The Role of Leaf Height in Plant Competition for Sunlight

Analysis of a canopy partitioning model

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Abstract

A global method of nullcine endpoint analysis is employed to determine the outcome of competition for sunlight between two hypothetical plant species with clonal growth form that differ solely in the height at which they place their leaves above the ground. This difference in vertical leaf placement, or *canopy partitioning*, produces species differences in sunlight energy capture and stem metabolic maintenance costs. The competitive interaction between these two species is analyzed by considering a special case of the Canopy Partitioning Model (RR Vance and AL Nevai, J. Theor. Biol. 2007, 245:210-219; AL Nevai and RR Vance, J. Math. Biol. 2007, 55:105-145). Nullcline endpoint analysis is used to partition parameter space into regions within which either competitive exclusion or competitive coexistence occurs. The principal conclusion is that two clonal plant species which compete for sunlight and place their leaves at different heights above the ground but differ in no other way can, under suitable parameter values, experience stable coexistence even though they occupy an environment which varies neither over horizontal space nor through time.

Keywords: canopy partitioning model – canopy structure model – plant competition – light competition – stable coexistence – mathematical model

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1 Introduction

Intuitively, it seems that plant species that compete for the same limiting resources (water, nutrients, and sunlight) should not be able to coexist at stable equilibrium abundances unless they partition these resources in some way [1, 2]; indeed, without such resource partitioning, it seems that the strongest competitor will simply drive all others to extinction [3, 4]. We have formulated a Canopy Partitioning Model [5, 6] specifically to determine whether two plant species with clonal growth form that compete only for sunlight can coexist when they differ only in the heights at which they place their leaves. This difference in vertical leaf placement generates a partitioning of the canopy into different height ranges within which either or both species' leaves lie.

In the spirit of addressing just one complicated problem at a time, we have employed assumptions that purposely eliminate other potential mechanisms of plant competitive coexistence known to be important in nature. In particular, we assume that the environment remains homogeneous through horizontal space and through time, that herbivores are absent, and that all resources other than sunlight always occur in excess. In addition, we purposely simplify descriptions of some plant structural and physiological properties. As explained in [5] and explored further in Nevai and Vance (in preparation), we feel that understanding of some subjects in plant competition is likely to come most easily by beginning with somewhat idealized models and then reintroducing realism gradually. The purpose of this paper is to complete analysis of the two-species competition problem begun in [6].

We show in [6] that if two such light-limited clonal species share the same vertical leaf profile, then no combination of other species differences will enable them to coexist stably. Thus, canopy partitioning is a necessary condition for competitive coexistence to occur. This conclusion agrees with similar results obtained by others [2, 7]. We also show in [6] that canopy partitioning can produce competitive coexistence, but our analysis failed to disentangle the role of leaf height *per se* from the roles of other features of plant structure and function such as stem density, tissue metabolic rate, and so on. That analysis merely showed that there exists a region in multi-dimensional parameter space within which coexistence occurs. What that analysis did not reveal is the role of each feature of plant structure and function individually in producing this coexistence.

In this paper, we ask whether two plant species that compete for sunlight can coexist simply by deploying their leaves at different heights above the ground. That is, we consider a converse to the earlier result: Is canopy partitioning *by itself* ever sufficient for two hypothetical clonal plant species to coexist competitively, even when they experience no environmental variation through horizontal space or time and they differ in no other way?

1.1 Statement of the problem

Consider two species ($i = 1, 2$) that satisfy the Kolmogorov-type [8] system of competition equations

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

We assume that $x_1(0) > 0$ and $x_2(0) > 0$, so that both species are initially present. The *allocation* functions $\mathtt{s}_1(z)$ and $\mathtt{s}_2(z)$ are probability density functions defined for $z \geq 0$. Their complementary cumulative distribution functions are denoted by $\mathtt{S}_i(z) = \int_z^\infty \mathtt{s}_i(\zeta)\,d\zeta$. We assume that the *gain* function $\phi(x)$ has the following properties:

P$_1$. ϕ is a continuously differentiable function of $x \geq 0$;

P$_2$. $\phi > 0$ for $x \geq 0$;

P$_3$. $\phi' < 0$ for $x \geq 0$;

P$_4$. $\phi \to 0$ as $x \to \infty$.

Observe that properties P$_1$-P$_4$ imply several additional "average value" properties,

P$_5$. $\phi(vx) < \frac{1}{v-u}\int_u^v \phi(\alpha x)\,d\alpha < \phi(ux)$ for $x > 0$ and $0 \leq u < v$;

P$_6$. $\int_u^v \phi(\alpha x)\,d\alpha$ is a continuous and strictly decreasing function of $x \geq 0$ for $0 \leq u < v$;

P$_7$. $\int_u^v \phi(\alpha x)\,d\alpha \to 0$ as $x \to \infty$ for $0 \leq u < v$.

The growth and cost parameters (γ_i and C_i) are both assumed to be positive. Let $s_i = \int_0^\infty z\mathtt{s}_i(z)\,dz$ denote the mean value of species i's allocation function.

The dynamical system (1.1) arises in the study of plant competition for sunlight [5]. Modeled are two interacting clonal plant species whose leaves partition the canopy vertically according to the allocation functions (or *vertical leaf profiles*). Biologically, $x_i = x_i(t)$ represents the total leaf area per unit ground area of species i at time t; the vertical leaf area density of species i at height z is $\mathtt{s}_i(z)$; the fraction of species i's leaves that overlie height z is $\mathtt{S}_i(z)$; the area of leaves overlying height z that belong to species i is $\mathtt{S}_i(z)x_i$; and the rate of instantaneous gross photosynthesis performed by a unit area of horizontal leaf surface belonging to either species that lies beneath combined leaf area x is $\phi(x)$. Although higher leaves belonging to either species receive more sunlight and therefore perform photosynthesis at higher rates than lower leaves, the former must also be supported by taller stems. The energetic cost of maintaining the stems that support a given vertical leaf profile is reflected in the species cost parameter C_i. A full description of the model, including biological explanations of all parameters and functions, appears in [5]. We remark that our decision to use allocation functions $\mathtt{s}_i(z)$ to describe vertical leaf placement was inspired by [7], in which similar functions are used to describe the vertical distribution of phytoplankton populations that compete for sunlight in a lake. Also, our model's description of various plant structures and their functions is based in part on many previous plant models (e.g., [9, 10, 11]).

The dynamics of (1.1) has been examined recently in special cases [6, 12]. As the competitive system (1.1) is dissipative and planar, it follows that every solution converges to an equilibrium [13]. Therefore, the long-term outcome of competition is determined entirely by the relative positions of the two species' non-trivial nullclines, which are defined by

$$\int_0^\infty \phi\big(\mathtt{S}_1(z)x_1 + \mathtt{S}_2(z)x_2\big)\mathtt{s}_i(z)\,dz = C_i, \quad i = 1, 2. \tag{1.2}$$

We will assume that these two plant species are identical in all ways except for the heights at which they place their leaves (as represented by the allocation functions), and that their cost parameter difference $(C_2 - C_1)$ is proportional to the difference in their mean leaf height $(s_2 - s_1)$.

We assume that each species has a rectangular (or uniform) allocation function of thickness $T > 0$, i.e.,

$$\mathbf{s}_1(z) = \begin{cases} \sigma, & z \in [s_1 - T/2, s_1 + T/2], \\ 0, & \text{elsewhere}, \end{cases}$$
$$\mathbf{s}_2(z) = \begin{cases} \sigma, & z \in [s_2 - T/2, s_2 + T/2], \\ 0, & \text{elsewhere}, \end{cases} \tag{1.3}$$

where $\sigma = 1/T$ and $s_2 \geq s_1 \geq T/2$. We also assume that the species cost difference is proportional to the allocation difference. That is, by letting $\tau = s_2 - s_1$, we assume that

$$C_2 = C_1 + b\tau \tag{1.4}$$

for some positive constant b. In view of (1.3), species 2 is τ units taller than species 1. The leaves of species 2 which reside in the overstory (i.e., at heights greater than $s_1 + T/2$) capture more sunlight than the highest leaves of species 1 simply because there are fewer leaves above them to cast shade. However, this advantage in energy capture is accompanied by the additional energetic cost of maintaining taller stems to support these higher leaves, which is represented in (1.4). The purpose of this paper is to examine this tradeoff explicitly for different values of τ.

Incorporating (1.3) and (1.4) into (1.2) yields a simplified form for the nullcline equations

$$\begin{aligned} \int_0^1 \phi\big(\alpha x_1 + \min\{\alpha + \sigma\tau, 1\} x_2\big)\, d\alpha &= C_1, \\ \int_0^1 \phi\big(\max\{\alpha - \sigma\tau, 0\} x_1 + \alpha x_2\big)\, d\alpha &= C_1 + b\tau. \end{aligned} \tag{1.5}$$

As shown in [6, Theorems 2.4 and 2.5], these nullclines coincide at most once within the closed first quadrant when $\tau > 0$ (they coincide everywhere when $\tau = 0$). When $\tau > 0$ and they do coincide, their intersection forms an equilibrium point for the competitive system whose stability is determined entirely by the manner in which the nullclines meet there. Unfortunately, inspection of the Jacobian at this equilibrium point proves unhelpful. However, since the nullclines can coincide at most once, it suffices to determine the relative magnitudes of the nullcline endpoints. That is, if $(x_1^\dagger, 0)$ and $(0, x_2^\ddagger)$ represent the endpoints of the species 1 nullcline, and $(x_1^\ddagger, 0)$ and

$(0, x_2^\dagger)$ represent the endpoints of the species 2 nullcline, then we need only determine the relative magnitudes of the pair $x_1^\dagger$ and $x_1^\ddagger$, and the relative magnitudes of the pair $x_2^\ddagger$ and $x_2^\dagger$, to determine the outcome of competition (see Figure 1). In particular, if $x_1^\dagger > x_1^\ddagger$ and $x_2^\ddagger > x_2^\dagger$ then the species 1 nullcline lies farther from the origin than the species 2 nullcline, and so species 1 always drives species 2 to extinction. (Stochastic fluctuations in the biological system which our deterministic model is meant to approximate together with the fact that nullclines can coincide at most once imply that the same conclusion holds in the improbable event that the nullclines meet and are tangent at a single point [14].) If one or both of these inequalities is reversed then other outcomes are potentially possible, including species 2 driving species 1 to extinction ($x_1^\dagger < x_1^\ddagger$ and $x_2^\ddagger < x_2^\dagger$), the stable coexistence of both species ($x_1^\dagger < x_1^\ddagger$ and $x_2^\ddagger > x_2^\dagger$), and bistability (or founder control) in which either species can drive the other to extinction with the identity of the surviving species depending on initial conditions ($x_1^\dagger > x_1^\ddagger$ and $x_2^\ddagger < x_2^\dagger$).

Since the value of a nullcline endpoint (which we identify from now on by its non-zero component) depends on the parameters of the model, it follows that different combinations of parameters may give rise to different outcomes of competition. Thus, we would like to divide parameter space into regions associated with these possible outcomes. Nevai and Vance [6] have produced such a bifurcation diagram for two species that can differ in multiple ways at the same time in a manner described by several composite parameters. However, this diagram provides information about the competitive system studied here only when τ is fixed. To determine the outcome of competition as τ varies, we must perform further analysis.

The defining equations for the four nullcline endpoints arise from (1.5) by setting either $x_1 = 0$ or $x_2 = 0$. These are displayed as (I)-(IV) in Table 1. There, we make use of the following notation: $C^{\mathrm{m}} \stackrel{\mathrm{def}}{=} \phi(0)$, $\tau^{\mathrm{m}} \stackrel{\mathrm{def}}{=} (C^{\mathrm{m}} - C_1)/b$,

$$C_2(\tau) = C_1 + b\tau, \tag{1.6}$$

and $\overline{\sigma\tau} \stackrel{\mathrm{def}}{=} \min(\sigma\tau, 1)$. Observe from the second relation that

$$C^{\mathrm{m}} = C_1 + b\tau^{\mathrm{m}}. \tag{1.7}$$

If $C_1 \geq C^{\mathrm{m}}$ (or $\tau^{\mathrm{m}} \leq 0$) then neither species nullcline exists (except perhaps at the origin) by (1.5) and the properties of ϕ. In this case, both species always become extinct because their cost parameters are too high. Furthermore, if $C_1 < C^{\mathrm{m}}$ (or $\tau^{\mathrm{m}} > 0$) and $\tau > \tau^{\mathrm{m}}$, then only the species 1 nullcline exists and species 1 always excludes species 2. Thus, τ^{m} is a threshold value for τ, beyond which species 2 cannot persist even when living alone. Consequently, we restrict our attention in this paper to cases in which $C_1 < C^{\mathrm{m}}$ (or $\tau^{\mathrm{m}} > 0$) and $\tau \in [0, \tau^{\mathrm{m}}]$, so that both species nullclines exist in the closed first quadrant. To simplify parts of our analysis, whenever a nullcline exists but does not intersect one of the coordinate axes, we will by convention set that nullcline endpoint equal to infinity.

Observe that if $\tau^{\mathrm{m}} > T$, then the nullcline for species 2 can exist in the closed first quadrant even when the allocation functions share no support, provided that $\tau \in [T, \tau^{\mathrm{m}}]$. However, if $\tau^{\mathrm{m}} < T$ then the nullcline for species 2 cannot exist when the supports of the two allocation functions do not overlap.

Our ultimate goal is to compare the relative magnitudes of $x_1^{\ddagger}$ and $x_1^{\dagger}$, and the relative magnitudes of $x_2^{\ddagger}$ and $x_2^{\dagger}$, for fixed values of $\sigma \geq 0$ as the allocation difference τ increases from 0 to τ^{m}. We will explore this problem by partitioning the σ-τ parameter plane into regions within which both pairs of nullcline endpoints maintain fixed orders. Although $x_1^{\dagger}$ does not depend on τ, we sometimes emphasize the τ-dependence of the other nullcline endpoints by writing them as $x_1^{\ddagger}(\tau)$, $x_2^{\dagger}(\tau)$, and $x_2^{\ddagger}(\tau)$. Inspection of (II) and (IV) in Table 1 reveals that the endpoints $x_1^{\ddagger}$ and $x_2^{\ddagger}$ depend not only on τ but also on σ. However, we will treat σ as fixed (albeit arbitrary) throughout and thus avoid (usually) any need to consider the σ-dependence of $x_1^{\ddagger}$ and $x_2^{\ddagger}$ explicitly.

The phrases "$x \geq 0$" and "$x > 0$" always imply that x is finite unless it is explicitly stated otherwise or it is clear from context. To simplify notation, we will write "$x \preceq y$ for $u \preceq v$" to represent the situation in which $x < y$ when $u < v$, $x = y$ when $u = v$, and $x > y$ when $u > v$. Also, we will write "$x \preccurlyeq y$ for $u \preccurlyeq v$" to represent the situation in which $x = y$ when $u = 0$ and $x \preceq y$ for $u \preceq v$ when $u > 0$. Some situations may require the first "$\preceq$" or "$\preccurlyeq$" in each pair to be replaced by "$\succeq$" or "$\succcurlyeq$", respectively.

1.2 Statement of the main results

In §2, we identify a region in parameter space in which $x_1^\ddagger(\tau) < x_1^\dagger$ and another region in which $x_1^\ddagger(\tau) > x_1^\dagger$ (see Figure 2a). Let $\tau^{-\mathrm{m}} \stackrel{\mathrm{def}}{=} 1/\tau^{\mathrm{m}}$.

Theorem 1. *Let $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$. There exists some $\sigma^* \in (0, \tau^{-\mathrm{m}})$ with the following properties:*

(a) *If $\sigma \leq \sigma^*$ then $x_1^\ddagger(\tau) \leq x_1^\dagger$ with equality if and only if $\tau = 0$;*

(b) *If $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$ then there exists some $\tau_1(\sigma) \in (0, \tau^{\mathrm{m}})$ such that $x_1^\ddagger(\tau) \gtrless x_1^\dagger$ for $\tau \lessgtr \tau_1$;*

(c) *If $\sigma \geq \tau^{-\mathrm{m}}$ then $x_1^\ddagger(\tau) \geq x_1^\dagger$ with equality if and only if $\tau = 0$;*

(d) *τ_1 is a continuous and strictly increasing function of $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$;*

(e) *$\tau_1 \to 0$ as $\sigma \to \sigma^*$ and $\tau_1 \to \tau^{\mathrm{m}}$ as $\sigma \to \tau^{-\mathrm{m}}$.*

In §3, we identify regions in parameter space in which $x_2^\ddagger(\tau)$ and $x_2^\dagger(\tau)$ maintain fixed orders (see Figure 2b). Let $\tau^{-*} \stackrel{\mathrm{def}}{=} 1/\tau^*$.

Theorem 2. *Let $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$. There exists some $\tau^* \in (0, \tau^{\mathrm{m}})$ with the following properties:*

(a) *If $\sigma \leq \sigma^*$ then $x_2^\ddagger(\tau) \geq x_2^\dagger(\tau)$ with equality if and only if $\tau = 0$;*

(b) *If $\sigma \in (\sigma^*, \tau^{-*})$ then there exists some $\tau_2(\sigma) \in (0, \tau^*)$ such that $x_2^\ddagger(\tau) \lessgtr x_2^\dagger(\tau)$ for $\tau \lessgtr \tau_2$;*

(c) *If $\sigma \geq \tau^{-*}$ then $x_2^\ddagger(\tau) \lessgtr x_2^\dagger(\tau)$ for $\tau \lessgtr \tau^*$;*

(d) *τ_2 is a continuous and strictly increasing function of $\sigma \in (\sigma^*, \tau^{-*})$;*

(e) *$\tau_2 \to 0$ as $\sigma \to \sigma^*$ and $\tau_2 \to \tau^*$ as $\sigma \to \tau^{-*}$.*

Finally, in §4 we establish regions in parameter space within which both pairs of nullcline endpoints maintain fixed orders (see Figure 2c).

Theorem 3. *$\tau_1(\sigma) > \tau_2(\sigma)$ for $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$.*

The biological implications of these results are presented in the Discussion.

2 The First Bifurcation

In this section, we examine the relative magnitudes of $x_1^\dagger$ and $x_1^\ddagger(\tau)$ for $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$. Recall that these endpoints satisfy equations (I) and (II) in Table 1, respectively. First, we show that $x_1^\dagger$ is finite, and we consider regions in parameter space within which $x_1^\ddagger(\tau)$ is either finite or infinite. Then we determine some additional properties of the function $x_1^\ddagger(\tau)$ within the region where it is finite. Next, we divide parameter space into regions within which the sign of $dx_1^\ddagger/d\tau$ is constant. Finally, we establish the existence, shape, and location of the function τ_1 in Theorem 1 whose graph divides parameter space into regions within which $x_1^\ddagger(\tau)$ and $x_1^\dagger$ maintain a fixed order.

For the remainder of this section, we assume that $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$. Then, as is evident from (1.6) and (1.7), the function $C_2(\tau)$ will always take values within the interval $[C_1, C^{\mathrm{m}}]$.

2.1 Elementary properties of $x_1^\dagger$ and $x_1^\ddagger(\tau)$

Define τ_∞ by the relation

$$C_2(\tau_\infty) = \sigma \tau_\infty C^{\mathrm{m}}. \tag{2.1}$$

We rearrange this equation to obtain

$$\tau_\infty = \frac{C_1}{\sigma C^{\mathrm{m}} - b}. \tag{2.2}$$

We will usually omit the argument σ in the function τ_∞ and in the τ_i-functions that follow. It is clear by inspection that τ_∞ is a positive, continuous, and strictly decreasing function of $\sigma \geq \tau^{-\mathrm{m}}$, from (1.7) that $\tau_\infty = \tau^{\mathrm{m}}$ when $\sigma = \tau^{-\mathrm{m}}$, and that $\tau_\infty \to 0$ as $\sigma \to \infty$.

We now show that $x_1^\dagger$ is finite and that the graph of τ_∞ divides parameter space into a region in which $x_1^\ddagger(\tau)$ is finite, and another in which it is infinite (see Figure 3).

Lemma 2.1. *Let $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$. Then $x_1^\dagger$ and $x_1^\ddagger(\tau)$ exist, they are unique, and $x_1^\dagger > 0$. Furthermore,*

(a) *If $\sigma < \tau^{-\mathrm{m}}$ then $x_1^\ddagger(\tau) \geq 0$;*

(b) *If $\sigma \geq \tau^{-\mathrm{m}}$ then $x_1^\ddagger(\tau) \geq 0$ for $\tau < \tau_\infty$ and $x_1^\ddagger(\tau) = \infty$ for $\tau \geq \tau_\infty$.*

Proof. By property P_6, the function $\Phi(x;u) = uC^{\mathrm{m}} + \int_0^{1-u} \phi(\alpha x)\, d\alpha$ is a continuous and strictly decreasing function of $x \geq 0$ for $u \in [0,1)$. Furthermore, $\Phi(0;u) = C^{\mathrm{m}}$ and $\Phi(x;u) \to uC^{\mathrm{m}}$ as $x \to \infty$ by property P_7. Eq. (I) and the properties of Φ with $u = 0$ imply that $x_1^{\dagger}$ exists, it is unique, and that $x_1^{\dagger} > 0$. We now consider the endpoint $x_1^{\ddagger}(\tau)$.

(a) Suppose first that $\sigma < \tau^{-\mathrm{m}}$. Then $0 \leq \sigma\tau < 1$. If follows from (1.6) and (1.7) that

$$C_2(\tau) = C_1 + b\tau \geq \tau^{-\mathrm{m}}\tau C_1 + b\tau = \tau^{-\mathrm{m}}\tau(C_1 + b\tau^{\mathrm{m}}) > \sigma\tau C^{\mathrm{m}}.$$

Eq. (II) and the properties of Φ with $u = \sigma\tau$ imply that $x_1^{\ddagger}(\tau)$ exists, it is unique, and that $x_1^{\ddagger}(\tau) \geq 0$ (with equality if and only if $\tau = \tau^{\mathrm{m}}$).

(b) Suppose now that $\sigma \geq \tau^{-\mathrm{m}}$. Eq. (II) and the properties of Φ with $u = \sigma\tau$ imply that if $\sigma\tau C^{\mathrm{m}} < C_2(\tau)$ then again $x_1^{\ddagger}(\tau)$ exists, it is unique, and $x_1^{\ddagger}(\tau) \geq 0$; but if $\sigma\tau C^{\mathrm{m}} \geq C_2(\tau)$ then $x_1^{\ddagger}(\tau)$ is undefined and so by convention is equal to infinity. By (2.2), if $\tau < \tau_\infty$ then

$$\tau < \frac{C_1}{\sigma C^{\mathrm{m}} - b}.$$

The positivity of $\sigma C^{\mathrm{m}} - b$ (which follows from the positivity of τ_∞) and (1.6) together imply that $\sigma\tau C^{\mathrm{m}} < C_2(\tau)$. A similar argument shows that if $\tau \geq \tau_\infty$ then $\sigma\tau C^{\mathrm{m}} \geq C_2(\tau)$ (with equality if and only if $\tau = \tau_\infty$). The conclusion follows from the remarks above. □

We now restrict our attention to values of $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$ for which $x_1^{\ddagger}(\tau)$ is finite. The next lemma describes elementary properties of the endpoint $x_1^{\ddagger}$ as a function of τ within the region where it is finite.

Lemma 2.2. *Let $\sigma \geq 0$. Then*

(a) $x_1^{\ddagger}(0) = x_1^{\dagger}$;

(b) $x_1^{\ddagger}$ *is a continuously differentiable function of τ (where it is finite), with*

$$\frac{dx_1^{\ddagger}}{d\tau} = \frac{b - \sigma\big[C^{\mathrm{m}} - \phi\big((1-\sigma\tau)x_1^{\ddagger}\big)\big]}{\int_0^{1-\sigma\tau} \phi'(\alpha x_1^{\ddagger})\alpha\, d\alpha}; \tag{2.3}$$

(c) *If $\sigma < \tau^{-\mathrm{m}}$ then $x_1^{\ddagger}(\tau^{\mathrm{m}}) = 0$;*

(d) *If* $\sigma > \tau^{-\mathrm{m}}$ *then* $x_1^\ddagger(\tau) \to \infty$ *as* $\tau \to \tau_\infty$.

Proof.

(a) This part follows from (II), (1.6) with $\tau = 0$, (I), and property P_6.

(b) Suppose that $x_1^\ddagger(\tau)$ is finite for some value of $\tau \in [0, \tau^{\mathrm{m}}]$. Then $x_1^\ddagger$ is continuously differentiable at τ by the implicit function theorem. To obtain an expression for $dx_1^\ddagger/d\tau$, we differentiate (II) implicitly with respect to τ and rearrange to get

$$b = \sigma\big[C^{\mathrm{m}} - \phi\big((1-\sigma\tau)x_1^\ddagger\big)\big] + \frac{dx_1^\ddagger}{d\tau}\int_0^{1-\sigma\tau} \phi'(\alpha x_1^\ddagger)\alpha \, d\alpha,$$

where $x_1^\ddagger = x_1^\ddagger(\tau)$. The conclusion follows from solving for $dx_1^\ddagger/d\tau$.

(c) Suppose that $\sigma < \tau^{-\mathrm{m}}$. Letting $\tau = \tau^{\mathrm{m}}$ in (II) yields

$$C^{\mathrm{m}} = \sigma\tau^{\mathrm{m}}C^{\mathrm{m}} + \int_0^{1-\sigma\tau^{\mathrm{m}}} \phi(\alpha x_1^\ddagger)\, d\alpha,$$

where $\sigma\tau^{\mathrm{m}} \in [0,1)$ and $x_1^\ddagger = x_1^\ddagger(\tau^{\mathrm{m}})$. The properties of ϕ imply that $x_1^\ddagger(\tau^{\mathrm{m}}) = 0$.

(d) Suppose that $\sigma > \tau^{-\mathrm{m}}$ and let $\tau_j \in [0, \tau_\infty)$ be a sequence with $\tau_j \to \tau_\infty$ as $j \to \infty$. Eq. (II) with $\tau = \tau_j$ yields

$$C_2(\tau_j) - \sigma\tau_j C^{\mathrm{m}} = \int_0^{1-\sigma\tau_j} \phi(\alpha x_j)\, d\alpha,$$

where $x_j = x_1^\ddagger(\tau_j) \geq 0$ by Lemma 2.1 (b). The left-hand side converges to 0 as $j \to \infty$ by (2.1). Therefore, the right-hand side must also vanish in the limit. In view of the fact that $0 \leq \sigma\tau_j < \sigma\tau_\infty = C_2(\tau_\infty)/C^{\mathrm{m}} < 1$, it follows from property P_2 that the truncated integral

$$\int_0^{1-\sigma\tau_\infty} \phi(\alpha x_j)\, d\alpha$$

converges to 0 as $j \to \infty$. Property P_7 implies that $x_j \to \infty$ as $j \to \infty$. □

2.2 The sign of $dx_1^\ddagger/d\tau$

We would like to determine regions in parameter space within which $dx_1^\ddagger/d\tau$ in (2.3) has constant sign. First, we observe from integration by parts and property P_1 that

$$\int_0^u \phi(\alpha x)\, d\alpha = u\phi(ux) - x\int_0^u \phi'(\alpha x)\alpha\, d\alpha, \quad \text{for } x, u \geq 0. \tag{2.4}$$

We shall say that a function $f(x)$ is *α-increasing* on an interval I if f is a continuously differentiable function of $x \in I$ and $f' > 0$ for $x \in \mathrm{int}(I)$. Functions which are *α-decreasing* are defined in a similar manner. We now prove a preliminary result concerning the behavior of the product $(1-\sigma\tau)x_1^\ddagger(\tau)$ appearing in (2.3) as a function of τ.

Lemma 2.3. *Let $\sigma \geq 0$.*

(a) *If $\sigma < \tau^{-\mathrm{m}}$ then $(1-\sigma\tau)x_1^\ddagger(\tau)$ α-decreases from $x_1^\dagger$ to 0 as τ increases from 0 to τ^{m};*

(b) *If $\sigma = \tau^{-\mathrm{m}}$ then $(1-\sigma\tau)x_1^\ddagger(\tau)$ is equal to $x_1^\dagger$ for all $\tau \in [0, \tau^{\mathrm{m}})$;*

(c) *If $\sigma > \tau^{-\mathrm{m}}$ then $(1-\sigma\tau)x_1^\ddagger(\tau)$ α-increases from $x_1^\dagger$ to ∞ as τ increases from 0 to τ_∞.*

Proof.

(a) Suppose that $\sigma < \tau^{-\mathrm{m}}$ and let $\tau \in [0, \tau^{\mathrm{m}}]$. Then $x_1^\ddagger(\tau) \geq 0$ by Lemma 2.1 (a) and $0 \leq \sigma\tau \leq \sigma\tau^{\mathrm{m}} < 1$. It is clear from Lemma 2.2 (b) that $(1-\sigma\tau)x_1^\ddagger(\tau)$ is continuously differentiable at τ. Observe from (1.7) that

$$\sigma C^{\mathrm{m}} - b = \sigma C_1 + b(\sigma\tau^{\mathrm{m}} - 1) < \sigma C_1.$$

We subtract $\sigma\tau(\sigma C^{\mathrm{m}} - b)$ from both sides and divide by $1-\sigma\tau$ to get

$$\sigma C^{\mathrm{m}} - b < \frac{\sigma C_1 - \sigma\tau(\sigma C^{\mathrm{m}} - b)}{1-\sigma\tau}.$$

It follows from (1.6) and (II) that

$$\sigma C^{\mathrm{m}} - b < \frac{\sigma}{1-\sigma\tau}\int_0^{1-\sigma\tau} \phi(\alpha x_1^\ddagger)\, d\alpha,$$

where $x_1^\ddagger = x_1^\ddagger(\tau)$. Eq. (2.4) with $x = x_1^\ddagger$ and $u = 1 - \sigma\tau$ implies that

$$\sigma C^{\mathrm{m}} - b < \sigma \left[\phi\big((1-\sigma\tau)x_1^\ddagger\big) - \frac{x_1^\ddagger}{1-\sigma\tau} \int_0^{1-\sigma\tau} \phi'(\alpha x_1^\ddagger)\alpha \, d\alpha \right].$$

Noting that the integral on the right-hand side is negative by property P_3, we rearrange to get

$$\frac{b - \sigma\big[C^{\mathrm{m}} - \phi\big((1-\sigma\tau)x_1^\ddagger\big)\big]}{\int_0^{1-\sigma\tau} \phi'(\alpha x_1^\ddagger)\alpha \, d\alpha} < \frac{\sigma x_1^\ddagger}{1-\sigma\tau}.$$

It follows from (2.3) that

$$\frac{dx_1^\ddagger}{d\tau} < \frac{\sigma x_1^\ddagger}{1-\sigma\tau}.$$

The positivity of $1 - \sigma\tau$ implies that

$$\frac{d}{d\tau}\Big[(1-\sigma\tau)x_1^\ddagger\Big] = (1-\sigma\tau)\frac{dx_1^\ddagger}{d\tau} - \sigma x_1^\ddagger < 0.$$

Consequently, $(1-\sigma\tau)x_1^\ddagger$ is an α-decreasing function of $\tau \in [0, \tau^{\mathrm{m}}]$. Lemma 2.2 (a, c) implies that $(1-\sigma\tau)x_1^\ddagger = x_1^\dagger$ when $\tau = 0$ and $(1-\sigma\tau)x_1^\ddagger = 0$ when $\tau = \tau^{\mathrm{m}}$.

(b) Suppose that $\sigma = \tau^{-\mathrm{m}}$ and let $\tau \in [0, \tau^{\mathrm{m}})$. Then $x_1^\ddagger(\tau) \geq 0$ by Lemma 2.1 (b) and $0 \leq \sigma\tau < \sigma\tau^{\mathrm{m}} = 1$. As before, Lemma 2.2 (b) implies that $(1-\sigma\tau)x_1^\ddagger(\tau)$ is continuously differentiable at τ. This time, however, (1.7) implies that

$$\sigma C^{\mathrm{m}} - b = \sigma C_1 + b(\sigma\tau^{\mathrm{m}} - 1) = \sigma C_1,$$

where $x_1^\ddagger = x_1^\ddagger(\tau)$. The proof that $(1-\sigma\tau)x_1^\ddagger$ takes on a constant value is similar to the argument in part (a) but with all inequalities replaced by equalities, and Lemma 2.2 (a) implies that this value must be $x_1^\dagger$.

(c) Suppose that $\sigma > \tau^{-\mathrm{m}}$ and let $\tau \in [0, \tau_\infty)$. Then $x_1^\ddagger(\tau) \geq 0$ by Lemma 2.1 (b) and $0 \leq \sigma\tau < \sigma\tau_\infty = C_2(\tau_\infty)/C^{\mathrm{m}} < 1 < \sigma\tau^{\mathrm{m}}$. Once again, Lemma 2.2 (b) implies that $(1-\sigma\tau)x_1^\ddagger(\tau)$ is continuously differentiable at τ. Now, (1.7) implies that

$$\sigma C^{\mathrm{m}} - b = \sigma C_1 + b(\sigma\tau^{\mathrm{m}} - 1) > \sigma C_1,$$

where $x_1^\ddagger = x_1^\ddagger(\tau)$. The proof that $(1-\sigma\tau)x_1^\ddagger$ is an α-increasing function of τ is similar to the argument in part (a) but with all inequalities reversed. Furthermore, Lemma 2.2 (a, d) implies that $(1-\sigma\tau)x_1^\ddagger = x_1^\dagger$ when $\tau = 0$ and $(1-\sigma\tau)x_1^\ddagger \to \infty$ as $\tau \to \tau_\infty$. $\square$

Observe from (1.7), (I), and property P_5 that

$$C^{\mathrm{m}} = C_1 + b\tau^{\mathrm{m}} = \int_0^1 \phi(\alpha x_1^\dagger)\, d\alpha + b\tau^{\mathrm{m}} > \phi(x_1^\dagger) + b\tau^{\mathrm{m}}.$$

We conclude that the constant

$$\sigma^* = \frac{b}{C^{\mathrm{m}} - \phi(x_1^\dagger)}$$

satisfies $\sigma^* \in (0, \tau^{-\mathrm{m}})$. It will be useful to note that if $\sigma \geq 0$ then

$$\sigma\big[C^{\mathrm{m}} - \phi(x_1^\dagger)\big] \preceq b \quad \text{for} \quad \sigma \preceq \sigma^*. \tag{2.5}$$

We now divide the parameter plane into regions within which $dx_1^\ddagger/d\tau$ has constant sign.

Lemma 2.4. *Let $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$.*

(a) *If $\sigma \leq \sigma^*$ then $dx_1^\ddagger/d\tau \leq 0$ with equality if and only if $(\sigma, \tau) = (\sigma^*, 0)$;*

(b) *If $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$ then there exists some $\tau_0 \in (0, \tau^{\mathrm{m}})$ such that $dx_1^\ddagger/d\tau \succeq 0$ for $\tau \preceq \tau_0$;*

(c) *If $\sigma \geq \tau^{-\mathrm{m}}$ then $dx_1^\ddagger/d\tau > 0$ for $\tau \in [0, \tau_\infty)$.*

Proof.

(a) Let $\sigma \in [0, \sigma^*]$. Then $x_1^\ddagger(\tau)$ is finite for $\tau \in [0, \tau^{\mathrm{m}}]$. In view of (2.3) we introduce the function

$$G(\tau) = b - \sigma\big[C^{\mathrm{m}} - \phi\big((1-\sigma\tau)x_1^\ddagger(\tau)\big)\big].$$

Lemma 2.2 (b) implies that G is a continuous function of $\tau \in [0, \tau^{\mathrm{m}}]$. Lemma 2.3 (a), the relation $C^{\mathrm{m}} = \phi(0)$, and property P_3 together imply that G strictly increases from

$$G(0) = b - \sigma\big[C^{\mathrm{m}} - \phi(x_1^\dagger)\big]$$

to $G(\tau^{\mathrm{m}}) = b$ as τ increases from 0 to τ^{m}. Eq. (2.5) implies that $G(0) \geq 0$, with equality if and only if $\sigma = \sigma^*$. Therefore, $G(\tau) \geq 0$ for all $\tau \in [0, \tau^{\mathrm{m}}]$, with equality if and only if $(\sigma, \tau) = (\sigma^*, 0)$. The conclusion follows from the fact that $G(\tau)$ and $dx_1^\ddagger/d\tau$ have opposite signs, as is evident by inspection of (2.3) and property P_3.

(b) Let $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$. Then $x_1^\ddagger(\tau)$ is finite for $\tau \in [0, \tau^{\mathrm{m}}]$. The function $G(\tau)$ defined in part (a) is again a continuous and strictly increasing function of $\tau \in [0, \tau^{\mathrm{m}}]$. This time, (2.5) implies that $G(0) < 0 < G(\tau^{\mathrm{m}})$. Therefore, there exists some $\tau_0 \in (0, \tau^{\mathrm{m}})$ such that $G(\tau) \preceq 0$ for $\tau \preceq \tau_0$. Again, the result follows from the fact that $G(\tau)$ and $dx_1^\ddagger/d\tau$ have opposite signs.

(c) Let $\sigma \geq \tau^{-\mathrm{m}}$. Then $x_1^\ddagger(\tau)$ is finite for $\tau \in [0, \tau_\infty)$. This time, the function $G(\tau)$ defined in part (a) is a continuous and nonincreasing function of $\tau \in [0, \tau_\infty)$. Furthermore, (2.5) implies that $G(0) < 0$. Therefore, $G(\tau) < 0$ for all $\tau \in [0, \tau_\infty)$. As before, the conclusion follows from the fact that $G(\tau)$ and $dx_1^\ddagger/d\tau$ have opposite signs. □

The following lemma establishes the shape and location of the function τ_0 (see Figure 3).

Lemma 2.5. *The quantity τ_0 has the following properties:*

(a) *τ_0 is a continuous and strictly increasing function of $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$;*

(b) *$\tau_0 \to 0$ as $\sigma \to \sigma^*$ and $\tau_0 \to \tau^{\mathrm{m}}$ as $\sigma \to \tau^{-\mathrm{m}}$.*

Proof. Throughout this proof, we emphasize the σ-dependence of the endpoint $x_1^\ddagger$ in (II) by writing $x_1^\ddagger(\sigma, \tau)$ instead of $x_1^\ddagger(\tau)$.

(a) Let $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$ and $\tau \in [0, \tau^{\mathrm{m}}]$. The function $x_1^\ddagger(\sigma, \tau)$ is continuously differentiable at σ by the implicit function theorem. To obtain an expression for $\partial x_1^\ddagger/\partial\sigma$, we differentiate (II) implicitly with respect to σ and rearrange to get

$$0 = \tau\big[C^{\mathrm{m}} - \phi\big((1-\sigma\tau)x_1^\ddagger\big)\big] + \frac{\partial x_1^\ddagger}{\partial\sigma}\int_0^{1-\sigma\tau} \phi'(\alpha x_1^\ddagger)\alpha\, d\alpha,$$

where $x_1^\ddagger = x_1^\ddagger(\sigma, \tau)$. Solving for $\partial x_1^\ddagger/\partial\sigma$ yields

$$\frac{\partial x_1^\ddagger}{\partial\sigma} = \frac{\tau\big[\phi\big((1-\sigma\tau)x_1^\ddagger\big) - C^{\mathrm{m}}\big]}{\int_0^{1-\sigma\tau} \phi'(\alpha x_1^\ddagger)\alpha\, d\alpha}. \tag{2.6}$$

It follows from Lemma 2.4 (b) that $\tau_0 \in (0, \tau^{\rm m})$ exists and that $\partial x_1^\ddagger/\partial\tau$ vanishes when $\tau = \tau_0$. Eq. (2.3) with $\tau = \tau_0$ implies then that

$$\sigma\left[C^{\rm m} - \phi\big(\psi(\sigma,\tau_0)\big)\right] = b$$

where $\psi(\sigma,\tau) = (1-\sigma\tau)x_1^\ddagger(\sigma,\tau)$ and $\tau_0 = \tau_0(\sigma)$. Note that $\sigma\tau_0 \in (0,1)$ because $\sigma \in (\sigma^*, \tau^{-\rm m})$ and $\tau_0 \in (0, \tau^{\rm m})$. We differentiate the equation above implicitly with respect to σ and rearrange to get

$$b = \sigma^2\phi'(\psi(\sigma,\tau_0))\frac{d\left[\psi(\sigma,\tau_0)\right]}{d\sigma}.$$

The derivative $\phi'\big(\psi(\sigma,\tau_0)\big)$ is negative by property P_3. Therefore, the total derivative

$$\frac{d\left[\psi(\sigma,\tau_0)\right]}{d\sigma} = \frac{\partial\psi}{\partial\sigma} + \frac{\partial\psi}{\partial\tau}\frac{d\tau_0}{d\sigma}\bigg|_{(\sigma,\tau_0)}$$

must also be negative. The partial derivative $\partial\psi/\partial\tau(\sigma,\tau_0)$ is negative by Lemma 2.3 (a). It only remains to show that the partial derivative $\partial\psi/\partial\sigma(\sigma,\tau_0)$ is positive, as this would force $d\tau_0/d\sigma$ to be positive also. It follows from the relation $C^{\rm m} = \phi(0)$ and property P_5 that

$$C^{\rm m} > \frac{1}{1-\sigma\tau_0}\int_0^{1-\sigma\tau_0}\phi(\alpha x_1^\ddagger)\,d\alpha,$$

where $x_1^\ddagger = x_1^\ddagger(\sigma,\tau_0)$. Eq. (2.4) with $x = x_1^\ddagger$ and $u = 1-\sigma\tau_0$ implies that

$$C^{\rm m} > \phi\big((1-\sigma\tau_0)x_1^\ddagger\big) - \frac{x_1^\ddagger}{1-\sigma\tau_0}\int_0^{1-\sigma\tau_0}\phi'(\alpha x_1^\ddagger)\alpha\,d\alpha.$$

Noting that the integral on the right-hand side is negative by property P_3, we rearrange to get

$$\frac{\phi\big((1-\sigma\tau_0)x_1^\ddagger\big) - C^{\rm m}}{\int_0^{1-\sigma\tau_0}\phi'(\alpha x_1^\ddagger)\alpha\,d\alpha} > \frac{x_1^\ddagger}{1-\sigma\tau_0}.$$

Recalling (2.6) with $\tau = \tau_0$,

$$\frac{\partial x_1^\ddagger}{\partial\sigma} > \frac{\tau_0 x_1^\ddagger}{1-\sigma\tau_0}.$$

The positivity of $1-\sigma\tau_0$ implies that

$$\frac{\partial\psi}{\partial\sigma}(\sigma,\tau_0) = \frac{\partial}{\partial\sigma}\Big[(1-\sigma\tau_0)x_1^{\ddagger}\Big] = (1-\sigma\tau_0)\frac{\partial x_1^{\ddagger}}{\partial\sigma} - \tau_0 x_1^{\ddagger} > 0.$$

The claim is proved, and we conclude that $d\tau_0/d\sigma > 0$.

(b) Let $\sigma_j \in (\sigma^*, \tau^{-\mathrm{m}})$ be a strictly decreasing sequence with $\sigma_j \to \sigma^*$ as $j \to \infty$. According to part (a) and Lemma 2.4 (b), the sequence $\tau_0(\sigma_j)$ is strictly decreasing and bounded within the interval $(0, \tau^{\mathrm{m}})$. Thus, there exists some $\tilde{\tau} \in [0, \tau^{\mathrm{m}})$ such that $\tau_0(\sigma_j) \to \tilde{\tau}$ as $j \to \infty$. We argue by contradiction. Suppose that $\tilde{\tau} \in (0, \tau^{\mathrm{m}})$ and let $\hat{\tau} \in (0, \tilde{\tau})$. Since $\hat{\tau} < \tilde{\tau} < \tau_0(\sigma_j)$, we obtain from Lemma 2.4 (b) that $\partial x_1^{\ddagger}/\partial\tau(\sigma_j, \hat{\tau}) > 0$. It follows from taking limits that $\partial x_1^{\ddagger}/\partial\tau(\sigma^*, \hat{\tau}) \geq 0$. But Lemma 2.4 (a) with $\tau = \hat{\tau}$ implies that $\partial x_1^{\ddagger}/\partial\tau(\sigma^*, \hat{\tau}) < 0$, a contradiction. We conclude that $\tilde{\tau} = 0$, and thus $\tau_0 \to 0$ as $\sigma \to \sigma^*$. A similar argument shows that $\tau_0 \to \tau^{\mathrm{m}}$ as $\sigma \to \tau^{-\mathrm{m}}$. □

2.3 The relative magnitudes of $x_1^{\ddagger}(\tau)$ and $x_1^{\dagger}$

We now prove the main result of this section by establishing the existence, shape, and location of the bifurcation function τ_1 in Theorem 1.

Proof of Theorem 1.

(a) Let $\sigma \leq \sigma^*$. It follows from Lemmas 2.2 (a, c) and 2.4 (a) that $x_1^{\ddagger}(\tau)$ strictly decreases from $x_1^{\dagger}$ to 0 as τ increases from 0 to τ^{m}. Therefore $x_1^{\ddagger}(\tau) \leq x_1^{\dagger}$ with equality if and only if $\tau = 0$.

(b) Let $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$. It follows from Lemmas 2.2 (a, c) and 2.4 (b) that $x_1^{\ddagger}(\tau)$ strictly increases from $x_1^{\dagger}$ to some maximum value as τ increases from 0 to τ_0, and then $x_1^{\ddagger}(\tau)$ strictly decreases from this maximum to 0 as τ continues to increase beyond τ_0 to τ^{m}. Therefore, there exists some $\tau_1 \in (\tau_0, \tau^{\mathrm{m}})$ such that $x_1^{\ddagger}(\tau) \gtrless x_1^{\dagger}$ for $\tau \lessgtr \tau_1$. (Note that this conclusion is slightly stronger than what is stated in the theorem because it ensures that τ_1 is not only positive but also greater than τ_0; this additional fact is needed to prove parts (d) and (e) of this theorem.)

(c) Let $\sigma \geq \tau^{-\mathrm{m}}$. It follows from Lemmas 2.2 (a, d) and 2.4 (c) that $x_1^{\ddagger}(\tau)$ strictly increases from $x_1^{\dagger}$ to ∞ as τ increases from 0 to τ_∞. By convention, $x_1^{\ddagger}(\tau) = \infty$ for $\tau \in [\tau_\infty, \tau^{\mathrm{m}}]$. Therefore

$x_1^\ddagger(\tau) \geq x_1^\dagger$ with equality if and only if $\tau = 0$.

(d) Let $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$. Then $\tau_1 \in (\tau_0, \tau^{\mathrm{m}})$ exists and is defined by the equation $x_1^\ddagger(\tau_1) = x_1^\dagger$. Equivalently, τ_1 satisfies (II) with $x_1^\dagger$ in place of $x_1^\ddagger(\tau_1)$,

$$C_2(\tau_1) = \sigma\tau_1 C^{\mathrm{m}} + \int_0^{1-\sigma\tau_1} \phi(\alpha x_1^\dagger)\, d\alpha$$

with $\sigma\tau_1 \in (0,1)$. In view of (1.6), we differentiate the equation above implicitly with respect to σ and rearrange to get

$$b \cdot \frac{d\tau_1}{d\sigma} = \left[\tau_1 + \sigma\frac{d\tau_1}{d\sigma}\right]\big[C^{\mathrm{m}} - \phi\big((1-\sigma\tau_1)x_1^\dagger\big)\big].$$

Further rearrangement gives

$$\frac{d\tau_1}{d\sigma} = \frac{\tau_1\big[C^{\mathrm{m}} - \phi\big((1-\sigma\tau_1)x_1^\dagger\big)\big]}{dx_1^\ddagger/d\tau \int_0^{1-\sigma\tau_1} \phi'(\alpha x_1^\dagger)\alpha\, d\alpha},$$

where we have used (2.3) with $\tau = \tau_1$ and $x_1^\ddagger(\tau_1) = x_1^\dagger$. The bracketed expression in the numerator is positive because of the relation $C^{\mathrm{m}} = \phi(0)$, property P_3, and the fact that $(1-\sigma\tau_1)x_1^\dagger > 0$ by Lemma 2.3 (a) with $\tau = \tau_1 < \tau^{\mathrm{m}}$. The derivative $dx_1^\ddagger/d\tau$ is negative by Lemma 2.4 (b) with $\tau = \tau_1 > \tau_0$. The integral in the denominator is negative by property P_3. We conclude then that $d\tau_1/d\sigma > 0$.

(e) Let $\sigma_j \in (\sigma^*, \tau^{-\mathrm{m}})$ be a strictly decreasing sequence with $\sigma_j \to \sigma^*$ as $j \to \infty$. According to parts (b) and (d) and Lemma 2.5, the sequence $\tau_1(\sigma_j)$ is strictly decreasing and bounded within the interval $(0, \tau^{\mathrm{m}})$. Thus, there exists some $\tilde{\tau} \in [0, \tau^{\mathrm{m}})$ such that $\tau_1(\sigma_j) \to \tilde{\tau}$ as $j \to \infty$. We argue by contradiction. Suppose that $\tilde{\tau} \in (0, \tau^{\mathrm{m}})$ and let $\hat{\tau} \in (0, \tilde{\tau})$. Since $\hat{\tau} < \tilde{\tau} < \tau_1(\sigma_j)$, we obtain from part (b) that $x_1^\ddagger(\sigma_j, \hat{\tau}) > x_1^\dagger$, where we now express the σ-dependence of $x_1^\ddagger$ in (II). It follows from taking limits that $x_1^\ddagger(\sigma^*, \hat{\tau}) \geq x_1^\dagger$. But part (a) with $\tau = \hat{\tau}$ implies that $x_1^\ddagger(\sigma^*, \hat{\tau}) < x_1^\dagger$, a contradiction. We conclude that $\tilde{\tau} = 0$. Finally, let $\sigma_j \in (\sigma^*, \tau^{-\mathrm{m}})$ be a sequence with $\sigma_j \to \tau^{-\mathrm{m}}$ as $j \to \infty$. Part (b) implies that $\tau_0(\sigma_j) < \tau_1(\sigma_j) < \tau^{\mathrm{m}}$ for all j. Lemma 2.5 (b) implies that $\tau_0(\sigma_j) \to \tau^{\mathrm{m}}$ as $j \to \infty$. It follows then that $\tau_1(\sigma_j) \to \tau^{\mathrm{m}}$ as $j \to \infty$. □

3 The Second Bifurcation

In this section, we examine the relative magnitudes of $x_2^\dagger(\tau)$ and $x_2^\ddagger(\tau)$ for $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$. Recall that these endpoints satisfy equations (III) and (IV) in Table 1, respectively. First, we show that $x_2^\ddagger(\tau)$ and $x_2^\dagger(\tau)$ are finite throughout parameter space. Next, we determine their relative magnitudes within the upper portion of this region. In the remaining lower region, we introduce functions $M(\tau)$ and $N(\tau)$ which have the property that $x_2^\ddagger(\tau) \preceq x_2^\dagger(\tau)$ for $M(\tau) \preceq N(\tau)$. Finally, we establish the existence, shape, and location of the function τ_2 in Theorem 2 whose graph divides parameter space into regions within which $x_2^\ddagger(\tau)$ and $x_2^\dagger(\tau)$ maintain a fixed order. The analysis in this section differs from the previous one because both $x_2^\ddagger$ and $x_2^\dagger$ are functions of τ.

As before, we assume throughout this section that $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$. Thus, the function $C_2(\tau)$ will always take values within the interval $[C_1, C^{\mathrm{m}}]$.

3.1 Elementary properties of $x_2^\ddagger(\tau)$ and $x_2^\dagger(\tau)$

We begin by showing that $x_2^\ddagger$ and $x_2^\dagger$ exist and are finite everywhere. We also describe elementary properties of the endpoints as functions of τ.

Lemma 3.1. *Let $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$. Then*

(a) $x_2^\ddagger(\tau)$ *and* $x_2^\dagger(\tau)$ *exist, they are unique,* $x_2^\ddagger(\tau) > 0$, *and* $x_2^\dagger(\tau) \geq 0$*;*

(b) $x_2^\ddagger(0) = x_2^\dagger(0) = x_1^\dagger$ *and* $x_2^\dagger(\tau^{\mathrm{m}}) = 0$*;*

(c) $x_2^\ddagger$ *is a continuously differentiable and nonincreasing function of* τ *with*

$$\frac{dx_2^\ddagger}{d\tau} = \frac{\sigma\big[\phi(\overline{\sigma\tau}x_2^\ddagger) - \phi(x_2^\ddagger)\big]}{\overline{\sigma\tau}\phi'(x_2^\ddagger) + \int_{\overline{\sigma\tau}}^1 \phi'(\alpha x_2^\ddagger)\alpha\, d\alpha} \leq 0. \tag{3.1}$$

The inequality is strict unless $\sigma = 0$ *or* $\sigma\tau \geq 1$, *in which case equality holds;*

(d) $x_2^\dagger$ *is a continuously differentiable and strictly decreasing function of* τ *with*

$$\frac{dx_2^\dagger}{d\tau} = \frac{b}{\int_0^1 \phi'(\alpha x_2^\dagger)\alpha\, d\alpha} < 0. \tag{3.2}$$

Proof.

(a) By properties P_1, P_3, and P_6, the function $\Phi(x;u) = u\phi(x) + \int_u^1 \phi(\alpha x)\,d\alpha$ is a continuous and strictly decreasing function of $x \geq 0$ when $u \in [0,1]$. Furthermore, $\Phi(0;u) = \phi(0) = C^{\mathrm{m}}$ and $\Phi(x;u) \to 0$ as $x \to \infty$ by properties P_4 and P_7. It follows from (IV) and the properties of Φ with $u = \overline{\sigma\tau} = \min\{\sigma\tau, 1\}$ that $x_2^\ddagger(\tau)$ exists, it is unique, and that $x_2^\ddagger(\tau) > 0$. It also follows from (III) and the properties of Φ with $u = 0$ that $x_2^\dagger(\tau)$ exists, it is unique, and that $x_2^\dagger(\tau) \geq 0$ (with equality if and only if $\tau = \tau^{\mathrm{m}}$).

(b) The first part follows from (IV), (III), (1.6) with $\tau = 0$, (I), and property P_6. The second part was obtained in the proof of part (a).

(c) The endpoint $x_2^\ddagger$ is a continuously differentiable function of $\tau \in [0, \tau^{\mathrm{m}}]$ by the implicit function theorem. The expression for the derivative in (3.1) arises from implicit differentiation of (IV) in the two cases $\sigma\tau < 1$ and $\sigma\tau \geq 1$ separately, and its sign from property P_3.

(d) The endpoint $x_2^\dagger$ is a continuously differentiable function of $\tau \in [0, \tau^{\mathrm{m}}]$ by the implicit function theorem. The expression for the derivative in (3.2) arises from implicit differentiation of (III) and its sign from property P_3. □

3.2 The upper portion of parameter space

Eq. (IV) implies that the endpoint $x_2^\ddagger(\tau)$ takes on the same fixed value, which we now denote by $z^\ddagger$, anytime $\sigma\tau \geq 1$. This $z^\ddagger$ satisfies the equation

$$\phi(z^\ddagger) = C_1. \tag{3.3}$$

We conclude from (I), the relation $C_1 < C^{\mathrm{m}}$, and property P_5 that $z^\ddagger \in (0, x_1^\dagger)$. It follows from Lemma 3.1 (b, c) that $x_2^\ddagger(\tau) > z^\ddagger$ whenever $\sigma\tau < 1$. Furthermore, the properties of $x_2^\dagger(\tau)$ in Lemma 3.1 (b, d) imply that there exists some $\tau^* \in (0, \tau^{\mathrm{m}})$ such that

$$x_2^\dagger(\tau) \succeq z^\ddagger \quad \text{for} \quad \tau \preceq \tau^*. \tag{3.4}$$

At this point, we can already establish the relative magnitudes of $x_2^\ddagger(\tau)$ and $x_2^\dagger(\tau)$ within the upper portion of parameter space. We first set $\tau^{-*} \stackrel{\text{def}}{=} 1/\tau^*$ and observe from the relation $\tau^* < \tau^{\mathrm{m}}$ that

$\tau^{-*} > \tau^{-\mathrm{m}}$ (see Figure 4).

Lemma 3.2. *Let $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$.*

(a) *If $\sigma < \tau^{-*}$ and $\tau \geq \tau^*$ then $x_2^{\ddagger}(\tau) > x_2^{\dagger}(\tau)$.*

(b) *If $\sigma \geq \tau^{-*}$ and $\sigma\tau \geq 1$ then $x_2^{\ddagger}(\tau) \preceq x_2^{\dagger}(\tau)$ for $\tau \preceq \tau^*$.*

Proof.

(a) Let $\sigma < \tau^{-*}$ and $\tau \geq \tau^*$. If $\sigma\tau < 1$ then $x_2^{\ddagger}(\tau) > z^{\ddagger} \geq x_2^{\dagger}(\tau)$ by (3.4). If $\sigma\tau \geq 1$ then $x_2^{\ddagger}(\tau) = z^{\ddagger} > x_2^{\dagger}(\tau)$ by (3.4) with $\tau \geq 1/\sigma > \tau^*$.

(b) If $\sigma \geq \tau^{-*}$ and $\sigma\tau \geq 1$ then the conclusion follows directly from (3.4) with $x_2^{\ddagger}(\tau) = z^{\ddagger}$. □

3.3 The lower portion of parameter space

In view of Lemmas 3.1 (b, c, d) and 3.2, it only remains to determine the relative magnitudes of $x_2^{\ddagger}(\tau)$ and $x_2^{\dagger}(\tau)$ for $\sigma > 0$ and $\tau \in (0, \tau^\circ)$, where

$$\tau^\circ = \begin{cases} \tau^*, & \sigma < \tau^{-*} \\ 1/\sigma, & \sigma \geq \tau^{-*}. \end{cases}$$

We now determine the relative values of $dx_2^{\ddagger}/d\tau$ and $dx_2^{\dagger}/d\tau$ along the line $\tau = 0$.

Lemma 3.3. *If $\sigma > 0$ then $\left[dx_2^{\ddagger}/d\tau\right]_{\tau=0} \succeq \left[dx_2^{\dagger}/d\tau\right]_{\tau=0}$ for $\sigma \preceq \sigma^*$.*

Proof. Observe from (3.1) and (3.2), Lemma 3.1 (b), and the relation $\phi(0) = C^{\mathrm{m}}$ that if $\tau = 0$ then

$$\left.\frac{dx_2^{\ddagger}/d\tau}{dx_2^{\dagger}/d\tau}\right|_{\tau=0} = \frac{\sigma\left[C^{\mathrm{m}} - \phi(x_1^{\dagger})\right]}{b}.$$

The derivatives that appear on the left-hand side are both negative by Lemma 3.1 (c, d) because $\sigma > 0$ and $\sigma\tau = 0 < 1$, and the numerator on the right-hand side is positive because $C^{\mathrm{m}} = \phi(0) > \phi(x_1^{\dagger})$ by property P_3. It follows that $dx_2^{\ddagger}/d\tau \succeq dx_2^{\dagger}/d\tau$ for $\sigma\left[C^{\mathrm{m}} - \phi(x_1^{\dagger})\right] \preceq b$, where each derivative is evaluated at $\tau = 0$. The conclusion follows from (2.5). □

We now introduce the functions

$$M(\tau) = \sigma\phi\big(x_2^\dagger(\tau)\big) + b, \qquad \text{for } \tau \in [0, \tau^\circ] \tag{3.5}$$

and

$$N(\tau) = \begin{cases} \sigma\phi(0), & \text{for } \tau = 0 \\ \dfrac{\sigma}{\tau}\displaystyle\int_0^\tau \phi\big(\sigma\alpha x_2^\dagger(\tau)\big)\,d\alpha, & \text{for } \tau \in (0, \tau^\circ]. \end{cases} \tag{3.6}$$

In the next lemma, we determine some elementary properties of M and N as functions of τ.

Lemma 3.4. *Let $\sigma > 0$. Then M and N are continuous and strictly increasing and decreasing functions of $\tau \in [0, \tau^\circ]$, respectively.*

Proof. Observe from Lemma 3.1 (b, d) and the relation $\tau^\circ < \tau^{\mathrm{m}}$ that $x_2^\dagger(\tau)$ is a positive and strictly decreasing function of $\tau \in [0, \tau^\circ]$. Properties P_1 and P_3 imply then that M in (3.5) is a continuous and strictly increasing function of $\tau \in [0, \tau^\circ]$. We now consider the function N. Observe from (3.6) that

$$\lim_{\tau\to 0} N(\tau) = \sigma \lim_{\tau\to 0}\left[\phi\big(\sigma\tau x_2^\dagger(\tau)\big) + \frac{dx_2^\dagger}{d\tau}\int_0^\tau \phi'\big(\sigma\alpha x_2^\dagger(\tau)\big)\sigma\alpha\,d\alpha\right] = N(0),$$

where we have used L'Hospital's Rule, the fact that $x_2^\dagger(\tau) \to x_1^\dagger$ as $\tau \to 0$, and the finiteness of $dx_2^\dagger/d\tau$ as established in Lemma 3.1 (d). We conclude that N is continuous (from the right) at $\tau = 0$. Furthermore, (3.6) and property P_5 together imply that if $\tau \in (0, \tau^\circ]$ then

$$N(\tau) = \frac{\sigma}{\tau}\int_0^\tau \phi\big(\sigma\alpha x_2^\dagger(\tau)\big)\,d\alpha < \sigma\phi(0) = N(0).$$

It only remains to show that N is a continuous and strictly decreasing function of $\tau \in (0, \tau^\circ]$. Thus, we now fix $\tau \in (0, \tau^\circ]$. Changing the variable of integration in (3.6) to $\chi = \sigma\alpha x_2^\dagger(\tau)$ yields

$$N(\tau) = \frac{1}{\tau x_2^\dagger(\tau)}\int_0^{\sigma\tau x_2^\dagger(\tau)} \phi(\chi)\,d\chi.$$

If we define

$$\psi(\tau) = \sigma\tau x_2^\dagger(\tau) \quad \text{and} \quad \theta(x) = \frac{\sigma}{x}\int_0^x \phi(\chi)\,d\chi,$$

then $N(\tau) = \theta\big(\psi(\tau)\big)$. It is clear from Lemma 3.1 (d) and the positivity of $x_2^\dagger(\tau)$ that ψ is positive and continuously differentiable at τ. It is also clear from property P_1 that θ is a continuously differentiable function of $x > 0$. Consequently, N is continuously differentiable at τ and $N'(\tau) = \theta'\big(\psi(\tau)\big)\psi'(\tau)$. To finish the proof, it suffices to show that $N'(\tau) < 0$ for $\tau \in (0, \tau^\circ)$ and $N'(\tau^\circ) \le 0$. It follows from differentiating θ, changing the variable of integration back to α, and property P_5 that

$$\theta'(x) = \frac{\sigma}{x}\left[\phi(x) - \frac{1}{x}\int_0^x \phi(\chi)\,d\chi\right] = \frac{\sigma}{x}\left[\phi(x) - \int_0^1 \phi(\alpha x)\,d\alpha\right] < 0.$$

Therefore $\theta'\big(\psi(\tau)\big) < 0$. To determine the sign of $\psi'(\tau)$ we differentiate ψ with respect to τ and rearrange to get

$$\psi'(\tau) = \sigma x_2^\dagger + \sigma\tau\frac{dx_2^\dagger}{d\tau} = \frac{\sigma}{\int_0^1 \phi'(\alpha x_2^\dagger)\alpha\,d\alpha}\left[x_2^\dagger\int_0^1 \phi'(\alpha x_2^\dagger)\alpha\,d\alpha + b\tau\right],$$

where $x_2^\dagger = x_2^\dagger(\tau)$ and we have used (3.2). Since the fraction on the right-hand side is negative by property P_3, we consider only the expression in brackets,

$$\begin{aligned} x_2^\dagger\int_0^1 \phi'(\alpha x_2^\dagger)\alpha\,d\alpha + b\tau &= \phi(x_2^\dagger) - \int_0^1 \phi(\alpha x_2^\dagger)\,d\alpha + b\tau \\ &= \phi(x_2^\dagger) - C_2(\tau) + b\tau \\ &= \phi(x_2^\dagger) - C_1 \\ &\le \phi\big(z^\ddagger\big) - C_1 \\ &= 0, \end{aligned}$$

where we have used (2.4) with $x = x_2^\dagger$ and $u = 1$, (III), (1.6), (3.4) with $\tau \le \tau^*$, property P_3, and (3.3). The inequality above is strict except in the case that $\tau = \tau^*$. It follows from these remarks that $\psi'(\tau) \ge 0$ for $\tau \in (0, \tau^\circ]$, with equality occurring only when $\tau = \tau^*$. Therefore, $N'(\tau) < 0$ for $\tau \in (0, \tau^\circ)$ and $N'(\tau^\circ) \le 0$. □

We will write "$x \preceq y \iff u \preceq v$" to emphasize that if $x \preceq y$ for $u \preceq v$ then $u \preceq v$ for $x \preceq y$

also holds. We now connect the relative magnitudes of $x_2^\ddagger(\tau)$ and $x_2^\dagger(\tau)$ to the relative values of $M(\tau)$ and $N(\tau)$.

Lemma 3.5. *Let $\sigma > 0$ and $\tau \in (0, \tau^\circ)$. Then $x_2^\ddagger(\tau) \preceq x_2^\dagger(\tau) \iff M(\tau) \preceq N(\tau)$.*

Proof. Inspired by (IV) with $\sigma\tau < 1$, we introduce the function

$$\Theta(\tau, x) = \sigma\tau\phi(x) + \int_{\sigma\tau}^{1} \phi(\alpha x) d\alpha.$$

It is clear from properties P_1, P_3, and P_6 that Θ is a continuous and strictly decreasing function of $x \geq 0$. We first suppose that $M(\tau) < N(\tau)$ for some $\tau \in (0, \tau^\circ)$. Let $x_2^\ddagger = x_2^\ddagger(\tau)$ and $x_2^\dagger = x_2^\dagger(\tau)$. Then $\sigma\tau \in (0, 1)$ and

$$\begin{aligned}
\Theta(\tau, x_2^\dagger) &= \sigma\tau\phi(x_2^\dagger) + \int_{\sigma\tau}^{1} \phi(\alpha x_2^\dagger)\, d\alpha \\
&= \sigma\tau\phi(x_2^\dagger) + \int_{0}^{1} \phi(\alpha x_2^\dagger)\, d\alpha - \int_{0}^{\sigma\tau} \phi(\alpha x_2^\dagger)\, d\alpha \\
&= \sigma\tau\phi(x_2^\dagger) + C_2(\tau) - \sigma \int_{0}^{\tau} \phi(\sigma\tilde{\alpha} x_2^\dagger)\, d\tilde{\alpha} \\
&= \sigma\tau\phi(x_2^\dagger) + C_2(\tau) - \tau N(\tau) \\
&< \sigma\tau\phi(x_2^\dagger) + C_2(\tau) - \tau M(\tau) \\
&= \sigma\tau\phi(x_2^\dagger) + C_2(\tau) - \tau\big[\sigma\phi(x_2^\dagger) + b\big] \\
&= C_1 \\
&= \sigma\tau\phi(x_2^\ddagger) + \int_{\sigma\tau}^{1} \phi(\alpha x_2^\ddagger)\, d\alpha \\
&= \Theta(\tau, x_2^\ddagger),
\end{aligned}$$

where we have used (III), (3.6), the assumption $M(\tau) < N(\tau)$, (3.5), (1.6), and (IV) with $\sigma\tau < 1$. Since Θ is a strictly decreasing function of x, it follows that $x_2^\ddagger(\tau) < x_2^\dagger(\tau)$. Similar arguments show that $x_2^\ddagger(\tau) = x_2^\dagger(\tau)$ when $M(\tau) = N(\tau)$, and that $x_2^\ddagger(\tau) > x_2^\dagger(\tau)$ when $M(\tau) > N(\tau)$. Therefore, $x_2^\ddagger(\tau) \preceq x_2^\dagger(\tau)$ for $M(\tau) \preceq N(\tau)$. □

3.4 The relative magnitudes of $x_2^{\ddagger}(\tau)$ and $x_2^{\dagger}(\tau)$

We now prove the main result of this section by establishing the existence, shape, and location of the bifurcation function τ_2 in Theorem 2.

Proof of Theorem 2.

(a) Let $\sigma \leq \sigma^*$ so that $\tau^\circ = \tau^*$. If $\tau = 0$ then Lemma 3.1 (b) applies, i.e., $x_2^{\ddagger}(0) = x_2^{\dagger}(0)$. We now restrict our attention to $\tau \in (0, \tau^{\mathrm{m}}]$. If $\sigma = 0$ then Lemma 3.1 (c, d) implies that $x_2^{\ddagger}(\tau) = x_1^{\dagger} > x_2^{\dagger}(\tau)$. If $\sigma > 0$ and $\tau \in (0, \tau^*)$ then

$$
\begin{aligned}
M(\tau) &> M(0) && \text{by Lemma 3.4} \\
&= \sigma\phi(x_1^{\dagger}) + b && \text{by (3.5) and Lemma 3.1 (b)} \\
&\geq \sigma C^{\mathrm{m}} && \text{by (2.5) with } \sigma \leq \sigma^* \\
&= N(0) && \text{by (3.6) and the relation } C^{\mathrm{m}} = \phi(0) \\
&> N(\tau) && \text{by Lemma 3.4.}
\end{aligned}
$$

We conclude from Lemma 3.5 that $x_2^{\ddagger}(\tau) > x_2^{\dagger}(\tau)$. If $\sigma > 0$ and $\tau \geq \tau^*$ then Lemma 3.2 (a) applies.

(b) Let $\sigma \in (\sigma^*, \tau^{-*})$ so that $\tau^\circ = \tau^*$. If $\tau = 0$ then Lemma 3.1 (b) applies, i.e., $x_2^{\ddagger}(0) = x_2^{\dagger}(0)$. Suppose now that $\tau \in (0, \tau^*)$. It follows from Lemma 3.3 with $\sigma > \sigma^*$ that $x_2^{\ddagger}(\tau) < x_2^{\dagger}(\tau)$ for $0 < \tau \ll 1$ and from Lemma 3.2 (a) that $x_2^{\ddagger}(\tau^*) > x_2^{\dagger}(\tau^*)$. The continuity of $x_2^{\ddagger}(\tau)$ and $x_2^{\dagger}(\tau)$ with respect to τ implies that there exists some $\tau_2 \in (0, \tau^*)$ such that $x_2^{\ddagger}(\tau_2) = x_2^{\dagger}(\tau_2)$. Lemma 3.5 implies that $M(\tau_2) = N(\tau_2)$. Lemma 3.4 implies that $M(\tau) \preceq N(\tau)$ for $\tau \preceq \tau_2$. We conclude from Lemma 3.5 again that $x_2^{\ddagger}(\tau) \preceq x_2^{\dagger}(\tau)$ for $\tau \preceq \tau_2$. If $\tau \geq \tau^*$ then Lemma 3.2 (a) applies.

(c) Let $\sigma \geq \tau^{-*}$ so that $\tau^\circ = 1/\sigma \leq \tau^*$. If $\tau = 0$ then Lemma 3.1 (b) applies. Suppose now that $\tau \in (0, 1/\sigma)$. Then

$$
\begin{aligned}
M(\tau) &< M(1/\sigma) && \text{by Lemma 3.4} \\
&= \sigma\phi\big(x_2^{\dagger}(1/\sigma)\big) + b && \text{by (3.5)}
\end{aligned}
$$

$\leq \sigma\phi(z^{\ddagger}) + b$	by (3.4) with $1/\sigma \leq \tau^*$ and property P_3
$= \sigma\big[C_1 + b/\sigma\big]$	by (3.3)
$= \sigma C_2(1/\sigma)$	by (1.6)
$= \sigma \int_0^1 \phi\big(\alpha x_2^{\dagger}(1/\sigma)\big)\, d\alpha$	by (III)
$= \sigma^2 \int_0^{1/\sigma} \phi\big(\sigma\tilde{\alpha} x_2^{\dagger}(1/\sigma)\big)\, d\tilde{\alpha}$	by the change of variable $\alpha = \sigma\tilde{\alpha}$
$= N(1/\sigma)$	by (3.6)
$< N(\tau)$	by Lemma 3.4.

We conclude from Lemma 3.5 that $x_2^{\ddagger}(\tau) < x_2^{\dagger}(\tau)$. If $\tau \geq 1/\sigma$ then Lemma 3.2 (b) applies.

(d) Let $\sigma \in (\sigma^*, \tau^{-*})$. Then $\tau_2 \in (0, \tau^*)$ exists and is defined by the equation $x_2^{\ddagger}(\sigma, \tau_2) = x_2^{\dagger}(\tau_2)$, where we now express the σ-dependence of $x_2^{\ddagger}$ in (IV). The uniqueness of τ_2 and the continuity of $x_2^{\ddagger}$ and $x_2^{\dagger}$ in the σ-τ plane guarantee that τ_2 is continuous at σ. It suffices to show that τ_2 is strictly increasing in a small neighborhood around σ. Observe that τ_2 satisfies (IV) with $x_2^{\dagger}(\tau_2)$ in place of $x_2^{\ddagger}(\sigma, \tau_2)$,

$$C_1 = \sigma\tau_2\phi(x_2^{\dagger}) + \int_{\sigma\tau_2}^1 \phi(\alpha x_2^{\dagger})\, d\alpha,$$

where $\sigma\tau_2 \in (0, 1)$ and $x_2^{\dagger} = x_2^{\dagger}(\tau_2)$. If $d\tau_2/d\sigma$ exists, we can differentiate the equation above implicitly with respect to σ and rearrange to get

$$0 = \left[\tau_2 + \sigma\frac{d\tau_2}{d\sigma}\right]\big[\phi(x_2^{\dagger}) - \phi(\sigma\tau_2 x_2^{\dagger})\big] + \frac{dx_2^{\dagger}}{d\tau}\frac{d\tau_2}{d\sigma}\left[\sigma\tau_2\phi'(x_2^{\dagger}) + \int_{\sigma\tau_2}^1 \phi'(\alpha x_2^{\dagger})\alpha\, d\alpha\right].$$

Further rearrangement gives

$$\frac{d\tau_2}{d\sigma} = \frac{\tau_2\big[\phi(\sigma\tau_2 x_2^{\dagger}) - \phi(x_2^{\dagger})\big]}{dx_2^{\dagger}/d\tau\left[\sigma\tau_2\phi'(x_2^{\dagger}) + \int_{\sigma\tau_2}^1 \phi'(\alpha x_2^{\dagger})\alpha\, d\alpha\right] - \sigma\big[\phi(\sigma\tau_2 x_2^{\dagger}) - \phi(x_2^{\dagger})\big]}.$$

Eq. (3.1) with $x_2^\ddagger(\sigma,\tau_2) = x_2^\dagger(\tau_2)$ implies that

$$\frac{\sigma}{\tau_2}\cdot\frac{d\tau_2}{d\sigma} = \frac{\partial x_2^\ddagger/\partial\tau}{dx_2^\dagger/d\tau - \partial x_2^\ddagger/\partial\tau}.$$

The numerator on the right-hand side is negative by Lemma 3.1 (c), and the denominator is nonpositive because $x_2^\ddagger(\tau_2) = x_2^\dagger(\tau_2)$ and $x_2^\ddagger(\tau) > x_2^\dagger(\tau)$ for $\tau > \tau_2$. We conclude then that $d\tau_2/d\sigma > 0$ if the derivative exists, and that τ_2 has a vertical tangent otherwise. In either case, τ_2 must be strictly increasing in a small neighborhood around σ.

(e) Let $\sigma_j \in (\sigma^*, \tau^{-*})$ be a strictly decreasing sequence with $\sigma_j \to \sigma^*$ as $j \to \infty$. According to parts (b) and (d), the sequence $\tau_2(\sigma_j)$ is strictly decreasing and bounded within the interval $(0, \tau^*)$. Thus, there exists some $\tilde{\tau} \in [0, \tau^*)$ such that $\tau_2(\sigma_j) \to \tilde{\tau}$ as $j \to \infty$. We argue by contradiction. Suppose that $\tilde{\tau} \in (0, \tau^*)$ and let $\hat{\tau} \in (0, \tilde{\tau})$. Since $\hat{\tau} < \tilde{\tau} < \tau_2(\sigma_j)$, we obtain from part (b) that $x_2^\ddagger(\sigma_j, \hat{\tau}) < x_2^\dagger(\hat{\tau})$, where we again express the σ-dependence of $x_2^\ddagger$ in (IV). It follows from taking limits that $x_2^\ddagger(\sigma^*, \hat{\tau}) \le x_2^\dagger(\hat{\tau})$. But part (a) with $\tau = \hat{\tau}$ implies that $x_2^\ddagger(\sigma^*, \hat{\tau}) > x_2^\dagger(\hat{\tau})$, a contradiction. We conclude that $\tilde{\tau} = 0$, and thus $\tau_2 \to 0$ as $\sigma \to \sigma^*$. A similar argument shows that $\tau_2 \to \tau^*$ as $\sigma \to \tau^{-*}$. □

4 Order of the Bifurcations

We now prove Theorem 3, which is the last main result of this paper. Its proof is adapted from [6].

Proof of Theorem 3. We first show that if $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$ and $\tau \in (0, \tau^{\mathrm{m}})$ then $(1-\sigma\tau)x_1^\ddagger(\tau) > x_2^\dagger(\tau)$. We argue by contradiction. Suppose that $(1-\sigma\tau)x_1^\ddagger(\tau) \le x_2^\dagger(\tau)$ for some $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$ and $\tau \in (0, \tau^{\mathrm{m}})$. Observe that $\sigma\tau \in (0,1)$. Also, Lemmas 2.1 (a) and 3.1 (a) imply that $x_1^\ddagger(\tau)$ and $x_2^\dagger(\tau)$ are both finite. We apply (II) with $x_1^\ddagger = x_1^\ddagger(\tau)$, change the variable of integration, use property P_6, apply (III) with $x_2^\dagger = x_2^\dagger(\tau)$, and then use the relation $C_2(\tau) < C^{\mathrm{m}}$ to get

$$\begin{aligned}
C_2(\tau) &= \sigma\tau C^{\mathrm{m}} + \int_0^{1-\sigma\tau} \phi(\alpha x_1^\ddagger)\,d\alpha \\
&= \sigma\tau C^{\mathrm{m}} + (1-\sigma\tau)\int_0^1 \phi(\tilde{\alpha}(1-\sigma\tau)x_1^\ddagger)\,d\tilde{\alpha} \\
&\ge \sigma\tau C^{\mathrm{m}} + (1-\sigma\tau)\int_0^1 \phi(\tilde{\alpha}x_2^\dagger)\,d\tilde{\alpha}
\end{aligned}$$

$$= \sigma\tau C^{\mathrm{m}} + (1-\sigma\tau)C_2(\tau)$$

$$= C_2(\tau) + \sigma\tau\big[C^{\mathrm{m}} - C_2(\tau)\big]$$

$$> C_2(\tau),$$

a contradiction. We conclude that if $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$ and $\tau \in (0, \tau^{\mathrm{m}})$ then $(1-\sigma\tau)x_1^{\ddagger}(\tau) > x_2^{\dagger}(\tau)$.

Recall from Theorems 1 and 2 that $\tau_1(\sigma^*) = 0 = \tau_2(\sigma^*)$, that τ_1 and τ_2 are continuous functions of $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$, and that $\tau_1(\tau^{-\mathrm{m}}) = \tau^{\mathrm{m}} > \tau_2(\tau^{-\mathrm{m}})$. We now show that $\tau_1(\sigma) > \tau_2(\sigma)$ for $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$. We argue by contradiction. Suppose that $\tau_1(\sigma) \le \tau_2(\sigma)$ for some $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$. Since the functions τ_1 and τ_2 are continuous, we may choose σ so that $\tau_1(\sigma) = \tau_2(\sigma)$. Let $\tau = \tau_1(\sigma) = \tau_2(\sigma)$, $x_1^{\ddagger} = x_1^{\ddagger}(\tau)$, $x_2^{\dagger} = x_2^{\dagger}(\tau)$, and $x_2^{\ddagger} = x_2^{\ddagger}(\tau)$. Then $\sigma\tau \in (0,1)$ because $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$ and $\tau \in (0, \tau^{\mathrm{m}})$, and furthermore $x_1^{\ddagger} = x_1^{\dagger}$ by Theorem 1 (b) and $x_2^{\ddagger} = x_2^{\dagger}$ by Theorem 2 (b). It follows from the positivity of $x_2^{\dagger}$ and property P_5 that

$$\int_0^{\sigma\tau} \phi(\alpha x_2^{\dagger})\, d\alpha < \sigma\tau\phi(0) = \sigma\tau C^{\mathrm{m}}.$$

We add the same quantity to both sides,

$$\int_0^1 \phi(\alpha x_2^{\dagger})\, d\alpha < \sigma\tau C^{\mathrm{m}} + \int_{\sigma\tau}^1 \phi(\alpha x_2^{\dagger})\, d\alpha.$$

We apply (III) and rearrange to get

$$C_2(\tau) - \sigma\tau C^{\mathrm{m}} < \int_{\sigma\tau}^1 \phi(\alpha x_2^{\dagger})\, d\alpha.$$

We apply (II) with $x_1^{\dagger}$ in place of $x_1^{\ddagger}$ to get

$$\int_0^{1-\sigma\tau} \phi(\alpha x_1^{\dagger})\, d\alpha < \int_{\sigma\tau}^1 \phi(\alpha x_2^{\dagger})\, d\alpha. \tag{4.1}$$

We now obtain the reverse inequality. The positivity of $x_1^{\ddagger}$, property P_5, the inequality $(1-\sigma\tau)x_1^{\ddagger} > x_2^{\dagger}$ established at the beginning of this proof, and property P_3 imply that

$$\frac{1}{\sigma\tau}\int_{1-\sigma\tau}^1 \phi(\alpha x_1^{\ddagger})\, d\alpha < \phi((1-\sigma\tau)x_1^{\ddagger}) < \phi(x_2^{\dagger}),$$

from which we conclude that

$$\int_{1-\sigma\tau}^{1} \phi(\alpha x_1^{\ddagger})\, d\alpha < \sigma\tau\phi(x_2^{\dagger}).$$

We subtract both sides from the same quantity, and then replace $x_1^{\ddagger}$ and $x_2^{\dagger}$ with $x_1^{\dagger}$ and $x_2^{\ddagger}$, respectively, to get

$$C_1 - \int_{1-\sigma\tau}^{1} \phi(\alpha x_1^{\dagger})\, d\alpha > C_1 - \sigma\tau\phi(x_2^{\ddagger}).$$

We now apply (I) to the left-hand side and (IV) with $\sigma\tau < 1$ to the right-hand side to get

$$\int_{0}^{1-\sigma\tau} \phi(\alpha x_1^{\dagger})\, d\alpha > \int_{\sigma\tau}^{1} \phi(\alpha x_2^{\ddagger})\, d\alpha.$$

We replace $x_2^{\ddagger}$ with $x_2^{\dagger}$ to get

$$\int_{0}^{1-\sigma\tau} \phi(\alpha x_1^{\dagger})\, d\alpha > \int_{\sigma\tau}^{1} \phi(\alpha x_2^{\dagger})\, d\alpha. \tag{4.2}$$

Since (4.1) and (4.2) cannot both hold simultaneously, we have a contradiction. We conclude that $\tau_1(\sigma) > \tau_2(\sigma)$ for $\sigma \in (\sigma^*, \tau^{-\mathrm{m}})$. □

5 Discussion

We have determined the outcome of plant competition for sunlight in a model of canopy partitioning by employing a global method of nullcine endpoint analysis. The fact that the bifurcation function τ_1 lies entirely above the bifurcation function τ_2 in Figure 2d implies that all parameter values between them give rise to globally stable competitive coexistence. The existence of this parameter region establishes that two hypothetical clonal plant species, limited solely by sunlight and occupying an environment which varies neither in horizontal space nor in time, can coexist at a globally stable equilibrium even though their only difference is the height at which they place their leaves above the ground. In this sense, for these hypothetical species for which no other mechanism of coexistence can operate, canopy partitioning with suitable parameter values is sufficient by itself to produce competitive coexistence. Furthermore, in this special case of our canopy partitioning model, there exist no parameter combinations that produce founder control, in which either species can exclude the other with the identity of the surviving species depending on initial conditions.

5.1 The role of leaf height in plant competition for sunlight

Before we interpret Figure 2d biologically, we recall that the taller species is assumed to be τ units taller than the shorter species and to have a stem cost parameter that reflects this height difference. We also observe that since the lowest leaves of the shorter species cannot occur below the ground surface, it follows that T has an implicit upper limit of $2s_1$ and σ has a corresponding lower limit of $(2s_1)^{-1}$. Thus, Figure 2d strictly applies only for values of $\sigma \geq (2s_1)^{-1}$. However, because s_1 is arbitrary, we will simplify the interpretation of our results by making no explicit mention of these bounds.

If the vertical leaf profile (or VLP) thickness T is large (so that σ is small) then the shorter species will exclude the taller species for any positive height difference τ. In this case, the cost of the taller species' extra height can never be fully repaid by the increased photosynthesis it experiences in the overstory. If T is moderate (so that σ is also moderate) then as the species height difference τ increases, the competitive success of the taller species decreases from competitive superiority to competitive compatibility to competitive inferiority compared with the shorter species. Furthermore, the lower and upper limits for the range of height differences which produce competitive coexistence (τ_1 and τ_2) both increase as T decreases (or σ increases). But beyond certain thresholds these limits become constants because T is so small that the VLP of the taller species lies entirely above the VLP of the shorter species. Outside the coexistence region, the taller species excludes the shorter species when the height difference is small because it intercepts more sunlight at a relatively low cost, but the shorter species excludes the taller species when the height difference is large because the cost of the taller species' extra height is again not fully repaid by the increased photosynthesis it experiences in the overstory.

The central point of these conclusions is that a difference in mean leaf height between two otherwise identical clonal plant species can produce both competitive exclusion and stable coexistence, with the outcome depending not on initial abundances but rather on parameters that describe the competing species. In particular, a difference in leaf height by itself can make competitive coexistence possible even when the plant species experience no environmental variation through horizontal space or time.

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endpoint	defining equation	condition	(eq. no.)
$x_1^\dagger$	$C_1 = \int_0^1 \phi(\alpha x_1^\dagger)\, d\alpha$		(I)
$x_1^\ddagger$	$C_2(\tau) = \sigma\tau C^{\mathrm{m}} + \int_0^{1-\sigma\tau} \phi(\alpha x_1^\ddagger)\, d\alpha$	$C_2(\tau) > \sigma\tau C^{\mathrm{m}}$	(II)
$x_2^\dagger$	$C_2(\tau) = \int_0^1 \phi(\alpha x_2^\dagger)\, d\alpha$		(III)
$x_2^\ddagger$	$C_1 = \overline{\sigma\tau}\phi(x_2^\ddagger) + \int_{\overline{\sigma\tau}}^1 \phi(\alpha x_2^\ddagger)\, d\alpha$		(IV)

Table 1: Defining equations for the nullcline endpoints when $\sigma \geq 0$ and $\tau \in [0, \tau^{\mathrm{m}}]$. If $C_2(\tau) \leq \sigma\tau C^{\mathrm{m}}$ then we define $x_1^\ddagger = \infty$. The expression $\overline{\sigma\tau} = \min\{\sigma\tau, 1\}$.

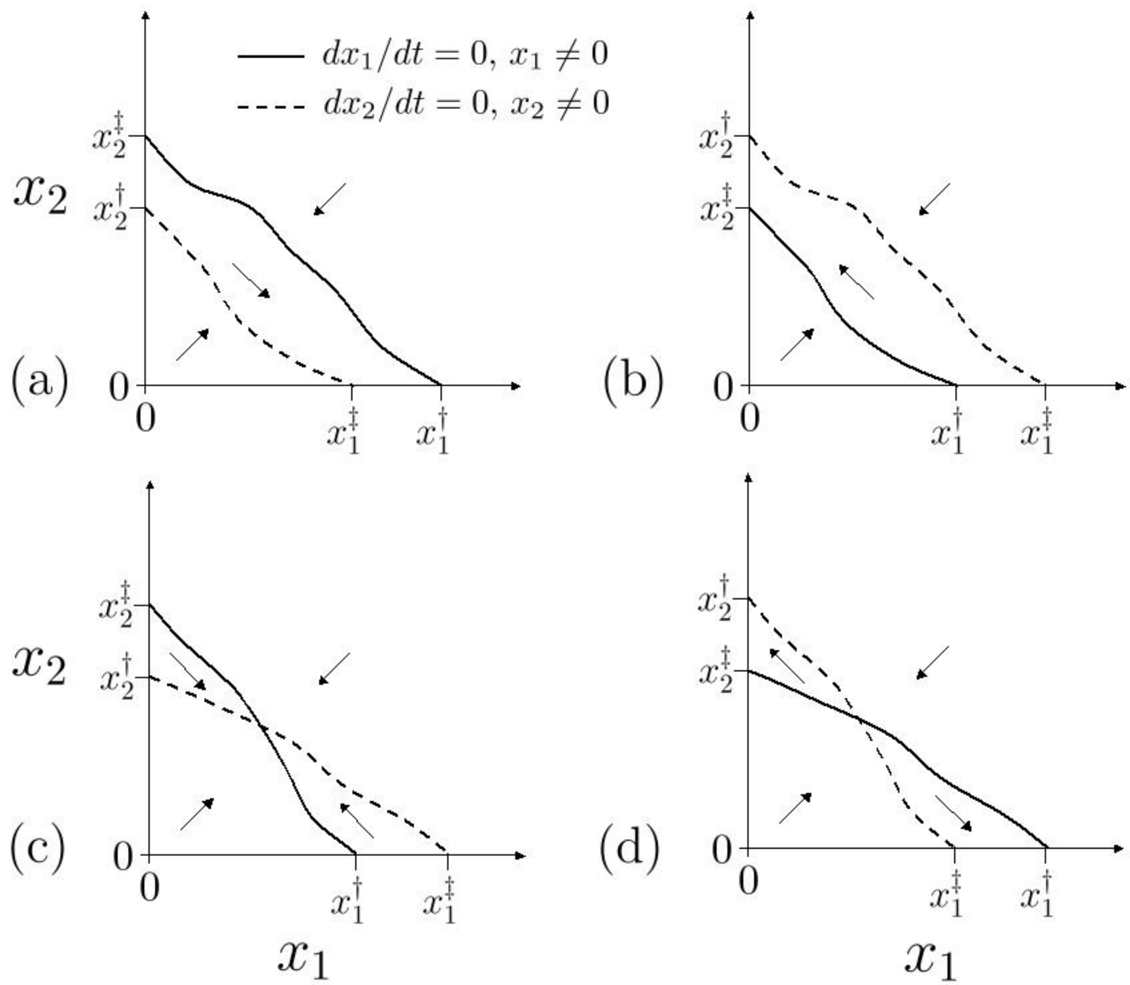

Figure 1: Some of the possible outcomes of competition: (a) species 1 excludes species 2; (b) species 2 excludes species 1; (c) the stable coexistence of both species; and (d) bistability (or founder control) in which either species can exclude the other. The arrows in each figure represent key trajectories.

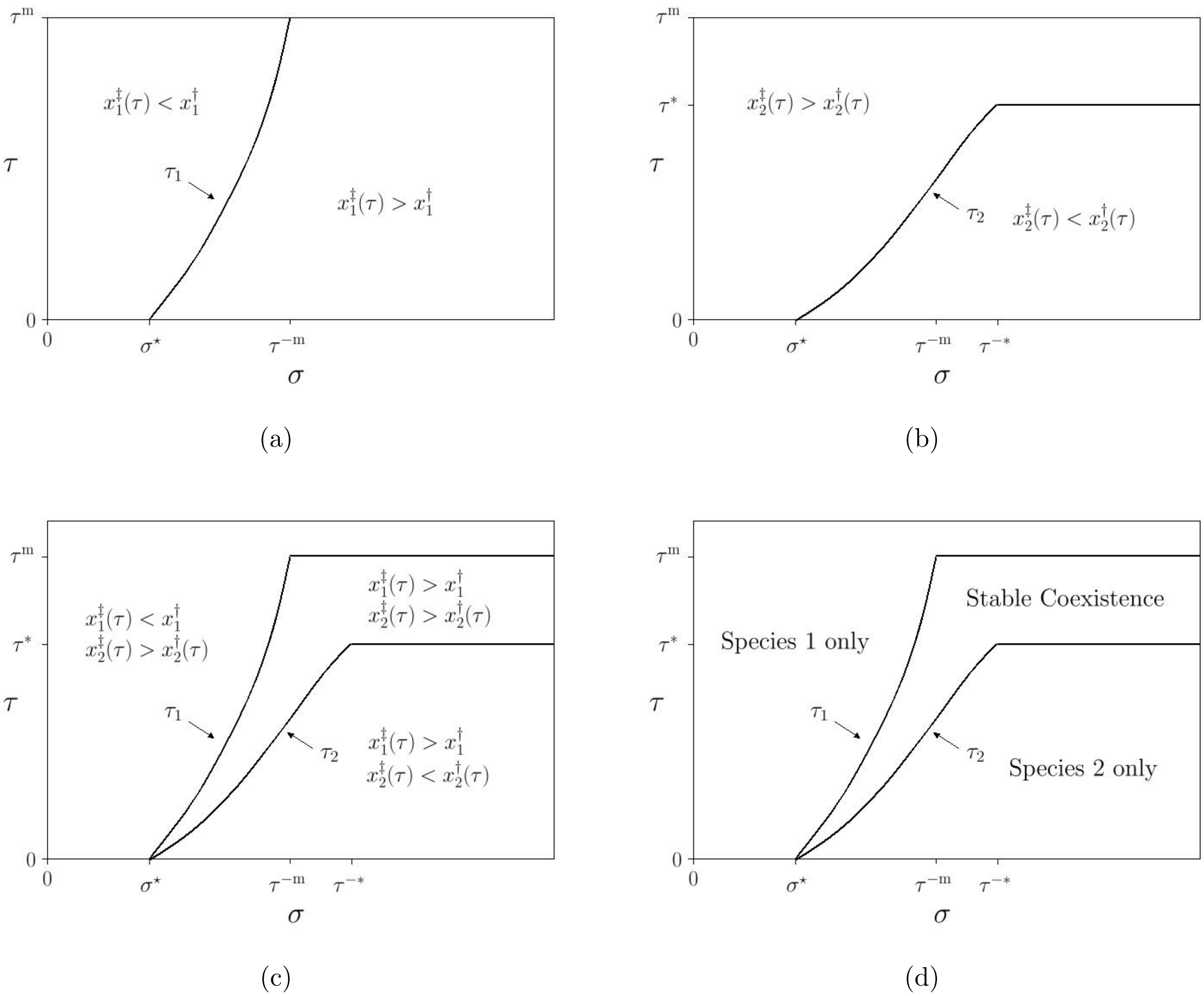

Figure 2: (a) The function τ_1 divides parameter space into regions in which the nullcline endpoints $x_1^{\ddagger}$ and $x_1^{\dagger}$ maintain a fixed order; (b) The function τ_2 divides parameter space into regions in which the nullcline endpoints $x_2^{\ddagger}$ and $x_2^{\dagger}$ maintain a fixed order; (c) Regions in parameter space in which both pairs of nullcline endpoints maintain fixed orders (we set $x_1^{\ddagger} = x_2^{\dagger} = 0$ when $\tau > \tau^{\mathrm{m}}$ because in this case the species 2 nullcline does not exist); (d) Regions in parameter space in which the various outcomes of competition occur. (By assumption, species 1 can persist when living alone, and so exclusion of both species cannot occur.)

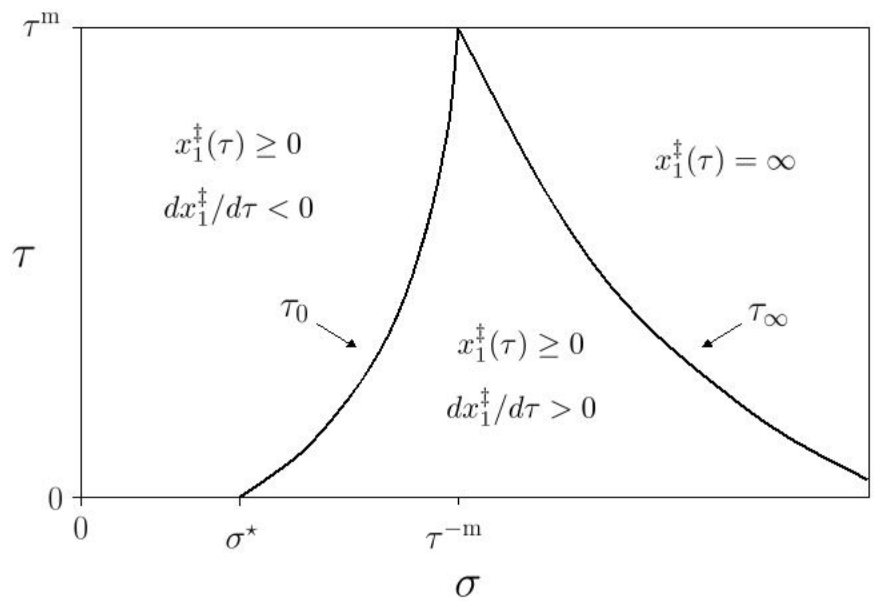

Figure 3: Intermediate results in §2.

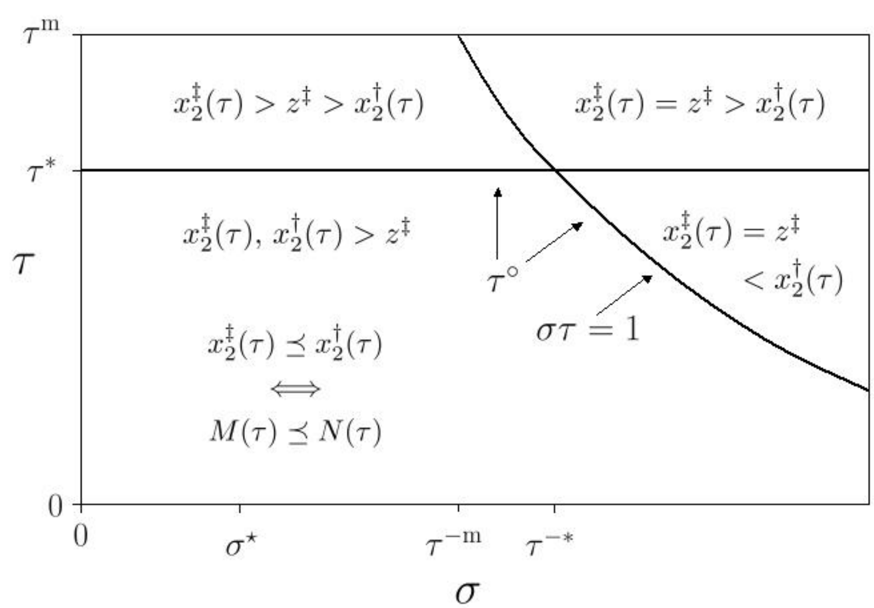

Figure 4: Intermediate results in §3.