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# Plant interspecies competition for sunlight

## A mathematical model of canopy partitioning

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**Abstract** We examine the influence of canopy partitioning on the outcome of competition between two plant species that interact only by mutually shading each other. This analysis is based on a Kolmogorov-type canopy partitioning model for plant species with clonal growth form and fixed vertical leaf profiles (R.R. Vance and A.L. Nevai, *J. Theor. Biol.*, 2007, to appear). We show that canopy partitioning is necessary for the stable coexistence of the two competing plant species. We also use implicit methods to show that, under certain conditions, the species' nullclines can intersect at most once. We use nullcline endpoint analysis to show that when the nullclines do intersect, and in such a way that they cross, then the resulting equilibrium point is always stable. We also construct surfaces that divide parameter space into regions within which the various outcomes of competition occur, and then study parameter dependence in the locations of these surfaces. The analysis presented here and in a companion paper (Nevai and Vance *in review*) together shows that canopy partitioning is both necessary and, under appropriate parameter values, sufficient for the stable coexistence of two hypothetical plant species whose structure and growth are described by our model.

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

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## 1 Introduction

The composition of ecological communities depends on the growth patterns of species populations which in turn arise partly from the physiological properties of the resident organisms. Unfortunately, the complexity of the processes involved usually prevents enlightening mathematical analysis of the causal pathways that connect community behavior to the physiological processes that ultimately drive it.

This paper examines how photosynthesis and energy allocation determine the ultimate fates of two species of plants that compete for sunlight. In particular, our analysis addresses the question of whether there exist species differences that promote competitive coexistence in an environment that varies neither through horizontal space nor through time. Previous empirical and numerical studies (Barnes *et al.* 1990, Ellsworth and Reich 1993, Kohyama 1993, Hirose and Werger 1995, Anten and Hirose 1998, Hikosaka *et al.* 1999, Anten and Hirose 2001, Anten and Hirose 2003) suggest that canopy partitioning (or different vertical leaf placement by different plant species) may help to promote the competitive coexistence of multiple plant species. However, a mathematical theory that examines this possibility has not yet been developed.

Our emphasis is not meant to imply that environmental variation through horizontal space and/or time plays no role in plant competitive coexistence in nature. On the contrary, there exist numerous studies, both empirical (*e.g.*, Pennings and Callaway 1992, Hubbell *et al.* 1999, Stoll and Prati 2001) and theoretical (*e.g.*, Shmida and Ellner 1984, Aikman and Benjamin 1994, Huston and DeAngelis 1994, Pacala and Levin 1997, Law and Dieckmann 2000, Perry *et al.* 2003, Zavala and Bravo de la Parra 2005) that strongly implicate environmental variation in determining plant community species composition (see Grace and Tilman 1990, Klausmeier and Tilman 2002, or Barot and Gignoux 2004). Unfortunately, however, and again because of the complexity involved, the mathematical theories of these phenomena typically overlook other mechanisms (*e.g.*, Pakes and Maller 1990) that do not depend on these kinds of environmental variation.

This study is meant to complement these theories. We ask whether structural and physiological differences can, in principle, produce plant species coexistence in the absence of these other mechanisms. If they can, then we will consider it probable that these mechanisms probably play some role, together with the others, in determining species composition of plant communities in nature.

Our analysis concerns a two-species plant competition model formulated specifically to examine whether a difference in height above the ground at which two competing species place their leaves can promote their competitive coexistence. Because this model must describe (at least in simplified form) how leaf height influences a plant's overall energy budget, this model must be mechanistic in character. Huisman *et al.* (1999) have shown that at least in phytoplankton, a mechanistic description of multispecies population dynamics can be assembled, with minimal loss in realism, from empirically validated mechanistic models of single species populations. Inspired by this demonstration, we developed the two-species CANOPY PARTITIONING MODEL to be studied here as a direct extension of our earlier mechanistic CANOPY STRUCTURE MODEL (Vance and Nevai 2007) that concerns a single plant species. Our analysis here amounts to an examination of

the physiological plausibility of competitive coexistence by canopy partitioning, a mechanism proposed by Weissing and Huisman (1994) and explored independently by D.E. Bunker, S.C. Stark, and W.P. Carson (*in preparation*). In this paper, we restrict our attention to species that possess a clonal growth form in which deeply shaded young stems receive growth energy subsidies from nearby taller stems by translocation through the roots that connect all stems in the same clone. This mechanism enables each hypothetical plant species to maintain a fixed vertical leaf distribution even though individual stems may sprout, grow in height, and ultimately die as time proceeds. Our model does not consider the potential role of the spectral composition of sunlight which Stomp *et al.* (2004) have shown to determine the outcome of competition in certain laboratory populations of phytoplankton.

This paper is organized as follows. In Sect. 2, we state the differential equations of the canopy partitioning model. We then begin asymptotic analysis by establishing the existence of each species nullcline and determining how these nullclines may meet in the phase plane. Sect. 3 examines the endpoints of the two nullclines on the coordinate axes to establish regions in parameter space in which the two nullcline endpoints on each axis maintain a fixed order. This examination shows that, under certain conditions, stable competitive coexistence is indeed possible, and that the surfaces which divide parameter space into regions that produce coexistence or exclusion can be projected onto a plane whose axes represent two of the parameters. Sect. 4 then examines how this projection depends on the values of other parameters. Because the analytical results of these sections concern somewhat different subjects, we will present their biological interpretations at the end of each section individually. In Sect. 5, we discuss some of the implications of both this study and its companion (Nevai and Vance *in review*), where we address the original question that motivated this whole exploration, namely whether canopy partitioning alone can promote competitive coexistence in a horizontally and temporally homogeneous environment, even if the two species differ only in height.

The two-species population growth model on which this study is based is rather idealized. The question consequently arises as to whether our findings can possibly apply in nature. Future papers will address this question by examining robustness and showing how enhancing the model's realism in various ways does not alter its basic qualitative properties.

## 2 Competition and Nullclines

In this section, we begin mathematical analysis of the canopy partitioning model. This model's basic structure has the classical Kolmogorov (1936) form in which the specific growth rate functions incorporate variation in the rates at which leaves perform photosynthesis when positioned at different heights within the light gradient. We start by presenting the model's differential equations and species nullcline equations. Next, we consider the special case in which each species has a uniform or rectangular vertical leaf area density function. For this case, we determine properties of each individual nullcline, and then we establish conditions under which the nullclines can coincide at most once within the closed first quadrant. After

we interpret the main results of this section biologically, we pause to consider a special case of competition between grossly unequal competitors.

## 2.1 Competition equations

Consider two clonal plant species ( $i = 1, 2$ ) that compete only for sunlight and obey the CANOPY PARTITIONING MODEL of Vance and Nevai (2007). The population growth equations are

$$\frac{dx_i}{dt} = x_i \gamma_i \left( \int_0^\infty \phi_i(S_1(z)x_1, S_2(z)x_2) s_i(z) dz - C_i \right), \quad i = 1, 2,$$

where  $x_i \geq 0$  is the total leaf area per unit ground area of species  $i$  at time  $t \geq 0$ ; the vertical leaf area density of species  $i$  at height  $z \geq 0$  is  $s_i(z) \geq 0$ , with  $\int_0^\infty s_i(z) dz = 1$ ; the fraction of species  $i$ 's leaves that overlie height  $z$  is  $S_i(z) = \int_z^\infty s_i(\zeta) d\zeta$ ; the area of leaves overlying height  $z$  that belong to species  $i$  is  $S_i(z)x_i$ ; the rate of instantaneous gross photosynthesis performed by  $1 \text{ m}^2$  of horizontal leaf surface belonging to species  $i$  that lies beneath leaf area  $\chi_1$  of species 1 and leaf area  $\chi_2$  of species 2 is  $\phi_i(\chi_1, \chi_2)$ ; and the growth factor  $\gamma_i$  and the cost parameter  $C_i$  are positive functions of primary scalar plant parameters, including mean leaf height  $s_i = \int_0^\infty z s_i(z) dz$ . Table 1 displays these and related quantities to be defined below. For a full description of all parameters and functions see Vance and Nevai (2007).

We remark here that Weissing and Huisman (1994) introduce functions that resemble  $s_i(z)$  to describe the vertical distribution of phytoplankton populations that compete for sunlight in a lake. Our model differs from theirs primarily in how this vertical structure is achieved: each of our leaves must be supported by a stem, while each of their neutrally buoyant phytoplankton cells is supported solely by the lake water in which it resides. Consequently, our model is structurally identical to theirs and differs only in assumed properties of the component parameters and functions. Namely, our cost parameter  $C_i$  depends on mean leaf height  $s_i$ , while their cost parameter does not depend on depth. In this paper, we extend their theoretical results by treating the interesting case of overlapping but distinct vertical leaf profiles.

We also note that vertical leaf area distributions have been measured empirically for a variety of single-species and mixed-plant canopies (*e.g.*, Hutchinson *et al.* 1986).

For mathematical simplicity, we assume that the two plant species have the same light extinction coefficient, so that the value of  $\phi_i(\chi_1, \chi_2)$  depends only on the sum  $\chi_1 + \chi_2$ . Consequently, the two-variable function  $\phi_i(\chi_1, \chi_2)$  is given by a related single-variable function  $\phi_i(\chi)$ , with  $\chi = \chi_1 + \chi_2$ . We further assume that (with  $\chi$  now replaced by  $x$ )

- P<sub>1</sub>.**  $\phi_i$  is a continuously differentiable (or  $C^1$ ) function of  $x \geq 0$ ;
- P<sub>2</sub>.**  $\phi_i > 0$  for  $x \geq 0$ ;
- P<sub>3</sub>.**  $\phi_i' < 0$  for  $x \geq 0$ ;
- P<sub>4</sub>.**  $\phi_i \rightarrow 0$  as  $x \rightarrow \infty$ .

Figure 1 displays qualitatively the features of  $\phi_i$  described by these properties. Vance and Nevai (2007) show how properties P<sub>1</sub>-P<sub>4</sub> arise from light absorption

by leaves positioned at different heights (Monsi and Saeki 1953, Thornley and Johnson 1990).

Finally, we remark that properties P<sub>1</sub>-P<sub>4</sub> imply several additional “average value” properties,

- P<sub>5</sub>.  $\phi_i(bx) < \frac{1}{b-a} \int_a^b \phi_i(\alpha x) d\alpha < \phi_i(ax)$  for  $x > 0$  and  $0 \leq a < b$ ;
- P<sub>6</sub>.  $\frac{1}{a} \int_{1-a}^1 \phi_i(\alpha x) d\alpha < \int_0^1 \phi_i(\alpha x) d\alpha < \frac{1}{a} \int_0^a \phi_i(\alpha x) d\alpha$  for  $x > 0$  and  $a \in (0, 1)$ ;
- P<sub>7</sub>.  $\frac{1}{b-a} \int_a^b \phi_i(\alpha x) d\alpha$  is a strictly decreasing function of  $x \geq 0$  for  $0 \leq a < b$ ;
- P<sub>8</sub>.  $\int_0^1 \phi_i(\alpha x) d\alpha \rightarrow 0$  as  $x \rightarrow \infty$ .

These properties have obvious geometric interpretations (see Figure 1).

With these assumptions, and given any nonnegative initial condition, a solution to the dynamical system exists for all time, it is unique, and it approaches a finite equilibrium as  $t \rightarrow \infty$  (Hirsch *et al.* 2004, pp. 144 and 250). Thus, to determine the asymptotic behavior of the dynamical system, it suffices to restrict our attention to nullclines and their intersections with each other and with the coordinate axes.

## 2.2 Nullcline equations

The (non-trivial) nullcline equation for species  $i$  is

$$\int_0^\infty \phi_i(\mathcal{S}_1(z)x_1 + \mathcal{S}_2(z)x_2) \mathfrak{s}_i(z) dz = C_i, \quad i = 1, 2. \quad (2.1)$$

If a solution of (2.1) exists with  $x_i > 0$  then we say that the *nullcline* for species  $i$  also exists and that it is given by all solutions of (2.1) that lie within the closed first quadrant. Otherwise, we say that it does not exist. When the nullcline for species  $i$  does exist, and it intersects a coordinate-axis in the phase plane, then we call this point (and its nonzero coordinate) a *nullcline endpoint*. Because (2.1) defines each nullcline only implicitly (*i.e.*, neither  $x_1$  nor  $x_2$  can be expressed explicitly as a function of the other), we are forced to use implicit methods in all further analysis.

Our entire treatment concerns a particular class of vertical leaf area density functions to be described next.

## 2.3 Vertical leaf profiles

To expedite analysis, we will suppose that species  $i$  has a uniform or rectangular vertical leaf area density function of thickness  $T_i > 0$ , *i.e.*,

$$\mathfrak{s}_i(z) = \begin{cases} 1/T_i, & z \in [s_i - T_i/2, s_i + T_i/2], \\ 0, & \text{elsewhere,} \end{cases} \quad (2.2)$$

where the mean leaf height  $s_2$  of species 2 is greater than or equal to the mean leaf height  $s_1$  of species 1. For brevity, we will usually refer to (2.2) as the *vertical leaf profile* (or VLP) of species  $i$ . Let  $z_i = s_i - T_i/2$  and  $z^i = s_i + T_i/2$  be the heights of the lowest and highest leaves of species  $i$ , respectively. We assume that  $0 \leq z_1 \leq z_2$ ,

so that the lowest leaves of species 1 lie at or above the ground surface and at or below the lowest leaves of species 2; and that  $z^1 \leq z^2$ , so that the highest leaves of species 1 lie at or below the highest leaves of species 2. We do not consider here cases in which the support of one VLP lies entirely in the interior of the support of the other.

If  $z_2 < z^1$ , so that the VLPs of the two species overlap, then the leaf canopy is partitioned into these three height zones:

$$\begin{aligned} \{z : z \in (z^1, z^2)\}, & \quad \text{species 2 only,} \\ \{z : z \in [z_2, z^1]\}, & \quad \text{both species,} \\ \{z : z \in [z_1, z_2)\}, & \quad \text{species 1 only.} \end{aligned}$$

If  $z_2 > z^1$ , so that the VLPs of the two species do not overlap, then the leaf canopy is partitioned into these three height zones:

$$\begin{aligned} \{z : z \in [z_2, z^2]\}, & \quad \text{species 2 only,} \\ \{z : z \in (z^1, z_2)\}, & \quad \text{neither species,} \\ \{z : z \in [z_1, z^1]\}, & \quad \text{species 1 only.} \end{aligned}$$

By convention, we say that if  $z_2 = z^1$  then the VLPs of the two species are adjacent but do not overlap.

It is convenient to introduce two composite parameters (see Figure 2),

$$h = \frac{z_2 - z_1}{T_1} \quad \text{and} \quad k = \frac{z^2 - z^1}{T_2}. \quad (2.3)$$

If  $z_2 < z^1$ , so that the VLPs of the two species overlap, then a fraction  $h \in [0, 1)$  of the leaves of species 1 lie at or below height  $z_2$ , and the remaining fraction  $1 - h$  of its leaves overlap with the leaves of species 2; similarly, a fraction  $k \in [0, 1)$  of the leaves of species 2 lie at or above height  $z^1$ , and the remaining fraction  $1 - k$  of its leaves overlap with the leaves of species 1. Thus  $h$  and  $k$ , which we call the *understory index* and the *overstory index*, respectively, each quantify in a different way the degree to which species 2's leaves lie above those of species 1. If  $z_2 = z^1$ , so that the VLPs of the two species are adjacent, then  $h = k = 1$ . If  $z_2 > z^1$ , so that the VLP of species 2 lies entirely above the VLP of species 1, then  $h, k \in (1, \infty)$ . In summary,  $h$  and  $k$  are *simultaneously* less than, equal to, or greater than 1, and because we assumed that  $z_2 \geq z_1$  and  $z^2 \geq z^1$ , both  $h$  and  $k$  are restricted to nonnegative values.

We note that our analysis includes the possibility that either the understory index  $h$  may vanish (which occurs when  $z_2 = z_1$ ) or the overstory index  $k$  may vanish (which occurs when  $z^2 = z^1$ ). In particular, if both these conditions hold simultaneously (*i.e.*,  $h = k = 0$ ) then the two species share the same VLP.

We now define the composite parameter  $\omega = T_1/T_2$  (the ratio of VLP thicknesses) and its reciprocal  $\hat{\omega} = 1/\omega$ . We obtain the following useful result when the VLPs overlap.

**Lemma 2.1** *Suppose that  $z_2 < z^1$ . Then*

- (a)  $\omega = \frac{1-k}{1-h}$ ;  
 (b)  $S_2(z) = \omega S_1(z) + k$  for  $z \in [z_2, z^1]$ .

*Proof*

- (a) It follows from (2.3) and the relation  $T_i = z^i - z_i$  that

$$\left(\frac{1-k}{1-h}\right) \hat{\omega} = \frac{(1-k)T_2}{(1-h)T_1} = \frac{(z^2 - z_2) - (z^2 - z^1)}{(z^1 - z_1) - (z_2 - z_1)} = 1 = \omega \hat{\omega}.$$

- (b) This part follows from a direct calculation involving (2.2) and (2.3).  $\square$

## 2.4 Nullcline existence theorems

We now obtain information about the individual nullclines, which are defined by (2.1) and (2.2). The structure of these equations forces use of implicit arguments to determine the existence, uniqueness, continuity, shape, and location of each nullcline. To simplify notation in later arguments, we define the continuous ramp functions

$$r_1(\alpha) = \begin{cases} \omega\alpha + k, & \alpha \in [0, 1-h] \\ 1, & \alpha \in [1-h, 1], \end{cases} \quad (2.4a)$$

$$r_2(\alpha) = \begin{cases} 0, & \alpha \in [0, k] \\ \hat{\omega}(\alpha - k), & \alpha \in [k, 1], \end{cases} \quad (2.4b)$$

for  $z_2 < z^1$  (see Figure 3). Observe that if  $h = k = 0$  then  $r_2(\alpha) = \alpha = r_1(\alpha)$  for  $\alpha \in (0, 1)$ , but if either  $h > 0$  or  $k > 0$  then  $r_2(\alpha) < \alpha < r_1(\alpha)$  for  $\alpha \in (0, 1)$ . If  $z_2 \geq z^1$ , then we define  $r_1(\alpha) \equiv 1$  and  $r_2(\alpha) \equiv 0$ . Intuitively, species 1 and species 2 maintain fixed fractions  $\alpha = S_1(z)$  and  $r_1(\alpha)$ , respectively, of their leaves above height  $z \in [z_1, z^1]$ , and they maintain fixed fractions  $r_2(\alpha)$  and  $\alpha = S_2(z)$ , respectively, of their leaves above height  $z \in [z_2, z^2]$ .

We begin by stating and proving the main properties of the species 1 nullcline.

**Theorem 2.1 (Species 1 Nullcline)** *Species 1 has a nullcline if and only if  $\phi_1(0) > C_1$ . If this condition holds, then this nullcline  $(x_1, x_2^1)$  satisfies the equation*

$$\int_0^1 \phi_1(\alpha x_1 + r_1(\alpha) x_2^1) d\alpha = C_1; \quad (2.5)$$

*there exist unique  $x_1^\dagger, x_2^\ddagger \in (0, \infty)$  such that  $(x_1^\dagger, 0)$  and  $(0, x_2^\ddagger)$  satisfy (2.5); and  $x_2^1$  is a  $C^1$ -function of  $x_1 \in [0, x_1^\dagger]$ . If the two species share the same vertical leaf profile then  $x_1 + x_2^1 \equiv x_1^\dagger$ ; otherwise  $dx_2^1/dx_1 \in (-1, 0)$  everywhere.*

*Proof* We consider the two cases  $z_2 < z^1$  and  $z_2 \geq z^1$  separately.

- (a) Suppose first that  $z_2 < z^1$ , so that the VLPs overlap. Recall that species 1 has a nullcline provided that the equation

$$\Theta(x_1, x_2) \stackrel{\text{def}}{=} \int_{z_1}^{z^1} \phi_1(\mathcal{S}_1(z)x_1 + \mathcal{S}_2(z)x_2) \mathfrak{s}_1(z) dz = C_1$$

has a solution  $(x_1, x_2)$  with  $x_1 > 0$  and  $x_2 \geq 0$ . We apply Lemma 2.1 (b) and change the variable of integration from  $z$  to  $\alpha = \mathcal{S}_1(z)$  to obtain

$$\begin{aligned} \Theta(x_1, x_2) &= \int_{z_1}^{z_2} \phi_1(\mathcal{S}_1(z)x_1 + x_2) \mathfrak{s}_1(z) dz \\ &\quad + \int_{z_2}^{z^1} \phi_1(\mathcal{S}_1(z)x_1 + [\omega\mathcal{S}_1(z) + k]x_2) \mathfrak{s}_1(z) dz \\ &= \int_{1-h}^1 \phi_1(\alpha x_1 + x_2) d\alpha + \int_0^{1-h} \phi_1(\alpha x_1 + (\omega\alpha + k)x_2) d\alpha \\ &= \int_0^1 \phi_1(\alpha x_1 + \mathfrak{r}_1(\alpha)x_2) d\alpha. \end{aligned}$$

Since  $\Theta(0, 0) = \phi_1(0)$  and  $\Theta$  is a positive, continuous, and strictly decreasing function of  $x_1 \geq 0$  and  $x_2 \geq 0$ , we conclude that if  $\phi_1(0) \leq C_1$  then the nullcline does not exist. We now assume otherwise, *i.e.*, that  $\phi_1(0) > C_1$ . Then by property P<sub>8</sub>,

$$\lim_{x_1 \rightarrow \infty} \Theta(x_1, 0) = \lim_{x_1 \rightarrow \infty} \int_0^1 \phi_1(\alpha x_1) d\alpha = 0 < C_1.$$

Consequently, there exists a unique  $x_1^\dagger \in (0, \infty)$  such that  $\Theta(x_1^\dagger, 0) = C_1$ , and the nullcline exists. Similarly, and because  $\mathfrak{r}_1(\alpha) \geq \alpha$  on  $[0, 1]$ , we obtain from property P<sub>3</sub> that there exists a unique  $x_2^\ddagger \in (0, \infty)$  such that  $\Theta(0, x_2^\ddagger) = C_1$ . For each  $x_1 \in (0, x_1^\dagger)$ , we have  $\Theta(x_1, 0) > \Theta(x_1^\dagger, 0) = C_1 = \Theta(0, x_2^\ddagger) > \Theta(x_1, x_2^\ddagger)$ . Thus, there exists a unique  $x_2^1 \in (0, x_2^\ddagger)$  such that  $\Theta(x_1, x_2^1) = C_1$ . We extend the definition of  $x_2^1$  to all  $x_1 \in [0, x_1^\dagger]$  by defining  $x_2^1 = x_2^\ddagger$  when  $x_1 = 0$  and  $x_2^1 = 0$  when  $x_1 = x_1^\dagger$ . Indeed, continuity of both sides of the equation  $\Theta(x_1, x_2) = C_1$ , together with the uniqueness of its solution, guarantee that  $x_2^1$  is a continuous function of  $x_1 \in [0, x_1^\dagger]$ . If  $h = k = 0$  then  $\mathfrak{r}_1(\alpha) = \alpha$  for  $\alpha \in [0, 1]$ . In this case,

$$\int_0^1 \phi_1(\alpha(x_1 + x_2^1)) d\alpha = C_1 = \int_0^1 \phi_1(\alpha x_1^\dagger) d\alpha.$$

Property P<sub>7</sub> implies that  $x_1 + x_2^1 \equiv x_1^\dagger$  for  $x_1 \in [0, x_1^\dagger]$ . We now suppose that either  $h > 0$  or  $k > 0$ , so that  $\mathfrak{r}_1(\alpha) > \alpha$  for  $\alpha \in (0, 1)$ . The implicit function theorem (*e.g.*, Courant 1964) implies that  $dx_2^1/dx_1$  exists for  $x_1 \in (0, x_1^\dagger)$ . Thus, we can implicitly differentiate (2.5) with respect to  $x_1$  to obtain

$$\frac{dx_2^1}{dx_1} = - \left[ \frac{\int_0^1 \phi_1'(\alpha x_1 + \mathfrak{r}_1(\alpha)x_2^1) \alpha d\alpha}{\int_0^1 \phi_1'(\alpha x_1 + \mathfrak{r}_1(\alpha)x_2^1) \mathfrak{r}_1(\alpha) d\alpha} \right].$$

Since  $x_2^1$  is a continuous function of  $x_1 \in [0, x_1^\dagger]$ , its derivative  $dx_2^1/dx_1$  is also a continuous function of  $x_1 \in [0, x_1^\dagger]$ . Since  $\phi_1'$  has constant sign and  $r_1(\alpha) > \alpha$  for  $\alpha \in (0, 1)$ , we conclude that  $dx_2^1/dx_1 \in (-1, 0)$  everywhere.

- (b) If  $z_2 \geq z^1$ , so that the VLPs do not overlap, then a similar argument as in (a) applies, but with  $r_1(\alpha) \equiv 1$ .  $\square$

We now state a similar theorem regarding the species 2 nullcline. This time, the proof is more involved because the species 2 nullcline may or may not intersect the  $x_1$ -axis.

**Theorem 2.2 (Species 2 Nullcline)** *Species 2 has a nullcline if and only if  $\phi_2(0) > C_2$ . If this condition holds, then this nullcline  $(x_1, x_2^2)$  satisfies the equation*

$$\int_0^1 \phi_2(r_2(\alpha)x_1 + \alpha x_2^2) d\alpha = C_2, \quad (2.6)$$

and there exists a unique  $x_2^\dagger \in (0, \infty)$  such that  $(0, x_2^\dagger)$  satisfies (2.6).

- (a) *Suppose the vertical leaf profiles of the two species overlap.*
- (i) *If  $k\phi_2(0) < C_2$ , then there exists a unique  $x_1^\dagger \in (0, \infty)$  such that  $(x_1^\dagger, 0)$  satisfies (2.6), and  $x_2^2$  is a  $C^1$ -function of  $x_1 \in [0, x_1^\dagger]$ . If the two species share the same vertical leaf profile then  $x_1 + x_2^2 \equiv x_2^\dagger$ ; otherwise  $dx_2^2/dx_1 \in (-1, 0)$  everywhere.*
- (ii) *If  $k\phi_2(0) \geq C_2$ , then the nullcline does not intersect the  $x_1$ -axis;  $x_2^2$  is a  $C^1$ -function of  $x_1 \in [0, \infty)$ ; and  $dx_2^2/dx_1 \in (-1, 0)$  everywhere.*
- (b) *Suppose the vertical leaf profiles of the two species do not overlap. Then  $x_2^2 \equiv x_2^\dagger$  for  $x_1 \in [0, \infty)$ .*

*Proof* As before, we consider the two cases  $z_2 < z^1$  and  $z_2 \geq z^1$  separately.

- (a) Suppose first that  $z_2 < z^1$ , so that the VLPs overlap. This time, species 2 has a nullcline provided that

$$\Theta(x_1, x_2) \stackrel{\text{def}}{=} \int_{z_2}^{z^2} \phi_2(S_1(z)x_1 + S_2(z)x_2) s_2(z) dz = C_2$$

has a solution  $(x_1, x_2)$  with  $x_1 \geq 0$  and  $x_2 > 0$ . We apply Lemma 2.1 (b) and change the variable of integration from  $z$  to  $\alpha = S_2(z)$  to obtain

$$\begin{aligned} \Theta(x_1, x_2) &= \int_{z_2}^{z^1} \phi_2(\hat{\omega}(S_2(z) - k)x_1 + S_2(z)x_2) s_2(z) dz \\ &\quad + \int_{z^1}^{z^2} \phi_2(S_2(z)x_2) s_2(z) dz \\ &= \int_k^1 \phi_2(\hat{\omega}(\alpha - k)x_1 + \alpha x_2) d\alpha + \int_0^k \phi_2(\alpha x_2) d\alpha \\ &= \int_0^1 \phi_2(r_2(\alpha)x_1 + \alpha x_2) d\alpha. \end{aligned}$$

Since  $\Theta(0,0) = \phi_2(0)$  and  $\Theta$  is a positive, continuous, and strictly decreasing function of  $x_1 \geq 0$  and  $x_2 \geq 0$ , we conclude that if  $\phi_2(0) \leq C_2$  then the nullcline does not exist. We now assume otherwise, *i.e.*, that  $\phi_2(0) > C_2$ . Then by property P<sub>8</sub>,

$$\lim_{x_2 \rightarrow \infty} \Theta(0, x_2) = \lim_{x_2 \rightarrow \infty} \int_0^1 \phi_2(\alpha x_2) d\alpha = 0 < C_2.$$

Consequently, there exists a unique  $x_2^\dagger \in (0, \infty)$  such that  $\Theta(0, x_2^\dagger) = C_2$ , and the nullcline exists. However,

$$\begin{aligned} \lim_{x_1 \rightarrow \infty} \Theta(x_1, 0) &= \lim_{x_1 \rightarrow \infty} \int_0^1 \phi_2(r_2(\alpha)x_1) d\alpha \\ &= \lim_{x_1 \rightarrow \infty} \left[ \int_0^k \phi_2(0) d\alpha + \int_k^1 \phi_2(\hat{\omega}(\alpha - k)x_1) d\alpha \right] \\ &= k\phi_2(0) + (1 - k) \lim_{x_1 \rightarrow \infty} \int_0^1 \phi_2(\tilde{\alpha}(1 - h)x_1) d\tilde{\alpha} \\ &= k\phi_2(0), \end{aligned}$$

where we have used property P<sub>8</sub> in the last step with  $(1 - h)x_1$  in place of  $x$ . Thus, there exists  $x_1^\ddagger \in (0, \infty)$  such that  $\Theta(x_1^\ddagger, 0) = C_2$  if and only if  $k\phi_2(0) < C_2$ . We now consider the two subcases  $k\phi_2(0) < C_2$  and  $k\phi_2(0) \geq C_2$  separately.

(i) Suppose first that  $k\phi_2(0) < C_2$ , so that  $x_1^\ddagger$  exists. For each  $x_1 \in (0, x_1^\ddagger)$ , we have  $\Theta(x_1, 0) > \Theta(x_1^\ddagger, 0) = C_2 = \Theta(0, x_2^\dagger) > \Theta(x_1, x_2^\dagger)$ . Thus, there exists a unique  $x_2^2 \in (0, x_2^\dagger)$  such that  $\Theta(x_1, x_2^2) = C_2$ . As before, we extend the definition of  $x_2^2$  to all  $x_1 \in [0, x_1^\ddagger]$  by defining  $x_2^2 = x_2^\dagger$  when  $x_1 = 0$  and  $x_2^2 = 0$  when  $x_1 = x_1^\ddagger$ . An argument similar to the one used in the proof of Theorem 2.1 establishes that  $x_2^2$  is a continuous function of  $x_1 \in [0, x_1^\ddagger]$ , that  $x_1 + x_2^2 \equiv x_2^\dagger$  for  $x_1 \in [0, x_1^\ddagger]$  when  $h = k = 0$ , and that if either  $h > 0$  or  $k > 0$  then

$$\frac{dx_2^2}{dx_1} = - \left[ \frac{\int_0^1 \phi_2'(r_2(\alpha)x_1 + \alpha x_2^2) r_2(\alpha) d\alpha}{\int_0^1 \phi_2'(r_2(\alpha)x_1 + \alpha x_2^2) \alpha d\alpha} \right]$$

exists and is a continuous function of  $x_1 \in [0, x_1^\ddagger]$  with  $dx_2^2/dx_1 \in (-1, 0)$  everywhere.

(ii) Now suppose that  $k\phi_2(0) \geq C_2$ , so that  $x_1^\ddagger$  does not exist. For each  $x_1 \in (0, \infty)$ , we have  $\Theta(x_1, 0) > k\phi_2(0) \geq C_2 = \Theta(0, x_2^\dagger) > \Theta(x_1, x_2^\dagger)$ . Thus, there exists a unique  $x_2^2 \in (0, x_2^\dagger)$  such that  $\Theta(x_1, x_2^2) = C_2$ . Again, we extend the definition of  $x_2^2$  to all  $x_1 \in [0, \infty)$  by defining  $x_2^2 = x_2^\dagger$  when  $x_1 = 0$ . As before,  $x_2^2$  is a  $C^1$ -function of  $x_1 \in [0, \infty)$  with  $dx_2^2/dx_1 \in (-1, 0)$  everywhere.

(b) Now suppose that  $z_2 \geq z^1$ , so that the VLPs do not overlap. An argument similar to the one in (a), but with  $r_2(\alpha) \equiv 0$ , establishes that the nullcline exists if and only if  $\phi_2(0) > C_2$ . Furthermore, it is clear in this case that the nullcline does not depend on  $x_1$  and that with  $x_2^\dagger$  defined as in (a), the pair  $(x_1, x_2^\dagger)$  uniquely satisfies (2.6) for each  $x_1 \geq 0$ .  $\square$

## 2.5 Nullcline intersection theorems

Having determined individual properties of each nullcline separately, we now consider them in relation to each other. The first theorem concerns species with the same VLP.

**Theorem 2.3 (Identical Vertical Leaf Profiles)** *Suppose that  $C_1 < \phi_1(0)$  and  $C_2 < \phi_2(0)$ , so that both species nullclines exist, and that the two species share the same vertical leaf profile. Then the nullclines either do not coincide anywhere or they coincide everywhere.*

*Proof* Suppose that  $h = k = 0$  so that the two species share the same VLP. Theorems 2.1 and 2.2 establish that  $x_1 + x_2^1 \equiv x_1^\dagger$  and  $x_1 + x_2^2 \equiv x_2^\dagger$ . Thus, if  $x_1^\dagger < x_2^\dagger$  then the species 1 nullcline lies closer to the origin than the species 2 nullcline everywhere, if  $x_1^\dagger = x_2^\dagger$  then the nullclines coincide everywhere, and if  $x_1^\dagger > x_2^\dagger$  then the species 1 nullcline lies further from the origin than the species 2 nullcline everywhere.  $\square$

For parametric functions  $\phi_1$  and  $\phi_2$ , parameter values that produce coincident nullclines in Theorem 2.3 are confined to a region of parameter space that has measure zero, and consequently identical VLPs almost surely produce nullclines that coincide nowhere. We remark that Theorem 2.3 continues to hold even if two competing plant species possess identical but arbitrary (*i.e.*, non-rectangular) VLPs.

The next theorem concerns species with non-overlapping VLPs.

**Theorem 2.4 (Non-Overlapping Vertical Leaf Profiles)** *Suppose that  $C_1 < \phi_1(0)$  and  $C_2 < \phi_2(0)$ , so that both species nullclines exist, and that the vertical leaf profiles of the two species do not overlap. Then the nullclines coincide at most once.*

*Proof* If  $z_2 \geq z^1$ , so that the VLPs of the two species do not overlap, then the conclusion is immediate from Theorems 2.1 and 2.2 because the nullcline of species 1 is strictly decreasing for  $x_1 \in [0, x_1^\dagger]$ , whereas the nullcline of species 2 is a horizontal line for  $x_1 \in [0, \infty)$ .  $\square$

As before, Theorem 2.4 continues to hold even if two competing plant species possess arbitrary non-overlapping VLPs in which all of the leaves of species 2 lie entirely above all of the leaves of species 1.

The next theorem, which is our first major result, concerns species with overlapping but distinct VLPs. We write “ $\phi_1 \equiv \phi_2$ ” when  $\phi_1(x) = \phi_2(x)$  for  $x \geq 0$ .

**Theorem 2.5 (Overlapping but Distinct Vertical Leaf Profiles)** *Suppose that  $C_1 < \phi_1(0)$  and  $C_2 < \phi_2(0)$ , so that both species nullclines exist, and that the vertical leaf profiles of the two species overlap but are distinct. If  $\phi_1 \equiv \phi_2$  then the nullclines coincide at most once.*

*Proof* We argue by contradiction. Suppose that at least one of  $h$  or  $k$  lies strictly between 0 and 1, so that the VLPs of the two species overlap but are distinct, and that  $(\xi_1, \eta_1)$  and  $(\xi_2, \eta_2)$  are distinct points within the closed first quadrant at which the two nullclines agree with  $\xi_1 < \xi_2$ . Then  $\eta_1 > \eta_2$  because the

species 1 nullcline is strictly decreasing by Theorem 2.1. At any point  $(x_1, x_2^1)$  on the species 1 nullcline,

$$\frac{d(x_1 + x_2^1)}{dx_1} = 1 + \frac{dx_2^1}{dx_1} > 0,$$

and so  $\xi_1 + \eta_1 < \xi_2 + \eta_2$ . Because the points  $(\xi_1, \eta_1)$  and  $(\xi_2, \eta_2)$  lie on both nullclines, they each satisfy (2.5) and (2.6),

$$\int_0^1 \phi_1(\alpha \xi_i + r_1(\alpha) \eta_i) d\alpha = C_1, \quad i = 1, 2,$$

$$\int_0^1 \phi_2(r_2(\alpha) \xi_i + \alpha \eta_i) d\alpha = C_2, \quad i = 1, 2.$$

We subtract the first equation with  $i = 2$  from the first equation with  $i = 1$ , do the same for the second equation, and then apply the fundamental theorem of calculus to the resulting differences separately to obtain

$$\int_0^1 \int_{\theta_2(\alpha)}^{\theta_1(\alpha)} \phi_1'(\beta) d\beta d\alpha = 0, \quad (2.7a)$$

$$\int_0^1 \int_{\psi_2(\alpha)}^{\psi_1(\alpha)} \phi_2'(\beta) d\beta d\alpha = 0, \quad (2.7b)$$

where

$$\theta_i(\alpha) = \alpha \xi_i + r_1(\alpha) \eta_i, \quad i = 1, 2,$$

$$\psi_i(\alpha) = r_2(\alpha) \xi_i + \alpha \eta_i, \quad i = 1, 2.$$

By inspection, the functions  $\theta_i$  and  $\psi_i$  are both nonnegative for  $\alpha \in [0, 1]$  and  $i = 1, 2$ . We consider two cases, showing that each leads to the desired contradiction.

- (i) Suppose first that  $(1-h)\xi_1 + \eta_1 > (1-h)\xi_2 + \eta_2$ . If  $h = 0$  then we immediately obtain a contradiction, so we may assume that  $h > 0$ . Observe that  $\psi_i(\alpha)$  is continuous, non-decreasing, and piecewise linear for  $\alpha \in [0, 1]$  and  $i = 1, 2$ , with a single kink at  $\alpha = k$ ; that  $\psi_i(0) = 0$ ; that  $\psi_1(k) = k\eta_1 \geq k\eta_2 = \psi_2(k)$ , with equality only when  $k = 0$ ; and that  $\psi_1(1) = (1-h)\xi_1 + \eta_1 > (1-h)\xi_2 + \eta_2 = \psi_2(1)$ . Consequently,  $\psi_1(\alpha) > \psi_2(\alpha)$  for  $\alpha \in (0, 1)$ . Since  $\phi_2'$  is negative, we conclude that the left-hand side of (2.7b) is negative, a contradiction.
- (ii) Now suppose that  $(1-h)\xi_1 + \eta_1 \leq (1-h)\xi_2 + \eta_2$ . Observe that  $\theta_i(\alpha)$  is continuous, strictly increasing, and piecewise linear for  $\alpha \in [0, 1]$  and  $i = 1, 2$ , with a single kink at  $\alpha = 1-h$ ; that  $\theta_1(1-h) = (1-h)\xi_1 + \eta_1 \leq (1-h)\xi_2 + \eta_2 = \theta_2(1-h)$ ; and that  $\theta_1(1) = \xi_1 + \eta_1 < \xi_2 + \eta_2 = \theta_2(1)$ . Consequently,  $\theta_1(\alpha) < \theta_2(\alpha)$  for  $\alpha \in (1-h, 1)$ . Eq. (2.7a) and the definitions of  $\theta_i(\alpha)$  and  $r_1(\alpha)$  together imply that

$$\int_0^{1-h} \int_{\alpha \xi_2 + (\omega \alpha + k) \eta_2}^{\alpha \xi_1 + (\omega \alpha + k) \eta_1} \phi_1'(\beta) d\beta d\alpha + \int_{1-h}^1 \int_{\alpha \xi_2 + \eta_2}^{\alpha \xi_1 + \eta_1} \phi_1'(\beta) d\beta d\alpha = 0.$$

Similarly, (2.7b) and the definitions of  $\psi_i(\alpha)$  and  $r_2(\alpha)$  together imply that

$$\int_0^k \int_{\alpha \eta_2}^{\alpha \eta_1} \phi_2'(\beta) d\beta d\alpha + \int_k^1 \int_{\hat{\omega}(\alpha-k)\xi_2 + \alpha \eta_2}^{\hat{\omega}(\alpha-k)\xi_1 + \alpha \eta_1} \phi_2'(\beta) d\beta d\alpha = 0.$$

We change the variable of integration in the second integral on the left-hand side from  $\alpha$  to  $\pi = \hat{\omega}(\alpha - k)$  to get

$$\int_0^k \int_{\alpha\eta_2}^{\alpha\eta_1} \phi_2'(\beta) d\beta d\alpha + \omega \int_0^{1-h} \int_{\pi\xi_2+(\omega\pi+k)\eta_2}^{\pi\xi_1+(\omega\pi+k)\eta_1} \phi_2'(\beta) d\beta d\pi = 0.$$

We multiply this equation by  $\hat{\omega}$  and then subtract it from the one above involving  $\phi_1'$  to get, after rearrangement,

$$\begin{aligned} \int_0^{1-h} \int_{\theta_2(\alpha)}^{\theta_1(\alpha)} [\phi_1'(\beta) - \phi_2'(\beta)] d\beta d\alpha \\ = \hat{\omega} \int_0^k \int_{\alpha\eta_2}^{\alpha\eta_1} \phi_2'(\beta) d\beta d\alpha - \int_{1-h}^1 \int_{\alpha\xi_2+\eta_2}^{\alpha\xi_1+\eta_1} \phi_1'(\beta) d\beta d\alpha. \end{aligned}$$

The nonnegativity of the functions  $\theta_1$  and  $\theta_2$ , together with the assumption  $\phi_1 \equiv \phi_2$ , implies that the left-hand side vanishes. Since  $\eta_1 > \eta_2$  and  $\phi_2' < 0$ , the first double integral on the right-hand side is negative if  $k > 0$ , and it vanishes when  $k = 0$ . Since  $\alpha\xi_1 + \eta_1 = \theta_1(\alpha) < \theta_2(\alpha) = \alpha\xi_2 + \eta_2$  for  $\alpha \in (1-h, 1)$  and  $\phi_1' < 0$ , the second double integral on the right-hand side is positive if  $h > 0$ , and it vanishes when  $h = 0$ . Since  $h$  and  $k$  cannot both be zero, the right-hand side must be negative, a contradiction.  $\square$

The five theorems of this section together imply that if  $\phi_1 \equiv \phi_2$  then there are ten qualitatively distinct possible nullcline arrangements in the phase plane. Figure 4 displays each of these possibilities except for the improbable case that two species with identical VLPs possess everywhere coincident nullclines (which if  $\phi_1 \equiv \phi_2$  can occur only when  $C_1 = C_2$ ).

## 2.6 Nullcline tangency

The proof of Theorem 2.4 establishes that when two species have non-overlapping VLPs, their nullclines actually cross wherever they may meet because they have distinct slopes there. However, the proof of Theorem 2.5, in which two species have overlapping but distinct VLPs, does not exclude the possibility that a nullcline meeting may be a point of tangency. An isolated nullcline tangency point at which the nullclines do not cross constitutes a semistable equilibrium point of the dynamical system that repels trajectories from a nonzero continuous range of directions while attracting trajectories from all other directions [see Figure 4 (h, i)]. In practice such a semistable equilibrium point would exert little influence in the inherently stochastic biological system whose ‘‘average’’ behavior our deterministic model is meant to represent, because random variation will always eventually displace any trajectory near the model equilibrium point into its repelling region. Since the nullclines can coincide at most once, the biological system’s behavior will resemble that of the appropriate case of the deterministic model in which the nullclines do not meet at all. For this reason, we will assume from now on that if the nullclines meet at an isolated point within the interior of the first quadrant, then they cross there. Hirsch *et al.* (2004, p. 247) view ecological competition equations in this same way. However, we hasten to point out that if  $\phi_1 \equiv \phi_2$  then

it is not obvious whether this assumed crossing is generic, although one would certainly expect it when  $\phi_1$  and  $\phi_2$  are distinct.

## 2.7 Biological interpretations

We now interpret the preceding results.

According to Theorem 2.1, the shorter species can always persist when living alone provided that the rate  $\phi_1(0)$  at which its leaves perform photosynthesis when exposed to full sunlight (per unit leaf area) exceeds its cost parameter  $C_1$ . Theorem 2.2 states a similar result for the taller species. These statements both agree with biological intuition.

Theorem 2.2 also produces another conclusion. Suppose that the taller species attempts to invade a community in which the shorter species is living alone (but not necessarily at equilibrium), and that the two species have overlapping VLPs. Initially, the taller species will be present at an infinitesimal population size, and so all of its leaves within the overstory (*i.e.*, above height  $z^1$ ) will be exposed to essentially full sunlight. If the contribution  $k\phi_2(0)$  of these leaves alone to its rate of photosynthesis (per unit leaf area) exceeds its cost parameter  $C_2$ , then the taller species can always successfully invade. Otherwise, the shorter species can at very high densities (*i.e.*, leaf areas) prevent the taller species from invading. This pattern agrees with biological intuition because if the shorter species is present at a very high density, so that little sunlight penetrates below height  $z^1$ , then the taller species must rely entirely on the energy obtained from photosynthesis in the overstory. If overstory photosynthesis is sufficient to cover metabolic costs then it persists. Otherwise it does not.

We now restrict our attention to two species that can each persist when living alone.

Theorem 2.3 and the remark that follows it imply that if two species possess identical (but arbitrary) VLPs, then competitive exclusion will almost surely occur, with the identity of the winning species depending on parameters. In this case, the species which by itself can persist at a higher equilibrium leaf area will always exclude the other, with neutrally stable coexistence occurring only in the exceptional case that both species share the same equilibrium. Weissing and Huisman (1994) reach the same conclusion for phytoplankton “distributed in parallel”. Theorem 2.3 is also consistent with the competitive exclusion result of Armstrong and McGehee (1980). It follows that if competitive coexistence can occur in our hypothetical plant species, then it will arise from a difference in their VLPs.

Theorem 2.4 and its proof reveal that if two species possess non-overlapping VLPs, then, depending on parameters, either (i) the taller species excludes the shorter species or (ii) the two species can coexist at a globally attracting equilibrium point, *i.e.*, at an equilibrium point which globally attracts the interior of the first quadrant. However, we have not yet shown that parameter combinations actually exist for which the latter competitive outcome does occur. We will return to this matter in Sect. 3.

The principal subject of Sect. 3 concerns the fates of competitors with overlapping VLPs. Although Theorem 2.5 does not by itself resolve whether there exist parameter combinations for which such plant species can competitively coexist, it does ensure that species which share the same photosynthesis function can coexist

at no more than one equilibrium point. We hasten to point out that Theorem 2.5 concerns only plant species with distinct rectangular VLPs that share the same light extinction coefficient and the same photosynthesis function. We do not fully understand how nontrivial violations of these conditions might change the theorem's conclusion, although Just and Nevai (*in review*) have made some progress in this area.

## 2.8 Uniform competitive superiority

Before continuing our main analysis, we pause briefly to state a minor extension of Theorem 2.5 that concerns two similar kinds of grossly unequal competitive interactions. These extensions are unlikely to offer much help in understanding real-world cases of plant competitive coexistence because such cases necessarily involve species that have competitive abilities of about the same magnitude. We present this extension in the hope of inspiring future attempts to generalize Theorem 2.5 in more substantive ways.

**Theorem 2.6 (Uniform Competitive Superiority)** *Suppose that  $C_1 < \phi_1(0)$  and  $C_2 < \phi_2(0)$ , so that both species nullclines exist, and that the vertical leaf profiles of the two species overlap but are distinct. Let  $\mathcal{I} = [0, x_1^\dagger]$ .*

- (a) *If  $\phi_1(x) \leq \phi_2(x)$  for  $x \in \mathcal{I}$  and  $C_1 \geq C_2$  then species 2 excludes species 1;*
- (b) *If  $\phi_1(x) \geq \phi_2(x)$  for  $x \in \mathcal{I}$  and  $C_1 \leq C_2$  then species 1 excludes species 2.*

*Proof* Assume that at least one of  $h$  or  $k$  lies strictly between 0 and 1. Let  $(\xi, \eta)$  be any point within the closed first quadrant that lies along the species 1 nullcline. Then  $\xi$  and  $\eta$  are both nonnegative and at least one is positive. Since the point  $(x_1^\dagger, 0)$  also lies on the species 1 nullcline, it follows from  $dx_2^1/dx_1 \in (-1, 0)$  in Theorem 2.1 that  $\xi + \eta \leq x_1^\dagger$ . Moreover, since either  $h$  or  $k$  is different from 0, we have  $r_2(\alpha) < \alpha < r_1(\alpha)$  for  $\alpha \in (0, 1)$ . Thus, the functions  $\theta(\alpha) = \alpha\xi + r_1(\alpha)\eta$  and  $\psi(\alpha) = r_2(\alpha)\xi + \alpha\eta$  satisfy

$$0 \leq \psi(\alpha) < \theta(\alpha) < x_1^\dagger, \quad \text{for } \alpha \in (0, 1).$$

Property P<sub>7</sub>, the assumption  $\phi_1(x) \leq \phi_2(x)$  for  $x \in \mathcal{I}$ , eq. (2.5), and the assumption  $C_1 \geq C_2$  together imply that

$$\int_0^1 \phi_2(\psi(\alpha)) d\alpha > \int_0^1 \phi_2(\theta(\alpha)) d\alpha \geq \int_0^1 \phi_1(\theta(\alpha)) d\alpha = C_1 \geq C_2.$$

Since  $(\xi, \eta)$  was arbitrary, we conclude from (2.6) that the species 1 nullcline lies closer to the origin than the species 2 nullcline. This proves (a). The proof for (b) is similar.  $\square$

We conclude this section by interpreting the conclusions of Theorem 2.6 biologically for two species that possess overlapping but distinct VLPs. If the taller species is grossly competitive dominant (because of its rapid photosynthesis and lower cost parameter) then it will always exclude the shorter species. Conversely, if the shorter species is grossly competitive dominant (because its lowest leaves

perform photosynthesis more rapidly than the highest leaves of the taller species and it has a lower cost parameter) then it will always exclude the taller species. The fact that the grossly competitive dominant survives is of course expected, but what is surprising is that if the shorter species is the grossly competitive dominant then competitive exclusion occurs even when the VLP overlap is slight.

### 3 The Outcome of Competition

Examining local stability of equilibrium points proves impractical when the VLPs of the two species overlap and are distinct. Consequently, we proceed directly with global analysis by examining nullcline endpoint positions. Knowledge of the relative magnitudes of the nullcline endpoints along each axis, together with the fact that the nullclines can coincide (under certain conditions) at most once, can allow us to determine (i) whether coexistence is possible, and (ii) whether coexistence, when possible, is stable or unstable.

Our plan is to divide parameter space into regions in which the various outcomes of competition occur. We first identify the region in which each species can persist when living alone. This region can be further divided according to whether the two species have overlapping or non-overlapping VLPs. Most of the analysis in this section concerns the overlapping case. In this case, we demonstrate the existence of a surface  $k_1$  that partitions parameter space into regions within which the species 1-axis endpoints ( $x_1^\dagger$  and  $x_1^\ddagger$ ) maintain a fixed order. A corresponding surface  $k_2$  for the species 2-axis endpoints ( $x_2^\dagger$  and  $x_2^\ddagger$ ) is also shown to exist. Then for the case  $\phi_1 \equiv \phi_2$ , we determine the relative positions of these two surfaces, and hence regions in parameter space within which the various outcomes of competition occur. Finally, we interpret these and corresponding results for non-overlapping VLPs in biological terms.

For economy, we will employ the notation “ $x[<, =, >]y$  for  $a[<, =, >]b$ ” to represent the situation in which  $x < y$ ,  $x = y$ , or  $x > y$  if and only if  $a < b$ ,  $a = b$ , or  $a > b$ , respectively.

#### 3.1 Parameter space

Species  $i$  can persist when living alone if and only if its nullcline exists, which occurs if and only if  $C_i < \phi_i(0)$  by Theorems 2.1 and 2.2. In light of this observation, we define  $C_i^m = \phi_i(0)$ , where the superscript (m) denotes “maximum”. If  $C_1 \geq C_1^m$ , so that species 1 cannot persist when living alone, then species 2 excludes species 1 if  $C_2 < C_2^m$  but neither species persists if  $C_2 \geq C_2^m$ . If  $C_1 < C_1^m$ , so that species 1 can persist when living alone, then species 1 excludes species 2 if  $C_2 \geq C_2^m$ , but the outcome is presently uncertain if  $C_2 < C_2^m$ . Our goal is to resolve this last case. To this end, we assume that  $C_1 \in (0, C_1^m)$  and  $C_2 \in (0, C_2^m)$  for the remainder of this section, so that both nullclines exist. We will consider the cases  $z_2 < z^1$  and  $z_2 \geq z^1$  separately. In each case, the starting point will be the set of equations that define the nullcline endpoints in terms of the composite parameters  $C_1$ ,  $C_2$ ,  $h$ , and  $k$ , and the functions  $\phi_1$  and  $\phi_2$ .

Recall also from Theorems 2.1 and 2.2 that the species 1 nullcline intersects both axes, and that the species 2 nullcline intersects the  $x_2$ -axis, but that it may or

may not intersect the  $x_1$ -axis at a finite point. Use of a simple notational convention for the latter case greatly simplifies the presentation of portions of our analysis: we set  $x_1^\ddagger$  equal to  $\infty$  when the species 2 nullcline fails to intersect the  $x_1$ -axis at a finite point.

### 3.2 Overlapping vertical leaf profiles and the $C_2$ - $k$ plane

Suppose first that  $z_2 < z^1$ , so that the VLPs of the two species overlap. The equations for the nullcline endpoints emerge from the nullcline equations (2.5) and (2.6) with either  $x_1 = 0$  or  $x_2 = 0$ , the definition of the ramp functions in (2.4), and the expression for  $\omega$  in Lemma 2.1 (a). These endpoints and the conditions under which they exist appear as (I)–(IV) in Table 2. The endpoints depend on six quantities, namely the four composite parameters  $C_1$ ,  $C_2$ ,  $h$ , and  $k$  and the two functions  $\phi_1$  and  $\phi_2$ . However, analysis reveals that conditions that produce the various outcomes of competition can be portrayed in a projection of parameter space onto a plane. Several choices for this plane's dimensions are possible. We choose the parameters  $C_2$  and  $k$  as these two dimensions because this combination makes subsequent analysis easier than do the other combinations we have explored. It is helpful for the present to choose fixed (but arbitrary) values of  $C_1 \in (0, C_1^m)$  and  $h \in [0, 1)$ , and particular functions  $\phi_1$  and  $\phi_2$  that satisfy properties P<sub>1</sub>–P<sub>4</sub>. We will, however, allow the values of  $C_2 \in (0, C_2^m)$  and  $k \in [0, 1)$  to vary. Taking this perspective amounts to fixing all characteristics of species 1, including its cost parameter  $C_1$  and understory index  $h$ , but allowing some characteristics of species 2 to vary, including its cost parameter  $C_2$  and overstory index  $k$ . In Sect. 4, we will again allow  $C_1$  and  $h$  to vary, although  $\phi_1$  and  $\phi_2$  will still remain fixed.

Although the endpoint  $x_1^\ddagger$  is constant in the  $C_2$ - $k$  parameter plane, we sometimes emphasize the dependencies of the other endpoints on their positions in this plane by writing  $x_1^\ddagger = x_1^\ddagger(C_2, k)$ ,  $x_2^\ddagger = x_2^\ddagger(C_2)$ , and  $x_2^\ddagger = x_2^\ddagger(k)$  (see Table 2).

### 3.3 The bifurcation function $k_1$

In this section, we examine the relative magnitudes of the species 1-axis endpoints  $x_1^\ddagger$  and  $x_1^\ddagger$  when  $C_2 \in (0, C_2^m)$  and  $k \in [0, 1)$ . First, we introduce a function  $k_\infty$  that divides parameter space into regions in which  $x_1^\ddagger$  is finite or infinite. Then we determine regions in parameter space in which  $x_1^\ddagger$  and  $x_1^\ddagger$  maintain a fixed order.

We begin by introducing the linear function

$$k_\infty(C_2) = \frac{C_2}{C_2^m}, \quad (3.1)$$

whose graph passes through the origin and the point  $(C_2^m, 1)$  in the  $C_2$ - $k$  plane. We will usually suppress the argument  $C_2$  in  $k_\infty$  and in the  $k_i$ -functions to follow. Theorem 2.2 implies that  $k_\infty$  partitions the parameter plane into two regions: one in which  $x_1^\ddagger$  is positive and finite ( $k < k_\infty$ ) and one in which  $x_1^\ddagger$  is infinite ( $k \geq k_\infty$ ), as shown in Figure 5.

It follows from properties P<sub>2</sub> and P<sub>5</sub> and the relation  $\phi_2(0) = C_2^m$  that the constant expression

$$A = \frac{1}{1-h} \int_0^{1-h} \phi_2(\alpha x_1^\dagger) d\alpha \quad (3.2)$$

satisfies  $A \in (0, C_2^m)$ . We are now in a position to identify regions in parameter space within which the endpoints  $x_1^\ddagger$  and  $x_1^\dagger$  maintain a fixed order.

**Theorem 3.1 (First Bifurcation)** *Let  $C_1 \in (0, C_1^m)$ ,  $C_2 \in (0, C_2^m)$ , and  $h, k \in [0, 1)$ .*

- (a) *If  $C_2 < A$  then  $x_1^\ddagger > x_1^\dagger$ ;*  
 (b) *If  $C_2 \geq A$  then there exists a unique  $k_1 = k_1(C_2) \in [0, k_\infty)$  such that*

$$x_1^\ddagger [ <, =, > ] x_1^\dagger \quad \text{for} \quad k [ <, =, > ] k_1,$$

and  $k_1$  is given by

$$k_1(C_2) = \frac{C_2 - A}{C_2^m - A}. \quad (3.3)$$

*Proof* In view of (II) with  $x_1^\dagger$  in place of  $x_1^\ddagger$ , let  $F(k) = kC_2^m + (1-k)A$ . It is clear that the function  $F$  is continuous and strictly increases from  $A$  to  $C_2^m$  as  $k$  increases from 0 to 1, and that  $F(k_\infty) > C_2$ . We also obtain from property P<sub>7</sub> that

$$x_1^\ddagger [ <, =, > ] x_1^\dagger \quad \text{for} \quad F(k) [ <, =, > ] C_2.$$

These relations hold when  $k < k_\infty$  and also when  $k \geq k_\infty$ . The statement of the theorem now follows with  $k_1$  satisfying  $F(k_1) = C_2$ .  $\square$

The main result of the foregoing analysis is specific identification of a region in parameter space in which  $x_1^\ddagger > x_1^\dagger$  and another region in which  $x_1^\ddagger < x_1^\dagger$ . These regions, together with the bifurcation function  $k_1$  on which  $x_1^\ddagger = x_1^\dagger$ , are shown in Figure 6.

### 3.4 The bifurcation function $k_2$

In this section, we examine the relative magnitudes of the species 2-axis endpoints  $x_2^\ddagger$  and  $x_2^\dagger$  when  $C_2 \in (0, C_2^m)$  and  $k \in [0, 1)$ . We first define functions  $G$  and  $H$  and state some of their properties. We then determine regions in parameter space in which  $x_2^\ddagger$  and  $x_2^\dagger$  maintain a fixed order.

**Lemma 3.1** *Let  $x > 0$  and  $k \in [0, 1]$ . The function*

$$G(x, k) \stackrel{\text{def}}{=} \begin{cases} h\phi_1(x) + \frac{1-h}{1-k} \int_k^1 \phi_1(\alpha x) d\alpha, & k < 1 \\ \phi_1(x), & k = 1 \end{cases} \quad (3.4a)$$

$$(3.4b)$$

*has the following properties:*

- (a)  $G(x, k) \rightarrow C_1^m$  as  $x \rightarrow 0$ ;  
 (b)  $G$  is a continuous and strictly decreasing function of  $x > 0$ ;

- (c)  $G(x, k) \rightarrow 0$  as  $x \rightarrow \infty$ ;  
(d)  $G$  is a continuous and strictly decreasing function of  $k \in [0, 1]$ .

*Proof* Parts (a), (b), and (c) follow directly from (3.4) and the properties of  $\phi_1$ . As for (d), it is clear that if  $x > 0$  then  $G$  is a continuous function of  $k \in [0, 1]$  and  $G(x, k) \rightarrow G(x, 1)$  as  $k \rightarrow 1$ . Therefore,  $G$  is a continuous function of  $k \in [0, 1]$ . Furthermore, the properties of  $\phi_1$  imply that if  $x > 0$  then  $G$  is a strictly decreasing function of  $k \in [0, 1]$ .  $\square$

Lemma 3.1 and the properties of  $x_2^\ddagger$  in (III) immediately imply the following result.

**Lemma 3.2** *Let  $C_2 \in (0, C_2^m)$  and  $k \in [0, 1]$ . The function*

$$H(C_2, k) \stackrel{\text{def}}{=} G(x_2^\ddagger(C_2), k) \quad (3.5)$$

*has the following properties:*

- (a)  $H(C_2, k) \rightarrow 0$  as  $C_2 \rightarrow 0$ ;  
(b)  $H$  is a continuous and strictly increasing function of  $C_2 \in (0, C_2^m)$ ;  
(c)  $H(C_2, k) \rightarrow C_1^m$  as  $C_2 \rightarrow C_2^m$ ;  
(d)  $H$  is a continuous and strictly decreasing function of  $k \in [0, 1]$ .

We are now in a position to identify regions in parameter space within which the endpoints  $x_2^\ddagger$  and  $x_2^\dagger$  maintain a fixed order.

**Theorem 3.2 (Second Bifurcation)** *Let  $C_1 \in (0, C_1^m)$ ,  $C_2 \in (0, C_2^m)$ , and  $h, k \in [0, 1]$ . There exist  $B, D \in (0, C_2^m)$  with  $B < D$  such that*

- (a) *If  $C_2 < B$  then  $x_2^\ddagger < x_2^\dagger$ ;*  
(b) *If  $C_2 \in [B, D)$  then there exists a unique  $k_2 = k_2(C_2) \in [0, 1)$  such that*

$$x_2^\ddagger [ >, =, < ] x_2^\dagger \quad \text{for} \quad k [ <, =, > ] k_2;$$

- (c) *If  $C_2 \geq D$  then  $x_2^\ddagger > x_2^\dagger$ .*

*Moreover,  $B, D$ , and  $k_2$  satisfy  $H(B, 0) = C_1$ ,  $H(D, 1) = C_1$ , and  $H(C_2, k_2) \equiv C_1$ . Finally,  $k_2$  is continuous and strictly increases from 0 to 1 as  $C_2$  increases from  $B$  to  $D$ .*

*Proof* It follows from Lemma 3.2 with  $k = 0$  or  $1$  that there exist unique  $B, D \in (0, C_2^m)$  such that  $H(B, 0) = H(D, 1) = C_1$ , and that

$$H(B, 0) = C_1 = H(D, 1) < H(D, 0).$$

Lemma 3.2 (b) implies that  $B < D$ . Suppose now that  $H(C_2, k) < C_1$ , and let  $x_2^\ddagger = x_2^\ddagger(C_2)$  and  $x_2^\ddagger = x_2^\ddagger(k)$ . It follows from (3.4a), (IV), and (3.5) that

$$G(x_2^\ddagger, k) = C_1 > H(C_2, k) = G(x_2^\dagger, k).$$

Lemma 3.1 (b) implies that  $x_2^\ddagger < x_2^\dagger$ . Similar arguments show that

$$x_2^\ddagger [ <, =, > ] x_2^\dagger \quad \text{for} \quad H(C_2, k) [ <, =, > ] C_1. \quad (3.6)$$

We now distinguish three cases.

(a) Let  $C_2 < B$ . Lemma 3.2 (b, d) implies that

$$H(C_2, k) < H(B, k) \leq H(B, 0) = C_1.$$

It follows from (3.6) that  $x_2^\ddagger < x_2^\dagger$ .

(b) Let  $C_2 \in [B, D)$ . Lemma 3.2 (b) implies that

$$H(C_2, 0) \geq H(B, 0) = C_1 = H(D, 1) > H(C_2, 1).$$

By Lemma 3.2 (d), there exists a unique  $k_2 = k_2(C_2) \in [0, 1)$  such that

$$H(C_2, k) [>, =, <] C_1 \text{ for } k [<, =, >] k_2.$$

It follows from (3.6) that  $x_2^\ddagger [>, =, <] x_2^\dagger$  for  $k [<, =, >] k_2$ .

(c) Let  $C_2 \geq D$ . Lemma 3.2 (b, d) implies that

$$H(C_2, k) \geq H(D, k) > H(D, 1) = C_1.$$

It follows from (3.6) that  $x_2^\ddagger > x_2^\dagger$ .

Clearly,  $k_2(B) = 0$  and  $k_2(D) = 1$ . Finally, Lemma 3.2 (b, d) and the implicit function theorem establish that  $k_2$  is a continuous and strictly increasing function of  $C_2$ .  $\square$

The main result of the foregoing analysis is specific identification of a region in parameter space in which  $x_2^\ddagger > x_2^\dagger$  and another region in which  $x_2^\ddagger < x_2^\dagger$ . These regions, together with the bifurcation function  $k_2$  on which  $x_2^\ddagger = x_2^\dagger$ , are shown in Figure 7.

### 3.5 The relative order of the bifurcation functions $k_1$ and $k_2$

In this section, we divide parameter space into regions in which *both* pairs of nullcline endpoints maintain fixed orders. This analysis will establish the existence of regions in parameter space under which either species exclusion or species coexistence occurs. Moreover, it will also determine whether coexistence, when it occurs, is stable or unstable. First, we prove a lemma concerning the relative magnitudes of the two endpoints ( $x_1^\ddagger$  and  $x_2^\ddagger$ ) of the species 2 nullcline. We then establish in the main theorem of this section that if  $\phi_1 \equiv \phi_2$  then the bifurcation functions  $k_1$  and  $k_2$  maintain fixed relative positions on the rectangle  $(0, C_2^m) \times [0, 1]$ .

**Lemma 3.3** *Let  $C_2 \in (0, C_2^m)$  and  $h \in [0, 1)$ . Then  $(1-h)x_1^\ddagger = x_2^\ddagger$  when  $k = 0$  and  $(1-h)x_1^\ddagger > x_2^\ddagger$  when  $k \in (0, k_\infty)$ .*

*Proof* Suppose first that  $k = 0$ . Equating the right-hand sides of (III) and (II), and then changing the variable of integration, yields

$$\int_0^1 \phi_2(\alpha x_2^\ddagger) d\alpha = \frac{1}{1-h} \int_0^{1-h} \phi_2(\alpha x_1^\ddagger) d\alpha = \int_0^1 \phi_2(\tilde{\alpha}(1-h)x_1^\ddagger) d\tilde{\alpha}.$$

We conclude from property P<sub>7</sub> that  $(1-h)x_1^\ddagger = x_2^\ddagger$ .

Suppose now that  $k \in (0, k_\infty)$ . To obtain a contradiction, suppose that  $(1-h)x_1^\ddagger \leq x_2^\ddagger$ . Applying (II), changing the variable of integration, using property P<sub>7</sub>, and then applying (III) yields

$$\begin{aligned} C_2 &= kC_2^m + \frac{1-k}{1-h} \int_0^{1-h} \phi_2(\alpha x_1^\ddagger) d\alpha \\ &= kC_2^m + (1-k) \int_0^1 \phi_2(\tilde{\alpha}(1-h)x_1^\ddagger) d\tilde{\alpha} \\ &\geq kC_2^m + (1-k) \int_0^1 \phi_2(\tilde{\alpha}x_2^\ddagger) d\tilde{\alpha} \\ &= kC_2^m + (1-k)C_2 \\ &= C_2 + k(C_2^m - C_2) \\ &> C_2, \end{aligned}$$

a contradiction. We conclude that if  $k \in (0, k_\infty)$  then  $(1-h)x_1^\ddagger > x_2^\ddagger$ .  $\square$

We now state the main theorem of this section. Obviously, such a theorem is needed only in the case that  $A < D$  (see Figures 6 and 7).

**Theorem 3.3 (Order of Bifurcations)** *Let  $C_1 \in (0, C_1^m)$ ,  $C_2 \in (0, C_2^m)$ , and  $h, k \in [0, 1)$  with either  $h > 0$  or  $k > 0$ . Suppose also that  $\phi_1 \equiv \phi_2$  and  $A < D$ . Then  $A > B$  and  $k_1 < k_2$  over the interval  $[A, D]$ .*

*Proof* We argue by contradiction. Theorems 3.1 and 3.2 establish that both  $k_1$  and  $k_2$  exist for every  $C_2 \in [A, D] \cap [B, D]$ , with the relative values of  $A$  and  $B$  left unspecified. Suppose that  $k_1(C_2) \geq k_2(C_2)$  for some such value of  $C_2$ . Since the functions  $k_1$  and  $k_2$  are continuous, and  $k_1(D) < k_2(D)$ , it follows that there exists  $c_2 \in [C_2, D)$  for which  $k_1(c_2) = k_2(c_2)$ . Let  $k = k_1(c_2) = k_2(c_2)$ ,  $x_1^\ddagger = x_1^\ddagger(c_2, k)$ ,  $x_2^\ddagger = x_2^\ddagger(c_2)$ , and  $x_2^\ddagger = x_2^\ddagger(k)$ . Then  $x_1^\ddagger = x_1^\ddagger$  and  $x_2^\ddagger = x_2^\ddagger$ . We will treat three cases separately.

(a) Suppose first that  $h, k \in (0, 1)$ . It follows from property P<sub>5</sub> that

$$\int_0^k \phi_2(\alpha x_2^\ddagger) d\alpha < k\phi_2(0) = kC_2^m.$$

We add the same quantity to both sides,

$$\int_0^1 \phi_2(\alpha x_2^\ddagger) d\alpha < kC_2^m + \int_k^1 \phi_2(\alpha x_2^\ddagger) d\alpha.$$

We apply (III) and rearrange to get

$$C_2 - kC_2^m < \int_k^1 \phi_2(\alpha x_2^\ddagger) d\alpha.$$

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

$$\frac{1}{1-h} \int_0^{1-h} \phi_2(\alpha x_1^\ddagger) d\alpha < \frac{1}{1-k} \int_k^1 \phi_2(\alpha x_2^\ddagger) d\alpha. \quad (3.7)$$

We now obtain the reverse inequality with  $\phi_1$  in place of  $\phi_2$ . Properties P<sub>3</sub> and P<sub>5</sub> and Lemma 3.3 together imply that

$$\frac{1}{h} \int_{1-h}^1 \phi_1(\alpha x_1^\ddagger) d\alpha < \phi_1((1-h)x_1^\ddagger) < \phi_1(x_2^\ddagger),$$

from which we conclude that

$$\int_{1-h}^1 \phi_1(\alpha x_1^\ddagger) d\alpha < h\phi_1(x_2^\ddagger).$$

We subtract both sides from  $C_1$ , and then replace  $x_1^\ddagger$  and  $x_2^\ddagger$  with  $x_1^\dagger$  and  $x_2^\dagger$ , respectively, to get

$$C_1 - \int_{1-h}^1 \phi_1(\alpha x_1^\dagger) d\alpha > C_1 - h\phi_1(x_2^\dagger).$$

We now apply (I) to the left-hand side and (IV) to the right-hand side to get

$$\int_0^{1-h} \phi_1(\alpha x_1^\dagger) d\alpha > \frac{1-h}{1-k} \int_k^1 \phi_1(\alpha x_2^\dagger) d\alpha.$$

We replace  $x_2^\dagger$  with  $x_2^\ddagger$  and rearrange to get

$$\frac{1}{1-h} \int_0^{1-h} \phi_1(\alpha x_1^\dagger) d\alpha > \frac{1}{1-k} \int_k^1 \phi_1(\alpha x_2^\dagger) d\alpha. \quad (3.8)$$

But the relation  $\phi_1 \equiv \phi_2$  implies that (3.7) and (3.8) cannot both hold simultaneously. This contradiction implies that  $k_1(C_2) < k_2(C_2)$ .

- (b) Suppose now that  $h = 0$  and  $k \in (0, 1)$ . It follows from (I), and (IV) with  $h = 0$  and  $x_2^\dagger$  in place of  $x_2^\ddagger$ , that

$$\int_0^1 \phi_1(\alpha x_1^\dagger) d\alpha = \frac{1}{1-k} \int_k^1 \phi_1(\alpha x_2^\dagger) d\alpha. \quad (3.9)$$

An argument similar to that in (a) shows that (3.7) also holds but with  $h = 0$ . Since  $\phi_1 \equiv \phi_2$ , we again have a contradiction. Therefore,  $k_1(C_2) < k_2(C_2)$ .

- (c) Suppose finally that  $h \in (0, 1)$  and  $k = 0$ . It follows from (II) with  $k = 0$  and  $x_1^\dagger$  in place of  $x_1^\ddagger$ , and (III) that

$$\frac{1}{1-h} \int_0^{1-h} \phi_2(\alpha x_1^\dagger) d\alpha = \int_0^1 \phi_2(\alpha x_2^\dagger) d\alpha. \quad (3.10)$$

An argument similar to that in (a) shows that (3.8) also holds but with  $k = 0$ . As before, we have a contradiction. Therefore,  $k_1(C_2) < k_2(C_2)$ .

It remains only to show that  $A > B$ . If not, then the properties of  $k_1$  and  $k_2$  imply that

$$0 = k_1(A) \leq k_1(B) < k_2(B) = 0,$$

again a contradiction. We conclude that  $A > B$ .  $\square$

Figure 8, which combines the results of Theorems 3.1, 3.2, and 3.3, displays the outcome of competition when the VLPs of the two species overlap and  $\phi_1 \equiv \phi_2$ . The case  $\phi_1 \not\equiv \phi_2$  remains unresolved but is examined for a special case in (Just and Nevai, *in review*).

### 3.6 Non-overlapping vertical leaf profiles

Suppose now that  $z_2 \geq z^1$ , so that the VLPs of the two species do not overlap. Recall from Theorems 2.1 and 2.2 that the species 1 nullcline intersects both axes (so that  $x_1^\dagger$  and  $x_2^\ddagger$  are both positive and finite) and the species 2 nullcline is a horizontal line (so that  $x_2^\ddagger$  is positive and finite but  $x_1^\ddagger$  is infinite). Figure 9 displays the two possible relative positions of the nullclines: species 2 excludes species 1 if  $x_2^\ddagger \leq x_2^\dagger$ , but both species persist if  $x_2^\ddagger > x_2^\dagger$ .

With  $D$  defined as in Theorem 3.2, we show now that species 2 excludes species 1 if  $C_2 \leq D$ , but that both species persist if  $C_2 > D$ . The endpoints  $x_2^\ddagger$  and  $x_2^\dagger$  are defined by the nullcline equations (2.5) and (2.6) with  $x_1 = 0$ ,  $r_1(\alpha) \equiv 1$ , and  $r_2(\alpha) \equiv 0$ . These endpoints and the conditions under which they exist appear as (III) and (V) in Table 2.

**Theorem 3.4 (Third Bifurcation)** *Let  $C_1 \in (0, C_1^m)$ ,  $C_2 \in (0, C_2^m)$ , and  $h, k \in [1, \infty)$ . Then  $x_1^\ddagger > x_1^\dagger$  and  $x_2^\ddagger [ <, =, > ] x_2^\dagger$  for  $C_2 [ <, =, > ] D$ .*

*Proof* The fact that  $x_1^\ddagger > x_1^\dagger$  is immediate from the remarks that precede the statement of the theorem. Observe from (III) and (V) that  $x_2^\ddagger$  depends on  $C_2$ , but that  $x_2^\dagger$  does not. Let  $E = \int_0^1 \phi_2(\alpha x_2^\ddagger) d\alpha$ , which by properties P<sub>2</sub> and P<sub>5</sub> satisfies  $E \in (0, C_2^m)$ . Observe from (III) and property P<sub>7</sub> that  $x_2^\ddagger [ <, =, > ] x_2^\dagger$  for  $C_2 [ <, =, > ] E$ . It remains only to show that  $E = D$ . Observe from (3.4b), (3.5), Theorem 3.2, and (V) that

$$\phi_1(x_2^\ddagger(D)) = H(D, 1) = C_1 = \phi_1(x_2^\ddagger),$$

and from (III) that

$$\int_0^1 \phi_2(\alpha x_2^\ddagger) d\alpha = E = \int_0^1 \phi_2(\alpha x_2^\ddagger(E)) d\alpha.$$

Properties P<sub>3</sub> and P<sub>7</sub> imply that  $x_2^\ddagger(D) = x_2^\ddagger = x_2^\ddagger(E)$ . We conclude from the properties of  $x_2^\ddagger$  in (III) that  $D = E$ .  $\square$

Figure 10 combines the results of all four theorems in this section.

### 3.7 Biological interpretations

Figure 10 inspires the following observations.

When the species' VLPs do not overlap, then founder control (*i.e.*, competition that always eliminates one species but whose identity depends on initial abundances) is not possible for any combination of parameter values. Furthermore, when the species' VLPs do overlap and their individual leaves perform photosynthesis at the same rate when subject to the same overlying leaf area ( $\phi_1 \equiv \phi_2$ ), then founder control also is not possible; but what happens when  $\phi_1 \not\equiv \phi_2$  and neither species is a uniformly competitive dominant (as described in Sect. 2.8) remains to be discovered [but see (Just and Nevai *in review*)].

In any case, the analysis of this section establishes that for our hypothetical clonal plant species, there are combinations of species characteristics that produce competitive coexistence.

There exists a minimum value  $A$  for the cost parameter  $C_2$  of the taller species below which the shorter species cannot exclude the taller species, even if the overstory index  $k$  is small. There also exists a maximum value  $D$  for this cost parameter above which the taller species cannot exclude the shorter species, even if the overstory index  $k$  is large. When  $A < D$ , then between these two extremes there exist various combinations of parameters for which either species can exclude the other, or both species can persist together.

The fact that, for given  $C_1$ ,  $h$ , and  $\phi_1 \equiv \phi_2$ , the outcome of competition depends only on the composite parameters  $C_2$  and  $k$  establishes that other features influence species success in a way similar to the influence of mean leaf height. Indeed, even if the two species' VLPs are very similar (but not identical) then suitable differences in other single cost factors or combinations of multiple cost factors (*e.g.*, density of stem tissue, tissue metabolic rate) can make competitive coexistence possible. Vance and Nevai (2007) describe how these and other individual cost factors influence  $C_1$  and  $C_2$ .

With all else held constant, as the taller species' cost parameter  $C_2$  increases, its competitive ability decreases from competitive superiority to competitive compatibility to competitive inferiority compared with the shorter species. Also, with all else held constant, as the taller species' height  $z^2$  increases relative to the shorter species' height  $z^1$  (so that the overstory index  $k$  increases), its competitive vigor relative to the shorter species also increases. These trends make biological sense. However, the situation is not really this simple because all else can rarely be held constant. For example, increasing leaf height requires growing taller stems which in turn imposes increased physiological costs. Indeed, because most aspects of plant structure and function influence the values of more than one of our composite parameters, it is not immediately obvious how individual plant attributes influence the outcome of competition. Isolating these influences requires careful scrutiny of parameter dependence.

We begin this scrutiny in the next section by examining the effect of the other composite parameters ( $C_1$  and  $h$ ) on the outcome of competition. We focus in the companion paper (Nevai and Vance *in review*) on the influence of one particular plant attribute, namely the mean leaf height  $s_2$  of species 2. This latter influence is not straightforward because  $C_2$ ,  $k$ , and  $h$  all depend upon  $s_2$ .

#### 4 Parameter Dependence in the Outcome of Competition

In the previous section, we established the existence of the bifurcation functions  $k_1$  (along which  $x_1^\ddagger = x_1^\ddagger$ ) and  $k_2$  (along which  $x_2^\ddagger = x_2^\ddagger$ ) by fixing arbitrary values of the composite parameters  $C_1 \in (0, C_1^m)$  and  $h \in [0, 1)$ . In this section, we determine the manner in which these parameters influence the locations of  $k_1$  and  $k_2$  in the  $C_2$ - $k$  parameter plane. Again, we conclude this section with biological interpretations.

#### 4.1 The cost parameter $C_1$ and the bifurcation functions $k_1$ and $k_2$

Recall that the bifurcation function  $k_1$  in Sect. 3.3 was viewed as a function of  $C_2$  that applied only for a single fixed  $C_1 \in (0, C_1^m)$ . Since the original choice of  $C_1$  was arbitrary,  $k_1$  is actually a function of both  $C_2$  and  $C_1$ . Here we examine this dependence more closely by determining the influence of  $C_1$  on  $k_1$  and its endpoint  $A$ , which we write here as  $A(C_1)$ . Recall that  $C_1^m = \phi_1(0)$  and  $C_2^m = \phi_2(0)$ .

**Theorem 4.1** *Let  $C_1 \in (0, C_1^m)$ ,  $C_2 \in (A(C_1), C_2^m)$ , and  $h \in [0, 1)$ . Then*

- (a)  $A$  is a continuous and strictly increasing function of  $C_1$ ;
- (b)  $A \rightarrow 0$  as  $C_1 \rightarrow 0$  and  $A \rightarrow C_2^m$  as  $C_1 \rightarrow C_1^m$ ;
- (c)  $k_1$  is a continuous and strictly decreasing function of  $C_1$ .

*Proof* Recall that  $A(C_1)$  satisfies (3.2) with  $x_1^\dagger = x_1^\dagger(C_1)$ , and observe that  $x_1^\dagger$  in (I) is a continuous and strictly decreasing function of  $C_1$ . Properties P<sub>1</sub> and P<sub>7</sub> now imply (a). Part (b) is obtained from (3.2), the limits  $x_1^\dagger \rightarrow \infty$  as  $C_1 \rightarrow 0$  and  $x_1^\dagger \rightarrow 0$  as  $C_1 \rightarrow C_1^m$ , and property P<sub>8</sub> with  $x = (1-h)x_1^\dagger(C_1)$ . Finally,  $k_1$  in (3.3) satisfies (c) because  $A$  satisfies (a) and takes values within the interval  $(0, C_2^m)$ .  $\square$

The influence of  $C_1$  on the bifurcation function  $k_2$  and its endpoints  $B(C_1)$  and  $D(C_1)$  is as follows.

**Theorem 4.2** *Let  $C_1 \in (0, C_1^m)$ ,  $C_2 \in (B(C_1), D(C_1))$ , and  $h \in [0, 1)$ . Then*

- (a)  $B$  and  $D$  are continuous and strictly increasing functions of  $C_1$ ;
- (b)  $B, D \rightarrow 0$  as  $C_1 \rightarrow 0$  and  $B, D \rightarrow C_2^m$  as  $C_1 \rightarrow C_1^m$ ;
- (c)  $k_2$  is a continuous and strictly decreasing function of  $C_1$ .

*Proof* Recall from Theorem 3.2 that  $B, D$ , and  $k_2$  satisfy

$$H(B, 0) = C_1, \quad H(D, 1) = C_1, \quad \text{and} \quad H(C_2, k_2) \equiv C_1, \quad (4.1)$$

where  $H$  is as in Lemma 3.2. It is clear from (4.1), the implicit function theorem, and Lemma 3.2 (b) that  $B$  and  $D$  satisfy (a). We obtain (b) from (4.1) and Lemma 3.2. Finally, it is clear from (4.1), the implicit function theorem, and Lemma 3.2 (d) that  $k_2$  satisfies (c).  $\square$

The influence of  $C_1$  on  $k_1$  and  $k_2$  is shown in Figure 11 (a, b).

#### 4.2 The understory index $h$ and the bifurcation functions $k_1$ and $k_2$

We now examine the effect of  $h$  on the bifurcation function  $k_1$  and its endpoint  $A(h)$ . First, we observe from properties P<sub>2</sub> and P<sub>5</sub> that

$$K \stackrel{\text{def}}{=} \int_0^1 \phi_2(\alpha x_1^\dagger) d\alpha \quad (4.2)$$

satisfies  $K \in (0, C_2^m)$ .

**Theorem 4.3** *Let  $C_1 \in (0, C_1^m)$ ,  $h \in [0, 1)$ , and  $C_2 \in (A(h), C_2^m)$ . Then*

- (a)  $A$  is a continuous and strictly increasing function of  $h$ ;
- (b)  $A(0) = K$  and  $A \rightarrow C_2^m$  as  $h \rightarrow 1$ ;
- (c)  $k_1$  is a continuous and strictly decreasing function of  $h$ .

*Proof* The continuity of  $A$  follows directly from (3.2), and the properties of  $\phi_2$  imply that  $A$  is a strictly increasing function of  $h$ . Eqs. (3.2) and (4.2) imply (b). Finally,  $k_1$  in (3.3) satisfies (c) because  $A$  satisfies (a) and takes values within the interval  $(K, C_2^m)$ .  $\square$

The influence of  $h$  on the bifurcation function  $k_2$  and its endpoints  $B(h)$  and  $D(h)$  is as follows.

**Theorem 4.4** *Let  $C_1 \in (0, C_1^m)$ ,  $h \in [0, 1)$ , and  $C_2 \in (B(h), D(h))$ . Then*

- (a)  $B$  is a continuous and strictly increasing function of  $h$ ;
- (b)  $D$  is independent of  $h$ ;
- (c)  $B(0) = K$  and  $B \rightarrow D$  as  $h \rightarrow 1$ ;
- (d)  $k_2$  is a continuous and strictly decreasing function of  $h$ .

*Proof* Recall from Theorem 3.2 that  $B$ ,  $D$ , and  $k_2$  satisfy

$$H(B(h), 0; h) \equiv C_1, \quad H(D(h), 1; h) \equiv C_1, \quad \text{and} \quad H(C_2, k_2; h) \equiv C_1, \quad (4.3)$$

where we now explicitly include  $h$  as a parameter in the function  $H$  from Lemma 3.2. We first show that if  $k \in [0, 1)$  then  $H(C_2, k; h)$  is a continuous and strictly decreasing function of  $h$ . Indeed, it is clear from (3.4a) and (3.5) that  $H$  is a continuous function of  $h$ . Let  $h, \tilde{h} \in [0, 1)$  with  $h < \tilde{h}$ . Then by (3.4a),

$$G(x, k; \tilde{h}) - G(x, k; h) = (\tilde{h} - h) \left[ \phi_1(x) - \frac{1}{1-k} \int_k^1 \phi_1(\alpha x) d\alpha \right].$$

It follows from property  $P_5$  that the right-hand side is negative. Thus  $G$ , and hence  $H$ , are strictly decreasing functions of  $h$ .

- (a) It is clear from (4.3), the implicit function theorem, Lemma 3.2 (b), and the  $h$ -properties of  $H$  that  $B$  is a continuous and strictly increasing function of  $h$ .
- (b) Observe from (3.4b), (3.5), and (4.3) that

$$\phi_1(x_2^\dagger(D(h))) = H(D(h), 1; h) \equiv C_1 = H(D(0), 1; 0) = \phi_1(x_2^\dagger(D(0))).$$

We conclude from property  $P_3$  that  $x_2^\dagger(D(h)) = x_2^\dagger(D(0))$ . The properties of  $x_2^\dagger$  in (III) imply that  $D(h) = D(0)$ .

- (c) Observe from (4.2), (III) with  $C_2 = K$ , and property  $P_7$  that  $x_2^\dagger(K) = x_1^\dagger$ . Thus, (3.4a), (3.5), (4.3), and (I) with  $x_2^\dagger(K)$  in place of  $x_1^\dagger$  imply that

$$\int_0^1 \phi_1(\alpha x_2^\dagger(B(0))) d\alpha = H(B(0), 0; 0) = C_1 = \int_0^1 \phi_1(\alpha x_2^\dagger(K)) d\alpha.$$

We conclude from property  $P_7$  and the properties of  $x_2^\dagger$  in (III) that  $B(0) = K$ . Next, it is clear from (a) and the upper bound of  $C_2^m$  on  $B(h)$  that  $B$  has a limit  $\tilde{B}$  as  $h \rightarrow 1$ . This fact, (3.4a), (3.5), and (4.3) imply that

$$\phi_1(x_2^\dagger(\tilde{B})) = H(\tilde{B}, 0; 1) = C_1 = H(D, 1; 0) = \phi_1(x_2^\dagger(D)).$$

We conclude from property  $P_3$  and the properties of  $x_2^\dagger$  in (III) that  $\tilde{B} = D$ .

- (d) It follows from (4.3), the implicit function theorem, Lemma 3.2 (d), and the  $h$ -properties of  $H$  that  $k_2$  satisfies (d).  $\square$

The influence of  $h$  on  $k_1$  and  $k_2$  is shown in Figure 11 (c, d).

### 4.3 Biological interpretations

This section has shown the manner in which the locations of the bifurcation functions in Figure 10 depend upon the values of the composite parameters  $C_1$  and  $h$ .

Figure 11 (a, b) implies that with  $\phi_1$ ,  $\phi_2$ , and  $h$  held constant, as the cost parameter  $C_1$  experienced by the shorter species increases, the taller species becomes competitively superior or competitively viable over a larger range of values of  $C_2$  and  $k$ . That is, as the costs experienced by the shorter species increase, the costs that the taller species can experience and still remain competitively superior or competitively viable also increase.

Figure 11 (c, d) implies that for fixed  $\phi_1$ ,  $\phi_2$ , and  $C_1$ , as the understory index  $h$  increases, the relative competitive vigor of the taller species increases. That is, as the taller species' lowest leaves become relatively higher, the taller species becomes competitively superior or competitively viable over an increasing range of values of  $C_2$  and  $k$ , because its leaves are shaded by fewer leaves of the shorter species.

## 5 Discussion

The analysis described here advances our understanding of (i) the role of canopy partitioning in determining the outcome of competition between two plant species with clonal growth form that compete only for sunlight, and more generally (ii) the role of space in determining the outcome of competition. We begin by considering the implications of (ii).

Early empirical studies of resource competition (Gause 1934, Hutchinson 1961, and others) revealed that stable competitive coexistence is unlikely to occur among uniformly distributed competitors living in a homogeneous environment, and that the more likely outcome is competitive exclusion (Hardin 1960). Indeed, Armstrong and McGehee (1980) employ Lyapunov functions to show that  $n$  species cannot coexist at fixed densities on fewer than  $n$  abiotic resources in a time-invariant and spatially homogeneous environment when the dynamics of the competitors are described by a Kolmogorov-type (1936) system of equations. Furthermore, if multiple species compete for a single resource then the species able to subsist at the lowest resource level ( $R^*$ ) will exclude all others (Hsu *et al.* 1977, Tilman 1982, Passarge *et al.* 2006). Tilman (1988) relates these same ideas to plant competition for nutrients and sunlight using his detailed computer model ALLOCATE, upon which our canopy partitioning model is partly based.

Our theory of plant competition differs from this classical work by introducing a particular form of spatial heterogeneity in resource abundance. Specifically, it considers the vertical gradient in light intensity created by the plants themselves as their leaves absorb sunlight passing vertically downward through the plant canopy.

Our hypothetical plants compete solely for sunlight, and we consider how differences in their capture and use of this single resource might influence whether competition can produce stable coexistence. Our analysis confirms the central result of the general competition theory of Armstrong and McGehee (1980) and the more specialized theory of Weissing and Huisman (1994) concerning light competition by phytoplankton in a lake. This central result is that two plant species that exploit this resource in the same qualitative way almost surely cannot coexist. Rather, one species will somehow exploit the resource more effectively and thereby drive its competitor to extinction.

However, if the two plant species differ in their light capture and energy use properties, then competitive coexistence becomes a possibility. Our analysis here produces two main insights about mechanism. First, the region in parameter space within which competitive coexistence occurs involves nontrivial ranges in all parameter values. The implication is that every plant feature somehow influences the likelihood of competitive coexistence. Second, this coexistence region does not include the case in which the two species share the same vertical leaf profile. That is, under the assumptions of our model, canopy partitioning, or different patterns of vertical leaf placement by the two species, is a *necessary* condition for competitive coexistence.

A third related insight emerges from further examination of this same model to appear elsewhere (Nevai and Vance *in review*), namely that there exist parameter values under which competitive coexistence can occur in two competing plants that differ in mean leaf height but in no other way. That is, under the assumptions of our model, provided that all shared properties of the two competitors fall within some suitable range, canopy partitioning by two competing species is a *sufficient* condition for competitive coexistence.

This analysis confirms the qualitative finding of a much earlier model (Vance 1985) that stable coexistence of a tall plant species and a short plant species can occur even in an environment lacking environmental variation through horizontal space and time. This study greatly advances earlier understanding, however, because the model here is fully mechanistic. That is, rather than relying on the not very clear cut distinction between exploitation and interference competition as Vance (1985) does, this model describes (albeit in simplified form) the processes of energy acquisition and use that plants actually employ. Because of this mechanistic character, the various quantities in this model can actually be measured empirically, and an empirically validated version of this model can be employed to study plant competitive coexistence in nature. Extensions of this model that incorporate more realism can be used in this way, though the resulting increase in mathematical complexity may resist analytical approaches. The principal message of this study is that because there is a region in parameter space in which this simplified model produces plant species competitive coexistence, the same property very likely applies to augmented versions of this model that describe real-world plants more realistically.

Our model applies only to a simplified abstraction of clonal plants. However, the fact that leaf height and other factors play such a critical role in competitive success in this model suggests that they might play an important role in other kinds of plants also. The implication is that rigorous field studies of plant competitive

coexistence should include physiological measurements and empirical reconstruction of the plants' energy budgets.

As we will show in future papers, even though the hypothetical plants envisioned in our canopy partitioning model are rather stylized and simplistic, this competition argument continues to apply when some assumptions are relaxed to accommodate certain additional features of nature. Other enrichments do not exactly fit the form of the model studied here, but come close. That is, these enrichments produce differential equations that still have the Kolmogorov form. At minimum, their analysis and their properties probably resemble the analysis and properties of the simpler prototype model discussed here.

Even for clonal plants, the addition of several of these enrichments into the same model will probably place it beyond the reach of classical analysis. In particular, a model realistic enough to be used in an empirical competition study of real-world clonal plants will probably have to be studied numerically, with parameter values obtained from empirical measurements.

Developing a model with this level of realism that applies to nonclonal plants in seasonal environments will require introducing environmental variation through horizontal space and time and considering the fates of plants of all sizes and life cycle stages. The models that address such plants most effectively are individual-based computer models like SORTIE (Pacala *et al.* 1996) concerning forest trees and spatial moment method based models (*e.g.*, Bolker and Pacala 1999, Law and Dieckmann 2000). To date, such models do not incorporate detailed structural and physiological information about the competing plants. Explaining community-level and ecosystem-level dynamics in terms of the physiological properties of individual plants will require hybrid models that combine the best features of these individual-based computer models [as reviewed by Porté and Bartelink (2002)] and spatial moment method based models with the physiologically based descriptions of populations as appear in the analytical model presented here, in companion papers (Vance and Nevai 2007, Nevai and Vance *in review*), and in their extensions presently being developed.

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## References

1. Aikman, D.P., Benjamin, L.R.: A model for plant and crop growth, allowing for competition for light by the use of potential and restricted projected crown zone areas. *Ann. Bot.* **73**, 185-194 (1994)
2. Anten, N.P.R., Hirose, T.: Biomass allocation and light partitioning among dominant and subordinate individuals in *Xanthium canadense* stands. *Ann. Bot.* **82**, 665-674 (1998)
3. Anten, N.P.R., Hirose, T.: Limitations on photosynthesis of competing individuals in stands and the consequences for canopy structure. *Oecologia* **129**, 186-196 (2001)
4. Anten, N.P.R., Hirose, T.: Interspecific differences in structural and physiological characteristics in a tall-grass meadow and consequences for carbon gain. *Ecology* **84**, 955-968 (2003)
5. Armstrong, R.A., McGehee, R.: Competitive exclusion. *Am. Nat.* **115**, 151-170 (1980)

6. Barnes, P.W., Beyschlag, W., Ryel, R., Flint, S.D., Caldwell, M.M.: Plant competition for light analyzed with a multispecies canopy model. III. Influence of canopy structure in mixtures and monocultures of wheat and wild oat. *Oecologia* **82**, 560-566 (1990)
7. Barot, S., Gignoux, J.: Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? *OIKOS* **106**, 185-192 (2004)
8. Bolker, B.M. and Pacala, S.W.: Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *Am. Nat.*, **153**, 575-602 (1999)
9. Bunker, D.E., Stark, S.C. and Carson, W.P.: Competition for light between plant species with complex canopies: using invasibility criteria to predict competitive outcomes. In preparation.
10. Courant R.: Differential and integral calculus. Interscience, New York, USA, 1936 (reprinted 1964)
11. Ellsworth, D.S., Reich, P.B.: Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **96**, 169-178 (1993)
12. Gause, G.F.: The struggle for existence. Dover, New York, USA, 1934 (reprinted 1971)
13. Grace, J.B., Tilman, D. (ed.): Perspectives on plant competition, Academic Press Inc, New York, USA, 1990
14. Hardin, G.: The competitive exclusion principle. *Science* **131**, 1292-1297 (1960)
15. Hikosaka, K., Sudoh, S., Hirose, T.: Light acquisition and use by individuals competing in a dense stand of an annual herb, *Xanthium canadense*. *Oecologia* **118**, 388-396 (1999)
16. Hirose, T., Werger, M.J.A.: Canopy structure and photon flux partitioning among species in a herbaceous plant community. *Ecology* **76**, 466-474 (1995)
17. Hirsch, M.W., Smale, S., Devaney, R.L.: Differential equations, dynamical systems, and an introduction to chaos. Academic Press, San Diego, CA, USA, 2004
18. Hsu, S.B., Hubbell, S., Waltman, P.: A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms. *SIAM J. Appl. Math.* **32**, 366-383 (1977)
19. Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J., Loo de Lao, S.: Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* **283**, 554-557 (1999)
20. Huisman, J., Jonker, R.R., Zonneveld, C., Weissing, F.J.: Competition for light between phytoplankton species: experimental tests of mechanistic theory. *Ecology* **80**, 211-222 (1999)
21. Huston, M.A., DeAngelis, D.L.: Competition and coexistence: the effects of resource transport and supply rates. *Am. Nat.* **144**, 954-977 (1994)
22. Hutchinson, G.E.: The paradox of the plankton. *Am. Nat.* **85**, 137-145 (1961)
23. Hutchinson, B.A., Matt, D.R., McMillen, R.T., Gross, L.J., Tajchman, S.J., Norman, J.M.: The architecture of a deciduous forest canopy in eastern Tennessee. *J. Ecol.* **74**, 635-646 (1986)
24. Just, W., Nevai, A.L.: A Kolmogorov-type competition model with multiple coexistence states and its applications to plant competition for sunlight. MBI Technical Report No. 59. In review.
25. Klausmeier, C.A., Tilman, D.: Spatial models of competition. In: Sommer, U., Worm, B. (ed.), *Competition and coexistence*, Springer-Verlag, 2002, pp. 43-78
26. Kohyama, T.: Size-structured tree populations in gap-dynamic forest - the forest architecture hypothesis for the stable coexistence of species. *J. Ecol.* **81**, 131-143 (1993)
27. Kolmogorov, A.N.: Sulla teoria di Volterra della lotta per l'esistenza. *Giornale dell'Istituto Italiano Degli Attuari* **7**, 74-80 (1936)
28. Law, R., Dieckmann, U.: A dynamical system for neighborhoods in plant communities. *Ecology* **81**, 2137-2148 (2000)
29. Monsi, M., Saeki, T.: Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jap. J. Bot.* **14**, 22-52 (1953)
30. Nevai, A.L., Vance, R.R.: The role of leaf height in plant competition for sunlight: analysis of a canopy partitioning model. In review.
31. Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A. Jr., Kone, R.K., Ribbens, E.: Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* **66**, 1-43 (1996)
32. Pacala, S.W., Levin, S.A.: Biologically generated spatial pattern and the coexistence of competing species. In: Tilman, D., Kareiva, P. (ed.), *Spatial ecology*, Princeton University Press, 1997, pp. 185-203

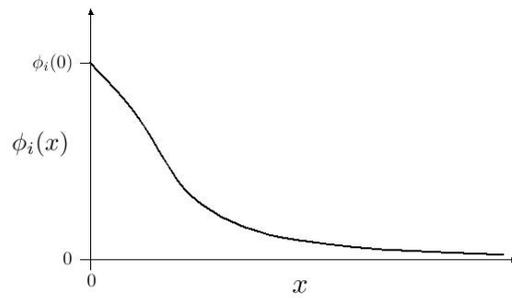
33. Pakes, A.G., Maller, R.A.: *Mathematical ecology of plant species competition: a class of deterministic models for binary mixtures of plant genotypes*. Cambridge University Press, Cambridge, UK, 1990.
34. Passarge, J., Hol, S., Escher, M., Huisman, J.: Competition for nutrients and light: stable coexistence, alternative stable states, or competitive exclusion? *Ecol. Monogr.* **76**, 57-72 (2006)
35. Pennings, S.C., Callaway, R.M.: Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology* **73**, 681-690 (1992)
36. Perry, L.G., Neuhauser, C., Galatowitsch, S.M.: Founder control and coexistence in a simple model of asymmetric competition for light. *J. Theor. Biol.* **222**, 425-436 (2003)
37. Porté, A., Bartelink, H.H.: Modelling mixed forest growth: a review of models for forest management. *Ecol. Mod.* **150**, 141-188 (2002)
38. Shmida, A., Ellner, S.: Coexistence of plant species with similar niches. *Vegetatio* **58**, 29-55 (1984)
39. Stoll, P., Prati, D.L.: Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* **82**, 319-327 (2001)
40. Stomp, M., Huisman, J., de Jongh, F., Veraart, A.J., Gerla, D., Rijkeboer, M., Ibelings, B.W., Wollenzien, U.I.A., Stal, L.J.: Adaptive divergence in pigment composition promotes phytoplankton biodiversity. *Nature* **432**, 104-107 (2004)
41. Thornley, J.H.M., Johnson, I.: *Plant and crop modelling - a mathematical approach to plant and crop physiology*, Clarendon Press, Oxford, UK, 1990
42. Tilman, D.: *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA, 1982
43. Tilman, D.: *Plant strategies and the dynamics and structure of plant communities*, Princeton University Press, Princeton, New Jersey, 1988
44. Vance, R.R.: The stable coexistence of two competitors for one resource. *Am. Nat.* **126**, 72-86 (1985)
45. Vance, R.R., Nevai, A.L.: Plant population growth and competition in a light gradient: a mathematical model of canopy partitioning. *J. Theor. Biol.* (2007). To appear.
46. Weissing, F., Huisman, J.: Growth and competition in a light gradient. *J. Theor. Biol.* **168**, 323-336 (1994)
47. Zavala, M.A., Bravo de la Parra, R.: A mechanistic model of tree competition and facilitation for Mediterranean forests: scaling from leaf physiology to stand dynamics. *Ecol. Mod.* **188**, 76-92 (2005)

notation	quantity	(eq. no.)	units
$t$	time		sec
$x_t$	upper leaf surface area of species $i$ at time $t$ per unit ground area		$\text{m}^2 \text{m}^{-2}$
$z$	height		m
$s_i(z)$	vertical leaf area density of species $i$ at height $z$		$\text{m}^{-1}$
$S_i(z)$	fraction of species $i$ 's leaves that overlie height $z$		—
$S_i(z)x_t$	area of leaves belonging to species $i$ that overlie height $z$ per unit ground area		$\text{m}^2 \text{m}^{-2}$
$\phi_i(\mathcal{K}_1, \mathcal{K}_2)$	species $i$ 's rate of photosynthesis per unit leaf area when shaded by ( $\mathcal{K}_1 \text{ m}^2, \mathcal{K}_2 \text{ m}^2$ ) of overlying leaf area		$\text{gC m}^{-2} \text{sec}^{-1}$
$\gamma_i$	species $i$ 's growth factor		$\text{m}^2 \text{gC}^{-1}$
$C_i$	species $i$ 's cost parameter		$\text{gC m}^{-2} \text{sec}^{-1}$
$\phi_i(x)$	species $i$ 's rate of photosynthesis per unit leaf area when shaded by $x \text{ m}^2$ of overlying leaf area		$\text{gC m}^{-2} \text{sec}^{-1}$
$T_i$	height range of species $i$ 's leaves		m
$s_i$	mean height of species $i$ 's leaves		m
$z_l$	height of species $i$ 's lowest leaves		m
$z^l$	height of species $i$ 's highest leaves		m
$h$	understorey index	(2.3)	—
$k$	overstorey index	(2.3)	—
$\omega$	vertical leaf profile thickness ratio	(2.3)	—
$\hat{\omega}$	inverse vertical leaf profile thickness ratio, $1/\omega$		—
$r_i(\alpha)$	species $i$ 's ramp function	(2.4)	—
$(x_1, x_1^2)$	species 1 mulcline	(2.5)	$\text{m}^2 \text{m}^{-2}$
$(x_1, x_2^2)$	species 2 mulcline	(2.6)	$\text{m}^2 \text{m}^{-2}$
$C_i^m$	species $i$ 's rate of photosynthesis per unit leaf area when shaded by no leaves, also equals $\phi_i(0)$		$\text{gC m}^{-2} \text{sec}^{-1}$
$x_1^+$	species 1 mulcline endpoint along the $x_1$ -axis	(I)	$\text{m}^2 \text{m}^{-2}$
$x_1^+$	species 2 mulcline endpoint along the $x_1$ -axis	(II)	$\text{m}^2 \text{m}^{-2}$
$x_2^+$	species 2 mulcline endpoint along the $x_2$ -axis	(III)	$\text{m}^2 \text{m}^{-2}$
$x_2^+$	species 1 mulcline endpoint along the $x_2$ -axis	(IV), (V)	$\text{m}^2 \text{m}^{-2}$

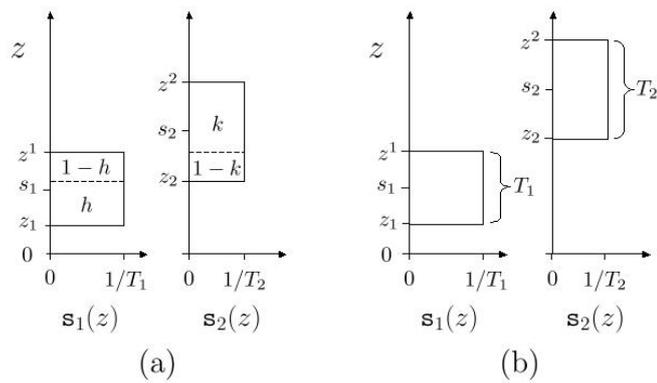
**Table 1** Notation used in this paper (gC = grams carbon and m = meters).

endpoint	defining equation	condition	(eq. no.)
$x_1^\dagger$	$C_1 = \int_0^1 \phi_1(\alpha x_1^\dagger) d\alpha$		(I)
$x_1^\ddagger$	$C_2 = kC_2^m + \frac{1-k}{1-h} \int_0^{1-h} \phi_2(\alpha x_1^\ddagger) d\alpha$	$C_2 > kC_2^m$	(II)
$x_2^\dagger$	$C_2 = \int_0^1 \phi_2(\alpha x_2^\dagger) d\alpha$		(III)
$x_2^\ddagger$	$C_1 = h\phi_1(x_2^\ddagger) + \frac{1-h}{1-k} \int_k^1 \phi_1(\alpha x_2^\ddagger) d\alpha$	$z_2 < z^1$	(IV)
$x_2^\ddagger$	$C_1 = \phi_1(x_2^\ddagger)$	$z_2 \geq z^1$	(V)

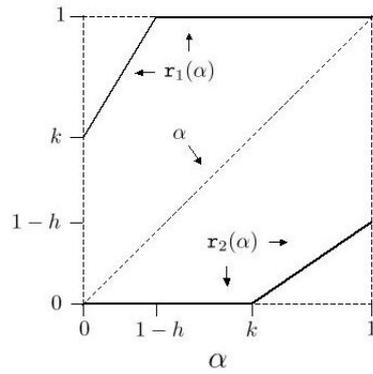
**Table 2** Defining equations for the nullcline endpoints when  $C_1 \in (0, C_1^m)$  and  $C_2 \in (0, C_2^m)$ , where  $C_i^m = \phi_i(0)$ . If  $C_2 \leq kC_2^m$  then we define  $x_1^\ddagger = \infty$ .



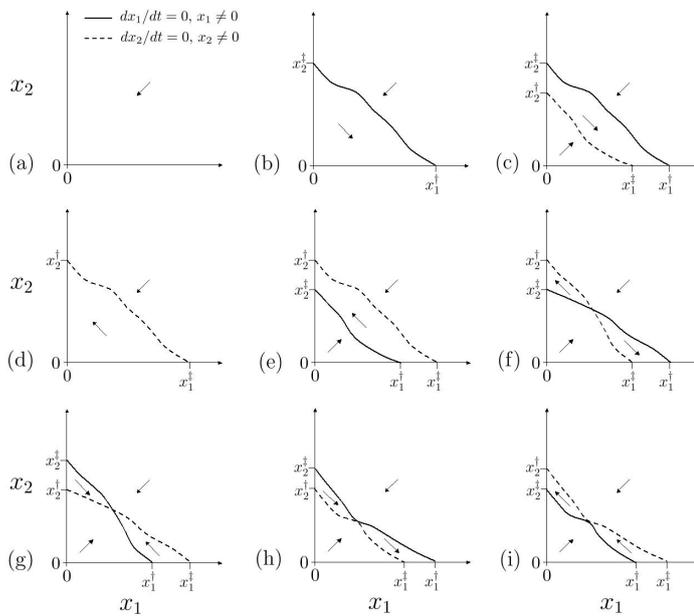
**Fig. 1** The qualitative form of a representative function  $\phi_i(x)$  satisfying properties P<sub>1</sub>-P<sub>4</sub>.



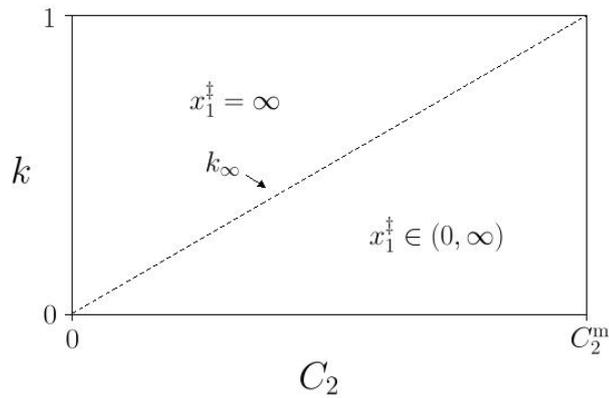
**Fig. 2** The VLPs of the two species overlap when (a)  $z_2 < z^1$ , but not when (b)  $z_2 \geq z^1$ .



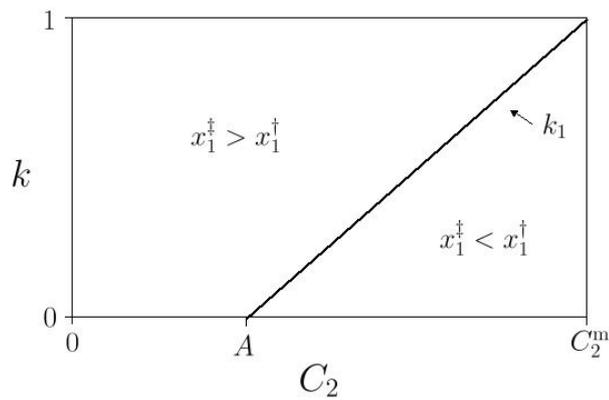
**Fig. 3** The ramp functions  $r_1$  and  $r_2$  when  $z_2 < z^1$ . This figure strictly applies when  $1 - h \leq k$ , so that there are no values of  $\alpha$  for which  $r_1$  and  $r_2$  are both ascending. If  $1 - h > k$ , then such values of  $\alpha$  do exist. However, this distinction does not influence any argument.



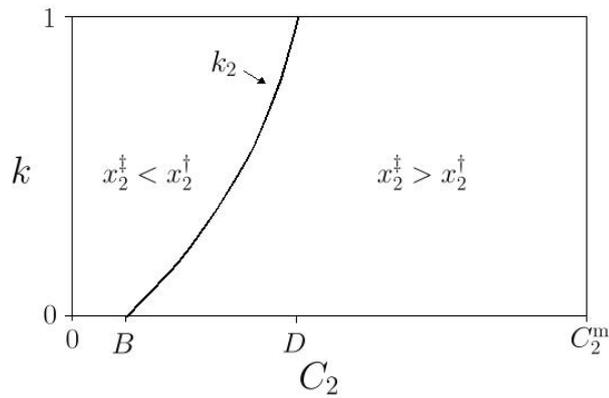
**Fig. 4** Nine qualitatively distinct possible arrangements of the species nullclines when  $\phi_1 \equiv \phi_2$ : (a) neither species persists, (b, c) species 1 excludes species 2, (d, e) species 2 excludes species 1, (f) unstable coexistence (or founder control), (g) stable coexistence, and (h, i) semistable coexistence. The arrows in each figure represent key trajectories. Note that when it exists, the species 2 nullcline may or may not intersect the  $x_1$ -axis at a finite point.



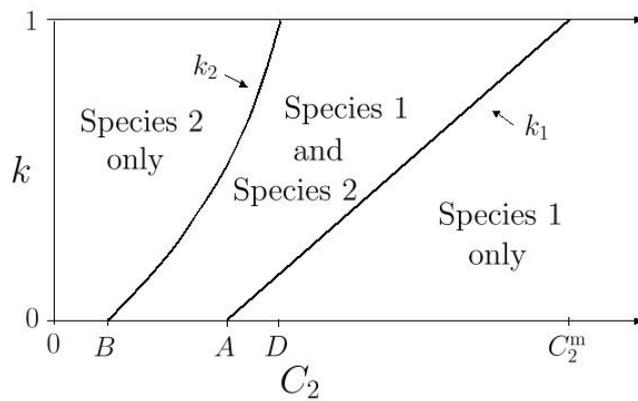
**Fig. 5** A portrayal of parameter space in the  $C_2$ - $k$  plane when  $C_1 \in (0, C_1^m)$  and  $h \in [0, 1)$ . If  $C_2 \in (0, C_2^m)$ , then the endpoints  $x_1^\dagger$ ,  $x_2^\dagger$ , and  $x_2^\ddagger$  are positive and finite for  $k \in [0, 1)$ , whereas the endpoint  $x_1^\ddagger$  is positive and finite for  $k \in [0, k_\infty)$  but infinite for  $k \in [k_\infty, 1)$ .



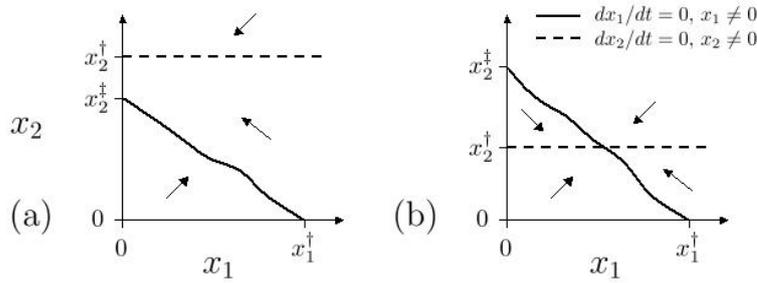
**Fig. 6** The bifurcation function  $k_1$  divides parameter space into regions in which the nullcline endpoints  $x_1^\ddagger$  and  $x_1^\dagger$  maintain a fixed order.



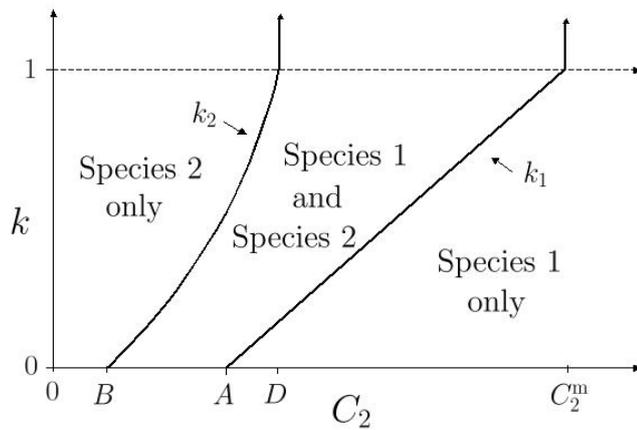
**Fig. 7** The bifurcation function  $k_2$  divides parameter space into regions in which the nullcline endpoints  $x_2^\dagger$  and  $x_2^\dagger$  maintain a fixed order.



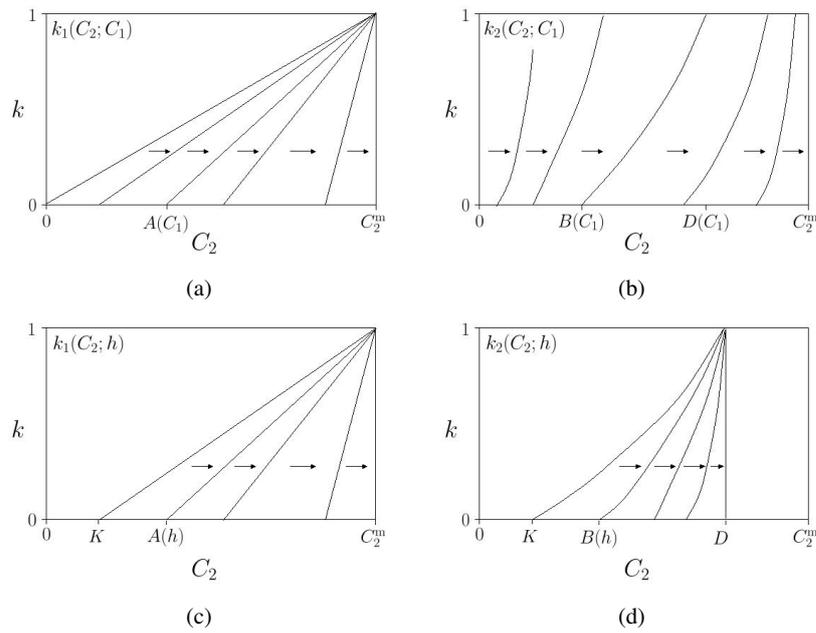
**Fig. 8** Regions in parameter space in which the various outcomes of competition occur when  $C_1 \in (0, C_1^m)$ ,  $h \in [0, 1)$ ,  $\phi_1 \equiv \phi_2$ , and  $A < D$ . All outcomes involve a globally attracting equilibrium point. If  $A \geq D$  then a similar figure applies.



**Fig. 9** The two possibilities that occur when  $C_1 \in (0, C_1^m)$ ,  $C_2 \in (0, C_2^m)$ , and  $z_2 \geq z^1$ : (a) species 2 excludes species 1 and (b) stable coexistence. The arrows in each figure represent key trajectories. In each case, the species 2 nullcline is a horizontal line.



**Fig. 10** Ranges of the parameters  $C_2$  and  $k$  over which the individual outcomes of competition occur when  $C_1 \in (0, C_1^m)$  and  $A < D$ . All outcomes involve a globally attracting equilibrium point. The region  $C_2 \in (0, C_2^m)$  and  $k \in [0, 1)$  applies only when  $\phi_1 \equiv \phi_2$ . If  $A \geq D$  then a similar figure applies.



**Fig. 11** (a) The function  $k_1$  and its endpoint  $A$  for different values of  $C_1$ ; (b) the function  $k_2$  and its endpoints  $B$  and  $D$  for different values of  $C_1$ ; (c)  $k_1$  and  $A$  for different values of  $h$ ; and (d)  $k_2$ ,  $B$ , and  $D$  for different values of  $h$ . The arrows in (a) and (b) indicate how quantities change as  $C_1$  increases from 0 to  $C_1^m$ . The arrows in (c) and (d) indicate how quantities change as  $h$  increases from 0 to 1.