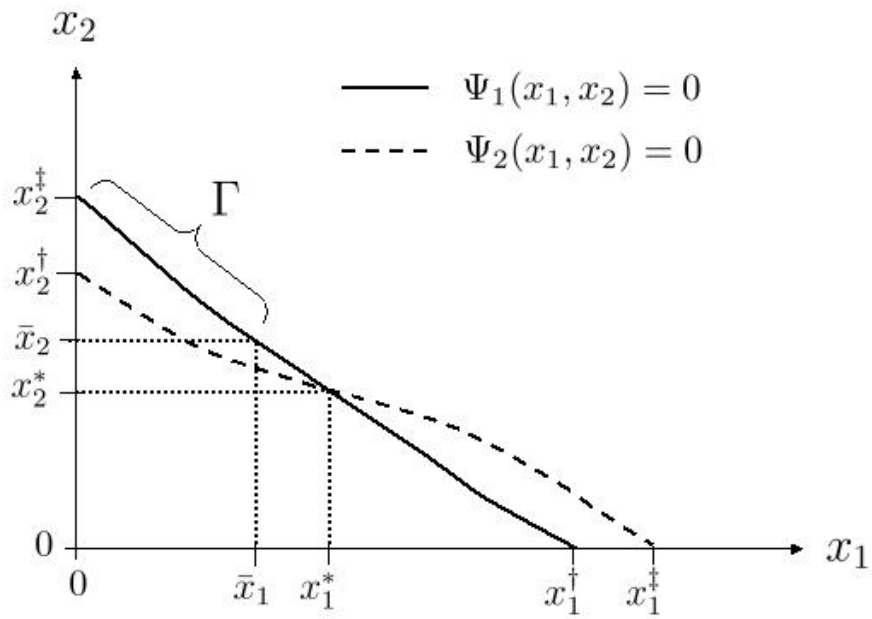

Figure 1: The species nullclines coincide at a unique equilibrium point, producing stable coexistence at $(x_1^*, x_2^*) \in K$. The point $(\bar{x}_1, \bar{x}_2)$ lies on the species 1 nullcline above and to the left of (x_1^*, x_2^*). This figure strictly applies only when $x_1^\ddagger$ is finite; however, a similar figure does apply when $x_1^\ddagger$ is infinite.

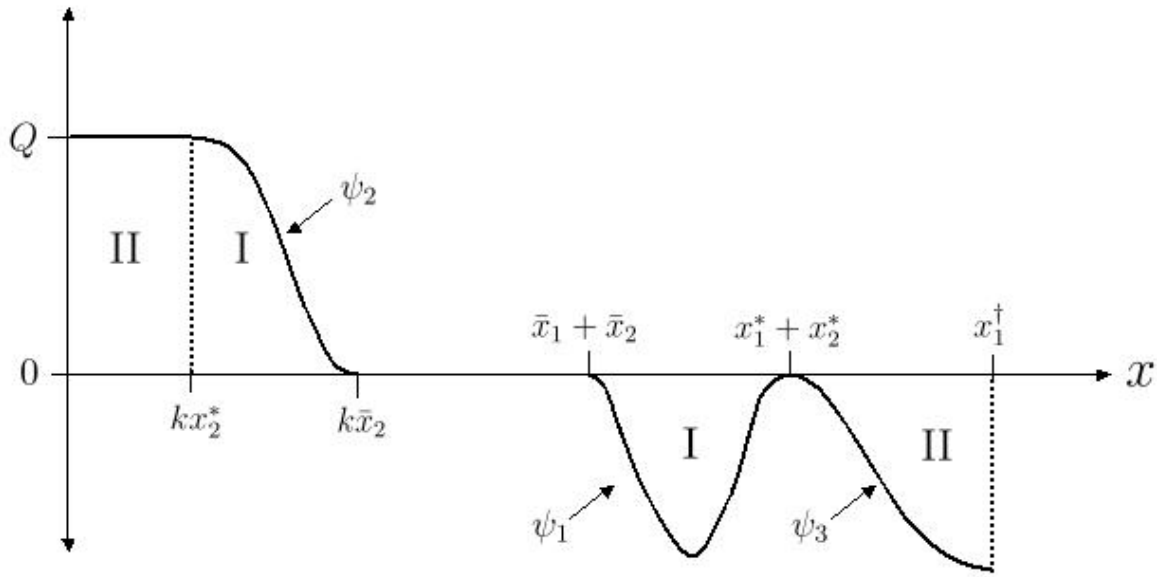

Figure 2: The functions ψ_1, ψ_2, and ψ_3. Areas with the same roman numerals corresponds to regions whose areas sum to zero.

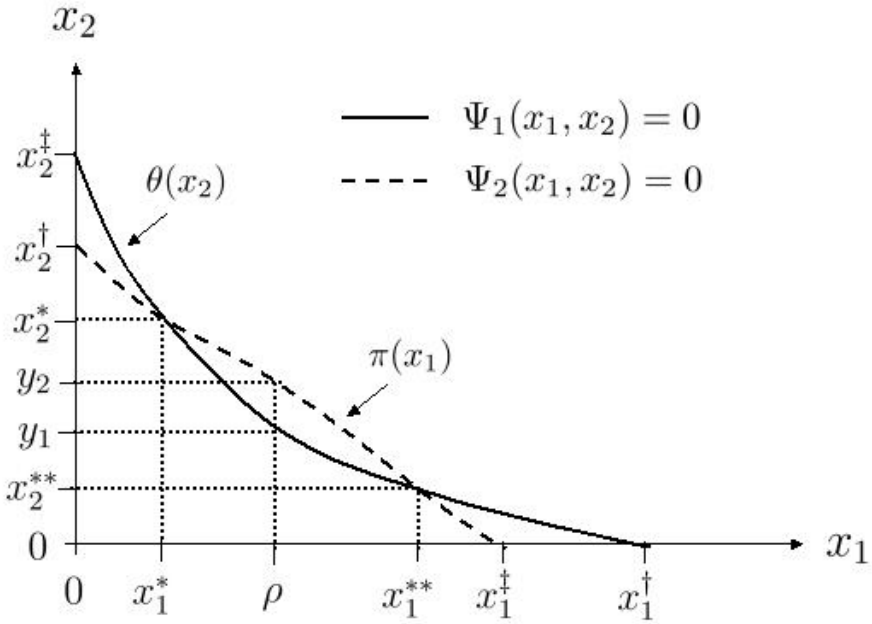

Figure 3: The species nullclines cross in at least two interior equilibrium points, producing locally stable coexistence at (x_1^*, x_2^*) and unstable coexistence at (x_1^{**}, x_2^{**}).

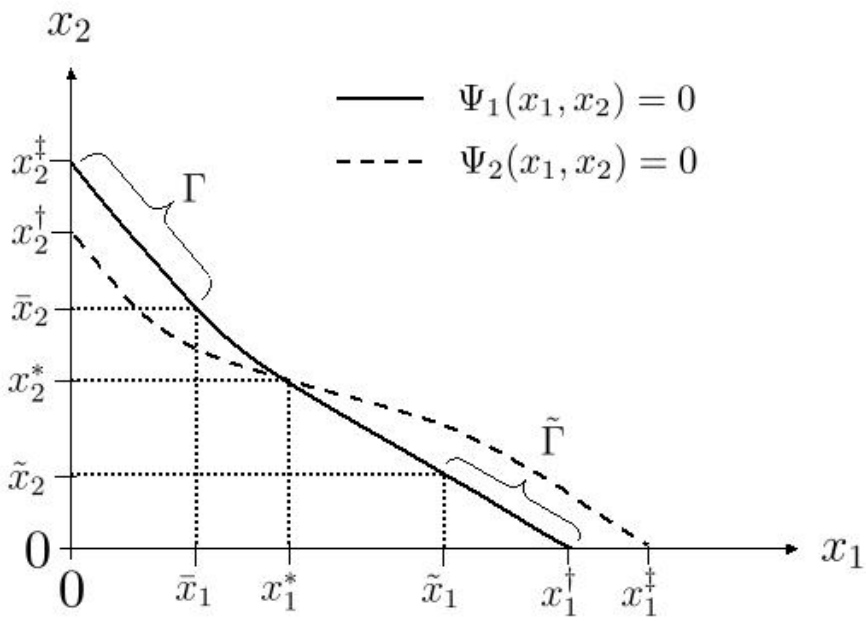

Figure 4: The sets of points Γ and $\tilde{\Gamma}$ on the species 1 nullcline.