



---

*Research article*

## Dynamics of coral–macroalgae interactions under crowding

Julie C. Blackwood<sup>1</sup>, Katerina Nik<sup>2,\*</sup> and Simon Nik<sup>2</sup>

<sup>1</sup> Department of Mathematics, Williams College, 180 Main Street, Williamstown, MA 01267, USA

<sup>2</sup> King Abdullah University of Science and Technology (KAUST), CEMSE Division, Thuwal 23955-6900, Saudi Arabia

\* **Correspondence:** Email: katerina.nik@kaust.edu.sa.

**Abstract:** We studied a planar ordinary differential equation (ODE) model for the benthic competition between coral, macroalgae, and algal turf on a reef, extending the classical model of Mumby, Hastings, and Edwards by a nonlinear, density-dependent coral mortality that accounts for crowding. The strength of crowding is set by an exponent  $\delta > 0$  that reshapes the coral nullcline and enriches the bifurcation structure of the system. We established positive invariance of the biologically relevant region and the absence of periodic orbits, classified the three boundary equilibria together with their local stability, and reduced the coexistence problem to a single scalar equation whose shape (in particular, its concavity) controls the number and local stability of the interior equilibria. When crowding makes this equation non-concave, the reef can support three coexistence equilibria and become locally tristable. The grazing intensity  $g$  organizes the dynamics through two thresholds  $g_0 < g_1$  determining the stability of the coral- and macroalgae-dominated states, and a further threshold  $g^*$  at which two interior equilibria collide. We proved that the system undergoes a transcritical bifurcation at the coral-dominated state and, for  $\delta \in \mathbb{N}$ , at the macroalgae-dominated state, together with a saddle-node bifurcation of interior equilibria, and we discussed the implications for coral reef resilience and hysteresis. We complemented these results with numerical simulations that illustrate the bifurcation sequence across the grazing regimes.

**Keywords:** coral reef ecosystems; crowding; equilibria; local stability; bifurcation analysis; multistability

---

### 1. Introduction

Coral reefs are among the most productive and diverse marine ecosystems, providing essential services that range from coastal protection and fisheries to tourism [1]. Across the globe, however, these ecosystems are increasingly threatened by stressors that are often exacerbated by anthropogenic activity: rising sea surface temperatures induce coral bleaching, while the over-harvesting of herbivorous reef fish promotes algal overgrowth that outcompetes and ultimately damages the coral [2–4].

There is both empirical and theoretical evidence that coral reef ecosystems admit two alternative stable states: a desirable state of high coral cover and a degraded, coral-depleted state dominated by macroalgae [5–8]. A well-documented illustration occurred in the Caribbean in the 1980s, when a disease-induced mass mortality of the sea urchin *Diadema antillarum*, until then the principal grazer, was followed by a marked decline of coral and a proliferation of algae [9]. In the absence of urchins, herbivorous reef fish such as parrotfish became the primary grazers, their scraping of algae from hard substrates helping to curb macroalgal overgrowth.

Maintaining the desirable state of high coral cover requires managing several interacting stressors simultaneously. Phase shifts between the two states may occur abruptly as exogenous conditions, such as the grazing rate, vary, and reversing them may then require improving these conditions well beyond the threshold at which the collapse occurred. This hysteresis underscores the importance of sustaining coral resilience [10, 11]. Alongside the management of grazing pressure, considerable effort is therefore devoted to active restoration, such as coral transplantation, coral gardening, and the deployment of artificial reefs [12]. Mathematical models of coral-macroalgae competition, in turn, have become a central tool for understanding the transitions between these states and the conditions under which a degraded reef may recover [8, 10, 13]. Recent work in this direction analyzes the deterministic and stochastic dynamics of a coral reef ecosystem with grazed macroalgae [14], examines how environmental stochasticity can destroy the persistence of macroalgae [15], and studies the global dynamics of a coral reef model with grazing by coral-mediated herbivores [16].

In the present work, we adapt the well-established Mumby–Hastings–Edwards model [8], which captures the central feedbacks between coral and algae competing for space on the reef, by incorporating the nonlinear effects of *coral crowding*: as coral cover increases, intraspecific competition raises the coral mortality rate. We model this density dependence through a mortality of the form  $m(C) = m_0 + dC^\delta$ , where  $m_0 > 0$  is the baseline mortality and the exponent  $\delta > 0$  tunes how steeply mortality grows with coral cover. Although such density dependence is ecologically well-documented [17], its consequences for the qualitative dynamics of coral-macroalgae models have received comparatively little rigorous attention. For comparison, the separate case  $d = 0$  reduces the model to the constant-mortality system of [8, 18], whose coral nullcline is a straight line. The crowding term reshapes this nullcline for every  $\delta > 0$ . As we show below, intermediate crowding  $1 < \delta < 2$  renders the reduced equation non-concave and can produce three coexistence equilibria and a tristable reef, a feature the constant-mortality model cannot exhibit [8, 10, 13, 18]. Ecologically, the locally asymptotically stable states represent coral dominance, macroalgae dominance, and a mixed coral-macroalgae community.

The aim of the present work is to provide a rigorous qualitative analysis of the resulting planar system, with particular emphasis on how the crowding exponent  $\delta$  reshapes the equilibrium and bifurcation structure. We determine all boundary and interior equilibria, characterize their local stability, identify the grazing thresholds at which the reef transitions from macroalgae dominance through bistability to coral dominance, and complement this analysis with numerical simulations. In particular, we reduce the coexistence problem to a single scalar equation whose concavity controls the number and local stability of the interior equilibria. The non-concave regime  $1 < \delta < 2$ , in which this reduction admits as many as three coexistence states, requires a more delicate analysis. We refer to [8, 11, 19] for the ecological background and for the parameter ranges underlying the model.

The article is organized as follows. In Section 2, we formulate the model, reduce it to a planar system

on a positively invariant region  $\Omega$ , and show the absence of periodic orbits (Lemma 2.1). In Section 3, we determine the three boundary equilibria and characterize their local stability in terms of two grazing thresholds  $g_0 < g_1$  (Lemma 3.2 and Theorems 3.3 and 3.5). In Section 4, we reduce the coexistence problem to a scalar equation  $L(y) = 0$ , relate the local stability of an interior equilibrium to the sign of  $L'(y)$ , and give a classification of the equilibria and their local stability across the low-, intermediate-, and high-grazing regimes, the last controlled by a further threshold  $g^*$  (Theorem 4.3). In Section 5, we rigorously establish the transcritical bifurcations at the boundary equilibria  $B$  and  $C$  (Theorems 5.1 and 5.3) and the saddle-node bifurcation of interior equilibria (Theorem 5.5), deferring to Appendix A accompanying normal-form reductions, which identify the local type of each degenerate equilibrium at its threshold as a saddle-node point. In Section 6, we specialize the analysis to the linear, quadratic, and intermediate crowding exponents and illustrate the resulting dynamics, including the bifurcation sequence, numerically. Section 7 discusses the ecological implications for coral reef resilience.

## 2. The coral reef model with crowding

We consider a benthic reef community composed of three constituents that compete for space: coral  $C$ , macroalgae  $M$ , and algal turf  $T$ , with their interactions depicted in Figure 1. Each variable denotes the fraction of the seabed occupied by the respective constituent, and the seabed is assumed to be fully covered, so that

$$C + M + T = 1. \quad (2.1)$$

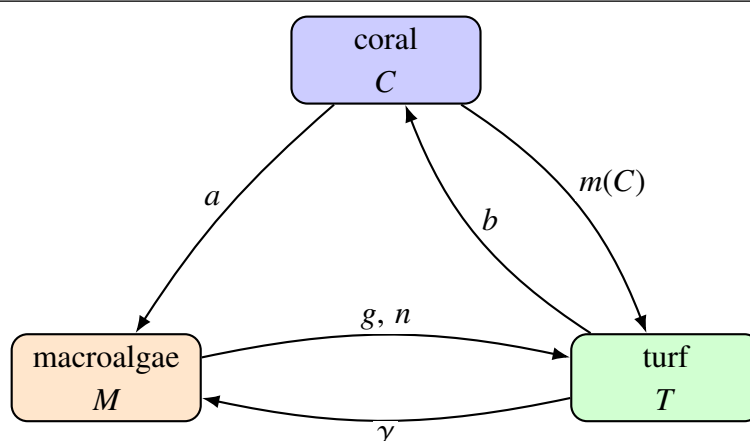
Building on the classical model of [8], in which coral and algae compete through overgrowth, grazing, and natural turnover, we incorporate a density-dependent coral mortality that accounts for crowding. The resulting dynamics are described by the system of three coupled nonlinear ordinary differential equations (ODEs)

$$\dot{M} = aMC + \gamma MT - \frac{gM}{M+T} - nM, \quad (2.2a)$$

$$\dot{C} = bCT - aMC - (m_0 + dC^\delta)C, \quad (2.2b)$$

$$\dot{T} = \frac{gM}{M+T} + nM + (m_0 + dC^\delta)C - bCT - \gamma MT, \quad (2.2c)$$

where the dot denotes differentiation with respect to time  $t$ .



**Figure 1.** Schematic of the benthic reef model (2.2). Coral  $C$ , macroalgae  $M$ , and algal turf  $T$  compete for the available space, with  $C + M + T = 1$ . Macroalgae overgrow coral at rate  $a$ , while coral overgrows turf at rate  $b$  and dies, from crowding or other reasons, at the rate  $m(C) = m_0 + dC^\delta$ . Macroalgae become turf through grazing at rate  $g$  and natural death at rate  $n$ , and they spread vegetatively over turf at rate  $\gamma$ .

The terms have the following ecological meaning, with the first five being those of [8]. Macroalgae overgrow coral at rate  $a$ , while grazers feed indiscriminately on macroalgae and turf at rate  $g$ , so that grazed macroalgae are converted into turf. Macroalgae spread vegetatively over turf at rate  $\gamma$  and die naturally at rate  $n$ , the latter producing turf, whereas coral overgrows turf at rate  $b$ . The original [8] model assumed that coral mortality is strictly density-independent, captured by  $m(C) = m_0$ . Here, however, we relax this assumption by accounting for both density-dependent and density-independent mortality such that

$$m(C) = m_0 + dC^\delta. \quad (2.3)$$

Corals still die at a baseline rate of  $m_0 > 0$ , while the term  $dC^\delta$  models the strengthening of intraspecific (coral-coral) competition as coral cover increases. The effect of the  $\delta$  term can be broken down as follows: When  $\delta < 1$ , mortality increases with coral density but at a decelerating rate; when  $\delta = 1$ , mortality increases linearly and proportionally to coral cover; and when  $\delta > 1$ , mortality increases at an accelerating rate. The case where  $\delta < 1$  represents environments where early post-settlement survival is only weakly density dependent. In contrast,  $\delta > 1$  may be most relevant for more vulnerable colonies or species due to compounding stressors such as self-shading [20–22]. As with the other loss terms, dead coral reverts to turf.

To remain consistent with the calibrated ranges of [11], the mortality (2.3) is required to satisfy

$$0.02 \leq m(C) \leq 0.30, \quad C \in [0, 1].$$

Since  $C \mapsto m(C)$  is increasing, with  $\min_{[0,1]} m = m(0) = m_0$  and  $\max_{[0,1]} m = m(1) = m_0 + d$ , this holds if and only if

$$m_0 \geq 0.02 \quad \text{and} \quad m_0 + d \leq 0.30.$$

Representative parameter ranges and their sources are collected in Table 1.

**Table 1.** Parameters of the model (2.2), with biologically plausible ranges and sources.

| Parameter | Description                              | Range             | Unit             | Source    |
|-----------|------------------------------------------|-------------------|------------------|-----------|
| $a$       | rate macroalgae overgrow coral           | 0–1.44            | yr <sup>-1</sup> | [11]      |
| $g$       | maximum grazing rate on algae            | 0.05–15           | yr <sup>-1</sup> | [11]      |
| $\gamma$  | rate macroalgae spread over turf         | 0–0.9             | yr <sup>-1</sup> | [11]      |
| $n$       | natural mortality rate of macroalgae     | 0–0.1             | yr <sup>-1</sup> | [13]      |
| $b$       | rate coral overgrows turf                | 0–1               | yr <sup>-1</sup> | [11]      |
| $m_0$     | density-independent coral mortality      | 0.02–0.30         | yr <sup>-1</sup> | [11]      |
| $d$       | crowding (density-dependent) coefficient | 0–(0.30 – $m_0$ ) | yr <sup>-1</sup> | this work |
| $\delta$  | crowding exponent                        | > 0               | —                | varies    |

Throughout, we impose the following general assumptions:

$$\begin{aligned}
 &a, b, \gamma, g, n, m_0, d, \delta \in \mathbb{R}_{>0}, \quad b > m_0, \quad a < \gamma, \\
 &0 < n < \min \left\{ a, \gamma - g, \frac{\gamma(a + m_0)}{a + b} \right\}, \\
 &0 < m_0 + d < \min \left\{ \frac{b}{2(a - n)} \left( \frac{\gamma(a + m_0)}{a + b} - n \right), \frac{b}{\sqrt{2(\gamma - a)}} \sqrt{\frac{\gamma(a + m_0)}{a + b} - n} \right\}.
 \end{aligned} \tag{GA}$$

Unless stated otherwise, all results below assume (GA), whose last condition is used in Section 3 to establish the strict ordering of the two grazing thresholds  $g_0$  and  $g_1$ .

### 2.1. Reduction to a planar system

Since  $T = 1 - C - M$  by (2.1), Eq (2.2c) is redundant, and using  $M + T = 1 - C$ , the dynamics reduce to the planar system

$$\dot{M} = aMC + \gamma M(1 - C - M) - \frac{gM}{1 - C} - nM, \tag{2.4a}$$

$$\dot{C} = bC(1 - C - M) - aMC - (m_0 + dC^\delta)C. \tag{2.4b}$$

Writing  $x := M$  and  $y := C$  for the macroalgae and coral cover, (2.4) takes the form

$$\dot{x} = x \left[ \gamma(1 - x) - n + (a - \gamma)y - \frac{g}{1 - y} \right] =: xF(x, y), \tag{2.5a}$$

$$\dot{y} = y \left[ b - m_0 - (a + b)x - by - dy^\delta \right] =: yG(x, y). \tag{2.5b}$$

We analyze (2.5) throughout, denoting partial differentiation by  $\partial$ , with a subscript indicating the variable, and the derivative of a function of a single variable by a prime.

## 2.2. Invariance and absence of periodic orbits

We work on the biologically relevant region

$$\Omega := \{(x, y) \in \mathbb{R}^2 : x > 0, y > 0, x + y < 1\}, \quad (2.6)$$

which is open and simply connected. The next result shows that  $\Omega$  is positively invariant and contains no periodic orbits.

**Lemma 2.1.** *Assume (GA). Then the region  $\Omega$  is positively invariant for (2.5) and contains no periodic orbit of the system.*

*Proof.* (i) Fix  $(x(0), y(0)) \in \Omega$ . Set  $\mathbf{V} := (xF, yG)$ . Since  $\mathbf{V} \in C^1(\mathbb{R} \times (0, 1), \mathbb{R}^2)$  for every  $\delta > 0$ , there exists a unique maximal solution on an interval  $[0, T_m)$ . Since  $\dot{x} = xF(x, y)$  and  $\dot{y} = yG(x, y)$ , the solution admits the representation

$$x(t) = x(0) \exp\left(\int_0^t F(x(s), y(s)) \, ds\right), \quad y(t) = y(0) \exp\left(\int_0^t G(x(s), y(s)) \, ds\right), \quad 0 \leq t < T_m,$$

so that  $x(t) > 0$  and  $y(t) > 0$  for  $0 \leq t < T_m$ . Thus a first exit from  $\Omega$  before  $T_m$  could only occur through the segment  $\{x + y = 1\}$ . Setting  $z := x + y$  and using  $x = 1 - y$  on this segment, we obtain

$$\dot{z} = \dot{x} + \dot{y} = -g - nx - m_0y - dy^{\delta+1} < 0, \quad (2.7)$$

since  $g, n, m_0, d > 0$  and  $x, y > 0$ . At a first contact  $t = \tau < T_m$ , however, one would have  $\dot{z}(\tau) \geq 0$ , contrary to (2.7). Hence the trajectory cannot reach  $\{x + y = 1\}$  on  $[0, T_m)$ . Moreover, (2.5b) and the comparison principle give

$$\dot{y} \leq y(b - m_0 - by), \quad 0 < y(t) \leq \eta := \max\left\{y(0), \frac{b - m_0}{b}\right\} < 1, \quad 0 \leq t < T_m.$$

Also,

$$G(x, y) = b(1 - x - y) - m_0 - ax - dy^\delta \geq -(a + m_0 + d), \quad (x, y) \in \Omega,$$

and hence

$$y(t) \geq y(0)e^{-(a+m_0+d)t}, \quad 0 \leq t < T_m.$$

If  $T_m < \infty$ , the orbit remains in the compact subset

$$[0, 1] \times [y(0)e^{-(a+m_0+d)T_m}, \eta] \subset \mathbb{R} \times (0, 1),$$

contrary to the continuation theorem. Hence  $T_m = \infty$ , and  $\Omega$  is positively invariant.

(ii) Choosing the Dulac function  $\psi(x, y) := \frac{1}{xy} > 0$ , for which  $\psi\mathbf{V}$  is of class  $C^1(\Omega)$  for every  $\delta > 0$ , we obtain

$$\partial_x(\psi xF) + \partial_y(\psi yG) = \frac{\partial_x F}{y} + \frac{\partial_y G}{x} = -\frac{\gamma}{y} - \frac{b + \delta dy^{\delta-1}}{x} < 0 \quad \text{on } \Omega.$$

Since  $\Omega$  is simply connected and this expression has a strict sign, the Bendixson–Dulac criterion rules out periodic orbits in  $\Omega$ .  $\square$

In view of Lemma 2.1, we assume henceforth that the initial data satisfies  $(x(0), y(0)) \in \Omega$ .

### 3. Boundary equilibria

In this section, we locate the boundary equilibria of (2.5) and determine their local stability. Equilibria are the intersections of the nullclines, which we therefore describe first. As we shall see, the grazing intensity  $g$  governs the stability of the non-trivial boundary equilibria through two thresholds  $0 < g_0 < g_1 < \gamma - n$  that separate a low-, an intermediate-, and a high-grazing regime.

#### 3.1. Nullclines

The equilibria of (2.5) are the points of  $\bar{\Omega} \setminus \{(0, 1)\}$  at which  $\dot{x} = \dot{y} = 0$ , that is, the intersections of the *macroalgae nullcline*  $\{x = 0\} \cup \{F = 0\}$  with the *coral nullcline*  $\{y = 0\} \cup \{G = 0\}$ . These nullclines and the equilibria at their intersections are illustrated, for several grazing rates, in Figure 2.

*The macroalgae nullcline.* Besides the  $y$ -axis  $\{x = 0\}$ , the macroalgae nullcline is the zero set of  $F$ . Since  $a < \gamma$ , multiplying  $F(x, y) = 0$  by  $1 - y > 0$  yields a quadratic in  $y$  whose branch lying in  $\bar{\Omega}$  is the graph

$$y = M(x) := \frac{1}{2(\gamma - a)} \left[ 2\gamma - a - n - \gamma x - \sqrt{(\gamma x + n - a)^2 + 4g(\gamma - a)} \right]. \quad (3.1)$$

The expression under the square root is bounded below by  $4g(\gamma - a) > 0$ , so  $M$  is smooth on  $[0, \infty)$ . The curve joins the point

$$A = (0, y_A), \quad y_A := M(0) = \frac{2\gamma - a - n - \sqrt{(n - a)^2 + 4g(\gamma - a)}}{2(\gamma - a)}, \quad (3.2)$$

on the  $y$ -axis to the point  $B = (x_B, 0)$  on the  $x$ -axis, where

$$x_B := 1 - \frac{g + n}{\gamma}, \quad (3.3)$$

and under (GA) both  $y_A \in (0, 1)$  and  $x_B \in (0, 1)$ . Differentiating (3.1) gives

$$M'(x) = -\frac{\gamma}{2(\gamma - a)} \left[ 1 + \frac{\gamma x + n - a}{\sqrt{(\gamma x + n - a)^2 + 4g(\gamma - a)}} \right] < 0, \quad (3.4)$$

so  $M$  is strictly decreasing on  $[0, x_B]$ .

*The coral nullcline.* Besides the  $x$ -axis  $\{y = 0\}$ , the coral nullcline is the zero set of  $G$ . As  $G$  is affine in  $x$ , the equation  $G(x, y) = 0$  is solved explicitly for  $x$ :

$$x = K(y) := \frac{b - m_0 - by - dy^\delta}{a + b}, \quad y \in [0, y_C], \quad (3.5)$$

where  $y_C \in (0, 1)$  is the unique solution of

$$H(y_C) = b - m_0, \quad H(y) := by + dy^\delta. \quad (3.6)$$

Indeed,  $H$  is continuous and strictly increasing on  $[0, \infty)$  with  $H(0) = 0 < b - m_0 < b + d = H(1)$ , so (3.6) admits a unique root  $y_C \in (0, 1)$ . The curve  $K$  joins  $C = (0, y_C)$  on the  $y$ -axis to  $D = (x_D, 0)$  on the  $x$ -axis, where

$$x_D := K(0) = \frac{b - m_0}{a + b} \in (0, 1). \quad (3.7)$$

For  $y > 0$ , we have

$$K'(y) = -\frac{b + \delta dy^{\delta-1}}{a + b} < 0, \quad (3.8)$$

so  $K$  is strictly decreasing and is smooth on  $(0, y_C]$ , extending as a curve of class  $C^1$  to  $[0, y_C]$  when  $\delta \geq 1$ . For later use, we record that

$$\partial_y F = (a - \gamma) - \frac{g}{(1 - y)^2} < 0 \quad \text{and} \quad \partial_y G = -(b + \delta dy^{\delta-1}) < 0 \quad \text{on } \Omega. \quad (3.9)$$

The boundary equilibria are now readily identified.

**Lemma 3.1.** *Under (GA), system (2.5) has exactly three boundary equilibria: the trivial state  $O = (0, 0)$ , the macroalgae-only state  $B = (x_B, 0)$  with  $x_B \in (0, 1)$  as in (3.3), and the coral-only state  $C = (0, y_C)$  with  $y_C \in (0, 1)$  as the unique root of (3.6).*

*Proof.* A boundary equilibrium lies on  $\partial\Omega$ . On the open segment  $\{x + y = 1\}$ , we have

$$G(x, 1 - x) = -m_0 - ax - d(1 - x)^\delta < 0,$$

so that  $\dot{y} = yG < 0$  whenever  $y > 0$ , and this segment therefore carries no equilibrium. On the  $x$ -axis, we have  $\dot{y} = 0$ , while  $\dot{x} = xF(x, 0)$  with

$$F(x, 0) = \gamma(1 - x) - n - g$$

strictly decreasing and vanishing only at  $x_B$ , so that the equilibria on  $\{y = 0\}$  are  $O$  and  $B$ . In the same way, on the  $y$ -axis, we have  $\dot{x} = 0$ , while  $\dot{y} = yG(0, y)$  with

$$G(0, y) = b - m_0 - by - dy^\delta$$

strictly decreasing and vanishing only at  $y_C$ , so that the equilibria on  $\{x = 0\}$  are  $O$  and  $C$ .  $\square$

### 3.2. Local stability of the boundary equilibria

Linearizing (2.5), and recalling (3.9) together with  $\partial_x F = -\gamma$  and  $\partial_x G = -(a + b)$ , the Jacobian is

$$J(x, y) = \begin{pmatrix} F + x\partial_x F & x\partial_y F \\ y\partial_x G & G + y\partial_y G \end{pmatrix} = \begin{pmatrix} F - \gamma x & x\partial_y F \\ -(a + b)y & G + y\partial_y G \end{pmatrix}, \quad (3.10)$$

where the entries are evaluated using  $\partial_y F$  and  $\partial_y G$  from (3.9). We evaluate (3.10) at each boundary equilibrium.

**Lemma 3.2.** *Under (GA), the trivial equilibrium  $O = (0, 0)$  is an unstable node.*

*Proof.* By (3.10),

$$J(0, 0) = \begin{pmatrix} \gamma - n - g & 0 \\ 0 & b - m_0 \end{pmatrix},$$

whose eigenvalues  $\gamma - n - g$  and  $b - m_0$  are both positive by (GA).  $\square$

We next turn to the macroalgae-only state  $B$ , whose stability is set by the threshold

$$g_1 := \frac{\gamma(a + m_0)}{a + b} - n. \quad (3.11)$$

**Theorem 3.3.** *Suppose (GA) holds. Then  $0 < g_1 < \gamma - n$ , and for every  $\delta > 0$ , the macroalgae-only state  $B$  is a stable node when  $g < g_1$ , a saddle when  $g > g_1$ , and nonhyperbolic at  $g = g_1$ .*

**Remark 3.4.** *As shown below, if  $\delta \in \mathbb{N}$  and (5.4) holds, the threshold  $g_1$  is a bifurcation value: system (2.5) undergoes a transcritical bifurcation at  $B$  as  $g$  crosses  $g_1$ , whereas  $B$  is a saddle-node point of the fixed system at  $g = g_1$  (Theorem 5.1 and Proposition 5.6(i)).*

*Proof.* At  $B = (x_B, 0)$ , the Jacobian (3.10) is upper triangular:

$$J(x_B, 0) = \begin{pmatrix} -(\gamma - g - n) & x_B(a - \gamma - g) \\ 0 & -(a + m_0) + \frac{g + n}{\gamma}(a + b) \end{pmatrix},$$

so that its eigenvalues are the diagonal entries. By (GA), the first is  $\lambda_1 = -(\gamma - g - n) < 0$ , while the second, by definition (3.11) of  $g_1$ , satisfies

$$\lambda_2 = -(a + m_0) + \frac{g + n}{\gamma}(a + b) = \frac{a + b}{\gamma}(g - g_1).$$

Thus  $\lambda_2 < 0$  for  $g < g_1$ ,  $\lambda_2 = 0$  for  $g = g_1$ , and  $\lambda_2 > 0$  for  $g > g_1$ , so that  $B$  is a stable node when  $g < g_1$ , nonhyperbolic when  $g = g_1$ , and a saddle when  $g > g_1$ . Finally  $g_1 < \gamma - n$  since  $m_0 < b$ , and  $g_1 > 0$  by (GA).  $\square$

The stability of the coral-only state  $C$  is governed by the threshold

$$g_0 := (1 - y_C)(\gamma - n + (a - \gamma)y_C), \quad (3.12)$$

with  $y_C$  as in (3.6).

**Theorem 3.5.** *Suppose (GA) holds. Then  $g_0 > 0$ , and for every  $\delta > 0$ , the coral-only state  $C$  is a stable node when  $g > g_0$ , a saddle when  $g < g_0$ , and nonhyperbolic at  $g = g_0$ .*

**Remark 3.6.** *As shown below, if (5.5) holds, the threshold  $g_0$  is a bifurcation value: system (2.5) undergoes a transcritical bifurcation at  $C$  as  $g$  crosses  $g_0$ , whereas  $C$  is a saddle-node point of the fixed system at  $g = g_0$  (Theorem 5.3 and Proposition 5.6(ii)).*

*Proof.* At  $C = (0, y_C)$ , the Jacobian (3.10) is lower triangular:

$$J(0, y_C) = \begin{pmatrix} \mu_1 & 0 \\ -(a + b)y_C & \mu_2 \end{pmatrix},$$

so that its eigenvalues are the diagonal entries  $\mu_1$  and  $\mu_2$ . The lower-right entry simplifies by (3.6) from  $b - m_0 - 2by_C - (1 + \delta)dy_C^\delta$  to

$$\mu_2 = -by_C - \delta dy_C^\delta < 0,$$

while the upper-left entry, by definition (3.12) of  $g_0$ , satisfies

$$\mu_1 = F(0, y_C) = \gamma - n + (a - \gamma)y_C - \frac{g}{1 - y_C} = \frac{g_0 - g}{1 - y_C}.$$

Since  $1 - y_C > 0$ , we have  $\mu_1 > 0$  for  $g < g_0$ ,  $\mu_1 = 0$  for  $g = g_0$ , and  $\mu_1 < 0$  for  $g > g_0$ , so that  $C$  is a saddle when  $g < g_0$ , nonhyperbolic when  $g = g_0$ , and a stable node when  $g > g_0$ . Moreover  $\gamma - n + (a - \gamma)y_C > a - n > 0$  since  $a > n$ , so that  $g_0 > 0$ .  $\square$

The two thresholds are ordered, which is what separates the grazing regimes studied in Section 4.

**Lemma 3.7.** *Under (GA), the thresholds satisfy  $0 < g_0 < g_1 < \gamma - n$ .*

*Proof.* We have already established  $g_0 > 0$  and  $0 < g_1 < \gamma - n$ , so it remains to prove  $g_0 < g_1$ . Since  $0 < y_C < 1$  and  $\delta > 0$  give  $0 < y_C^\delta < 1$ , relation (3.6) yields  $by_C = b - m_0 - dy_C^\delta > b - m_0 - d$ , that is,

$$1 - y_C < \frac{m_0 + d}{b}.$$

Using this lower bound for  $y_C$  once more,

$$\gamma - n + (a - \gamma)y_C = \gamma - n - (\gamma - a)y_C < (a - n) + (\gamma - a)\frac{m_0 + d}{b},$$

and therefore, by (3.12),

$$g_0 < \frac{m_0 + d}{b} \left[ (a - n) + (\gamma - a)\frac{m_0 + d}{b} \right] = \frac{(a - n)(m_0 + d)}{b} + \frac{(\gamma - a)(m_0 + d)^2}{b^2}. \quad (3.13)$$

By the last condition in (GA),  $m_0 + d < \frac{b}{2(a-n)}g_1$  and  $m_0 + d < b\sqrt{\frac{g_1}{2(\gamma-a)}}$ , so each summand in (3.13) is strictly less than  $\frac{g_1}{2}$ . Hence  $g_0 < g_1$ .  $\square$

**Remark 3.8.** *The two thresholds control the boundary stability monotonically in  $g$ . The proofs of Theorems 3.3 and 3.5 give*

$$\lambda_2 = \frac{a + b}{\gamma}(g - g_1), \quad \mu_1 = \frac{g_0 - g}{1 - y_C},$$

hence

$$\partial_g \lambda_2 = \frac{a + b}{\gamma} > 0, \quad \partial_g \mu_1 = -\frac{1}{1 - y_C} < 0.$$

As  $g$  increases,  $\lambda_2$  therefore increases through 0 at  $g = g_1$  and  $\mu_1$  decreases through 0 at  $g = g_0$ , so stronger grazing destabilizes  $B$  and stabilizes  $C$ . Since  $g_0 < g_1$  by Lemma 3.7, the coral state gains stability before the macroalgae state loses it, and  $B$  and  $C$  are simultaneously stable for  $g_0 < g < g_1$ . In terms of the nullcline intercepts (3.2), (3.3) and (3.7),

$$g > g_0 \quad \text{if and only if} \quad y_C > y_A, \quad g < g_1 \quad \text{if and only if} \quad x_D < x_B.$$

#### 4. Interior equilibria

An interior equilibrium is a point  $(x^*, y^*) \in \Omega$  at which  $F = G = 0$ , and it corresponds to the coexistence of coral, macroalgae, and turf, with the last occupying the remaining cover  $1 - x^* - y^* > 0$ . In this section, we reduce the search for such points to a scalar equation, relate the stability of an interior equilibrium to the derivative of the reduced function  $L$  introduced below, and classify the interior equilibria in each grazing regime.

##### 4.1. The reduced equation and its concavity

By (3.5), the coral nullcline is the graph  $x = K(y)$ ,  $y \in [0, y_C]$ , so every interior equilibrium has the form  $(K(y^*), y^*)$  with  $y^* \in (0, y_C)$  a root of  $F(K(y), y)$ . Since  $1 - K(y) = \frac{a+m_0+by+dy^\delta}{a+b}$ , we set

$$L(y) := F(K(y), y) = \frac{\gamma(a + m_0 + by + dy^\delta)}{a + b} - n + (a - \gamma)y - \frac{g}{1 - y}, \quad y \in [0, y_C]. \quad (4.1)$$

Every root of  $L$  in  $(0, y_C)$  indeed yields an interior equilibrium.

**Lemma 4.1.** *If  $y \in (0, y_C)$ , then  $(K(y), y) \in \Omega$ .*

*Proof.* Recall from (3.6) the strictly increasing function  $H(y) = by + dy^\delta$ . Since  $H(y) < H(y_C) = b - m_0$  for  $y < y_C$ , we have  $K(y) > 0$ . Moreover  $K(y) + y = \frac{b-m_0+ay-dy^\delta}{a+b} < 1$ , since  $ay - dy^\delta < a < a + m_0$  for  $0 < y < 1$ . Thus  $(K(y), y) \in \Omega$ .  $\square$

Consequently, the number of interior equilibria equals the number of roots of  $L$  in  $(0, y_C)$ . Evaluating  $L$  at the endpoints and using  $a + m_0 + by_C + dy_C^\delta = a + b$  from (3.6),

$$L(0) = g_1 - g, \quad L(y_C) = \frac{g_0 - g}{1 - y_C}, \quad (4.2)$$

with  $g_0, g_1$  from (3.12) and (3.11). The number of roots is determined by the shape of  $L$ , whose derivatives are

$$L'(y) = \frac{\gamma(b + \delta d y^{\delta-1})}{a + b} + (a - \gamma) - \frac{g}{(1 - y)^2}, \quad L''(y) = \frac{\gamma\delta(\delta - 1)dy^{\delta-2}}{a + b} - \frac{2g}{(1 - y)^3}, \quad (4.3)$$

for  $y \in (0, y_C]$ . We record when  $L$  is concave.

**Lemma 4.2.** *Let  $y \in (0, y_C]$ . (i) If  $0 < \delta \leq 1$ , then  $L''(y) < 0$ . (ii) If  $\delta \geq 2$  and*

$$2g \geq \frac{\gamma\delta(\delta - 1)d}{a + b} y_C^{\delta-2}, \quad (4.4)$$

*then  $L''(y) < 0$ . In either case,  $L$  is strictly concave on  $(0, y_C]$ .*

*Proof.* (i) For  $0 < \delta \leq 1$ , one has  $\delta(\delta - 1) \leq 0$ , so the first term of  $L''$  is nonpositive while the second is negative. (ii) For  $\delta \geq 2$ , the map  $y \mapsto y^{\delta-2}$  is nondecreasing, so

$$\frac{\gamma\delta(\delta - 1)d}{a + b} y^{\delta-2} \leq \frac{\gamma\delta(\delta - 1)d}{a + b} y_C^{\delta-2} \leq 2g$$

by (4.4), while  $\frac{2g}{(1-y)^3} > 2g$  for  $y > 0$ , and hence  $L''(y) < 0$ . Finally, since  $y_C^{\delta-2} \leq 1$ , the simpler bound  $2g \geq \frac{\gamma\delta(\delta-1)d}{a+b}$  already implies (4.4), so it too suffices.  $\square$

The remaining range  $1 < \delta < 2$ , where  $L$  fails to be concave near  $y = 0$ , is analyzed in Subsection 4.4.

#### 4.2. Stability of an interior equilibrium

Let  $E^* = (x^*, y^*)$  with  $x^* = K(y^*)$  be an interior equilibrium, with  $y^* \in (0, y_C)$  a root of  $L$ . As  $F(E^*) = G(E^*) = 0$ , the Jacobian (3.10) reduces to

$$J(E^*) = \begin{pmatrix} x^* \partial_x F(E^*) & x^* \partial_y F(E^*) \\ y^* \partial_x G(E^*) & y^* \partial_y G(E^*) \end{pmatrix}. \quad (4.5)$$

Its trace is

$$\text{tr } J(E^*) = x^* \partial_x F(E^*) + y^* \partial_y G(E^*) = -\gamma x^* - y^*(b + \delta d(y^*)^{\delta-1}) < 0. \quad (4.6)$$

For the determinant, the chain rule applied to (4.1) gives

$$L'(y^*) = \partial_x F(E^*) K'(y^*) + \partial_y F(E^*) = \frac{\gamma(b + \delta d(y^*)^{\delta-1})}{a + b} + \partial_y F(E^*), \quad (4.7)$$

so that  $(\partial_x F \partial_y G - \partial_y F \partial_x G)(E^*) = \gamma(b + \delta d(y^*)^{\delta-1}) + (a + b) \partial_y F(E^*) = (a + b) L'(y^*)$ , and therefore

$$\det J(E^*) = x^* y^* (\partial_x F \partial_y G - \partial_y F \partial_x G)(E^*) = (a + b) x^* y^* L'(y^*). \quad (4.8)$$

The off-diagonal entries  $x^* \partial_y F(E^*)$  and  $y^* \partial_x G(E^*) = -(a + b) y^*$  are both negative, so that their product is positive and the eigenvalues of  $J(E^*)$  are real. In view of (4.6) and (4.8), the equilibrium  $E^*$  is therefore a stable node when  $L'(y^*) > 0$  and a saddle when  $L'(y^*) < 0$ . Thus the graph of  $L$  determines the number of interior equilibria and the local stability of each hyperbolic one.

#### 4.3. Classification of the interior equilibria

It is convenient to write  $L(y) = \frac{\tilde{g}(y) - g}{1 - y}$ , where

$$\tilde{g}(y) := (1 - y) \left[ \frac{\gamma}{a + b} (a + m_0 + by + dy^\delta) - n + (a - \gamma)y \right], \quad y \in [0, y_C], \quad (4.9)$$

is independent of  $g$ . Then  $\tilde{g}(0) = g_1$  and  $\tilde{g}(y_C) = g_0$ , and a root of  $L$  is a point where  $\tilde{g}(y) = g$ , while  $L'(y^*)$  and  $\tilde{g}'(y^*)$  share the same sign there, so that an interior equilibrium is a stable node when  $\tilde{g}'(y^*) > 0$  and a saddle when  $\tilde{g}'(y^*) < 0$ . Set

$$g^* := \max_{y \in [0, y_C]} \tilde{g}(y) \in [g_1, \gamma - n]. \quad (4.10)$$

The interior equilibria are classified as follows.

**Theorem 4.3.** Suppose (GA) holds and, for the given  $g$ ,  $L$  is strictly concave on  $(0, y_C]$  (e.g.,  $0 < \delta \leq 1$ , or  $\delta \geq 2$  with (4.4)). The interior equilibria of (2.5) are classified by the grazing regime:

- (i) Low grazing. For  $0 < g < g_0$ , there is no interior equilibrium.
- (ii) Intermediate grazing. For  $g_0 < g < g_1$ , there is a unique interior equilibrium  $E^* = (K(y^*), y^*)$ , and it is a saddle.
- (iii) High grazing. Let  $g_1 < g < \gamma - n$ . If  $g^* = g_1$ , there is no interior equilibrium. If  $g^* > g_1$ , there is none for  $g^* < g < \gamma - n$ , exactly two for  $g_1 < g < g^*$ , a stable node  $E_1^* = (K(y_1^*), y_1^*)$  and a saddle  $E_2^* = (K(y_2^*), y_2^*)$  with  $0 < y_1^* < y_2^* < y_C$ , and a single nonhyperbolic equilibrium  $E_3^* = (K(y_3^*), y_3^*)$  at  $g = g^*$ .

*Proof.* (i) By (4.2),  $L(0) > 0$  and  $L(y_C) > 0$  (as  $g < g_0$ ). Writing  $y = (1 - \theta)y_C$  with  $\theta \in [0, 1]$ , concavity gives

$$L(y) \geq \theta L(0) + (1 - \theta)L(y_C) > 0,$$

so that  $L > 0$  on  $[0, y_C]$  and there is no root.

(ii) By (4.2),  $L(0) > 0 > L(y_C)$  (as  $g_0 < g < g_1$ ), so  $L$  has a root  $y^* \in (0, y_C)$ . If  $0 < y_1 < y_2 < y_C$  were two roots, then, writing  $y_1 = (1 - \theta)y_2$  with  $\theta \in (0, 1)$ , concavity would give

$$0 = L(y_1) \geq \theta L(0) + (1 - \theta)L(y_2) = \theta L(0) > 0,$$

which is a contradiction, so that the root is unique. Finally, by the mean value theorem, there is some  $c \in (0, y^*)$  with

$$L'(c) = \frac{L(y^*) - L(0)}{y^*} = -\frac{L(0)}{y^*} < 0,$$

and since  $L'$  is decreasing, we have  $L'(y^*) \leq L'(c) < 0$ , so that the corresponding equilibrium  $E^*$  is a saddle.

(iii) By (4.2),  $L(0) < 0$  and  $L(y_C) < 0$  (as  $g > g_1$ ). If  $g^* = g_1$ , then  $\tilde{g} \leq g_1 < g$ , hence  $L < 0$  on  $[0, y_C]$  and there is no interior equilibrium. Assume henceforth  $g^* > g_1$ , so that the maximum of  $\tilde{g}$  is attained at an interior point  $\hat{y} \in (0, y_C)$ , as  $\tilde{g}(0) = g_1 < g^*$  and  $\tilde{g}(y_C) = g_0 < g^*$ . We distinguish three cases.

(a) For  $g^* < g < \gamma - n$ , one has  $\tilde{g} < g$ , hence  $L < 0$  and there is no interior equilibrium.

(b) For  $g_1 < g < g^*$ ,

$$L(\hat{y}) = \frac{g^* - g}{1 - \hat{y}} > 0, \quad L(0) < 0, \quad L(y_C) < 0,$$

so  $L$  has roots  $y_1^* \in (0, \hat{y})$  and  $y_2^* \in (\hat{y}, y_C)$ . Strict concavity precludes a third root, since three roots  $y_1 < y_2 < y_3$  would force  $L(y_2) > 0$  by the argument of part (ii). As  $L > 0$  on  $(y_1^*, y_2^*)$  vanishes at the endpoints, and  $L'$  is strictly decreasing,

$$L'(y_1^*) > 0 > L'(y_2^*),$$

so the corresponding equilibria are a stable node  $E_1^*$  and a saddle  $E_2^*$ .

(c) For  $g = g^*$ ,  $L \leq 0$ . Since strict concavity would give  $L > 0$  between two distinct zeros, equality holds only at the unique maximizer  $y_3^*$  of  $\tilde{g}$ , where

$$L(y_3^*) = 0, \quad L'(y_3^*) = 0,$$

where the second equality holds because  $y_3^*$  is an interior maximum. By (4.8) and (4.6),

$$\det J(E_3^*) = 0, \quad \text{tr } J(E_3^*) < 0.$$

□

Together with Lemma 3.2 and Theorems 3.3 and 3.5, this yields the classification summarized in Table 2 and illustrated in Figure 2. When  $g^* > g_1$ , Section 5 shows that the coalescence of  $E_1^*$  and  $E_2^*$  into  $E_3^*$  at  $g = g^*$  is a saddle-node bifurcation (Theorem 5.5 and Proposition 5.6), illustrated in Figure 4.

**Table 2.** Classification of equilibria across the grazing regimes (Lemma 3.2 and Theorems 3.3, 3.5, and 4.3), where the last four rows assume  $g^* > g_1$ , since otherwise, there is no interior equilibrium for  $g \geq g_1$ . At  $g = g_0$  and  $g = g_1$ , the equilibria  $C$  and  $B$  are nonhyperbolic and undergo transcritical bifurcations, the latter for  $\delta \in \mathbb{N}$ , and at  $g = g^*$ , the interior equilibria undergo a saddle-node bifurcation (Section 5). For  $\delta \in (1, 2)$ , the counts can differ (Proposition 4.5).

|                        | $O$           | $B$           | $C$           | Interior equilibria                 |
|------------------------|---------------|---------------|---------------|-------------------------------------|
| $0 < g < g_0$          | unstable node | stable node   | saddle        | none                                |
| $g = g_0$              | unstable node | stable node   | nonhyperbolic | none                                |
| $g_0 < g < g_1$        | unstable node | stable node   | stable node   | $E^*$ saddle                        |
| $g = g_1$              | unstable node | nonhyperbolic | stable node   | $E_2^*$ saddle                      |
| $g_1 < g < g^*$        | unstable node | saddle        | stable node   | $E_1^*$ stable node, $E_2^*$ saddle |
| $g = g^*$              | unstable node | saddle        | stable node   | $E_3^*$ nonhyperbolic               |
| $g^* < g < \gamma - n$ | unstable node | saddle        | stable node   | none                                |

The two canonical crowding exponents, linear ( $\delta = 1$ ) and quadratic ( $\delta = 2$ ), are worked out explicitly in Subsection 6.1.

#### 4.4. The non-concave regime $1 < \delta < 2$

When  $1 < \delta < 2$ , (4.3) gives

$$\lim_{y \rightarrow 0^+} L''(y) = +\infty,$$

so that  $L$  is convex near  $y = 0$  and the concavity arguments of Subsection 4.3 no longer apply. We show that  $L''' < 0$  on  $(0, y_C)$  (Lemma 4.4), which limits the system to at most three interior equilibria and preserves the high-grazing conclusions of Theorem 4.3 (Proposition 4.5).

**Lemma 4.4.** Assume (GA) and  $1 < \delta < 2$ . Then  $L'''(y) < 0$  and  $\tilde{g}'''(y) < 0$  for  $y \in (0, y_C)$ . Consequently  $L'$  has at most one interior maximum, hence at most two zeros, and  $\tilde{g}$  has at most one interior local maximum and one interior local minimum.

*Proof.* By (4.3),

$$L'''(y) = \frac{\gamma\delta(\delta-1)(\delta-2)d}{a+b}y^{\delta-3} - \frac{6g}{(1-y)^4},$$

and for  $1 < \delta < 2$ , both terms are negative, since  $\delta(\delta-1) > 0$  and  $\delta-2 < 0$ , and hence  $L''' < 0$ . Moreover  $\tilde{g}(y) = (1-y)L(y) + g$ , so that  $\tilde{g}''' = -3L'' + (1-y)L'''$ , and substituting (4.3) gives

$$\tilde{g}'''(y) = \frac{\gamma\delta(\delta-1)d}{a+b}y^{\delta-3}[(\delta-2) - (\delta+1)y] < 0, \quad y \in (0, y_C),$$

with the bracket being negative because  $\delta-2 < 0$ . As  $L''' < 0$ ,  $L''$  is strictly decreasing, and since  $L''(0^+) = +\infty$ , it has at most one zero in  $(0, y_C)$ , so  $L'$  has at most one interior maximum and hence at most two zeros. As  $\tilde{g}''' < 0$ ,  $\tilde{g}'$  is strictly concave and so has at most two zeros, where  $\tilde{g}$  has at most one interior local maximum and one interior local minimum.  $\square$

**Proposition 4.5.** Assume (GA) and  $1 < \delta < 2$ . Then (2.5) has at most three interior equilibria  $(K(y^*), y^*)$ , each a stable node or a saddle according to  $L'(y^*) > 0$  or  $L'(y^*) < 0$  (Subsection 4.2). For  $g > g_1$ , there are at most two, and when two exist, the one of smaller coral cover is a stable node and the other a saddle. If all roots of  $L$  in  $(0, y_C)$  are simple, the number of interior equilibria is even for  $g < g_0$  and for  $g > g_1$ , and odd for  $g_0 < g < g_1$ .

*Proof.* (a) By Lemma 4.4,  $L'$  has at most two zeros in  $(0, y_C)$ , so by Rolle's theorem,  $L$  has at most three roots there. As the interior equilibria are exactly the points  $(K(y^*), y^*)$  with  $y^* \in (0, y_C)$ , a root of  $L$  (Subsection 4.1 and Lemma 4.1), there are at most three of them.

(b) For  $g > g_1$ , (4.2) gives  $L(0) = g_1 - g < 0$ . Were  $L$  to have three roots  $y_1 < y_2 < y_3$ , Rolle would yield two zeros of  $L'$ , which by Lemma 4.4 are its only zeros. As  $L'$  has a single interior maximum,  $L' < 0$  on  $(0, y_1)$ , where  $L(0) > L(y_1) = 0$ , contradicting  $L(0) < 0$ . Hence at most two roots remain. For two simple roots  $y_1 < y_2$ , the endpoint signs  $L(0), L(y_C) < 0$  force

$$L < 0 \text{ on } (0, y_1) \cup (y_2, y_C), \quad L > 0 \text{ on } (y_1, y_2),$$

so that

$$L'(y_1) > 0 > L'(y_2),$$

and hence  $(K(y_1), y_1)$  is a stable node and  $(K(y_2), y_2)$  a saddle.

(c) By (4.2),

$$\text{sign}L(0) = \text{sign}(g_1 - g), \quad \text{sign}L(y_C) = \text{sign}(g_0 - g).$$

If all roots of  $L$  in  $(0, y_C)$  are simple, each changes sign. Since  $g_0 < g_1$ , the endpoint signs agree for  $g < g_0$ , differ for  $g_0 < g < g_1$ , and agree for  $g > g_1$ , which gives the stated conclusion.  $\square$

On the grazing window of Proposition 4.7, which lies in  $(g_0, g_1)$ , there are exactly three simple interior equilibria, and the system is locally tristable, as illustrated in Figure 5.

**Remark 4.6.** By Proposition 4.5(a),(b), the high-grazing conclusion of Theorem 4.3(iii) remains valid for  $1 < \delta < 2$ : for  $g > g_1$ , there are at most two interior equilibria, a stable node and a saddle. The convexity of  $L$  near  $y = 0$  can give the strictly concave  $\tilde{g}'$  two interior zeros, so that  $\tilde{g}$  has an interior local minimum, and a second pair of interior equilibria then raises the count to three on the window of Proposition 4.7. When  $\tilde{g}$  is monotone on  $[0, y_C]$ , it can only decrease, since  $\tilde{g}(0) = g_1$  exceeds  $\tilde{g}(y_C) = g_0$  (Lemma 3.7), so  $g^* = g_1$ , leaving at most one interior equilibrium. A parameter set realizing three coexisting interior equilibria is examined in Subsection 6.1.

**Proposition 4.7.** Assume (GA) and  $1 < \delta < 2$ , and suppose that  $\tilde{g}'$  has two interior zeros  $\check{y} < \hat{y}$  in  $(0, y_C)$  and that

$$\max\{g_0, \tilde{g}(\check{y})\} < g < \min\{g_1, \tilde{g}(\hat{y})\}.$$

Then (2.5) has exactly three interior equilibria  $(K(y_i^*), y_i^*)$ ,  $i = 1, 2, 3$ , with

$$0 < y_1^* < \check{y} < y_2^* < \hat{y} < y_3^* < y_C,$$

all simple, saddles for  $i = 1, 3$ , and a stable node for  $i = 2$ , so that together with  $B$  and  $C$ , the system is locally tristable.

*Proof.* By Lemma 4.4, the function  $\tilde{g}'$  is strictly concave on  $(0, y_C)$ , so, having the two zeros  $\check{y} < \hat{y}$ , it is positive between them and negative outside:

$$\tilde{g}' < 0 \text{ on } (0, \check{y}), \quad \tilde{g}' > 0 \text{ on } (\check{y}, \hat{y}), \quad \tilde{g}' < 0 \text{ on } (\hat{y}, y_C),$$

and has no further zero. As  $\tilde{g}$  is continuous on  $[0, y_C]$ , it strictly decreases on  $[0, \check{y}]$ , strictly increases on  $[\check{y}, \hat{y}]$ , and strictly decreases on  $[\hat{y}, y_C]$ , so that  $\check{y}$  is its only interior local minimum and  $\hat{y}$  its only interior local maximum. By (4.9), the endpoint values are  $\tilde{g}(0) = g_1$  and  $\tilde{g}(y_C) = g_0$ , and an interior root of  $L$  is a point where  $\tilde{g}(y) = g$  with  $y \in (0, y_C)$ . The assumed grazing window places  $g$  strictly between the endpoint values of  $\tilde{g}$  on each monotone interval:

$$\tilde{g}(\check{y}) < g < g_1, \quad \tilde{g}(\check{y}) < g < \tilde{g}(\hat{y}), \quad g_0 < g < \tilde{g}(\hat{y}),$$

on  $[0, \check{y}]$ ,  $[\check{y}, \hat{y}]$ , and  $[\hat{y}, y_C]$ , respectively. By the intermediate value theorem, and strict monotonicity, each interval carries exactly one solution:

$$y_1^* \in (0, \check{y}), \quad y_2^* \in (\check{y}, \hat{y}), \quad y_3^* \in (\hat{y}, y_C),$$

while the strict inequalities exclude the endpoints themselves, so these three exhaust the interior roots of  $L$ . Each is simple, since  $\tilde{g}'(y_i^*) \neq 0$ ,  $i = 1, 2, 3$ . By Lemma 4.1, the states  $(K(y_i^*), y_i^*)$ ,  $i = 1, 2, 3$ , lie in  $\Omega$ .

By (4.9), we have  $\text{sign} L'(y_i^*) = \text{sign} \tilde{g}'(y_i^*)$ , since  $1 - y_i^* > 0$ , where

$$L'(y_1^*) < 0, \quad L'(y_2^*) > 0, \quad L'(y_3^*) < 0.$$

By (4.6) and (4.8), the eigenvalues of the Jacobian at each  $(K(y_i^*), y_i^*)$  are real with negative trace, and an interior equilibrium is a stable node when  $L'(y^*) > 0$  and a saddle when  $L'(y^*) < 0$ . Therefore  $(K(y_i^*), y_i^*)$  is a saddle for  $i = 1, 3$  and a stable node for  $i = 2$ .

Finally,  $\max\{g_0, \tilde{g}(\check{y})\} \geq g_0$  and  $\min\{g_1, \tilde{g}(\hat{y})\} \leq g_1$ , so the window forces  $g_0 < g < g_1$ . By Theorems 3.3 and 3.5, the states  $B$  and  $C$  are then stable and, together with the interior node, the system is locally tristable.  $\square$

## 5. Bifurcation analysis

We now describe the bifurcations through which the equilibria of (2.5) exchange stability and are created or destroyed as the grazing intensity  $g$  varies. The bifurcation diagrams of Figures 4 and 5 display these bifurcations. By Section 3, the boundary equilibria  $B$  and  $C$  are nonhyperbolic at  $g = g_1$  and  $g = g_0$ , and by Section 4, the two interior equilibria of the high-grazing regime coalesce into the nonhyperbolic equilibrium  $E_3^*$  at  $g = g^*$ . We show that  $C$  undergoes a transcritical bifurcation, that  $B$  does so for  $\delta \in \mathbb{N}$ , and that the interior equilibria undergo a saddle-node bifurcation. We write system (2.5) as

$$\dot{\mathbf{X}} = \mathbf{F}(\mathbf{X}, g), \quad \mathbf{X} = (x, y)^\top, \quad \mathbf{F}(\mathbf{X}, g) = \begin{pmatrix} xF(x, y) \\ yG(x, y) \end{pmatrix}, \quad (5.1)$$

and invoke Sotomayor's theorem [23, Section 4.2]: If  $\mathbf{F}(\mathbf{X}_0, g^\dagger) = 0$  and  $D\mathbf{F}(\mathbf{X}_0, g^\dagger)$  has a simple zero eigenvalue with right eigenvector  $\mathbf{U}$  and left eigenvector  $\mathbf{W}$ , then at  $g = g^\dagger$ , the system undergoes a *transcritical* bifurcation if

$$\mathbf{W}^\top \mathbf{F}_g(\mathbf{X}_0, g^\dagger) = 0, \quad \mathbf{W}^\top (D\mathbf{F}_g(\mathbf{X}_0, g^\dagger)\mathbf{U}) \neq 0, \quad \mathbf{W}^\top (D^2\mathbf{F}(\mathbf{X}_0, g^\dagger)(\mathbf{U}, \mathbf{U})) \neq 0, \quad (5.2)$$

and a *saddle-node* bifurcation if

$$\mathbf{W}^\top \mathbf{F}_g(\mathbf{X}_0, g^\dagger) \neq 0, \quad \mathbf{W}^\top (D^2 \mathbf{F}(\mathbf{X}_0, g^\dagger)(\mathbf{U}, \mathbf{U})) \neq 0. \quad (5.3)$$

Here  $\mathbf{F}_g = \partial_g \mathbf{F}$ ,  $D\mathbf{F}_g$  is its Jacobian in  $\mathbf{X}$ , and  $D^2 \mathbf{F}(\mathbf{U}, \mathbf{U}) = (\mathbf{U}^\top (D^2 F_1) \mathbf{U}, \mathbf{U}^\top (D^2 F_2) \mathbf{U})^\top$  with  $D^2 F_i$  is the Hessian of the  $i$ -th component.

### 5.1. Transcritical bifurcations at the boundary equilibria

**Theorem 5.1.** Suppose (GA) holds and  $\delta \in \mathbb{N}$ . If

$$g_1 \neq a - \gamma + \frac{\gamma}{a+b}(b + d\mathbb{1}_{\{\delta=1\}}), \quad (5.4)$$

then system (2.5) undergoes a transcritical bifurcation at  $B$  as  $g$  crosses  $g_1$ .

*Proof.* Center  $B$  at the origin by  $X = x - x_B$ ,  $Y = y$ , where  $x_B = 1 - \frac{g+n}{\gamma}$  depends on  $g$ , so that the origin is an equilibrium for every  $g$ . In these coordinates, (5.1) reads  $\dot{\mathbf{X}} = \mathbf{F}(\mathbf{X}, g)$  with  $\mathbf{X} = (X, Y)^\top$  and

$$\begin{aligned} \mathbf{F}(\mathbf{X}, g) &= \begin{pmatrix} F_1(\mathbf{X}, g) \\ F_2(\mathbf{X}, g) \end{pmatrix} = \begin{pmatrix} (X + x_B) F(X + x_B, Y) \\ Y G(X + x_B, Y) \end{pmatrix} \\ &= \begin{pmatrix} (X + x_B) [\gamma(1 - X - x_B) - n + (a - \gamma)Y - \frac{g}{1-Y}] \\ Y [-(a + m_0) + \frac{(a+b)(g+n)}{\gamma} - (a+b)X - bY - dY^\delta] \end{pmatrix}, \end{aligned}$$

where the lower entry is written using this value of  $x_B$ . For  $\delta \in \mathbb{N}$ , the component  $F_2$  is a polynomial in  $(X, Y)$ , so  $\mathbf{F}$  is smooth near the origin. At  $g = g_1$ , one has  $\frac{(a+b)(g_1+n)}{\gamma} = a + m_0$ , so

$$D\mathbf{F}(\mathbf{0}, g_1) = \begin{pmatrix} \lambda_1 & x_B(a - \gamma - g_1) \\ 0 & 0 \end{pmatrix}, \quad \lambda_1 = -(\gamma - g_1 - n) < 0,$$

and the zero eigenvalue is simple, with right and left eigenvectors

$$\mathbf{U} = \left( -\frac{x_B(a - \gamma - g_1)}{\lambda_1}, 1 \right)^\top, \quad \mathbf{W} = (0, 1)^\top.$$

As  $\mathbf{W} = (0, 1)^\top$ , the conditions (5.2) involve only  $F_2$ . From  $\partial_g F_2(\mathbf{X}, g) = \frac{a+b}{\gamma} Y$ ,

$$\mathbf{W}^\top \mathbf{F}_g(\mathbf{0}, g_1) = 0, \quad \mathbf{W}^\top (D\mathbf{F}_g(\mathbf{0}, g_1)\mathbf{U}) = DF_{2,g}(\mathbf{0}, g_1)\mathbf{U} = \frac{a+b}{\gamma} \neq 0.$$

Since  $F_2(\cdot, \cdot, g_1) = -(a+b)XY - bY^2 - dY^{\delta+1}$ , its Hessian at the origin is

$$D^2 F_2(\mathbf{0}, g_1) = \begin{pmatrix} 0 & -(a+b) \\ -(a+b) & -2(b + d\mathbb{1}_{\{\delta=1\}}) \end{pmatrix},$$

and therefore

$$\mathbf{W}^\top (D^2 \mathbf{F}(\mathbf{0}, g_1)(\mathbf{U}, \mathbf{U})) = \mathbf{U}^\top D^2 F_2(\mathbf{0}, g_1)\mathbf{U} = 2 \left( \frac{(a+b)x_B(a - \gamma - g_1)}{\lambda_1} - (b + d\mathbb{1}_{\{\delta=1\}}) \right),$$

which vanishes only for  $g_1 = a - \gamma + \frac{\gamma}{a+b}(b + d\mathbb{1}_{\{\delta=1\}})$ , which is excluded by hypothesis. Hence (5.2) holds, and as the centering is a smooth change of coordinates, (2.5) undergoes a transcritical bifurcation at  $B$ .  $\square$

**Remark 5.2.** The restriction  $\delta \in \mathbb{N}$  guarantees that  $Y^{\delta+1}$ , and thus  $F_2$ , is smooth on a full neighborhood of  $Y = 0$ , including  $Y < 0$ , as Sotomayor's theorem requires, and the crowding coefficient  $d$  enters the nondegeneracy condition (5.4) only when  $\delta = 1$ .

**Theorem 5.3.** Suppose (GA) holds. If

$$g_0 \neq (1 - y_C)^2 \left( a - \gamma + \frac{\gamma(b + \delta dy_C^{\delta-1})}{a + b} \right), \quad (5.5)$$

then for every  $\delta > 0$ , system (2.5) undergoes a transcritical bifurcation at  $C$  as  $g$  crosses  $g_0$ .

*Proof.* Since  $C = (0, y_C)$  is independent of  $g$ , we work directly with (5.1). At  $g = g_0$ , one has  $\mu_1 = F(0, y_C) = 0$ , so

$$D\mathbf{F}(C, g_0) = \begin{pmatrix} 0 & 0 \\ -(a+b)y_C & \mu_2 \end{pmatrix}, \quad \mu_2 = -by_C - \delta dy_C^\delta < 0,$$

and the zero eigenvalue is simple, with

$$\mathbf{U} = \left( \frac{\mu_2}{(a+b)y_C}, 1 \right)^\top, \quad \mathbf{W} = (1, 0)^\top.$$

As  $\mathbf{F}_g(\mathbf{X}, g) = \left( -\frac{x}{1-y}, 0 \right)^\top$  vanishes at  $C$  (where  $x = 0$ ),  $\mathbf{W}^\top \mathbf{F}_g(C, g_0) = 0$ , while

$$\mathbf{W}^\top (D\mathbf{F}_g(C, g_0)\mathbf{U}) = -\frac{U_1}{1-y_C} = -\frac{\mu_2}{(a+b)y_C(1-y_C)} > 0.$$

Since  $\mathbf{W} = (1, 0)^\top$ , the last condition involves only  $F_1(\mathbf{X}, g) = xF(x, y)$ , with the Hessian

$$D^2 F_1(C, g_0) = \begin{pmatrix} -2\gamma & (a-\gamma) - \frac{g_0}{(1-y_C)^2} \\ (a-\gamma) - \frac{g_0}{(1-y_C)^2} & 0 \end{pmatrix},$$

so that

$$\mathbf{W}^\top (D^2 \mathbf{F}(C, g_0)(\mathbf{U}, \mathbf{U})) = \mathbf{U}^\top D^2 F_1(C, g_0)\mathbf{U} = 2U_1 \left( a - \gamma - \frac{g_0}{(1-y_C)^2} - \gamma U_1 \right).$$

Using  $U_1 = -\frac{b+\delta dy_C^{\delta-1}}{a+b}$ , this vanishes only for  $g_0 = (1 - y_C)^2 \left( a - \gamma + \frac{\gamma(b+\delta dy_C^{\delta-1})}{a+b} \right)$ , which is excluded by hypothesis. Thus (5.2) holds and (2.5) undergoes a transcritical bifurcation at  $C$ .  $\square$

**Remark 5.4.** At  $g = g_0$ , both the macroalgal nullcline endpoint  $A = (0, y_A)$  of (3.2) and the interior equilibrium  $E^*$  coincide with the coral-only state  $C = (0, y_C)$ : there  $y_A = y_C$ , since  $g_0$  is the value at which  $F(0, y_C) = 0$ , while  $L(y_C) = 0$  by (4.2) and  $K(y_C) = 0$ , so that  $E^* = (K(y_C), y_C) = (0, y_C) = C$ . This crossing of the interior equilibrium with the boundary is the transcritical bifurcation of Theorem 5.3.

## 5.2. Saddle-node bifurcation of interior equilibria

**Theorem 5.5.** Suppose (GA) holds, that, at  $g = g^*$ , one of the conditions of Lemma 4.2 holds, and that  $g^* > g_1$ . Then system (2.5) undergoes a saddle-node bifurcation at the interior equilibrium  $E_3^* = (x_3^*, y_3^*)$  as  $g$  crosses  $g^*$ .

*Proof.* By Theorem 4.3(iii)(c), at  $g = g^*$ , the equilibrium  $E_3^*$  satisfies  $\det J(E_3^*) = 0$  and  $\text{tr } J(E_3^*) < 0$ , so its zero eigenvalue is simple. Using  $L'(y_3^*) = 0$ , equivalently,  $\partial_y F(E_3^*) = -\frac{\gamma(b+\delta d(y_3^*)^{\delta-1})}{a+b} = \gamma U_1$ , the eigenvectors are

$$\mathbf{U} = \left( -\frac{b + \delta d(y_3^*)^{\delta-1}}{a+b}, 1 \right)^\top, \quad \mathbf{W} = \left( 1, -\frac{\gamma x_3^*}{(a+b)y_3^*} \right)^\top.$$

Then  $\mathbf{W}^\top \mathbf{F}_g(E_3^*, g^*) = -\frac{x_3^*}{1-y_3^*} \neq 0$ , so the bifurcation is not transcritical. For the second condition, the Hessians of  $F_1(\mathbf{X}, g) = xF(x, y)$  and  $F_2(\mathbf{X}, g) = yG(x, y)$  at  $E_3^*$  give, using  $\partial_y F(E_3^*) = \gamma U_1$  and  $(a+b)U_1 = -(b + \delta d(y_3^*)^{\delta-1})$ ,

$$\begin{aligned} \mathbf{U}^\top D^2 F_1(E_3^*, g^*) \mathbf{U} &= -\frac{2g^* x_3^*}{(1-y_3^*)^3}, \\ \mathbf{U}^\top D^2 F_2(E_3^*, g^*) \mathbf{U} &= -2(a+b)U_1 - 2b - \delta(\delta+1)d(y_3^*)^{\delta-1}. \end{aligned}$$

Combining these with  $\mathbf{W} = (1, -\frac{\gamma x_3^*}{(a+b)y_3^*})^\top$  and simplifying by (4.3),

$$\mathbf{W}^\top (D^2 \mathbf{F}(E_3^*, g^*)(\mathbf{U}, \mathbf{U})) = -\frac{2g^* x_3^*}{(1-y_3^*)^3} + \frac{\gamma x_3^* \delta(\delta-1)d(y_3^*)^{\delta-2}}{a+b} = x_3^* L''(y_3^*).$$

By Lemma 4.2,  $L''(y_3^*) < 0$ , so this expression is nonzero. Thus (5.3) holds and (2.5) undergoes a saddle-node bifurcation at  $E_3^*$ .  $\square$

Beyond the bifurcation type, the nondegeneracy conditions (5.4) and (5.5), together with one of the conditions in Lemma 4.2 for the interior equilibrium, fix the local phase portrait of each nonhyperbolic equilibrium at its threshold.

**Proposition 5.6.** Suppose (GA) holds. Then each nonhyperbolic equilibrium is a saddle-node point in the sense of [23, Section 2.11], as follows.

- (i) The macroalgae-only state  $B$  at  $g = g_1$ , provided  $\delta \in \mathbb{N}$  and (5.4) holds.
- (ii) The coral-only state  $C$  at  $g = g_0$ , provided (5.5) holds.
- (iii) The interior equilibrium  $E_3^* = (K(y_3^*), y_3^*)$  at  $g = g^*$ , provided  $g^* > g_1$  and one of the conditions of Lemma 4.2 holds.

*Proof.* In each case, [23, Theorem 1, Section 2.11] applies with  $m = 2$ , and hence the equilibrium is a saddle node. The computations are deferred to Appendix A.  $\square$

Together, Theorems 5.1, 5.3, and 5.5 show that, as the grazing intensity increases, the reef passes through a transcritical bifurcation at  $g = g_0$  (where the coral-dominated state  $C$  gains stability), a transcritical bifurcation at  $g = g_1$  (where the macroalgae-dominated state  $B$  loses stability), and, when  $g^* > g_1$ , a saddle-node bifurcation at  $g = g^*$  (where the coexistence states annihilate one another). This sequence of bifurcations, with the corresponding phase portraits, is depicted for a representative parameter set in Figure 4. The ecological consequences are discussed in Section 7.

## 6. Examples and numerical simulations

While our previous sections mathematically define the boundaries of the bistable and tristable regimes, the following numerical simulations serve to visually illustrate the foregoing analysis (2.5) using representative baseline parameter sets. These simulations show the nullclines and phase portraits in the low-, intermediate-, and high-grazing regimes of Theorem 4.3 (Figure 2), the dependence of the interior equilibrium and the coral-only state on the crowding exponent, for  $\delta = 2$  and  $\delta = 5$  (Figure 3), the bifurcation diagram and phase portraits for a representative  $\delta = 1$  set with two interior equilibria (Figure 4), the bifurcation diagram and phase portrait for a  $\delta = 1.8$  set with three interior equilibria (Figure 5), and our final simulation maps of the number of interior equilibria across the  $(\delta, g)$  plane, gathering the regimes of Figures 2–5 (Figure 6). These figures are further explained in the following sections.

### 6.1. Special cases of the crowding exponent

We apply the foregoing analysis to three crowding regimes, linear ( $\delta = 1$ ), quadratic ( $\delta = 2$ ), and intermediate ( $1 < \delta < 2$ ). For  $\delta = 1$  and  $\delta = 2$ , the quantities of Section 4 become explicit: we specialize the coral nullcline (3.5), the reduced function (4.1) and its derivatives (4.3), the thresholds (3.12) and (3.11), and the maximizer  $\hat{y}$  of  $\tilde{g}$  given in (4.9) that determines  $g^*$  from (4.10).

*Linear crowding  $\delta = 1$ .* The nullcline (3.5) is a line,  $y_C$  from (3.6) is explicit, and (3.12) gives

$$K(y) = \frac{b - m_0 - (b + d)y}{a + b}, \quad y_C = \frac{b - m_0}{b + d}, \quad g_0 = \frac{d + m_0}{b + d} \left( \gamma - n + (a - \gamma) \frac{b - m_0}{b + d} \right).$$

The  $d$  term in (4.3) vanishes, leaving  $L''(y) = -\frac{2g}{(1-y)^3} < 0$ , so  $L$  is strictly concave for every  $g > 0$  (Lemma 4.2(i)) and Theorem 4.3 applies. Theorems 5.1 and 5.3 (the former since  $\delta \in \mathbb{N}$ ) give the transcritical bifurcations at  $B$  and  $C$  under (5.4) and (5.5), which here read

$$g_1 \neq a - \gamma + \frac{\gamma(b + d)}{a + b}, \quad g_0 \neq (1 - y_C)^2 \left( a - \gamma + \frac{\gamma(b + d)}{a + b} \right).$$

Here  $\tilde{g}$  (4.9) is the quadratic  $\tilde{g}(y) = (1 - y)(g_1 + (\frac{\gamma(b+d)}{a+b} + a - \gamma)y)$ . If  $\tilde{g}'(0) > 0$ , then  $\tilde{g}$  is strictly concave and its unique maximizer on  $[0, y_C]$  is the root of  $\tilde{g}'(y) = 0$ ,

$$\hat{y} = \frac{1}{2} \left( 1 - \frac{(a + b)g_1}{\gamma d + a(a + b - \gamma)} \right),$$

which lies in  $(0, y_C)$ . Thus  $g^* = \tilde{g}(\hat{y}) > g_1$ , and Theorem 5.5 yields a saddle node at  $g = g^*$ , as in Figure 4 (a  $\delta = 1$  set with two interior equilibria by Theorem 4.3(iii)). If  $\tilde{g}'(0) \leq 0$ , then  $g^* = g_1$ .

*Quadratic crowding  $\delta = 2$ .* The nullcline (3.5) is a parabola and (3.6) gives

$$K(y) = \frac{b - m_0 - by - dy^2}{a + b}, \quad y_C = \frac{-b + \sqrt{b^2 + 4d(b - m_0)}}{2d},$$

with  $g_0$  from (3.12). Now (4.3) gives  $L''(y) = \frac{2\gamma d}{a+b} - \frac{2g}{(1-y)^3}$ , so  $L$  is strictly concave on  $(0, y_C]$  exactly under the bound (4.4), that is,  $g \geq \frac{\gamma d}{a+b}$  (Lemma 4.2(ii)), and then Theorem 4.3 applies, as Figure 3

illustrates for  $\delta = 2$ . Theorems 5.1 and 5.3 (the former since  $\delta \in \mathbb{N}$ ) give the transcritical bifurcations at  $B$  and  $C$  under (5.4) and (5.5), which here read

$$g_1 \neq a - \gamma + \frac{\gamma b}{a + b}, \quad g_0 \neq (1 - y_C)^2 \left( a - \gamma + \frac{\gamma(b + 2dy_C)}{a + b} \right).$$

Here  $\tilde{g}$  (4.9) is cubic. If  $g^* > g_1$ , then the expression under the square root below is positive and the unique maximizer  $\hat{y} \in (0, y_C)$  is the larger root of  $\tilde{g}'(y) = 0$ ,

$$\hat{y} = \frac{a + b}{3\gamma d} \left[ -\left( \frac{\gamma(b - d)}{a + b} + a - \gamma \right) + \sqrt{\left( \frac{\gamma(b - d)}{a + b} + a - \gamma \right)^2 - \frac{3\gamma d}{a + b} \left( g_1 - \frac{\gamma b}{a + b} - a + \gamma \right)} \right],$$

with  $g^* = \tilde{g}(\hat{y}) > g_1$ . Otherwise  $g^* = g_1$ . In the first case, when (4.4) holds at  $g = g^*$ , Theorem 5.5 yields the saddle-node bifurcation at  $g = g^*$ . The set of Figure 4 (drawn for  $\delta = 1$ ) yields the same qualitative picture under  $\delta = 2$ , with  $g^* > g_1$  and two interior equilibria for  $g_1 < g < g^*$  by Theorem 4.3(iii).

*Intermediate crowding*  $1 < \delta < 2$ . Here  $L$  is no longer concave: the first term of  $L''$  in (4.3) diverges as  $y \rightarrow 0^+$ , so  $L''(0^+) = +\infty$  and  $L$  is convex near  $y = 0$ . Neither case of Lemma 4.2 holds, so Theorem 4.3 is replaced by Proposition 4.5 of Subsection 4.4, which permits as many as three interior equilibria, against at most two when  $L$  is concave. By Theorem 5.3, the transcritical bifurcation at  $C$  holds for every  $\delta > 0$  under (5.5), while Theorem 5.1 for  $B$  requires  $\delta \in \mathbb{N}$  and does not apply.

For the parameter set of Figure 5, which satisfies (GA), one finds

$$g_0 \approx 0.0072 < g_1 \approx 0.0215,$$

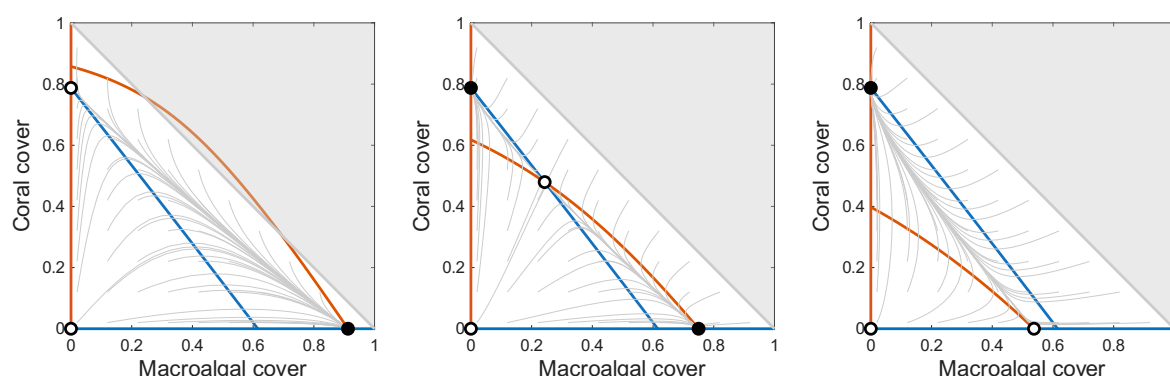
and  $\tilde{g}$  (4.9) has an interior local minimum at  $\check{y} \approx 0.120$ , of value  $\tilde{g}(\check{y}) \approx 0.0208$ , besides its maximizer  $\hat{y} \approx 0.388$  with  $g^* = \tilde{g}(\hat{y}) \approx g_1$ . At  $g \approx 0.0212$ , the reduced equation  $L(y) = 0$  has three roots,

$$y \approx 0.026, \quad y \approx 0.260, \quad y \approx 0.486,$$

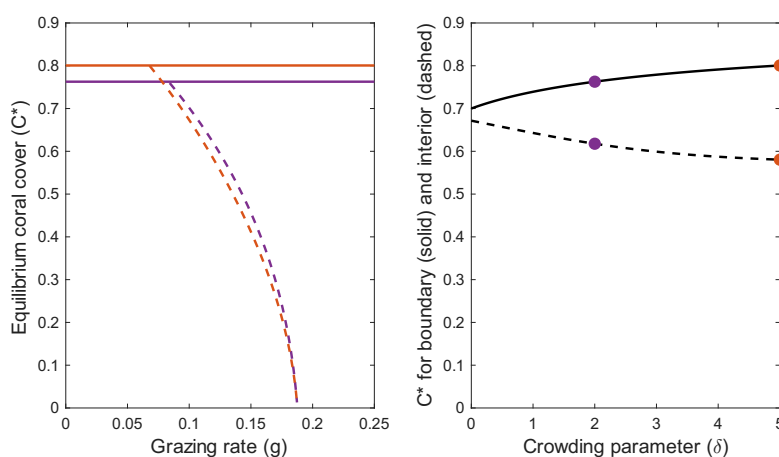
hence three interior equilibria  $(K(y_i), y_i)$ ,  $i = 1, 2, 3$ : a saddle, a stable node, and a saddle (Proposition 4.5), as in Figure 5. For  $g_0 < g < g_1$ , the boundary states  $B$  and  $C$  are also stable (Theorems 3.3 and 3.5), so  $B$ ,  $C$ , and the interior node give three stable states and the reef is tristable. These roots occur only for  $g \in (\tilde{g}(\check{y}), g_1)$ , a window of width about  $6.6 \times 10^{-4}$ , and require the interior minimum of  $\tilde{g}$ . When  $\tilde{g}$  is monotone on  $[0, y_C]$ , the ordering  $g_0 < g_1$  of Lemma 3.7 makes it decrease from  $\tilde{g}(0) = g_1$  to  $\tilde{g}(y_C) = g_0$ , so  $g^* = g_1$  and at most one interior equilibrium remains. Figure 6 places the  $1 < \delta < 2$  regime within the full  $(\delta, g)$  count.

## 6.2. Numerical illustrations

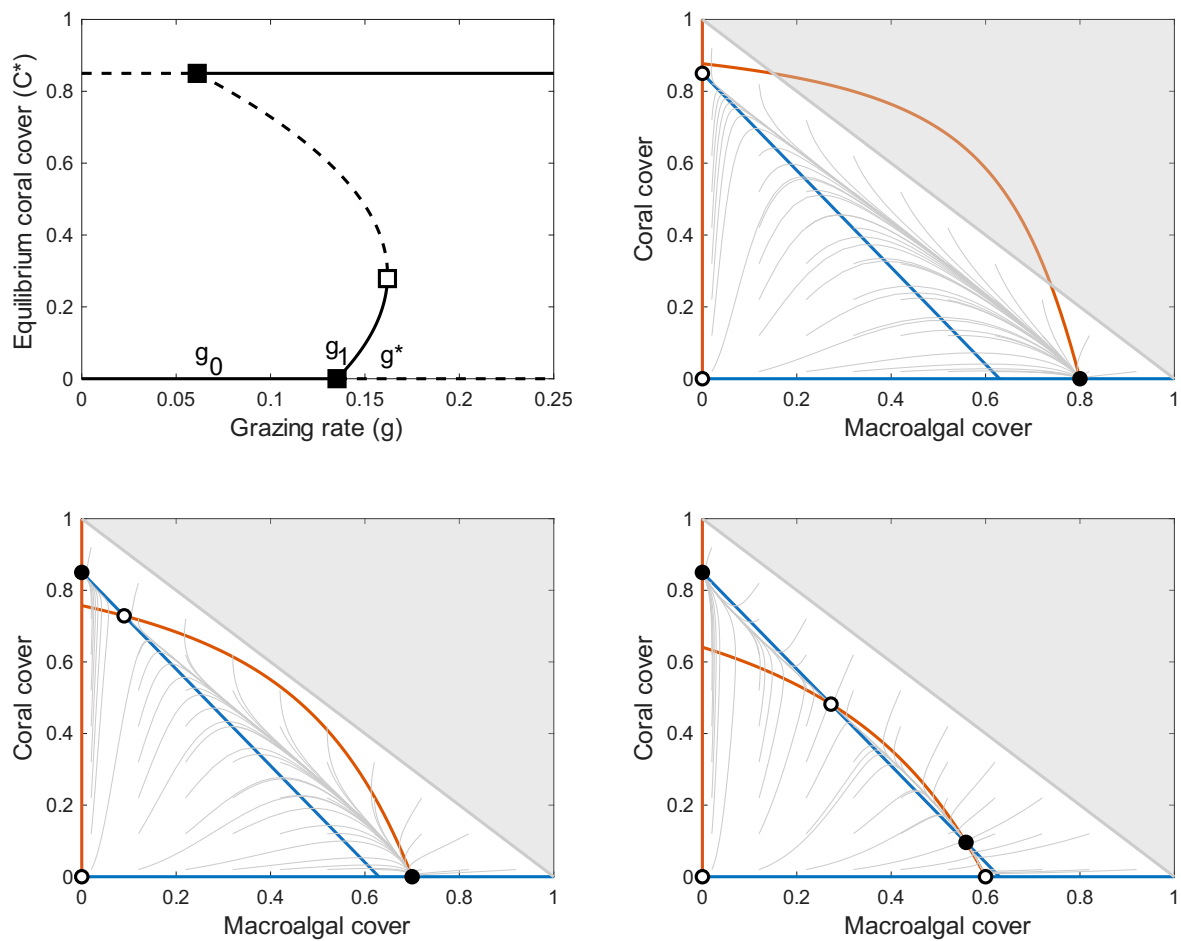
Figure 2 shows the nullclines and phase portraits in the low-, intermediate-, and high-grazing regimes of Theorem 4.3. Figure 3 shows the dependence of the interior equilibrium and the coral-only state on the crowding exponent, for  $\delta = 2$  and  $\delta = 5$ . Figure 4 shows the bifurcation diagram and phase portraits for a representative  $\delta = 1$  set with two interior equilibria. Figure 5 shows the bifurcation diagram and phase portrait for a  $\delta = 1.8$  set with three interior equilibria. Figure 6 maps the number of interior equilibria across the  $(\delta, g)$  plane, gathering the regimes of Figures 2–5.



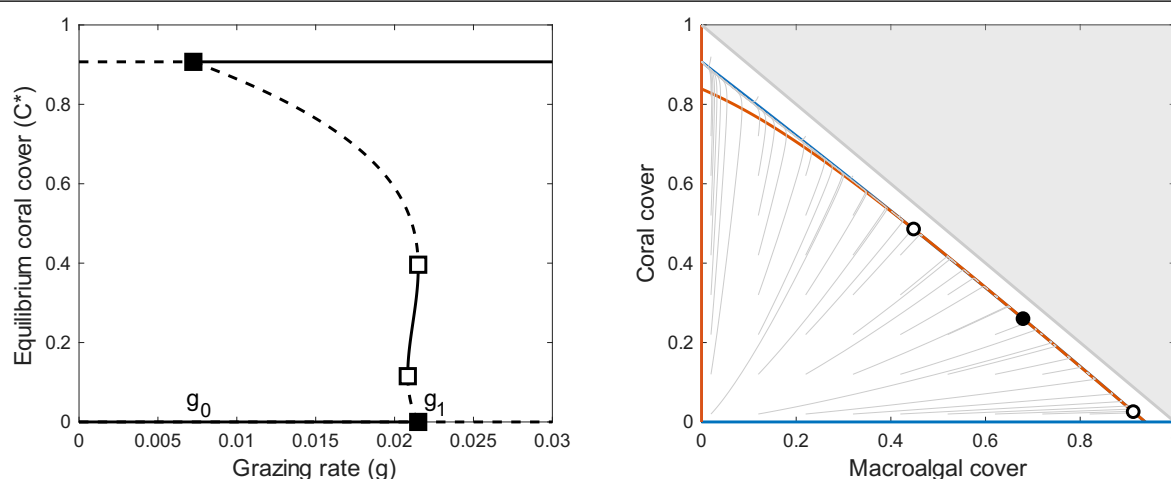
**Figure 2.** Nullclines, equilibria, and stability as the grazing rate increases ( $g = 0.05, 0.18$ , and  $0.35$  for the left, middle, and right panels, respectively). Orange curves are the  $\dot{x} = 0$  macroalgae nullclines, blue curves the  $\dot{y} = 0$  coral nullclines, and gray curves are sample trajectories. The gray triangle lies outside the domain. The crowding parameter is fixed at  $\delta = 2$ , and the remaining parameters  $(a, b, \gamma, m_0, d, n) = (0.3, 1, 0.8, 0.2, 0.02, 0.02)$  lie within the ranges of Table 1. Filled and open dots mark stable and unstable equilibria, respectively. The coral-only state  $C$  is stable for sufficiently high grazing, whereas the macroalgae-only state  $B$  is stable only for sufficiently low grazing. For intermediate grazing (middle panel), the interior equilibrium exists and is a saddle, producing local bistability. The trivial state  $O$  is unstable throughout. The three panels correspond to the low-, intermediate-, and high-grazing regimes of Theorem 4.3.



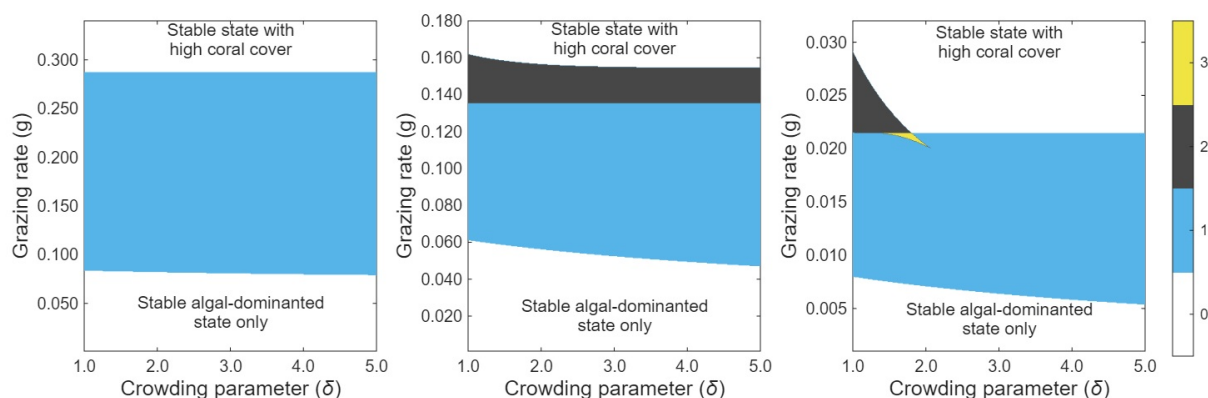
**Figure 3.** The effects of crowding when there is one interior equilibrium. (Left) Bifurcation diagram of the equilibrium coral cover ( $C^*$ ) versus the grazing rate  $g$ . Solid and dashed curves represent stable and unstable equilibria, respectively. The purple curves use  $\delta = 2$  and the red curves use  $\delta = 5$ . The horizontal curves represent  $y_C$  in the equilibrium  $C$ , which does not vary with  $g$  but increases as  $\delta$  increases. The interior equilibrium  $E^*$  shifts to the left as  $\delta$  increases. The remaining parameters are  $(a, b, \gamma, m_0, d, n) = (0.3, 1, 0.6, 0.15, 0.15, 0.02)$ . (Right) Summary of the values of the equilibria as  $\delta$  varies, with  $\delta = 2$  and  $\delta = 5$  indicated by dots matching the colors from the left figure. Here the grazing rate is fixed at  $g = 0.1$ .



**Figure 4.** Bifurcation and phase diagrams for the parameter set  $(a, b, \gamma, m_0, d, n, \delta) = (0.45, 0.9, 0.5, 0.05, 0.1, 0.05, 1)$  to summarize our findings when there are two interior equilibria. (Top left) Bifurcation diagram of the equilibrium coral cover ( $C^*$ ) versus grazing rate ( $g$ ). The solid and open squares indicate transcritical and saddle-node bifurcations, respectively, and  $g_0$ ,  $g_1$ , and  $g^*$  are labeled for clarity. The remaining panels are phase diagrams similar to those provided in Figure 2 but with this parameter set. The grazing rates used are 0.05 (top right), 0.1 (bottom left), and 0.15 (bottom right).



**Figure 5.** Bifurcation and phase diagrams for the parameter set  $(a, b, \gamma, m_0, d, n, \delta) = (0.035, 1, 0.82, 0.03, 0.075, 0.03, 1.8)$  to summarize our findings when there are three interior equilibria. (Left) Bifurcation diagram of the equilibrium coral cover ( $C^*$ ) versus grazing rate ( $g$ ). The solid and open squares indicate transcritical and saddle-node bifurcations, respectively, and  $g_0, g_1$  are labeled for clarity.  $g^*$  is not labeled because of its close proximity to  $g_1$ . The right panel is a phase diagram similar to those provided in Figure 2 but with this parameter set and a grazing rate ( $g$ ) of 0.0212. The marked bifurcations are determined numerically for this non-integer  $\delta$ . This parameter set is used as a mathematical illustration of the regime with three interior equilibria.



**Figure 6.** Parameter space showing the number of interior fixed points as the crowding parameter ( $\delta$ ) and grazing rate ( $g$ ) are varied. The panels summarize the dynamics from Figures 2–5 under different parameter regimes: left panel (parameters as in Figure 2), middle panel (Figure 4), and right panel (Figure 5). Note that the  $g$ -axis covers a smaller range in the right panel for visual clarity.

## 7. Conclusions

We have analyzed a coral-macroalgae competition model in which coral mortality increases with cover through a crowding term  $dC^\delta$ . The system has no nonconstant periodic solution in  $\Omega$  (Lemma 2.1), and its dynamics are organized by the grazing rate  $g$  through two ordered thresholds  $0 < g_0 < g_1 < \gamma - n$ : the coral-only state  $C$  is stable for  $g > g_0$  and the macroalgae-only state  $B$  for  $g < g_1$ , and both are stable on the intermediate range. As  $g$  crosses these thresholds,  $C$  and  $B$  exchange stability with a coexistence equilibrium through transcritical bifurcations (Theorems 5.3 and 5.1, the latter for  $\delta \in \mathbb{N}$ ). When the reduced function  $L$  is concave, as in the constant-mortality model of [8, 18], high grazing admits at most two coexistence states, a stable node and a saddle that collide in a saddle-node bifurcation at a third threshold  $g^*$  (Theorem 5.5). Intermediate crowding  $1 < \delta < 2$  makes  $L$  non-concave and can produce as many as three coexistence states (Proposition 4.7), so that the reef can be locally tristable, a regime beyond the reach of constant mortality. More broadly, the analysis shows how density-dependent crowding reshapes the coral-macroalgae dynamics across all crowding exponents: it alters the coral nullcline and the coexistence structure for every  $\delta > 0$ , whereas the possibility of three coexistence equilibria is established here in the intermediate regime  $1 < \delta < 2$ .

These results have direct ecological implications. We have characterized the local stability of the equilibria, while the phase portraits of Section 6 show sample trajectories for the parameter values specified there. As  $g$  decreases through  $g_0$ , the state  $C$  loses local stability, whereas  $B$  loses local stability as  $g$  increases through  $g_1$ . Hence  $g_1 - g_0$  is the width of the interval on which both boundary states are locally asymptotically stable. This local bistability underlies the hysteresis interpretation.

Beyond the two dominance states, the model also admits a mixed coral-macroalgae community. In the bistable regime, this interior equilibrium is a saddle. Under stronger grazing, it is joined by a stable node, and the two collide and disappear at  $g^*$  in the saddle-node bifurcation of Theorem 5.5, a further tipping point beyond which coral dominance is the only locally asymptotically stable state. Crowding adds one further possibility: for intermediate  $1 < \delta < 2$ , the mixed community can be stable alongside both dominance states, so that the reef is locally tristable.

## Use of AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

## Conflict of interest

The authors declare there is no conflict of interest.

## References

1. F. Moberg, C. Folke, Ecological goods and services of coral reef ecosystems, *Ecol. Econ.*, **29** (1999), 215–233. [https://doi.org/10.1016/S0921-8009\(99\)00009-9](https://doi.org/10.1016/S0921-8009(99)00009-9)
2. S. S. Ban, N. A. J. Graham, S. R. Connolly, Evidence for multiple stressor interactions and effects on coral reefs, *Glob. Change Biol.*, **20** (2014), 681–697. <https://doi.org/10.1111/gcb.12453>

3. A. R. Harborne, A. Rogers, Y. M. Bozec, P. J. Mumby, Multiple stressors and the functioning of coral reefs, *Annu. Rev. Mar. Sci.*, **9** (2017), 445–468. <https://doi.org/10.1146/annurev-marine-010816-060551>
4. T. P. Hughes, J. H. Connell, Multiple stressors on coral reefs: a long-term perspective, *Limnol. Oceanogr.*, **44** (1999), 932–940. [https://doi.org/10.4319/lo.1999.44.3\\_part\\_2.0932](https://doi.org/10.4319/lo.1999.44.3_part_2.0932)
5. D. R. Bellwood, T. P. Hughes, C. Folke, M. Nyström, Confronting the coral reef crisis, *Nature*, **429** (2004), 827–833. <https://doi.org/10.1038/nature02691>
6. T. P. Hughes, Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef, *Science*, **265** (1994), 1547–1551. <https://doi.org/10.1126/science.265.5178.1547>
7. N. Knowlton, Thresholds and multiple stable states in coral reef community dynamics, *Am. Zool.*, **32** (1992), 674–682.
8. P. J. Mumby, A. Hastings, H. J. Edwards, Thresholds and the resilience of Caribbean coral reefs, *Nature*, **450** (2007), 98–101. <https://doi.org/10.1038/nature06252>
9. H. A. Lessios, D. R. Robertson, J. D. Cubit, Spread of *Diadema* mass mortality through the Caribbean, *Science*, **226** (1984), 335–337. <https://doi.org/10.1126/science.226.4672.335>
10. J. C. Blackwood, A. Hastings, P. J. Mumby, The effect of fishing on hysteresis in Caribbean coral reefs, *Theor. Ecol.*, **5** (2012), 105–114. <https://doi.org/10.1007/s12080-010-0102-0>
11. T. Fung, R. M. Seymour, C. R. Johnson, Alternative stable states and phase shifts in coral reefs under anthropogenic stress, *Ecology*, **92** (2011), 967–982. <https://doi.org/10.1890/10-0378.1>
12. E. Bayraktarov, P. J. Stewart-Sinclair, S. Brisbane, L. Boström-Einarsson, M. I. Saunders, C. E. Lovelock, et al., Motivations, success, and cost of coral reef restoration, *Restor. Ecol.*, **27** (2019), 981–991. <https://doi.org/10.1111/rec.12977>
13. S. N. Zhao, S. L. Yuan, A coral reef benthic system with grazing intensity and immigrated macroalgae in deterministic and stochastic environments, *Math. Biosci. Eng.*, **19** (2022), 3449–3471. <https://doi.org/10.3934/mbe.2022159>
14. C. Xu, W. Chen, J. Hu, Deterministic and stochastic analysis of a coral reef ecosystem with grazed macroalgae, *Int. J. Biomath.*, **18** (2025), 2450039. <https://doi.org/10.1142/S1793524524500396>
15. C. Xu, Q. Chen, How environmental stochasticity can destroy the persistence of macroalgae in a coral reefs ecosystem, *Math. Biosci.*, **382** (2025), 109402. <https://doi.org/10.1016/j.mbs.2025.109402>
16. C. Xu, Y. Cai, L. Wan, Global dynamics of a coral reef model with grazing by coral-mediated herbivores, *J. Biol. Syst.*, (2026), 1–21. <https://doi.org/10.1142/S0218339026500300>
17. T. P. Hughes, Population dynamics based on individual size rather than age: a general model with a reef coral example, *Am. Nat.*, **123** (1984), 778–795. <https://doi.org/10.1086/284239>
18. X. Li, H. Wang, Z. Zhang, A. Hastings, Mathematical analysis of coral reef models, *J. Math. Anal. Appl.*, **416** (2014), 352–373. <https://doi.org/10.1016/j.jmaa.2014.02.053>
19. M. Tan, G. Lan, C. Wei, Mathematical insights into the influence of delay and external recruitment on coral–macroalgae system, *J. Franklin Inst.*, **361** (2024), 107329. <https://doi.org/10.1016/j.jfranklin.2024.107329>

20. C. Doropoulos, N. R. Evensen, L. A. Gómez-Lemos, R. C. Babcock, Density-dependent coral recruitment displays divergent responses during distinct early life-history stages, *R. Soc. Open Sci.*, **4** (2017), 170082. <https://doi.org/10.1098/rsos.170082>
21. J. S. Madin, A. H. Baird, M. Dornelas, S. R. Connolly, Mechanical vulnerability explains size-dependent mortality of reef corals, *Ecol. Lett.*, **17** (2014), 1008–1015. <https://doi.org/10.1111/ele.12306>
22. E. H. Meesters, M. Hilberman, E. Kardinaal, M. Keetman, M. de Vries, R. P. M. Bak, Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation, *Mar. Ecol. Prog. Ser.*, **209** (2001), 43–54. <https://doi.org/10.3354/meps209043>
23. L. Perko, *Differential Equations and Dynamical Systems*, 3<sup>rd</sup> edition, Springer, New York, 2001. <https://doi.org/10.1007/978-1-4613-0003-8>
24. Z. Zhang, T. Ding, W. Huang, Z. Dong, *Qualitative Theory of Differential Equations*, Translations of Mathematical Monographs, American Mathematical Society, Providence, RI, 1992. <https://doi.org/10.1090/mmono/101>

## Appendix

### Proof of Proposition 5.6

To prove Proposition 5.6, it remains, for each of the three nonhyperbolic equilibria, to apply the result of [23, Theorem 1, Section 2.11] (equivalently, [24, Theorem 7.1, Chap. 2]): Translate the equilibrium to the origin, write the transformed system in the form of the cited result, and read off the order  $m$  of the corresponding function  $\psi$ , with  $m = 2$  giving a saddle node. Throughout, a dot denotes differentiation with respect to the original time and a subscript  $\tau$  with respect to the rescaled time.

**(i) The macroalgae-only state  $B$  at  $g = g_1$ .** At  $g = g_1$ , the equilibrium  $B$  is nonhyperbolic, with eigenvalues  $\lambda_2 = 0$  and  $\lambda_1 < 0$ . Translating  $B$  to the origin by  $(X, Y) = (x - x_B, y)$ , with  $x_B$  as in (3.3), and expanding in a power series to fourth order, we obtain

$$\begin{aligned} \dot{X} = & \lambda_1 X + x_B(a - \gamma - g_1)Y + (a - \gamma - g_1)XY - \gamma X^2 - g_1 x_B Y^2 \\ & - g_1 X Y^2 - g_1 x_B Y^3 - g_1 X Y^3 - g_1 x_B Y^4 + P_1(X, Y), \end{aligned} \quad (\text{A.1a})$$

$$\dot{Y} = -(a + b)XY - bY^2 - dY^{\delta+1}, \quad (\text{A.1b})$$

where  $P_1(X, Y)$  is the power series collecting the terms  $X^i Y^j$  with  $i + j \geq 5$ . The linear change of variables

$$\begin{pmatrix} X \\ Y \end{pmatrix} = \begin{pmatrix} \frac{-x_B(a-\gamma-g_1)}{\lambda_1} & \frac{1}{\lambda_1} \\ 1 & 0 \end{pmatrix} \begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix}$$

brings the linear part of (A.1) to diagonal form, turning it into

$$\begin{aligned} \dot{\bar{x}} = & a_{1,1}\bar{x}\bar{y} + a_{2,0}\bar{x}^2 + a_{\delta+1,0}\bar{x}^{\delta+1}, \\ \dot{\bar{y}} = & b_{1,0}\bar{y} + b_{1,1}\bar{x}\bar{y} + b_{0,2}\bar{y}^2 + b_{2,0}\bar{x}^2 + b_{2,1}\bar{x}^2\bar{y} + b_{3,0}\bar{x}^3 + b_{\delta+1,0}\bar{x}^{\delta+1} + P_2(\bar{x}, \bar{y}), \end{aligned}$$

with

$$\begin{aligned} a_{1,1} &:= -\frac{a+b}{\lambda_1}, & a_{2,0} &:= \frac{x_B(a-\gamma-g_1)(a+b)}{\lambda_1} - b, & a_{\delta+1,0} &:= -d, \\ b_{1,0} &:= \lambda_1, & b_{0,2} &:= -\frac{\gamma}{\lambda_1}, & b_{2,1} &:= -g_1, \\ b_{1,1} &:= a-\gamma-g_1 + \frac{x_B(a-\gamma-g_1)(2\gamma-(a+b))}{\lambda_1}, \\ b_{2,0} &:= \frac{x_B^2(a-\gamma-g_1)^2(a+b-\gamma)}{\lambda_1} - x_B(a-\gamma-g_1)(a+b-\gamma-g_1) - \lambda_1 g_1 x_B, \\ b_{3,0} &:= g_1(x_B(a-\gamma-g_1) - \lambda_1 x_B), & b_{\delta+1,0} &:= -dx_B(a-\gamma-g_1), \end{aligned}$$

where  $P_2(\bar{x}, \bar{y})$  is a power series of order  $\geq 4$ . Rescaling time by  $\tau := \lambda_1 t$  then gives

$$\bar{x}_\tau = c_{1,1}\bar{x}\bar{y} + c_{2,0}\bar{x}^2 + c_{\delta+1,0}\bar{x}^{\delta+1}, \quad (\text{A.2a})$$

$$\bar{y}_\tau = \bar{y} + d_{1,1}\bar{x}\bar{y} + d_{0,2}\bar{y}^2 + d_{2,0}\bar{x}^2 + d_{2,1}\bar{x}^2\bar{y} + d_{3,0}\bar{x}^3 + d_{\delta+1,0}\bar{x}^{\delta+1} + P_3(\bar{x}, \bar{y}), \quad (\text{A.2b})$$

where  $c_{i,j} := \lambda_1^{-1}a_{i,j}$  and  $d_{i,j} := \lambda_1^{-1}b_{i,j}$ , and  $P_3(\bar{x}, \bar{y})$  is a power series of order  $\geq 4$ . For  $\delta \in \mathbb{N}$ , the system is thus in the normal form

$$\bar{x}_\tau = P(\bar{x}, \bar{y}), \quad \bar{y}_\tau = \bar{y} + Q(\bar{x}, \bar{y}), \quad (\text{A.3})$$

of [23, Theorem 1, Section 2.11], with  $P, Q$  analytic near the origin of order  $\geq 2$ . Set  $\mathcal{H}(\bar{x}, \bar{y}) := \bar{y} + Q(\bar{x}, \bar{y})$ . Since  $Q$  carries no constant or linear term,  $\mathcal{H}(0, 0) = 0$  and  $\mathcal{H}_{\bar{y}}(0, 0) = 1 \neq 0$ , so by the implicit function theorem  $\bar{y} + Q(\bar{x}, \bar{y}) = 0$  has near the origin a unique analytic solution  $\bar{y} = \phi(\bar{x})$  with  $\phi(\bar{x}) + Q(\bar{x}, \phi(\bar{x})) \equiv 0$  and  $\phi(0) = \phi'(0) = 0$ . Writing  $\phi(\bar{x}) = A_2\bar{x}^2 + A_3\bar{x}^3 + \dots$  and matching powers of  $\bar{x}$  in  $\mathcal{H}(\bar{x}, \phi(\bar{x})) = 0$  yields

$$\begin{aligned} 0 &= \mathcal{H}(\bar{x}, \phi(\bar{x})) = \phi(\bar{x}) + Q(\bar{x}, \phi(\bar{x})) \\ &= (A_2 + d_{2,0} + d_{\delta+1,0}\mathbb{1}_{\{\delta=1\}})\bar{x}^2 + (A_3 + d_{1,1}A_2 + d_{3,0} + d_{\delta+1,0}\mathbb{1}_{\{\delta=2\}})\bar{x}^3 + O(\bar{x}^4), \end{aligned}$$

as  $\bar{x} \rightarrow 0$ , where  $\mathbb{1}_{\{\delta=k\}} = 1$  if  $\delta = k$  and 0 otherwise, where  $A_2 = -(d_{2,0} + d_{\delta+1,0}\mathbb{1}_{\{\delta=1\}})$  and

$$\begin{aligned} A_3 &= -(d_{1,1}A_2 + d_{3,0} + d_{\delta+1,0}\mathbb{1}_{\{\delta=2\}}) \\ &= d_{1,1}(d_{2,0} + d_{\delta+1,0}\mathbb{1}_{\{\delta=1\}}) - d_{3,0} - d_{\delta+1,0}\mathbb{1}_{\{\delta=2\}}. \end{aligned}$$

Set  $\psi(\bar{x}) := P(\bar{x}, \phi(\bar{x}))$ , where  $P(\bar{x}, \bar{y}) = c_{1,1}\bar{x}\bar{y} + c_{2,0}\bar{x}^2 + c_{\delta+1,0}\bar{x}^{\delta+1}$  is the right-hand side of (A.2a). We obtain

$$\psi(\bar{x}) = (c_{2,0} + c_{\delta+1,0}\mathbb{1}_{\{\delta=1\}})\bar{x}^2 + (c_{1,1}A_2 + c_{\delta+1,0}\mathbb{1}_{\{\delta=2\}})\bar{x}^3 + O(\bar{x}^4)$$

as  $\bar{x} \rightarrow 0$ . The nondegeneracy condition (5.4) is equivalent, by  $\lambda_1 \neq 0$  and the identity

$$\frac{x_B(a-\gamma-g_1)(a+b)}{\lambda_1} = -\frac{(a-\gamma-g_1)(a+b)}{\gamma},$$

to  $c_{2,0} + c_{\delta+1,0}\mathbb{1}_{\{\delta=1\}} \neq 0$ , so that the leading term of  $\psi$  is quadratic. Hence  $m = 2$  and  $B$  is a saddle node by [23, Theorem 1, Section 2.11].

(ii) **The coral-only state  $C$  at  $g = g_0$ .** At  $g = g_0$ , the equilibrium  $C$  is nonhyperbolic, with eigenvalues  $\mu_1 = 0$  and  $\mu_2 < 0$ . Translating  $C$  to the origin by  $(X, Y) = (x, y - y_C)$  and expanding in a power series to fourth order, we obtain

$$\dot{X} = -\gamma X^2 + \left( (a - \gamma) - \frac{g_0}{(1 - y_C)^2} \right) XY - \frac{g_0}{(1 - y_C)^3} XY^2 - \frac{g_0}{(1 - y_C)^4} XY^3 + P_1(X, Y), \quad (\text{A.4a})$$

$$\begin{aligned} \dot{Y} = & -(a + b)y_C X + \mu_2 Y - (a + b)XY - \left( b + \frac{1}{2}d\delta(\delta + 1)y_C^{\delta-1} \right) Y^2 \\ & - \frac{1}{6}d(\delta - 1)\delta(\delta + 1)y_C^{\delta-2} Y^3 - \frac{1}{24}d(\delta - 2)(\delta - 1)\delta(\delta + 1)y_C^{\delta-3} Y^4 \\ & + Q_1(X, Y), \end{aligned} \quad (\text{A.4b})$$

where  $P_1(X, Y)$  and  $Q_1(X, Y)$  are power series collecting the terms  $X^i Y^j$  with  $i + j \geq 5$ . The change of variables  $\bar{x} = X$ ,  $\bar{y} = -(a + b)y_C X + \mu_2 Y$ ,  $\tau = \mu_2 t$  brings (A.4) into the normal form of [23, Eq (2), Section 2.11],

$$\bar{x}_\tau = P_2(\bar{x}, \bar{y}), \quad \bar{y}_\tau = \bar{y} + Q_2(\bar{x}, \bar{y}), \quad (\text{A.5})$$

with  $P_2$  and  $Q_2$  analytic near the origin of order  $\geq 2$ . Carrying out the substitution and expanding gives

$$\bar{x}_\tau = P_2(\bar{x}, \bar{y}) = A_{2,0}\bar{x}^2 + A_{1,1}\bar{x}\bar{y} + A_{3,0}\bar{x}^3 + A_{2,1}\bar{x}^2\bar{y} + A_{1,2}\bar{x}\bar{y}^2 + \dots, \quad (\text{A.6a})$$

where

$$\begin{aligned} A_{2,0} &:= \frac{(a + b)y_C}{\mu_2^2} \left( (a - \gamma) - \frac{g_0}{(1 - y_C)^2} \right) - \frac{\gamma}{\mu_2}, & A_{1,1} &:= \frac{1}{\mu_2^2} \left( (a - \gamma) - \frac{g_0}{(1 - y_C)^2} \right), \\ A_{3,0} &:= -\frac{(a + b)^2 y_C^2}{\mu_2^3} \frac{g_0}{(1 - y_C)^3}, & A_{2,1} &:= -\frac{2(a + b)y_C}{\mu_2^3} \frac{g_0}{(1 - y_C)^3}, \\ A_{1,2} &:= -\frac{1}{\mu_2^3} \frac{g_0}{(1 - y_C)^3}, \dots, \end{aligned}$$

and

$$\begin{aligned} \bar{y}_\tau &= \bar{y} + Q_2(\bar{x}, \bar{y}) \\ &= \bar{y} + B_{1,1}\bar{x}\bar{y} + B_{2,0}\bar{x}^2 + B_{0,2}\bar{y}^2 + B_{3,0}\bar{x}^3 + B_{0,3}\bar{y}^3 + B_{1,2}\bar{x}\bar{y}^2 + B_{2,1}\bar{x}^2\bar{y} + \dots, \end{aligned} \quad (\text{A.6b})$$

where

$$\begin{aligned}
 B_{1,1} &:= -\frac{(a+b)}{\mu_2} - \frac{(a+b)y_C}{\mu_2^2} \left( (a-\gamma) - \frac{g_0}{(1-y_C)^2} + 2b + d\delta(\delta+1)y_C^{\delta-1} \right), \\
 B_{2,0} &:= \frac{(a+b)y_C}{\mu_2} (\gamma - (a+b)) - \frac{(a+b)^2 y_C^2}{\mu_2^2} \left( (a-\gamma) - \frac{g_0}{(1-y_C)^2} + b + \frac{1}{2} d\delta(\delta+1)y_C^{\delta-1} \right), \\
 B_{0,2} &:= -\frac{d\delta(\delta+1)y_C^{\delta-1} + 2b}{2\mu_2^2}, \\
 B_{3,0} &:= \frac{(a+b)^3 y_C^3}{\mu_2^3} \left( \frac{g_0}{(1-y_C)^3} - \frac{d(\delta-1)\delta(\delta+1)y_C^{\delta-2}}{6} \right), \\
 B_{0,3} &:= -\frac{d(\delta-1)\delta(\delta+1)y_C^{\delta-2}}{6\mu_2^3}, \\
 B_{1,2} &:= \frac{(a+b)y_C}{\mu_2^3} \left( \frac{g_0}{(1-y_C)^3} - \frac{d(\delta-1)\delta(\delta+1)y_C^{\delta-2}}{2} \right), \\
 B_{2,1} &:= \frac{2(a+b)^2 y_C^2}{\mu_2^3} \left( \frac{g_0}{(1-y_C)^3} - \frac{d(\delta-1)\delta(\delta+1)y_C^{\delta-2}}{4} \right), \dots
 \end{aligned}$$

By the implicit function theorem there is, near  $\bar{x} = 0$ , a unique analytic  $\phi$  with  $\phi(\bar{x}) + Q_2(\bar{x}, \phi(\bar{x})) \equiv 0$ ,  $\phi(0) = 0$ , and  $\phi'(0) = 0$ , expanding as  $\phi(\bar{x}) = c_2 \bar{x}^2 + c_3 \bar{x}^3 + \dots$ . Since  $Q_2(\bar{x}, \bar{y}) = B_{1,1} \bar{x} \bar{y} + B_{2,0} \bar{x}^2 + B_{0,2} \bar{y}^2$  up to terms of degree  $\geq 3$ , inserting  $\bar{y} = \phi(\bar{x}) = c_2 \bar{x}^2 + O(\bar{x}^3)$  into  $\bar{y} + Q_2(\bar{x}, \bar{y}) = 0$  gives

$$0 = \phi(\bar{x}) + Q_2(\bar{x}, \phi(\bar{x})) = (c_2 + B_{2,0}) \bar{x}^2 + O(\bar{x}^3),$$

where  $c_2 = -B_{2,0}$  and  $\phi(\bar{x}) = -B_{2,0} \bar{x}^2 + O(\bar{x}^3)$ . The corresponding function  $\psi(\bar{x}) := P_2(\bar{x}, \phi(\bar{x}))$  then satisfies

$$\psi(\bar{x}) = A_{2,0} \bar{x}^2 + A_{1,1} \bar{x} \phi(\bar{x}) + A_{3,0} \bar{x}^3 + A_{2,1} \bar{x}^2 \phi(\bar{x}) + A_{1,2} \bar{x} \phi(\bar{x})^2 + \dots,$$

so that its leading term is  $A_{2,0} \bar{x}^2$ . The nondegeneracy condition (5.5) is equivalent, after rearrangement, to  $A_{2,0} \neq 0$ , so that  $m = 2$ . Hence  $C$  is a saddle node by [23, Theorem 1, Section 2.11].

**(iii) The interior equilibrium  $E_3^*$  at  $g = g^*$ .** At  $g = g^*$ , the interior equilibrium  $E_3^* = (x_3^*, y_3^*)$  is nonhyperbolic, with eigenvalues 0 and  $\nu_2 := \text{tr } J(E_3^*) < 0$  and with  $L'(y_3^*) = 0$  (Theorem 4.3). The right-hand side of (2.5) is real-analytic near  $E_3^*$  for every  $\delta > 0$ . Translating  $E_3^*$  to the origin by  $(X, Y) = (x - x_3^*, y - y_3^*)$  and expanding in a power series to fourth order, we obtain

$$\dot{X} = -x_3^* \gamma X + x_3^* \partial_y F(x_3^*, y_3^*) Y \tag{A.7a}$$

$$\begin{aligned}
 & - \gamma X^2 + \partial_y F(x_3^*, y_3^*) XY - \frac{g x_3^*}{(1-y_3^*)^3} Y^2 - \frac{g}{(1-y_3^*)^3} XY^2 \\
 & - \frac{g x_3^*}{(1-y_3^*)^4} Y^3 - \frac{g}{(1-y_3^*)^4} XY^3 - \frac{g x_3^*}{(1-y_3^*)^5} Y^4 + P_1(X, Y),
 \end{aligned}$$

$$\begin{aligned}
 \dot{Y} &= -(a+b)y_3^* X - y_3^* (b + \delta d(y_3^*)^{\delta-1}) Y \\
 & - (a+b)XY - \left( b + \frac{1}{2} \delta(\delta+1)d(y_3^*)^{\delta-1} \right) Y^2
 \end{aligned} \tag{A.7b}$$

$$\begin{aligned}
& -\frac{1}{6}\delta(\delta-1)(\delta+1)d(y_3^*)^{\delta-2}Y^3 \\
& -\frac{1}{24}\delta(\delta-2)(\delta-1)(\delta+1)d(y_3^*)^{\delta-3}Y^4 + Q_1(X, Y).
\end{aligned}$$

The functions  $P_1(X, Y)$  and  $Q_1(X, Y)$  are power series collecting the terms  $X^i Y^j$  with  $i + j \geq 5$ , the linear part is the Jacobian  $J(E_3^*)$  of (4.5), and  $\partial_y F(x_3^*, y_3^*) = (a - \gamma) - \frac{g}{(1-y_3^*)^2}$ ,  $\partial_y G(x_3^*, y_3^*) = -(b + \delta d(y_3^*)^{\delta-1})$ . The change of variables

$$\bar{x} = X - \frac{x_3^* \gamma}{(a+b)y_3^*} Y, \quad \bar{y} = -X - \frac{b + \delta d(y_3^*)^{\delta-1}}{a+b} Y, \quad \tau = v_2 t, \quad (\text{A.8})$$

with  $v_2 = -x_3^* \gamma - y_3^* (b + \delta d(y_3^*)^{\delta-1})$ , has  $Y$ -coefficients fixed by  $L'(y_3^*) = 0$ . Rearranging this equality via (4.7) gives  $\partial_y F(x_3^*, y_3^*) = -\frac{\gamma(b + \delta d(y_3^*)^{\delta-1})}{a+b}$ , hence  $\frac{\partial_y F(x_3^*, y_3^*)}{\partial_y G(x_3^*, y_3^*)} = \frac{\gamma}{a+b}$  on dividing by  $\partial_y G(x_3^*, y_3^*) = -(b + \delta d(y_3^*)^{\delta-1}) < 0$ , so that the constants in (A.8) are  $\kappa := \frac{x_3^* \gamma}{(a+b)y_3^*}$  and  $\sigma := \frac{1}{\gamma} \partial_y F(x_3^*, y_3^*) = -\frac{b + \delta d(y_3^*)^{\delta-1}}{a+b}$ . The change of variables (A.8) brings the system into the normal form  $\bar{x}_\tau = P_2(\bar{x}, \bar{y})$ ,  $\bar{y}_\tau = \bar{y} + Q_2(\bar{x}, \bar{y})$  of [23, Eq (2), Section 2.11], with  $P_2, Q_2$  analytic near the origin of order  $\geq 2$ . With  $\Delta := \sigma - \kappa = \frac{v_2}{(a+b)y_3^*}$ , carrying out the substitution and expanding give

$$\bar{x}_\tau = P_2(\bar{x}, \bar{y}) = \alpha_{2,0} \bar{x}^2 + \alpha_{1,1} \bar{x} \bar{y} + \alpha_{0,2} \bar{y}^2 + O(|(\bar{x}, \bar{y})|^3), \quad (\text{A.9a})$$

where

$$\begin{aligned}
\alpha_{2,0} &:= \frac{1}{v_2 \Delta^2} \left[ -\frac{g x_3^*}{(1-y_3^*)^3} + \kappa \left( (a+b)\sigma + b + \frac{1}{2} \delta (\delta+1) d(y_3^*)^{\delta-1} \right) \right], \\
\alpha_{1,1} &:= \frac{1}{v_2 \Delta^2} \left[ \Delta \partial_y F(x_3^*, y_3^*) - \frac{2g x_3^*}{(1-y_3^*)^3} + \kappa \left( (a+b)(\sigma + \kappa) + 2b + \delta (\delta+1) d(y_3^*)^{\delta-1} \right) \right], \\
\alpha_{0,2} &:= \frac{1}{v_2 \Delta^2} \left[ -\gamma \kappa^2 + \partial_y F(x_3^*, y_3^*) \kappa - \frac{g x_3^*}{(1-y_3^*)^3} + \kappa \left( (a+b)\kappa + b + \frac{1}{2} \delta (\delta+1) d(y_3^*)^{\delta-1} \right) \right].
\end{aligned}$$

Moreover,

$$\bar{y}_\tau = \bar{y} + Q_2(\bar{x}, \bar{y}) = \bar{y} + \beta_{2,0} \bar{x}^2 + \beta_{1,1} \bar{x} \bar{y} + \beta_{0,2} \bar{y}^2 + O(|(\bar{x}, \bar{y})|^3), \quad (\text{A.9b})$$

where

$$\begin{aligned}
\beta_{2,0} &:= \frac{1}{v_2 \Delta^2} \left[ \frac{g x_3^*}{(1-y_3^*)^3} - \sigma \left( (a+b)\sigma + b + \frac{1}{2} \delta (\delta+1) d(y_3^*)^{\delta-1} \right) \right], \\
\beta_{1,1} &:= \frac{1}{v_2 \Delta^2} \left[ -\Delta \partial_y F(x_3^*, y_3^*) + \frac{2g x_3^*}{(1-y_3^*)^3} - \sigma \left( (a+b)(\sigma + \kappa) + 2b + \delta (\delta+1) d(y_3^*)^{\delta-1} \right) \right], \\
\beta_{0,2} &:= \frac{1}{v_2 \Delta^2} \left[ \gamma \kappa^2 - \partial_y F(x_3^*, y_3^*) \kappa + \frac{g x_3^*}{(1-y_3^*)^3} - \sigma \left( (a+b)\kappa + b + \frac{1}{2} \delta (\delta+1) d(y_3^*)^{\delta-1} \right) \right].
\end{aligned}$$

Set  $\mathcal{H}(\bar{x}, \bar{y}) := \bar{y} + Q_2(\bar{x}, \bar{y})$ . Since  $Q_2$  has no constant or linear part,  $\mathcal{H}(0, 0) = 0$  and  $\mathcal{H}_{\bar{y}}(0, 0) = 1 \neq 0$ , so by the implicit function theorem  $\bar{y} + Q_2(\bar{x}, \bar{y}) = 0$  has near the origin a unique analytic solution

$\bar{y} = \phi(\bar{x})$  with  $\phi(\bar{x}) + Q_2(\bar{x}, \phi(\bar{x})) \equiv 0$  and  $\phi(0) = \phi'(0) = 0$ . Writing  $\phi(\bar{x}) = c_2\bar{x}^2 + c_3\bar{x}^3 + \dots$  and matching the  $\bar{x}^2$ -coefficients in  $\mathcal{H}(\bar{x}, \phi(\bar{x})) = 0$  gives

$$0 = (c_2 + \beta_{2,0})\bar{x}^2 + O(\bar{x}^3),$$

hence  $c_2 = -\beta_{2,0}$  and  $\phi(\bar{x}) = -\beta_{2,0}\bar{x}^2 + O(\bar{x}^3)$ . Introducing the function  $\psi(\bar{x}) := P_2(\bar{x}, \phi(\bar{x}))$ , we obtain the expansion

$$\psi(\bar{x}) = \alpha_{2,0}\bar{x}^2 + \alpha_{1,1}\bar{x}\phi(\bar{x}) + \alpha_{0,2}\phi(\bar{x})^2 + \dots,$$

so that the leading term of  $\psi$  is  $\alpha_{2,0}\bar{x}^2$ . It remains to check that  $\alpha_{2,0} \neq 0$ , which gives  $m = 2$ . Substituting  $\kappa$  and  $\sigma$  into  $\alpha_{2,0}$  and using (4.3) yields

$$\alpha_{2,0} = \frac{x_3^*}{2\nu_2\Delta^2} \left[ \frac{\gamma\delta(\delta-1)d(y_3^*)^{\delta-2}}{a+b} - \frac{2g}{(1-y_3^*)^3} \right] = \frac{x_3^*}{2\nu_2\Delta^2} L''(y_3^*) = \frac{(a+b)^2 x_3^* (y_3^*)^2}{2\nu_2^3} L''(y_3^*).$$

By Lemma 4.2,  $L''(y_3^*) < 0$ . Since  $x_3^*, y_3^* > 0$  while  $\nu_2^3 < 0$ , we have  $\alpha_{2,0} > 0$ . Hence  $m = 2$  and  $E_3^*$  is a saddle node by [23, Theorem 1, Section 2.11].



AIMS Press

©2026 the Author(s), licensee AIMS Press. This is an open access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0>)