



Modeling and analysis of stoichiometric two-patch consumer–resource systems

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Abstract

Ecological stoichiometry studies the balance of energy and multiple chemical elements in ecological interactions to establish how the laws of thermodynamics affect food-web dynamics and nutrient cycling in ecosystems. In this paper, we incorporate stoichiometric principles in a model with habitat heterogeneity and dispersal in order to better understand population growth dynamics. This model describes a situation where a resource is separated into two patches by a barrier. Growth of the resource in each patch is limited by soil fertility and self-crowding. The consumer disperses between the two patches and is not affected by the barrier. The consumer's growth is potentially limited by the phosphorus content of the acquired resource. Mathematical analysis of this model and simulations are performed.

Several biological implications, including an observed 'stoichiometric extinction effect,' are demonstrated with simulation where the stoichiometric mechanism appears to promote extinction in a patchy environment. This is in sharp contrast to the notion that stoichiometry mechanism promotes diversity in spatially homogeneous settings. Another important result is the rediscovery of a simple and plausible biological mechanism that generates local and global extinction. In this setting, which can be considered a spatially mediated form of apparent competition, the dispersal of the consumer from the rich patch can des the growth of the resource in the poor patch and in some situations can lead to the extinction of the resource in the poor patch.

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1. Introduction

All organisms are composed of several chemical elements such as carbon, nitrogen, and phosphorus. The relative abundance of these chemical elements can vary considerably among different species and across trophic levels [9–11]. However, at the same time, most studies of ecological consumer resource dynamics fail to consider such variations in chemical composition [21,30]. In particular, ecological models often emphasize how a single constituent, usually carbon (C) (which is generally considered to be the equivalent to energy) is transferred between the resource and consumer trophic levels. Implicitly, such models assume a chemical homogeneity within and among the various trophic levels. In reality, such chemical homogeneities are rarely observed. The issue of chemical heterogeneity is further complicated by the fact that autotrophic species (e.g., terrestrial plants, phytoplankton) exhibit significant intraspecific variation in chemical composition [6,7,19]. In sharp contrast to autotrophic species, the chemical composition of heterotrophic consumer species (e.g., terrestrial insects, aquatic arthropods and Crustacea) are often tightly regulated through homeostatic mechanisms [38]. Though such chemical heterogeneity has been long since recognized, it is only in recent years that the importance and the extent of these aspects have been studied by ecologists. This approach is often referred to as *ecological stoichiometry* [39]. In ecological stoichiometry, the primary focus is on how the relative abundance of essential elements such as carbon (C), nitrogen (N), and phosphorus (P) in organisms simultaneously affects ecological dynamics.

To motivate our employment of ecological stoichiometry, we begin with a stoichiometric observation from genetics and the physiology of organisms. Several studies have suggested that phosphorus-rich species appear to exhibit dramatically higher growth rates than their phosphorus-poor counterparts [9,33]. The growth rate variable is the *specific growth rate*, the exponential rate of change in mass per unit mass (μ). The specific growth rate may be reduced below its maximum value (μ_{\max}) by conditions affecting the abundance and/or quality of available resources. Phosphorus appears most critical because, in organisms lacking major mineral storage of P (as in bones), biomass C:N:P depends largely on the disproportionate demands for P-rich ribosomal RNA in rapidly growing cells [9]. This *growth rate hypothesis* provides a mechanism through which cellular allocation and ecological dynamics are connected. Our goal is to connect these ‘micro-scale’ phenomena to the study of ecosystems.

In a study by Helfield and Naiman [15], the effects of salmon-derived nitrogen on riparian forest growth were investigated. Isotopic analysis indicated that 22–24% of foliar nitrogen (N) in trees and shrubs is derived from spawning salmon. In turn, the riparian forests affected the quality of the instream habitat through shading, sediment, and nutrient filtration. Consequently, there is a positive feedback mechanism that in turn improves the spawning of the salmon. From these studies, it is clear that the role of a key nutrient, such as nitrogen (N) or phosphorous (P) should be considered in conjunction with carbon (C) in understanding species growth and dispersal dynamics [20,36,37].

In addition to this issue of the interplay between quantity and quality, biologists have been increasingly concerned with the unprecedented rate at which certain species have been declining and disappearing [29,34,35]. Despite the fact that the direct causes for the loss of biodiversity are

yet to be fully determined, several ecologists have noted that habitat fragmentation appears to be a significant factor in population dynamics that can lead to extinction. Habitat fragmentation and organism dispersal play a significant role in conservation and long term viability of endangered species. General conditions under which degrees of connectivity could synchronize local population fluctuations have been considered in recent studies [5,8]. Essential to the study of these fragmented habitats is the inclusion of conservation corridors that facilitate diffusion between the patches. A recurring question that appears in such investigations is whether a classical ‘rescue effect’ occurs and prevents extinction on the patches when migration is present. Recent studies (e.g., [28,41]) have demonstrated how attention to spatial structure and details of dispersal can yield new insights into ecological dynamics. Such spatial models may be particularly relevant for terrestrial systems, rather than the aquatic ones in which ecological stoichiometry was first developed. However, aquatic systems can and do feature a degree of habitat patchiness as well [22]. Most existing models only consider the interactions of food abundance and dispersal (e.g., [26]).

Alongside the work of these theoretical biologists, others have developed a variety of mathematical population models based on stoichiometry. Recently, Loladze et al. [31,32] reframed the issue of ecological stoichiometry using a more phenomenological model similar to those of the Lotka–Volterra type. This new framework, which we will refer to as a LKE model, facilitates further extensions to address several key ecological questions while retaining equation structures that are generally tractable for analysis. The LKE model and those proposed by Andersen [1,2], Grover [12], and Kooijman [24] all exhibit ‘indirect competition’ between two or more populations for phosphorus. Two species are said to compete indirectly if there exists a medium, such as predation by a consumer, that allows one of the species to become more efficient at finding or exploiting resources. This phenomenon has been widely observed both in nature and in laboratory experiments. Furthermore, these models feature complex dynamics with multiple positive equilibria featuring bistability and deterministic extinction. Expressing autotroph–herbivore interactions in stoichiometrically realistic terms is beginning to reveal quantitatively new and exciting dynamical behavior.

Although the issues of biological stoichiometry and habitat heterogeneity seem at best indirectly related, much might be gained by formulating models that capture key features of both subjects. We derive and conduct a rigorous mathematical analysis of such a model. Extensive numerical simulations and graphics are also provided.

In the construction of our model, we assume that our resource (plant) is divided into two patches. Both of these patches have a different soil phosphorus level. The growth rate of the resource is limited by its carrying capacity due to overcrowding and the amount of phosphorus that it can obtain from the soil. At the same time, a consumer species is distributed over the two-patch system. The rate at which the consumer acquires its food is carefully modeled using a divided time argument. We again employ stoichiometry by assuming that the growth of the consumer is potentially limited by the amount of phosphorus contained its food. One of our most important findings is an observed ‘stoichiometric extinction effect’. Fig. 5 suggests that although neither of the two patches alone can sustain the consumer, the consumer can persist if at least one of two patches is of sufficiently high quality in a two-patch system. Another important result from this work is the discovery of a simple and plausible biological mechanism that generates local extinction explained in Section 5.4: the dispersion of the consumer from the rich resource patch depresses the growth of the producer in the poor patch that in some situations can lead to the extinction of the resource in the poor patch.

This paper is organized as follows: In Section 2, we provide details for the formulation of our two-patch model. In Section 3, we present a preliminary analysis of the model. In Section 4, we conduct a systematic analysis of the one-patch model which reveals some novel dynamics. Section 5 deals with extinction scenarios of the two-patch model. Section 6 focuses on the existence and stability aspects of the positive steady states. The paper ends with a discussion section.

2. Derivation of the two-patch model

Let x_i be the resource density on patch i , and y be the density of the consumer found in both patches. We assume that the resource on each patch possesses logistic growth dynamics with intrinsic growth rate r_i and K_i as the autotroph's 'carrying capacity.' We first assume that the consumer's growth rate is proportional to the rate at which resource is consumed. With the above definitions, we arrive at

$$x'_i(t) = r_i x_i \left(1 - \frac{x_i}{K_i} \right) - f(x_1, x_2) y, \quad (2.1)$$

$$y'(t) = \epsilon f(x_1, x_2) y - d y. \quad (2.2)$$

Next, we derive a suitable candidate for the consumer's functional response, $f(x_1, x_2)$. We will follow a classical Holling time budget argument in the derivation of a suitable candidate for our functional response outlined in [18]. The consumer (predator) will be allowed to move freely between the two patches. The consumer's total time spent gathering food from the two patches, T , consists of four parts: the time spent searching in patch 1, T_{s_1} , the time spent searching in patch 2, T_{s_2} , the handling time for resource in patch 1, T_{h_1} , and the handling time for resource in patch 2, T_{h_2} . We now assume that the time that the consumer spends searching in patch i is proportional to its size, A_i . With proportionality constant κ , we have $T_{s_i} = \kappa A_i$. We can write

$$T_{s_1} = \frac{A_1}{A_2} T_{s_2} \equiv \beta T_{s_2}.$$

The expected total number of units of resource acquired by a consumer on patch i equals the product of the resource density x_i , searching efficiency, α_i , and the spent searching on the patch, T_{s_i} . Therefore, the total number of units of resource per consumer acquired in both patches = $\alpha_1 x_1 T_{s_1} + \alpha_2 x_2 T_{s_2}$. The total handling time on patch i is equal to the product of the total number of units of resource acquired per consumer and the expected handling time h_i per unit resource. Consequently, $T_{h_i} = \alpha_i h_i x_i T_{s_i}$. And, we have

$$T = T_{s_1} + T_{s_2} + \alpha_1 h_1 x_1 T_{s_1} + \alpha_2 h_2 x_2 T_{s_2} = (1 + \beta + \beta \alpha_1 h_1 x_1 + \alpha_2 h_2 x_2) T_{s_2}.$$

The number of units of resource acquired in the 1st patch per consumer per unit of time is

$$\frac{\alpha_1 x_1 T_{s_1}}{T} = \frac{\alpha_1 x_1 T_{s_1}}{(1 + \beta + \beta \alpha_1 h_1 x_1 + \alpha_2 h_2 x_2) T_{s_2}} = \frac{\alpha_1 \beta x_1}{1 + \beta + \beta \alpha_1 h_1 x_1 + \alpha_2 h_2 x_2}.$$

The number of units of resource acquired in the second patch per consumer per unit of time is

$$\frac{\alpha_2 x_2 T_{s_2}}{T} = \frac{\alpha_2 x_2 T_{s_2}}{(1 + \beta + \beta \alpha_1 h_1 x_1 + \alpha_2 h_2 x_2) T_{s_2}} = \frac{\alpha_2 x_2}{1 + \beta + \beta \alpha_1 h_1 x_1 + \alpha_2 h_2 x_2}.$$

Together, the total number of units of resource acquired in both patches per consumer per unit time is

$$f(x_1, x_2) = \frac{\alpha_1 \beta x_1 + \alpha_2 x_2}{1 + \beta + \beta \alpha_1 h_1 x_1 + \alpha_2 h_2 x_2}.$$

To simplify notation, let $c_1 = \beta \alpha_1$, $c_2 = \alpha_2$, $a = 1 + \beta$, $q_1 = h_1 c_1$ and $q_2 = h_2 c_2$.

With the above definitions, we arrive at the model

$$x_1'(t) = r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) - \frac{c_1 x_1 y}{a + q_1 x_1 + q_2 x_2}, \quad (2.3)$$

$$x_2'(t) = r_2 x_2 \left(1 - \frac{x_2}{K_2} \right) - \frac{c_2 x_2 y}{a + q_1 x_1 + q_2 x_2}, \quad (2.4)$$

$$y'(t) = \frac{\epsilon c_1 x_1 y}{a + q_1 x_1 + q_2 x_2} + \frac{\epsilon c_2 x_2 y}{a + q_1 x_1 + q_2 x_2} - dy. \quad (2.5)$$

Arditi and Michaelski [3] give several interpretations of this type of response including the incorporation of handling time and relative preferences between resources.

We will capture the ecological implications of biological stoichiometry in terms of ‘food quality,’ where one can interpret a species’ quality (as a resource relative to the stoichiometric demands of consumer species) in terms of the relative abundance of C (as an energy currency) and a nutrient element such as P. In contrast to the traditional C:X ratios found in most stoichiometric discussions, we will consider P:C. This formulation increases the mathematical tractability of our model, but does not alter the underlying biophysical framework. In incorporating stoichiometric properties into our model, we make the following assumptions:

Assumption 1. The soil of each resource patch has a fixed amount of phosphorus that is replenished as it is utilized by the resource.

We will refer to this phosphorus level, P_i (mg P/L) as the ‘richness’ of the soil.

Assumption 2. The consumer maintains a fixed P:C ratio, s . The plant has a minimum P:C ratio m , but can acquire excess P from the soil, in which its P:C ratio in patch i is P_i/x_i . Because of differences in consumer physiology from plant physiology, $s < m$.

Assumption 3. Growth of the plant depends on soil P, in that the carrying capacity of patch i can be P-limited. If growth is only limited by P, plant carrying capacity in patch i equals P_i/m . Under P-limitation, when x_i approaches carrying capacity, plant P:C approaches m .

Assumption 4. The plant’s carrying capacity can also be limited by light availability or by crowding, so that the carrying capacity is $\min(K_i, (P_i/m))$. Whenever x_i is less than the P-limited carrying capacity, the P:C ratio is P_i/x_i .

Urabe and Sterner [40] observed that algae density increased proportionately to increased light levels at moderately low light levels. However, as density further increased, the algae density

decreased due to overcrowding and self-shading. We consequently define K , as our autotrophic carrying capacity on patch i . Thus, $\min(K_i, (P_i - sy)/m)$, the minimum of the autotroph's self-crowding carrying capacity and maximum amount of resource density that can be produced given the available amount of phosphorus in the soil represents the more accurate measure of the carrying capacity. Since the total phosphorus stored in living consumers is often negligible when compared to the phosphorus stored in the soil, we have $P_i - sy \approx P_i$. Consequently, we will simply replace $(P_i - sy)/m$ with P_i/m .

Assumption 5. The plant's P:C ratio determines the trophic transfer efficiency of the consumer. Trophic transfer efficiency is at a minimum when plant P:C equals m . As plant P:C increases, trophic transfer efficiency increases to an upper bound of one. That is, the efficiency equals $\epsilon \min(1, (P_i/x_i)/s)$. Therefore, if the autotroph's P:C ratio is greater than or equal to s , then it constitutes optimal food for the consumer. If the autotroph's P:C ratio is less than s , then the consumer wastes the excess carbon (energy) in the ingested food. This lowers the transfer efficiency as measured in terms of carbon.

With the above five assumptions, the quantity m is analogous to 'structural P' or Q_{\min} that has been utilized in DEB and quota models, respectively. There is sufficient evidence to suggest that autotroph P:C can reach lower levels than consumer P:C under P-limitation. The assumption that plants acquire any and all available P implies that P uptake and recycling occurs at a relatively rapid rate with respect to the time scales in the model. Since the model does not include many of the complex processes concerning nutrient uptake and storage, we can view P_i as a 'supply parameter' rather than the explicit P density of the soil. However, since the model's population growth dynamics of the plants and consumers are slower than microbial nutrient cycling and fine root turnover, the assumptions that plants rapidly uptake P, recycle P, and acquire a pool of plant-available P is biologically reasonable.

Within this framework, we propose the following simple stoichiometric two-patch consumer–resource model:

$$x'_1(t) = r_1 x_1 \left(1 - \frac{x_1}{\min(K_1, (P_1/m))} \right) - \frac{c_1 x_1 y}{a + q_1 x_1 + q_2 x_2}, \quad (2.6)$$

$$x'_2(t) = r_2 x_2 \left(1 - \frac{x_2}{\min(K_2, (P_2/m))} \right) - \frac{c_2 x_2 y}{a + q_1 x_1 + q_2 x_2}, \quad (2.7)$$

$$y'(t) = \frac{\epsilon \min(1, (P_1/x_1)/s) c_1 x_1 y}{a + q_1 x_1 + q_2 x_2} + \frac{\epsilon \min(1, (P_2/x_2)/s) c_2 x_2 y}{a + q_1 x_1 + q_2 x_2} - dy. \quad (2.8)$$

where $(x_1(0), x_2(0), y(0)) > (0, 0, 0)$.

3. Preliminary analysis

For biological realism, we require that both $x_i(0) > 0$ and $y(0) > 0$ in the work that follows. To simplify notation, define (Table 1)

Table 1
Description of variables and parameters of the model

	Description	Units
<i>Variable</i>		
x_i	Density of resource on patch i	mg C/l
y_i	Density of consumer on patch i	mg C/l
<i>Parameter</i>		
P_i	Density of P in the soil on patch i	mg P/l
r_i	Intrinsic growth rate of the patches	day ⁻¹
d	Death rate of the consumer incl. loss and resp.	day ⁻¹
K_i	Constant carrying capacity	mg C/l
ϵ	Maximal growth efficiency of consumer	none
s	Fixed ratio of P to C in the consumer	mg P/mg C
a	Half saturation constant of the consumer	none
h_i	Handling time per unit of resource i	day ⁻¹
c_i	Searching efficiency of the consumer on patch i	(mg C/l day) ⁻¹
α_i	Searching efficiency of the consumer on patch i	(mg C/l day) ⁻¹
κ	Consumer's time spent per unit area of patch searching for food	day/area
q_i	Product of handling time and searching efficiency	(mg C/l) ⁻¹
m	Minimum ratio of P to C in the resource	mg P/mg C

$$\bar{k}_1 = \min(K_1, (P_1/m)) \quad \text{and} \quad \bar{k}_2 = \min(K_2, (P_2/m)).$$

For simplicity, we re-scale the above system by non-dimensionalizing the population variables and time with the following substitutions

$$t \rightarrow r_1 t, \quad x_1 \rightarrow \frac{x_1}{\bar{k}_1}, \quad x_2 \rightarrow \frac{x_2}{\bar{k}_2}, \quad y \rightarrow \frac{c_1}{r_1 a} y.$$

Then, the system takes the form

$$x'_1(t) = x_1 \left(1 - x_1 - \frac{y}{1 + \alpha_1 x_1 + \alpha_2 x_2} \right), \tag{3.1}$$

$$x'_2(t) = x_2 \left(\beta(1 - x_2) - \frac{\gamma y}{1 + \alpha_1 x_1 + \alpha_2 x_2} \right), \tag{3.2}$$

$$y'(t) = y \left(\frac{k_1 \min(x_1, p_1)}{1 + \alpha_1 x_1 + \alpha_2 x_2} + \frac{\gamma k_2 \min(x_2, p_2)}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \right), \tag{3.3}$$

where

$$\alpha_1 = \frac{q_1 \bar{k}_1}{a}, \quad \alpha_2 = \frac{q_2 \bar{k}_2}{a}, \quad \beta = \frac{r_2}{r_1}, \quad \gamma = \frac{c_2}{c_1}, \quad \delta = \frac{d}{r_1},$$

$$k_1 = \frac{\epsilon c_1 \bar{k}_1}{r_1 a}, \quad k_2 = \frac{\epsilon c_2 \bar{k}_2}{r_1 a}, \quad p_1 = \frac{P_1}{s \bar{k}_1}, \quad \text{and} \quad p_2 = \frac{P_2}{s \bar{k}_2}.$$

It should be noted that the dimensionless parameter β is the ratio of the intrinsic growth rates of the two patches, and the parameter δ can be regarded as the scaled death rate of the consumer.

$$x'_1(t) = x_1F_1(x_1, x_2, y),$$

$$x'_2(t) = x_2F_2(x_1, x_2, y),$$

$$y'(t) = yG(x_1, x_2),$$

where we define

$$F_1(x_1, x_2, y) = 1 - x_1 - y\Delta(x_1, x_2), \tag{3.4}$$

$$F_2(x_1, x_2, y) = \beta(1 - x_2) - \gamma y\Delta(x_1, x_2), \tag{3.5}$$

$$G(x_1, x_2) = (k_1 \min(x_1, p_1) + \gamma k_2 \min(x_2, p_2))\Delta - \delta, \tag{3.6}$$

where $\Delta(x_1, x_2) = (1 + \alpha_1x_1 + \alpha_2x_2)^{-1}$.

The Jacobian of the above system is given by

$$J(x_1, x_2, y) = (a_{ij})_{3 \times 3} = \begin{pmatrix} F_1 + \frac{\partial F_1}{\partial x_1}x_1 & \frac{\partial F_1}{\partial x_2}x_1 & \frac{\partial F_1}{\partial y}x_1 \\ \frac{\partial F_2}{\partial x_1}x_2 & F_2 + \frac{\partial F_2}{\partial x_2}x_2 & \frac{\partial F_2}{\partial y}x_2 \\ \frac{\partial G}{\partial x_1}y & \frac{\partial G}{\partial x_2}y & G + \frac{\partial G}{\partial y}y \end{pmatrix}.$$

Our partial derivatives are

$$\frac{\partial F_1}{\partial x_1} = -1 + \alpha_1y\Delta^2, \quad \frac{\partial F_1}{\partial x_2} = \alpha_2y\Delta^2, \quad \frac{\partial F_1}{\partial y} = -\Delta,$$

$$\frac{\partial F_2}{\partial x_1} = \gamma\alpha_1y\Delta^2, \quad \frac{\partial F_2}{\partial x_2} = -\beta + \gamma\alpha_2y\Delta^2, \quad \frac{\partial F_2}{\partial y} = -\gamma\Delta,$$

$$\frac{\partial G}{\partial x_1} = \begin{cases} k_1 + (k_1\alpha_2 - \gamma k_2\alpha_1)x_2\Delta^2 & \text{if } x_1 < p_1 \text{ and } x_2 < p_2, \\ -\alpha_1(k_1p_1 + \gamma k_2x_2)\Delta^2 & \text{if } x_1 > p_1 \text{ and } x_2 < p_2, \\ k_1(1 + \alpha_2x_2) - \gamma k_2\alpha_1p_2\Delta^2 & \text{if } x_1 < p_1 \text{ and } x_2 > p_2, \\ -\alpha_1(k_1p_1 + \gamma k_2p_2)\Delta^2 & \text{if } x_1 > p_1 \text{ and } x_2 > p_2, \end{cases}$$

$$\frac{\partial G}{\partial x_2} = \begin{cases} (\gamma k_2 - (k_1\alpha_2 - \gamma k_2\alpha_1)x_1)\Delta^2 & \text{if } x_1 < p_1 \text{ and } x_2 < p_2, \\ (\gamma k_2(1 + \alpha_1x_1) - \alpha_2k_1p_1)\Delta^2 & \text{if } x_1 > p_1 \text{ and } x_2 < p_2, \\ (-\alpha_2(k_1x_1 + \gamma k_2p_2))\Delta^2 & \text{if } x_1 < p_1 \text{ and } x_2 > p_2, \\ (-\alpha_2(k_1p_1 + \gamma k_2p_2))\Delta^2 & \text{if } x_1 > p_1 \text{ and } x_2 > p_2, \end{cases}$$

$$\frac{\partial G}{\partial y} = 0.$$

Before beginning a detailed analysis of our system, we mention some preliminary results such as positivity, boundedness, existence, and uniqueness.

Theorem 1. For $x_1(0) > 0, x_2(0) > 0, y(0) > 0$, (3.1)–(3.3) has a unique solution defined for all $t \geq 0$ that is positive and bounded for all $t \geq 0$. Furthermore, for any $0 < \epsilon_1, \epsilon_2 < 1$, $x_1(t) < 1 + \epsilon_1$ and $x_2(t) < 1 + \epsilon_2$ for sufficiently large $t > 0$.

The proof of Theorem 1 can be found in Appendix A.

As a result of the re-scaling of the variables of our system and the definition of new parameters from old, some observations should be made. First of all, with regards to phosphorus content, we have the following equivalent expressions:

$$p_i = \frac{P_i}{s\bar{k}_i} = \frac{P_i}{s \min(K_i, P_i/m)} = \frac{1}{s \min\left(\frac{K_i}{P_i}, \frac{1}{m}\right)}.$$

To facilitate the subsequent analysis, we have two definitions.

Definition 1. The condition $p_i > 1$ will be referred to as the *absolute good quality* scenario since we can rewrite the condition $p_i > 1$ as

$$\max\left(\frac{P_i}{K_i}, m\right) > s.$$

This condition is equivalent to the maximum of the P:C ratio of the soil's phosphorous content (mg P) to the resources carrying capacity (mg C) and the resources homeostatic P:C ratio being greater than the P:C ratio of the consumer.

Definition 2. In the analysis that follows, we will determine and discuss positive resource equilibria, x_i^* . We will refer to the case $x_i^* > p_i$, where $i = 1, 2$, as patch i as having *relatively poor quality*. And, cases where $x_i^* < p_i$ and $x_j^* > p_j$ where $i \neq j$ will be referred to as *mixed quality*. Finally, the case described by $x_i^* < p_i$, where $i = 1, 2$, will be referred to as patches having *relatively good quality*.

4. Analysis of the one-patch model

Before we begin a more detailed analysis of our stoichiometric two-patch system, we will investigate the one patch version of our model.

If we set $x_2 = 0$ in (3.1)–(3.3) and drop subscripts, our two-patch system reduces to the system:

$$x'(t) = x \left(1 - x - \frac{y}{1 + \alpha x} \right) = xF(x, y), \quad (4.1)$$

$$y'(t) = y \left(\frac{k \min(x, p)}{1 + \alpha x} - \delta \right) = yG(x), \quad (4.2)$$

where

$$F(x, y) = 1 - x - y\Delta(x), \quad (4.3)$$

$$G(x) = k \min(x, p)\Delta(x) - \delta, \tag{4.4}$$

and $\Delta(x) = (1 + \alpha x)^{-1}$.

4.1. Equilibria and their local stability

The total extinction equilibrium, $E_0 = (0, 0)$, always exists and is an unstable saddle. For $E_1 = (1, 0)$, the consumer-free equilibrium, we have two cases to consider.

Case 1: If $x^* = 1 < p$ then $E_{100} = (1, 0)$, is locally asymptotically stable (L.A.S.) if and only if $k(1 + \alpha)^{-1} < \delta$.

Case 2: If $x^* = 1 > p$ then $E_{10} = (1, 0)$, is L.A.S. if $kp(1 + \alpha)^{-1} < \delta$.

Up to two other equilibria may exist. These equilibria are solutions of the system

$$k \min(x, p) - \delta\alpha x = \delta, \quad y = (1 - x)\Delta^{-1}.$$

We have the following theorem regarding their existence.

Theorem 2. *If p satisfies $0 < \frac{\delta}{k - \delta\alpha} \leq p \leq \frac{kp - \delta}{\alpha\delta} < 1$, then the one-patch model has two positive equilibria. And, if $p \leq \frac{kp - \delta}{\alpha\delta} \leq \min\{\frac{\delta}{k - \delta\alpha}, 1\}$, or $\max\{0, \frac{kp - \delta}{\alpha\delta}\} \leq \frac{\delta}{k - \alpha\delta} \leq \min\{1, p\}$ then the one-patch model has exactly one positive equilibrium.*

Proof. Let (x^*, y^*) be a potential positive equilibrium. Clearly, the number of solutions of the equation $k \min(x, p) - \delta\alpha x = \delta$ depend on the parameter p . We have the following cases to consider:

Case 1: If $x^* < p$ then $x_{\text{good}}^* \equiv \frac{\delta}{k - \delta\alpha}$. We will refer to this equilibrium as the relatively good quality equilibrium.

Case 2: If $p \leq x^*$ then $x_{\text{poor}}^* \equiv \frac{kp - \delta}{\alpha\delta}$. This equilibrium will be referred to as the relatively poor quality equilibrium.

Thus, we have $x_{\text{good}}^* \leq p \leq x_{\text{poor}}^*$ implying the existence of two positive equilibria. If $p \leq x_{\text{poor}}^* \leq \min\{1, x_{\text{good}}^*\}$, then only (x_{poor}^*, y^*) exists. Similarly, if $\max\{Q, x_{\text{poor}}^*\} \leq x_{\text{good}}^* \leq \min\{1, p\}$ then only (x_{good}^*, y^*) exists. \square

We will now state and prove a theorem concerning their local stability.

Theorem 3

(i) $x_{\text{good}}^* = \frac{\delta}{k - \delta\alpha}$ is L.A.S. if $\delta < \frac{(\alpha - 1)k}{\alpha(1 + \alpha)}$.

(ii) $x_{\text{poor}}^* = \frac{kp - \delta}{\alpha\delta}$ is an unstable saddle.

Proof. At any positive equilibrium (x^*, y^*) , the Jacobian of our system is given by

$$J(x^*, y^*) = (a_{ij})_{2 \times 2} = \begin{pmatrix} \frac{\partial F}{\partial x}(x^*, y^*)x^* & \frac{\partial F}{\partial x}(x^*, y^*)y^* \\ \frac{\partial G}{\partial x}(x^*)y^* & \frac{\partial G}{\partial y}(x^*)y^* \end{pmatrix}.$$

Now, our partial derivatives are

$$\frac{\partial F}{\partial x} = -1 + \alpha y \Delta^2, \quad \frac{\partial F}{\partial y} = -\Delta, \quad \frac{\partial G}{\partial x} = \begin{cases} k\Delta^2 & \text{if } x < p, \\ -\alpha k p \Delta^2 & \text{if } x > p, \end{cases} \quad \frac{\partial G}{\partial y} = 0.$$

The characteristic polynomial corresponding to the above Jacobian is

$$\Psi(\lambda) = \lambda^2 + \left(-x \frac{\partial F}{\partial x}\right)\lambda - xy \frac{\partial F}{\partial y} \frac{\partial G}{\partial x} = 0$$

evaluated at (x^*, y^*) .

We will abbreviate the above as $\Psi(\lambda) = \lambda^2 + a_1\lambda + a_2$. For local stability of $E_* = (x^*, y^*)$, we need by the Routh–Hurwitz criteria that $a_1 > 0$ and $a_2 > 0$.

For the good quality case $x^* = x_{\text{good}}^* < p$ we have

$$a_1 = \frac{\partial F}{\partial x}(x^*, y^*)x^* = -x^* + \frac{\alpha y^* x^*}{(1 + \alpha x^*)^2},$$

$$a_2 = -x^* y^* \frac{\partial F}{\partial y}(x^*, y^*) \frac{\partial G}{\partial x}(x^*, y^*) = \frac{kx^* y^*}{(1 + \alpha x^*)^3} > 0.$$

Thus, in this case, we always have $a_2 > 0$. And, the condition $a_1 > 0$ is equivalent to requiring $x_{\text{good}}^* < \frac{\alpha-1}{2\alpha}$. And, this inequality can be rewritten as $\delta < \frac{(\alpha-1)k}{\alpha(1+\alpha)}$.

For the poor quality case $x^* = x_{\text{poor}}^* > p$ we have

$$a_1 = \frac{\partial F}{\partial x}(x^*, y^*)x^* = -x^* + \frac{\alpha y^* x^*}{(1 + \alpha x^*)^2},$$

$$a_2 = -x^* y^* \frac{\partial F}{\partial y}(x^*, y^*) \frac{\partial G}{\partial x}(x^*, y^*) = \frac{-\alpha k p x^* y^*}{(1 + \alpha x^*)^3} < 0.$$

Thus, in this case, we always have $a_2 < 0$. Thus, this poor quality positive equilibrium is an unstable saddle. \square

Fig. 1 indicates that the one-patch model exhibits multiple attractors. Consequently, bistability is observed in the stoichiometric one-patch model. This bistability property will also be inherited by the stoichiometric two-patch model in the work that follows. The simulation confirms that as we increase p from 0.49 to the value $p = 0.5$ a single positive (and locally asymptotically stable) equilibrium is born. If we increase p from 0.5 we see the coexistence of two positive equilibria. The left one of these equilibria is L.A.S while the right one equilibria is unstable. As we continue increasing p , the right, unstable, positive equilibrium merges with the boundary equilibrium $(1, 0)$, resulting in a possible global attractor consisting of the left positive equilibrium.

4.2. Limit cycles in the one-patch system

For the two-patch model, we have shown that solutions satisfy $x_i(t) \leq 1 + \epsilon_i$ where $\epsilon_i > 0$ for sufficiently large t . For the one-patch model, this is equivalent to $x(t) \leq 1 + \epsilon$ where $\epsilon > 0$ for sufficiently large t . Thus, if $p \geq 1$, then for sufficiently large t , we have $\min(x, p) \leq \min(x, 1) \leq x$. Therefore, for $p \geq 1$ we have the non-stoichiometric (conventional) system.

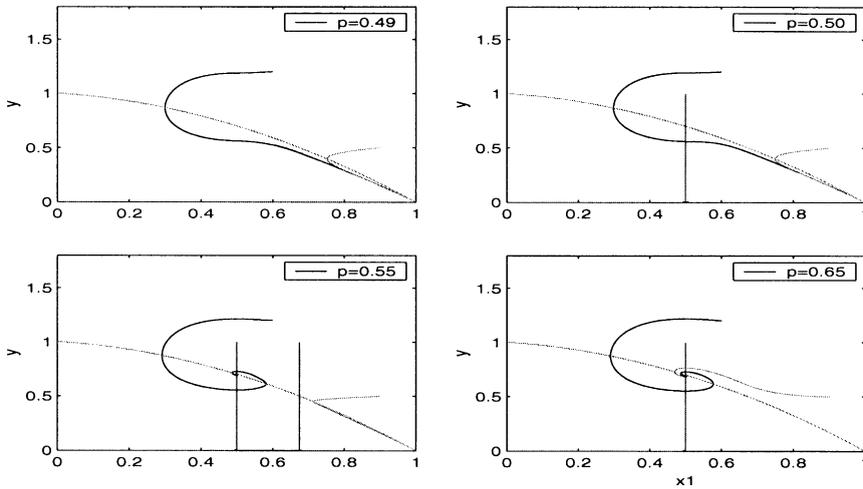


Fig. 1. One-patch nullclines (for the parameter values: $\alpha = 0.8$, $\delta = 0.5$ and $k = 1.4$ for four different values of the quality parameter p).

$$x'(t) = x \left(1 - x - \frac{y}{1 + \alpha x} \right) = P(x, y), \tag{4.5}$$

$$y'(t) = y \left(\frac{kx}{1 + \alpha x} - \delta \right) = Q(x, y). \tag{4.6}$$

Under assumption that $p \geq 1$, we observe that P and Q are continuously differentiable on R_2^+ . We are now ready to prove a theorem regarding conditions on parameters that excludes the existence of limit cycles in the one-patch model [16,25].

Theorem 4. *If x^* exists, $p \geq 1$, and $\alpha < 1$, then there are no limit cycles in the one-patch system given by (4.1) and (4.2).*

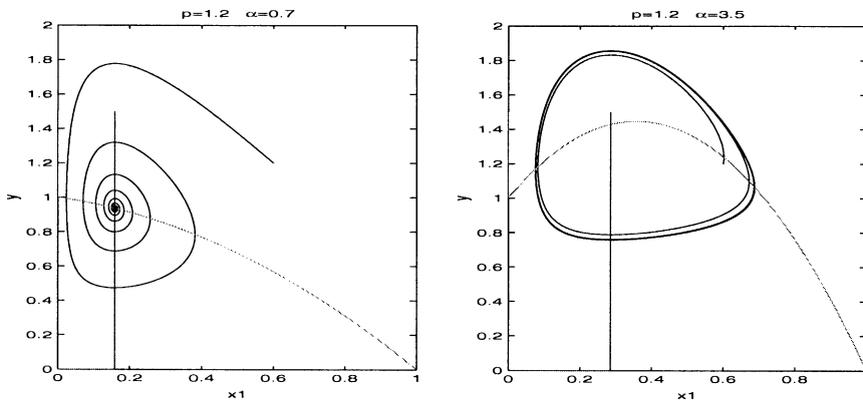


Fig. 2. One-patch equilibria and limit cycles (for the parameter values: $\delta = 0.5$ and $k = 1.4$ while varying the parameters p and α).

Proof. Consider the following continuously differentiable Dulac function.

$$B(x, y) = \left(\frac{1 + \alpha x}{x} \right) y^{\sigma-1}, \quad \sigma = \frac{1 - \alpha}{k - \delta \alpha}.$$

If $p > 1$ then,

$$\begin{aligned} \Omega(x, y) &= \frac{\partial}{\partial x}(BP) + \frac{\partial}{\partial y}(BQ) \\ &= -\frac{y^{\sigma-1}}{x} ((1 - \alpha)x + 2\alpha x^2 - \sigma(kx - \delta(1 + \alpha x))) \\ &\leq -\frac{y^{\sigma-1}}{x} \left(2\alpha x^2 + \left(\frac{1 - \alpha}{k - \delta \alpha} \right) \delta \right) \\ &= -\frac{y^{\sigma-1}}{x} (2\alpha x^2 + (1 - \alpha)x^*). \end{aligned}$$

Thus, $\Omega(x, y) < 0$, if $p \geq 1$, $\alpha < 1$, and x^* exists.

By the Bendixon–Dulac criterion (since $\Omega(x, y)$ does not change sign) the one-patch system given by (4.1) and (4.2) has no limit cycles if $p \geq 1$, $\alpha \geq 1$, and x^* exists. \square

Fig. 2 illustrates the above result.

5. Extinction dynamics

This section deals with the boundary dynamics of our system. We will first study the local stability analysis of the consumer free equilibria. In addition, several theorems prescribing conditions for global stability of this equilibrium are stated. The second subsection deals with the bistability aspect of the model. In the third subsection, we look at the stoichiometry mediated extinction and persistence of the consumer population. In the last subsection we study the local stability of equilibria with one patch extinct.

Before we begin our analysis of the equilibria for this system, we first notice that any equilibria for our model fall into one of the following four cases outlined in Table 2.

5.1. Consumer-free boundary dynamics

Our stoichiometric two-patch system (3.1)–(3.3) has three consumer-free equilibria that always exist but are unstable saddles and as such are unlikely to occur. We shall denote these as $E_{000} = (0, 0, 0)$, $E_{100} = (1, 0, 0)$, $E_{010} = (0, 1, 0)$. Since the origin, $E_{000} = (0, 0, 0)$, is always a saddle node, there cannot be total extinction of the system for positive initial conditions $x_1(0) > 0$, $x_2(0) > 0$, and $y(0) > 0$. Furthermore, in the absence of the consumer, both resource patches will survive regardless of how poor their quality may be.

Although the fourth consumer-free equilibrium, $E_{110} = (1, 1, 0)$ always exists, its stability varies for various parameters. The following theorem gives precise conditions for this equilibrium’s local asymptotic stability. For convenience, we define $D \equiv \Delta(1, 1) = (1 + \alpha_1 + \alpha_2)^{-1}$.

Table 2
Four cases for equilibria in the two-patch model

Case	Conditions on x_i^*
1	$x_1^* < p_1$ and $x_2^* < p_2$
2	$x_1^* > p_1$ and $x_2^* < p_2$
3	$x_1^* < p_1$ and $x_2^* > p_2$
4	$x_1^* > p_1$ and $x_2^* > p_2$

Theorem 5. *The equilibrium $E_{110} = (1, 1, 0)$ is locally asymptotically stable if and only if exactly one of the following cases hold*

- Case 1. $x_1^* = 1 \leq p_1, x_2^* = 1 \leq p_2$, and $(k_1 + \gamma k_2)D < \delta$.
- Case 2. $x_1^* = 1 > p_1, x_2^* = 1 \leq p_2$, and $(k_1 p_1 + \gamma k_2)D < \delta$.
- Case 3. $x_1^* = 1 \leq p_1, x_2^* = 1 > p_2$, and $(k_1 + \gamma k_2 p_2)D < \delta$.
- Case 4. $x_1^* = 1 > p_1, x_2^* = 1 > p_2$, and $(k_1 p_1 + \gamma k_2 p_2)D < \delta$.

The proof of Theorem 5 consists of straightforward analysis of Jacobians at E_{110} in these specific cases. Our next theorem extends this local stability result globally if the death rate does not exceed a specific value. This value and its significance are described below.

Theorem 6. *If $\delta \geq k_1 \min\left(1, p_1, \frac{1}{\alpha_1}\right) + \gamma k_2 \min\left(1, p_2, \frac{1}{\alpha_2}\right)$, then*

$$\lim_{t \rightarrow \infty} (x_1(t), x_2(t), y(t)) = (1, 1, 0).$$

The proof of this theorem can be found in Appendix B. This result states that the consumer goes extinct if it cannot acquire resources from both patches of sufficient quality (phosphorus content) at a sufficiently high rate.

In the case of both resource patches having absolute high quality, i.e. $p_i \geq 1$, we can get such a sharp result if we choose parameters that identify the patches as equivalent under predation. The proof of this theorem can be found in Appendix C.

Theorem 7. *Let $(x_1(0), x_2(0)) \in [0, 1] \times [0, 1]$. Assume $p_1 \geq 1$ and $p_2 \geq 1$. If*

- (i) $\frac{k_1}{\alpha_1} = \frac{\gamma k_2}{\alpha_2}$, and
- (ii) $\frac{k_1 + \gamma k_2}{1 + \alpha_1 + \alpha_2} - \delta < 0$, then,

$$\lim_{t \rightarrow \infty} (x_1(t), x_2(t), y(t)) = (1, 1, 0).$$

We observe that under absolutely good quality, we can obtain a global stability result for our consumer-free equilibrium by assuring that its death rate is sufficiently large.

Theorem 8. *Suppose that $p_1 \geq 1$ and $p_2 \geq 1$. Let $\bar{\sigma} = \max_{(x_1, x_2) \in [0, 1] \times [0, 1]} \left(\frac{k_1 x_1 + \gamma k_2 x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta\right)$. If $\bar{\sigma} < 0$, then $\lim_{t \rightarrow \infty} y(t) = 0$.*

Proof. First, we recall that $\lim_{t \rightarrow \infty} \sup x_i(t) \leq 1$, we have that $x_1(t) < 1 + \epsilon_1$ for large $t > t_1$ and $x_2(t) < 1 + \epsilon_2$ for large $t > t_2$. And, from (2.3) for sufficiently large $t > \max\{t_1, t_2\}$ we have

$$\begin{aligned}
 y' &= y \left(\frac{k_1 \min(x_1, p_1) + \gamma k_2 \min(x_2, p_2)}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \right) \\
 &\leq y \left(\frac{k_1 \min(x_1, 1) + \gamma k_2 \min(x_2, 1)}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \right) \\
 &\leq y \left(\frac{k_1 x_1 + \gamma k_2 x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \right) \\
 &< \bar{\sigma} y
 \end{aligned}$$

since $\bar{\sigma} = \max_{(x_1, x_2) \in [0,1] \times [0,1]} \left(\frac{k_1 x_1 + \gamma k_2 x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \right)$.

Now, since $y' < \bar{\sigma} y$ and $\bar{\sigma} < 0$, then $\lim_{t \rightarrow \infty} y(t) = 0$. \square

The following proposition provides explicit conditions for the above theorem.

Proposition 1. Suppose that $p_1 \geq 1$ and $p_2 \geq 1$. Let $\bar{\sigma} = \max_{(x_1, x_2) \in [0,1] \times [0,1]} \left(\frac{k_1 x_1 + \gamma k_2 x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \right)$.

- (i) If $k_1 + \alpha_2 k_1 - \alpha_1 \gamma k_2 < 0$ and $(1 + \alpha_1) \gamma k_2 > (1 + \alpha_2) k_1$ then $\bar{\sigma} = \frac{\gamma k_2}{1 + \alpha_2} - \delta$.
- (ii) If $\gamma k_2 + \alpha_1 \gamma k_2 - \alpha_1 k_1 < 0$ and $(1 + \alpha_2) k_1 > (1 + \alpha_2) \gamma k_2$ then $\bar{\sigma} = \frac{k_1}{1 + \alpha_1} - \delta$. Furthermore, if both (i) and (ii) fail to hold, then $\bar{\sigma} = \frac{k_1 + \gamma k_2}{1 + \alpha_1 + \alpha_2} - \delta$.

The proof of Proposition 1 can be found in Appendix D.

In Fig. 3, we provide a scenario in which the consumer can persist on one of the single patches, but not on the other, and fails to persist when the two patches are linked. We see that combining resource patches can lead to consumer extinction by extending the amount of time required to search for prey on both patches. This observed extinction effect from the combining of resource

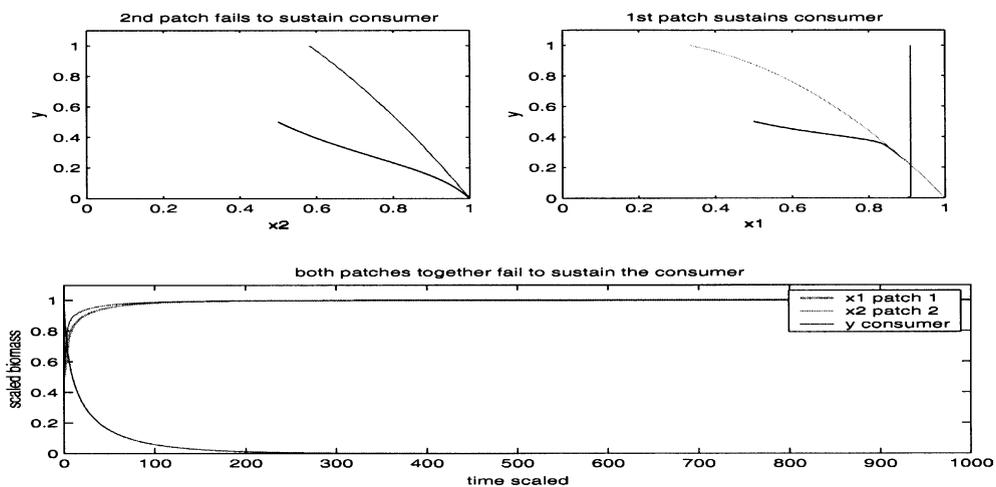


Fig. 3. Scenario where a consumer goes extinct by combining resource patches without stoichiometry for initial values $x_i(0) = 0.5$ and $y(0) = 1.0$, with parameter values $\alpha = 1.5$, $\alpha_2 = 0.9$, $\gamma = 0.7$, $\beta = 1.1$, $\delta = 0.5$, $k_1 = 1.3$ and $k_2 = 0.5$.

patches may lead to greater understanding of important ecological issues such as endangered species protection and species conservation [27]. In particular, caution must be exercised when we try to recover the damages resulted from patch fragmentation. Simply merge patches or provide passages between patches may expand a local extinction to global extinction. In other words, conservation policies must not be guided by intuition only [4].

5.2. Bistability in the case of $p_i < 1$

One might suspect a more general condition that guarantees global stability of the consumer-free equilibrium, $(1, 1, 0)$ that is often found in most conventional models. However, our stoichiometric two-patch model does not permit this. Since the consumer can dynamically uptake more or less nutrient depending on the quality of the resource, predictable outcomes found in non-stoichiometric systems are unobtainable. To investigate what mechanisms prohibit such an otherwise expected global result, we begin with our previous local stability analysis. We have seen that $(1, 1, 0)$ has eigenvalues

$$\lambda_1 = -1, \quad \lambda_2 = -\beta, \quad \lambda_3 = f(p_1, p_2)D - \delta,$$

where

$$f(p_1, p_2) = \begin{cases} k_1 + \gamma k_2 & \text{if } p_1 \geq 1 \text{ and } p_2 \geq 1, \\ k_1 p_1 + \gamma k_2 & \text{if } p_1 < 1 \text{ and } p_2 \geq 1, \\ k_1 + \gamma k_2 p_2 & \text{if } p_1 \geq 1 \text{ and } p_2 < 1, \\ k_1 p_1 + \gamma k_2 p_2 & \text{if } p_1 < 1 \text{ and } p_2 < 1. \end{cases}$$

Thus, it is natural to investigate the behavior of the critical quantity

$$A(x_1, x_2) = \frac{k_1 \min(x_1, p_1) + \gamma k_2 \min(x_2, p_2)}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta.$$

Although $A(1, 1) < 0$ guarantees local asymptotic stability for $(1, 1, 0)$, it is not sufficient for global asymptotic stability. With $A(1, 1) < 0$, solutions with different initial conditions do not necessarily tend to $(1, 1, 0)$ as $t \rightarrow \infty$ as suggested by the local asymptotic stability conditions.

Fig. 4 depicts the three-dimensional phase-space exhibiting two solutions with different initial data that have drastically different dynamics. One solution tends to the consumer-free equilibrium $(1, 1, 0)$ and the other solution tends to a locally asymptotically stable limit cycle.

In Fig. 5, we fix four different initial conditions for the initial value of the state variable, x_2 . And, we vary the initial values of x_1 and y . The set of values that converge to $(1, 1, 0)$ appears to have a very complicated and ‘fractal-like’ boundary.

5.3. Stoichiometry mediated coexistence and consumer extinction

Varying the patch quality p_i can lead to either consumer extinction or persistence of both resource species and the consumer. As noted in Section 3, values of p_i that satisfy $p_i > 1$ will be referred to as absolutely good quality. That is, the P:C (phosphorous to carbon) ratio of the consumed resource is always higher than the P:C ratio of the consumer. And, $p_i < 1$ will correspond to a potentially lower quality scenario where the P:C ratio of the consumed resource

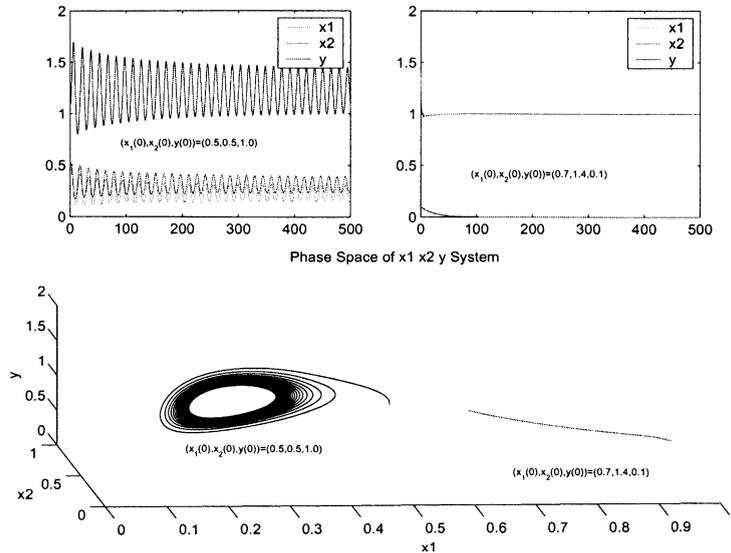


Fig. 4. Multiple attractors for the parameters $p_1 = 0.35$, $p_2 = 0.6$, $\alpha_1 = 0.9$, $\alpha_2 = 1.2$, $\gamma = 0.8$, $\beta = 0.9$, $\delta = 0.40$, $k_1 = 1.5$ and $k_2 = 1.2$.

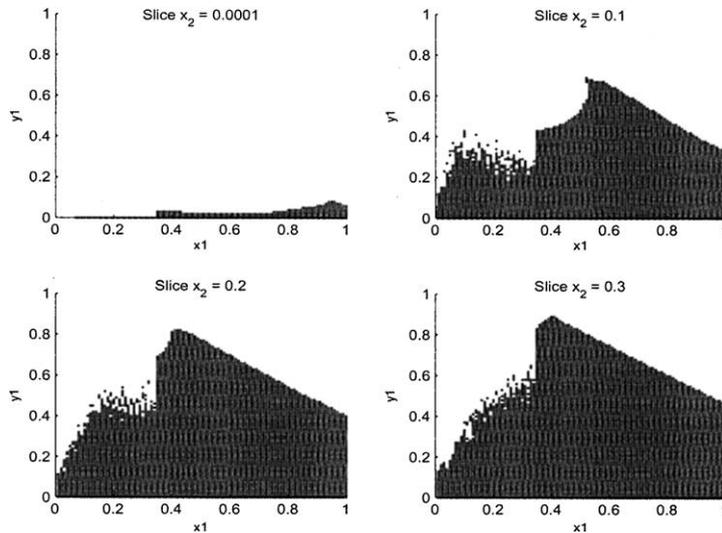


Fig. 5. Initial conditions for solutions tending to equilibrium $(1, 1, 0)$ for the parameter values: $p_1 = 0.35$, $p_2 = 1.4$, $\alpha_1 = 0.9$, $\alpha_2 = 1.1$, $\gamma = 0.8$, $\beta = 0.9$, $\delta = 0.40$, $k_1 = 1.5$ and $k_2 = 0.4$.

variably compares to the P:C ratio of the consumer. In Fig. 6 we start with the same set of initial conditions (initial density) of the state variables and compare long-term behavior of solutions while holding the first patch at quality $p_1 = 0.3$ and considering two different values for the quality of the second patch. With p_1 fixed at 0.3, the first graph features the simulation of the system of equations with $p_2 = 0.4$. This scenario corresponds to both patches having poor quality resource.

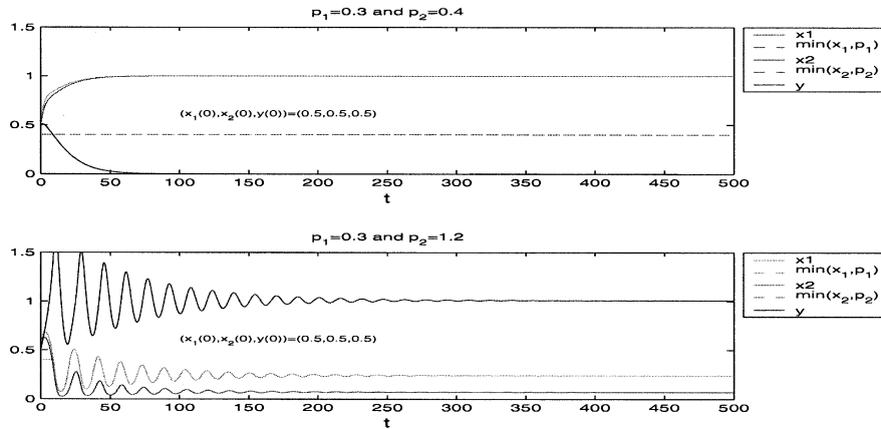


Fig. 6. Simulation of the system with poor and absolutely good quality with $x_i(0) = 0.5$ and $y(0) = 1.0$, and parameter values: $\alpha_1 = 1.1$, $\alpha_2 = 0.9$, $\gamma = 1.1$, $\beta = 0.9$, $\delta = 0.3$, $k_1 = 1.5$ and $k = 0.5$.

Obviously, the consumer goes extinct. In the second graph, we still hold p_1 fixed at 0.3. But, we consider $p_2 = 1.2$. This corresponds to the first patch having poor quality. And, the second patch has absolutely-good quality. We immediately notice that the system with at least one patch of absolutely good quality obtains an equilibrium with all three populations persisting. Thus, having poor quality can potentially lead to consumer extinction. Whereas, a system having at least one patch of absolutely good resource quality may sustain the consumer and the resource on both patches.

We now observe that simulation suggests that the stoichiometric growth constraint on the consumer can drive it to extinction. We refer to this phenomenon as ‘the stoichiometric extinction effect.’ Simulation demonstrates that although the two patches alone cannot sustain the consumer, the consumer can be sustained if the two patches are combined. However, this may merely be the effect of combining the densities of the two patches and increasing the amount of available resource for the consumer. The observed extinction effect is the result of the stoichiometrically modeled growth of the consumer. If both of the resource patches have relatively poor quality the stoichiometric growth factor reduces the growth rate of the consumer. One possible explanation of this follows from the idea that since the consumer’s density is limited by quantity on the first patch, it ‘over-grazes’ on the second patch which is of low quality. Consequently, the consumer’s growth is inhibited by this ‘poor quality’ food source. Thus, resulting reduced growth rate prohibits the consumer from growing fast enough to overcome its constant death rate. Fig. 7 demonstrates this intriguing extinction effect. We will further elaborate on this phenomenon in the discussion section of this paper.

5.4. Local extinction of the resource in one patch

The following analysis shows that the system can reach an equilibrium where one of the resource patches is extinct, and yet the consumer and other patch coexist at a positive equilibrium. Furthermore, this equilibrium is stable if the steady state population of the surviving patch is bounded above and below specific levels. The dispersal of the consumer from the rich patch

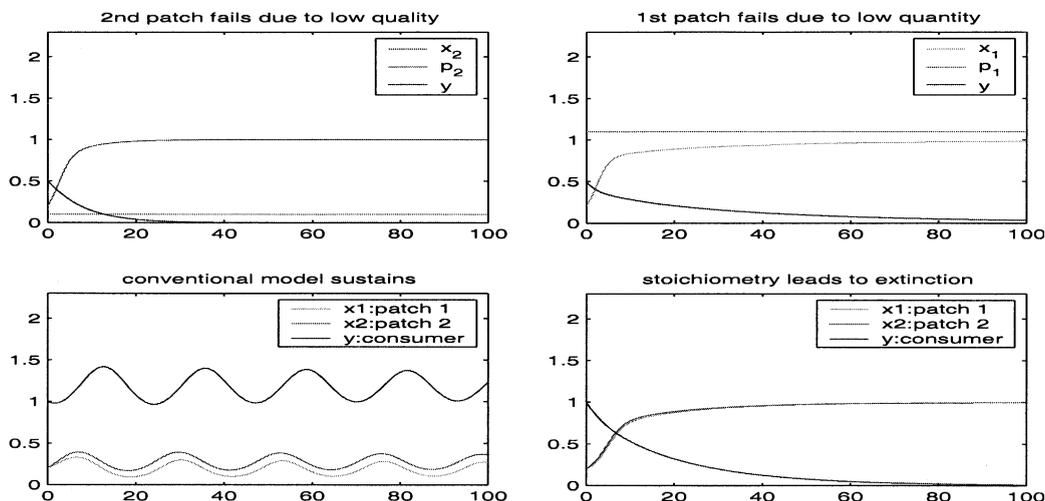


Fig. 7. Simulation of the system with one of each patch missing and then both patches together. (In the conventional model, the consumer persists. But, in the stoichiometric model, the consumer goes extinct.) The initial populations of the existing patch are $x_i(0) = 0.2$ and $y(0) = 0.5$ with parameter values: $\beta = 0.9$, $k_1 = 0.3$, $k_2 = 0.9$, $p_1 = 1.1$, $p_2 = 0.1$, $\delta = 0.17$, $\gamma = 0.8$, $\alpha_1 = 1.0$, $\alpha_2 = 1.0$.

depresses the growth of the resource in the poor patch and this can lead to the extinction of the resource in one of the two patches. Because the consumer population can be sustained locally by feeding on the high quality patch, it can feed on the other resource patch (of lower quantity) until it is extinct. Upon extinction of the resource in one patch, the total consumer population eventually resides on the surviving resource patch at some equilibrium level.

There may exist two equilibria in which the consumer is present and one of the resource patches is extinct. These equilibria will be denoted by $E_{0**} = (0, x_2^*, y^*)$, where $x_2^* > 0$ and $y^* > 0$, and $E_{*0*} = (x_1^*, 0, y^*)$, where $x_1^* > 0$ and $y^* > 0$. We provide the existence and local stability criteria for these equilibria in Table 3.

In Fig. 8, we see that reducing the quality parameter p_2 of the second patch from $p_2 = 1.3$ to $p_2 = 0.2$ prevents the extinction of the first patch. A possible explanation for this phenomenon is the stoichiometric growth of the consumer. If the quality of the second patch is reduced, then the growth rate of the consumer is decreased. Consequently, the total consumer population found on both resource patches is reduced. And, since there is a smaller population of consumers feeding on the first patch, it is not over-grazed, and the resource in the first patch does not go extinct. In this

Table 3
Explicit equilibria, conditions for existence, and stability type for E_{0**} and E_{*0*}

Value of x_i^*	Existence conditions	Stability conditions
$x_2^* = \frac{\delta}{\gamma k_2 - \delta \alpha_2}$	$x_2^* < p_2$ and $\gamma k_2 > \delta \alpha_2$	L.A.S if $\frac{\alpha_2 - 1}{2\alpha_2} < x_2^* < \frac{\beta - \gamma}{\beta}$
$x_2^* = \frac{\gamma k_2 p_2 - \delta}{\delta \alpha_2}$	$x_2^* > p_2$ and $\gamma k_2 p_2 > \delta$	Unstable saddle
$x_1^* = \frac{\delta}{k_1 - \delta \alpha_1}$	$x_1^* < p_1$ and $k_1 > \delta \alpha_1$	L.A.S if $\frac{\alpha_1 - 1}{2\alpha_1} < x_1^* < 1 - \frac{\beta}{\gamma}$
$x_1^* = \frac{k_1 p_1 - \delta}{\delta \alpha_1}$	$x_1^* > p_1$ and $k_1 p_1 > \delta$	Unstable saddle

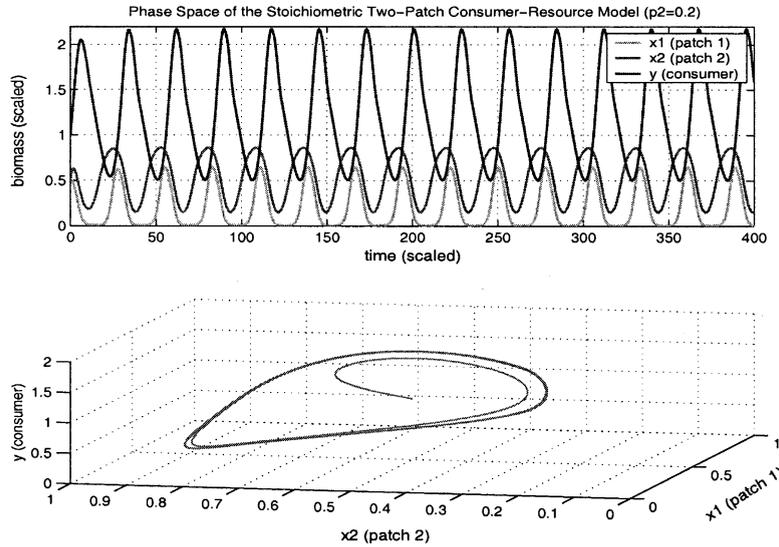


Fig. 8. Persistence of the first resource patch. Initial conditions: $x_1(0) = 0.5$, $x_2(0) = 0.5$ and $y(0) = 1.0$, and parameter values: $\alpha_1 = 1.2$, $\alpha_2 = 0.9$, $\gamma = 0.8$, $\beta = 1.4$, $\delta = 0.27$, $p_1 = 1.35$, $p_2 = 0.2$, $k_1 = 1.5$ and $k_2 = 1.4$.

sense, we see that stoichiometric constraints can promote resource renewal and ecosystem persistence.

In Fig. 9, we observe that boundary dynamics (on the plane $x_1 = 0$ or $x_2 = 0$) the system has two vertical consumer nullclines. This is due to the stoichiometric minimum function in the

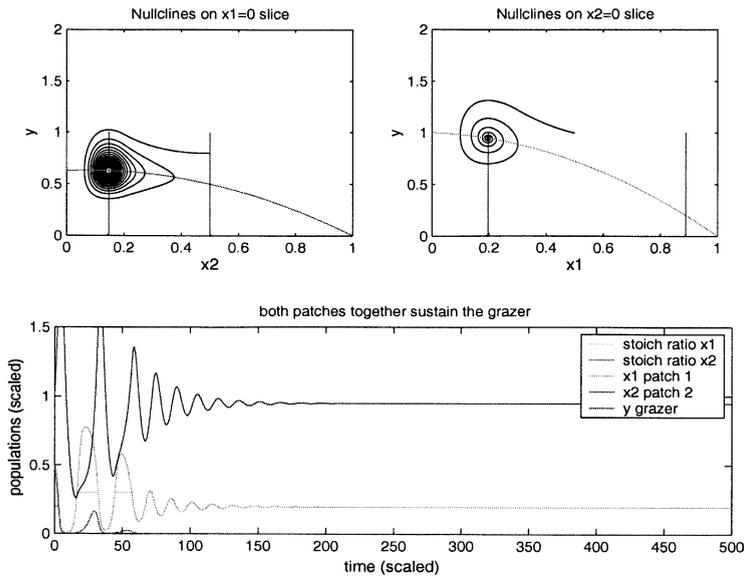


Fig. 9. Local extinction (in unsealed variables and original parameters) with initial conditions, $x_i(0) = 0.5$ and $y(0) = 1.0$, and parameter values: $b_1 = 0.85$, $b_2 = 0.8$, $K_1 = 3.5$, $K_2 = 2.0$, $p_1 = 0.15$, $p_2 = 0.10$, $d = 0.5$, $m = 0.04$, $\epsilon = 0.8$, $c_1 = 0.7$, $c_2 = 0.80$, $q_1 = 1.0$, $q_2 = 1.0$, $h = 0.01$, $a = 0.7$.

consumer growth equation. These vertical nullclines remind us that the amount of phosphorus in the soil is assumed to be constant. (The position of these vertical nullclines changes for different quality levels.)

6. The positive equilibrium

In order to locate the positive equilibrium, we set the equations in system (3.1)–(3.3) equal to zero and divide by $x_1^* > 0$, $x_2^* > 0$, and $y^* > 0$. We obtain

$$1 - x_1 - y\Delta(x_1, x_2) = 0, \tag{6.1}$$

$$\beta - \beta x_2 - \gamma y\Delta(x_1, x_2) = 0, \tag{6.2}$$

$$[k_1 \min(x_1, p_1) + \gamma k_2 \min(x_2, p_2)]\Delta(x_1, x_2) = \delta. \tag{6.3}$$

Let $D^* \equiv \Delta(x_1^*, x_2^*) = (1 + \alpha_1 x_1^* + \alpha_2 x_2^*)^{-1}$. Notice that $D^* \neq 0$. Upon division and replacing and rearranging terms, we have at equilibrium a 2×2 linear system in x_1^* and x_2^* of the form

$$\gamma x_1^* - \beta x_2^* = (\gamma - \beta), \tag{6.4}$$

$$k_1 \min(x_1^*, p_1) + \gamma k_2 \min(x_2^*, p_2) = \delta D^*. \tag{6.5}$$

Although one can write explicit formulae for the positive equilibrium by separating the above system of equations into four possible cases depending on x_i^* and p_i , we will omit this work and proceed to investigate its stability.

6.1. Relatively good quality case

Case I: $x_1^* < p_1$ and $x_2^* < p_2$.

To simplify notation, define $\omega = k_1 \alpha_2 - k_2 \alpha_1 \gamma$. In this case, the variational matrix of (3.1)–(3.3) at E_* is given by

$$M = J(x_1^*, x_2^*, y^*) = \begin{pmatrix} m_{11} & m_{12} & m_{13} \\ m_{21} & m_{22} & m_{23} \\ m_{31} & m_{32} & 0 \end{pmatrix}, \tag{6.6}$$

where

$$m_{11} = -x_1^* + \alpha_1 x_1^* y^* (D^*)^2 = x_1^* (-1 + \alpha_1 y^* (D^*)^2), \tag{6.7}$$

$$m_{12} = \alpha_2 y^* x_1^* (D^*)^2 = \alpha_2 y^* x_1^* (D^*)^2, \tag{6.8}$$

$$m_{13} = -x_1^* D^* = -x_1^* D^*, \tag{6.9}$$

$$m_{21} = \alpha_1 \gamma y^* x_2^* (D^*)^2 = \alpha_1 \gamma y^* x_2^* (D^*)^2, \tag{6.10}$$

$$m_{22} = -\beta x_2^* + \alpha_2 \gamma x_2^* y^* (D^*)^2 = x_2^* (-\beta + \alpha_2 \gamma y^* (D^*)^2), \tag{6.11}$$

$$m_{23} = -\gamma x_2^* D^* = -\gamma x_2^* D^*, \tag{6.12}$$

$$m_{31} = (k_1 y^* + (k_1 \alpha_2 - k_2 \alpha_1 \gamma) y^* x_2^*) (D^*)^2 = y^* ((k_1 + \omega x_2^*) (D^*)^2), \tag{6.13}$$

$$m_{32} = (\gamma k_2 y^* - (k_1 \alpha_2 - k_2 \alpha_1 \gamma) x_1^* y^*) (D^*)^2 = y^* ((\gamma k_2 - \omega x_1^*) (D^*)^2). \tag{6.14}$$

The characteristic polynomial of M is

$$\begin{aligned} f(\lambda) &= \det(M - \lambda I) \\ &= (-\lambda)((m_{11} - \lambda)(m_{22} - \lambda) - m_{12}m_{21}) + m_{13}(m_{21}m_{32} - m_{31}(m_{22} - \lambda)) \\ &\quad - m_{23}(m_{32}(m_{11} - \lambda) - m_{31}m_{12}). \end{aligned}$$

Now, the roots λ of $f(\lambda) = 0$ are the solutions of

$$\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0,$$

where

$$A_1 = -m_{11} - m_{22},$$

$$A_2 = m_{11}m_{22} - m_{12}m_{21} - m_{13}m_{31} - m_{23}m_{32},$$

$$A_3 = m_{31}m_{13}m_{22} + m_{23}m_{32}m_{11} - m_{13}m_{21}m_{32} - m_{23}m_{31}m_{12}.$$

Theorem 9. *If the positive equilibrium, E_* , exists, $A_1 > 0$, and $A_1 A_2 - A_3 > 0$ then it is locally asymptotically stable.*

Proof. From the Routh–Hurwitz criterion, E_* is locally asymptotically stable if and only if $A_1 > 0$, $A_3 > 0$, and $A_1 A_2 - A_3 > 0$. Now, it can be shown that the condition $A_3 > 0$ is equivalent to $x_i^* > 0$ and $y^* > 0$. The proof of this algebraic result can be found in Appendix E. \square

Since a sharp set of conditions that guarantees the local asymptotic stability of E_* is not mathematically tractable, we turn our attention to a local stability and existence diagram for E_* defined over the $\delta\beta$ -parameter space. The shape of the stability region suggests that values of β near 1 and δ values near 0.75 yield locally asymptotically stable and positive equilibrium. In terms of our original parameters, β values near 1 correspond to almost equal intrinsic growth rates of the resources on each patch. Thus, similarity between patches increases the likelihood of persistence for the consumer. Fig. 10 is a diagram of such a region.

With parameter values $\alpha_1 = 0.8$, $\alpha_2 = 1.4$, $\gamma = 0.9$, $k_1 = 1.5$, $k_2 = 1.4$, $\delta = 0.6$, $\beta = 0.8$, $p_1 = 1.5$, and $p_2 = 1.4$ which correspond to the shaded region of Fig. 10, $E_* = (0.6164, 0.7842, 0.9938)$ is locally asymptotically stable by the Routh–Hurwitz criterion.

6.2. Mixed quality case

Without loss of generality, we assume that $p_1 > 1$ and $p_2 < 1$ so that the first patch, $i = 1$ is of good quality. The variational matrix of (3.11)–(3.13) at E_* is given by

$$M = J(x_1^*, x_2^*, y^*) = \begin{pmatrix} m_{11} & m_{12} & m_{13} \\ m_{21} & m_{22} & m_{23} \\ m_{31} & m_{32} & 0 \end{pmatrix}. \tag{6.15}$$

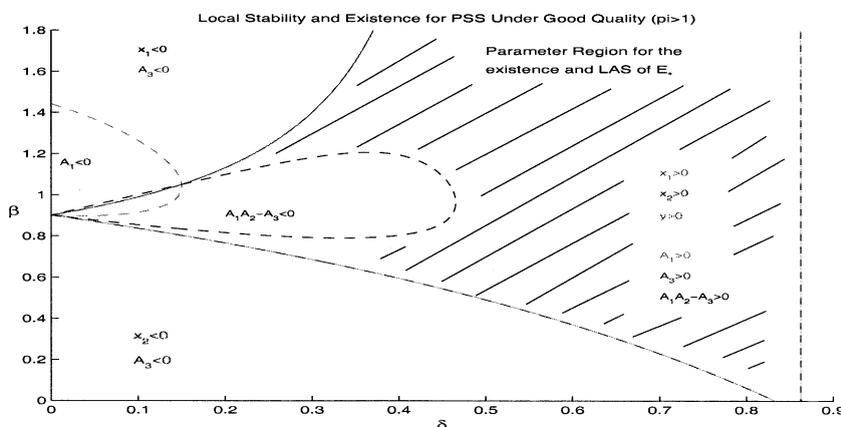


Fig. 10. Region of local asymptotic stability for the positive equilibrium in the good quality case $p_i > 1$ for initial data: $x_i(0) = 0.5$ and $y(0) = 1.0$, and for the parameter values: $p_1 = 1.4$, $p_2 = 1.5$, $\alpha_1 = 0.8$, $\alpha_2 = 1.4$, $\gamma = 0.9$, $k_1 = 1.5$ and $k_2 = 1.4$. The shaded region depicts the parameter region that guarantees both existence (positivity) and local stability of E_* .

With the exception of

$$m_{31} = (k_1(1 + \alpha_2 x_2^*) - \gamma k_2 \alpha_1 p_2)(D^*)^2,$$

$$m_{32} = (-\alpha_2(k_1 x_1^* + \gamma k_2 p_2))(D^*)^2,$$

the entries of the variational matrix are given by (6.7)–(6.14). The eigenvalues, λ_i , are the solutions of

$$\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0,$$

where

$$A_1 = -m_{11} - m_{22},$$

$$A_2 = m_{11}m_{22} - m_{12}m_{21} - m_{13}m_{31} - m_{23}m_{32},$$

$$A_3 = m_{31}m_{13}m_{22} + m_{23}m_{32}m_{11} - m_{13}m_{21}m_{32} - m_{23}m_{31}m_{12}.$$

From the Routh–Hurwitz criterion, E_* is locally asymptotically stable if and only if $A_1 > 0$, $A_3 > 0$, and $A_1 A_2 - A_3 > 0$.

With parameter values $\alpha_1 = 0.8$, $\alpha_2 = 1.4$, $\gamma = 0.9$, $k_1 = 1.5$, $k_2 = 1.4$, $\delta = 0.6$, and $\beta = 1.6$, $p_1 = 1.5 > 1$, and $p_2 = 0.5 < 1$, which correspond to the shaded region of Fig. 11, $E_* = (0.6164, 0.7842, 0.9938)$ is locally asymptotically stable by the Routh–Hurwitz criterion.

Again, the actual conditions that satisfy the above criteria are mathematically intractable. In Fig. 11 we create a existence and local stability diagram by varying the parameters β and δ .

6.3. Poor quality case

Theorem 10. *If E_* exists (is positive) then it is unstable.*

Proof. The positive equilibrium, E_* is locally asymptotically stable if and only if $A_1 > 0$, $A_3 > 0$, and $A_1 A_2 - A_3 > 0$ in the characteristic polynomial is $\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0$. In Appendix F, we show that the positivity of x_1^* , x_2^* , and y^* implies that $A_3 < 0$. Thus, the Routh–Hurwitz criterion implies that E_* is unstable in this case. \square

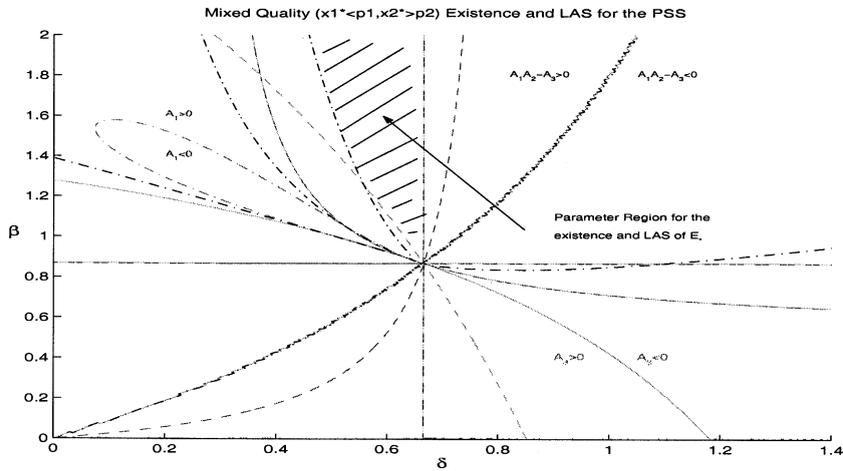


Fig. 11. Region of local asymptotic stability for the positive equilibrium in the case of mixed resource quality $p_1 = 1.5 > 1$, $p_2 = 0.5 < 1$ for initial data: $x_i(0) = 0.5$ and $y(0) = 1.0$, and for the parameter values: $\alpha_1 = 0.8$, $\alpha_2 = 1.4$, $\gamma = 0.9$, $k_1 = 1.5$, and $k_2 = 1.4$. The shaded region depicts the parameter region that guarantees both existence (positivity) and local stability of E_* .

6.4. Limit cycles and bifurcation of the positive equilibrium

The following bifurcation diagram shows that the positive steady state undergoes a supercritical Hopf bifurcation into an attracting limit cycle while we hold the parameter β fixed, and decrease δ towards zero. However, with the further decreasing of δ , we observe that the limit cycle's amplitude grows until a critical value of δ is reached. Then, the stoichiometric growth of the consumer reduces the amplitude of the limit cycles for a range of δ . Further decreases in the

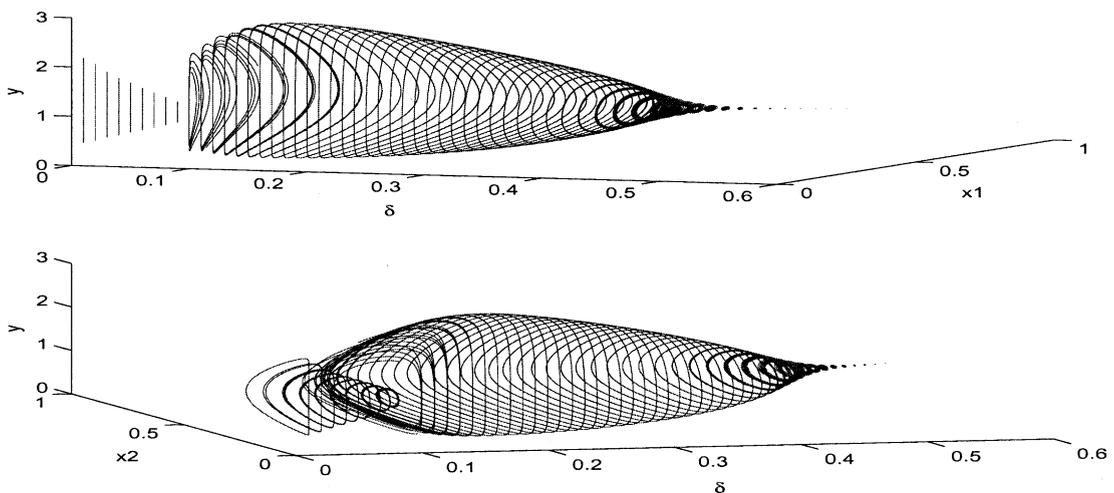


Fig. 12. Bifurcation of the positive equilibrium. $x_1(0) = 0.5$, $x_2(0) = 0.5$ and $y(0) = 1.0$ for the parameter values: $\alpha_1 = 0.9$, $\alpha_2 = 1.1$, $\gamma = 0.8$, $\beta = 0.9$, $k_1 = 1.5$, $k_2 = 1.4$, $p_1 = 0.35$ and $p_2 = 0.4$.

value of δ increase the amplitude of the limit cycles. This unusual behavior is depicted in Fig. 12. The program used to create the graphic was written in MATLAB. It loops over the bifurcation parameter δ and plots the approximate limit cycle after discarding transient solutions.

7. Discussion

Through analysis and simulation, our model demonstrates that diverse and intriguing dynamics are possible in a model that considers both stoichiometry and habitat heterogeneity. By including the more realistic assumption that an organism's growth depends on both the quality and quantity of the food it consumes, we can develop models that contain new population dynamics. Consideration of ecological stoichiometry and consumer dispersal in heterogeneous habitats can bring new insight to the study of biodiversity and stability in ecosystems. For example, we can examine under what conditions ecosystems that are divided into resource patches with different stoichiometric properties provide enhanced or reduced opportunities for sustaining species. When patches harbor resources of different quality, permitting consumers to disperse between patches can lead to the extinction of a resource species. This was observed in our 'stoichiometric extinction effect.' In a conventional setting without stoichiometry, this resource extinction can be the result of apparent competition imposed by the consumer's searching efficiencies on each patch [17]. The extinction of a consumer (predator) population from the combining (or connecting) of resource (prey) patches has been observed on islands [4]. However, we can enrich our discussion of this phenomenon with stoichiometry. That is, we can propose a scenario where a rich neighboring patch can increase the overall population of consumers on both patches, and subsequent dispersal of the consumer to the rich patch can depress the growth of the consumer on the poor patch. As we have seen in Section 5.4, this can lead to the local extinction of the resource in a single patch. In some situations, if the quality of the resource is poor, then the extinction of the resource can be prevented. Therefore, stoichiometric mechanisms may determine whether fragmented ecosystems can persist, an issue that has implications both for the study of biodiversity and aspects of conservation.

Extinction is a complex biological process. To explain this phenomenon, many mathematical and theoretical ecologists often resort to random event hypotheses. This random event hypothesis forms the key assumption and foundation in metapopulation theory [14]. Stoichiometry may provide another analytical framework; one which provides a deterministic mechanism for extinction. In addition, permitting a consumer species to disperse between patches can sometimes rescue the consumer from extinction [23]. But, in Section 5.1, we have seen that when the resource quality can determine the growth of the consumer, the consumer can go extinct even with dispersal.

The presence of multiple attractors in both the one-patch and two-patch models suggests that the ecological implications of stoichiometric and heterogeneous habitat models depend closely on the initial populations of the resource and consumers being studied. Under the same set of parameters in the model, we observe that with some initial conditions, the system may reach an equilibrium where the consumer population is extinct, whereas, with other initial conditions, the consumer and resource populations persist (Fig. 4). In addition to creating a descriptive framework for modeling ecological systems, the inclusion of stoichiometric growth functions has

enriched the computational and analytical results of our work. The bistability of the one-patch model (4.1)–(4.2) is a fascinating feature that indicates the possible existence of new and interesting mathematical results from models with explicit stoichiometric mechanisms.

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Appendix A

Proof of Theorem 1. For $x_1(0) > 0$, $x_2(0) > 0$, $y(0) > 0$, (3.1)–(3.3) has a unique solution defined for all $t \geq 0$ that is positive and bounded for all $t \geq 0$. Furthermore, for any $0 < \epsilon_1, \epsilon_2 < 1$, $x_1(t) < 1 + \epsilon_1$ and $x_2(t) < 1 + \epsilon_2$ for sufficiently large $t > 0$.

Proof. Uniqueness and positivity follow from careful but standard mathematical arguments. To show that solutions are bounded for positive initial conditions are bounded, we observe that $x_1' \leq x_1(1 - x_1)$ which implies that $\lim_{t \rightarrow \infty} \sup x_1(t) \leq 1$. And, $x_2' \leq \beta x_2(1 - x_2)$ which implies that $\lim_{t \rightarrow \infty} \sup x_2(t) \leq 1$. Thus, for any $0 < \epsilon_1 < 1$ and $0 < \epsilon_2 < 1$, we have for large t

$$x_1(t) \leq 1 + \epsilon_1, \quad x_2(t) \leq 1 + \epsilon_2.$$

Furthermore, it can be shown that solutions with initial data satisfying $x_i(0) < 1$ and $y(0) > 0$ satisfy $x_i(t) < 1$ for all $t \geq 0$ by a simple comparison to the logistic equation. Then,

$$\begin{aligned} (k_1x_1 + k_2x_2 + y)' &= k_1x_1(1 - x_1) + k_2\beta x_2(1 - x_2) - \delta y + y(k_1(\min(x_1, p_1) - x_1) \\ &\quad + \gamma k_2(\min(x_2, p_2) - x_2))\Delta \\ &\leq k_1x_1 + k_2\beta x_2 - \delta y + y(k_1(\min(x_1, p_1) - x_1) + \gamma k_2(\min(x_2, p_2) - x_2))\Delta \\ &\leq k_1x_1 + k_2x_2 - \delta y \\ &= k_1(1 + \delta)x_1 + k_2(\beta + \delta)x_2 - \delta(k_1x_1 + k_2x_2 + y). \end{aligned}$$

Now, let $z(t) = k_1x_1(t) + k_2x_2(t) + y(t)$. Then,

$$z'(t) \leq ((1 + \delta)k_1(1 + \epsilon_1) + (\beta + \delta)k_2(1 + \epsilon_2)) - \delta z.$$

Now, define $\zeta = (1 + \delta)k_1(1 + \epsilon_1) + (\beta + \delta)k_2(1 + \epsilon_2)$. Then,

$$z'(t) \leq \zeta - \delta z$$

Therefore,

$$z(t) \leq \frac{\zeta}{\delta} + \epsilon_3 \quad \text{for } 0 < \epsilon_3 < 1 \text{ and sufficiently large } t.$$

So,

$$\limsup_{t \rightarrow \infty} z(t) = \limsup_{t \rightarrow \infty} (k_1 x_1(t) + k_2 x_2(t) + y(t)) \leq \frac{\zeta}{\delta}.$$

Therefore, $y(t)$ is bounded for $y(0) > 0$.

Now, it can easily be shown that $F_1(x_1, x_2, y)$, $F_2(x_1, x_2, y)$ and $yG(x_1, x_2)$ given by (3.4)–(3.6) are locally Lipschitz for x_i and y in $R_+^3 = \{(x_1, x_2, y) : x_1 \geq 0, x_2 \geq 0, y \geq 0\}$. The local uniqueness and existence of solutions follows from the Picard–Lindelof theorem (Theorem 3.1 in [13]). Furthermore, since solutions are positive and bounded in R_+^3 , then with a standard continuation argument ([13], pp. 17–18) we have that solutions are defined for all $t \geq 0$. \square

Appendix B

Proof of Theorem 6. If $\delta \geq k_1 \min(1, p_1, \frac{1}{\alpha_1}) + \gamma k_2(1, p_2, \frac{1}{\alpha_2})$, then

$$\lim_{t \rightarrow \infty} (x_1(t), x_2(t), y(t)) = (1, 1, 0).$$

Proof. From (3.13) we have

$$\begin{aligned} y' &= -y \left(\delta - \frac{k_1 \min(x_1, p_1)}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \frac{\gamma k_2 \min(x_2, p_2)}{1 + \alpha_1 x_1 + \alpha_2 x_2} \right) \\ &\leq -y \left(\delta - k_1 \min \left(\frac{x_1}{1 + \alpha_1 x_1 + \alpha_2 x_2}, \frac{p_1}{1 + \alpha_1 x_1 + \alpha_2 x_2} \right) \right) \\ &\quad - y \left(-\gamma k_2 \min \left(\frac{x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2}, \frac{p_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} \right) \right) \\ &\leq -y \left(\delta - k_1 \min \left(\frac{x_1}{1 + \alpha_1 x_1}, p_1 \right) - \gamma k_2 \min \left(\frac{x_2}{1 + \alpha_2 x_2}, p_2 \right) \right) \\ &\leq -y \left(\delta - k_1 \min \left(1, \frac{1}{\alpha_1}, p_1 \right) - \gamma k_2 \min \left(1, \frac{1}{\alpha_2}, p_2 \right) \right) \\ &< 0 \end{aligned}$$

since $\delta \geq k_1 \min(1, \frac{1}{\alpha_1}, p_1) + \gamma k_2 \min(1, \frac{1}{\alpha_2}, p_2)$ and $x_i \leq 1$.

Therefore, we have $y' < 0$. Furthermore, since the model is dissipative, there exists a positive constant, say, M , such that for large t , for $t > t_3 > t_1 > t_0$, $1 + \alpha_1 x_1 + \alpha_2 x_2 < M$.

Thus,

$$y' < -\frac{\delta}{M} y$$

which implies that $\lim_{t \rightarrow \infty} y(t) = 0$.

Again, since the model is dissipative, we must have a positive constant, say, M , such that for large t , for $t > t_0 > 0$, $1 + \alpha_1 x_1 + \alpha_2 x_2 < M$. Now, since $\lim_{t \rightarrow \infty} y(t) = 0$, then, for any $0 < \epsilon_1 < 1$, there exists a $t_4 > t_3$, such that for $t > t_4$, $y(t) < \epsilon_1 M$. Thus,

$$x_1'(t) > x_1 \left(1 - x_1 - \frac{y}{M} \right) > x_1 (1 - \epsilon_1 - x_1).$$

Simple comparison argument shows that $\liminf_{t \rightarrow \infty} x_1(t) \geq 1 - \epsilon_1$. Thus, upon letting $\epsilon_1 \rightarrow 0$, we have $\lim_{t \rightarrow \infty} x_1(t) = 1$.

Also, since $\lim_{t \rightarrow \infty} y(t) = 0$, then, for any $0 < \epsilon_2 < \gamma$, there exists a $t_5 > t_4$, such that for $t > t_5$, $y(t) < \frac{\beta M \epsilon_2}{\gamma}$. Thus,

$$x_2'(t) > x_2(\beta(1 - x_2) - \gamma y) > x_2(\beta(1 - x_2) - \beta \epsilon_2) > \beta x_2(1 - \epsilon_2 - x_2).$$

Again, a simple comparison argument shows that $\liminf_{t \rightarrow \infty} x_2(t) \geq 1 - \epsilon_2$. Thus, upon letting $\epsilon_2 \rightarrow 0$, we have $\lim_{t \rightarrow \infty} x_2(t) = 1$.

Therefore, under the above assumptions $\lim_{t \rightarrow \infty} (x_1(t), x_2(t), y(t)) = (1, 1, 0)$. \square

Appendix C

Proof of Theorem 7. Let $(x_1(0), x_2(0)) \in [0, 1] \times [0, 1]$. Assume $p_1 \geq 1$ and $p_2 \geq 1$. If

- (i) $\frac{k_1}{\alpha_1} = \frac{\gamma k_2}{\alpha_2}$, and
- (ii) $\frac{\alpha_1 k_1 + \gamma k_2}{1 + \alpha_1 + \alpha_2} - \delta < 0$,

then $\lim_{t \rightarrow \infty} (x_1(t), x_2(t), y(t)) = (1, 1, 0)$.

Proof. First, we recall that $\lim_{t \rightarrow \infty} \sup x_i(t) \leq 1$, we have that $x_1(t) < 1 + \epsilon_1$ for large $t > t_1$ and $x_2(t) < 1 + \epsilon_2$ for large $t > t_2$. And, from (2.3) for sufficiently large $t > \max\{t_1, t_2\}$ we have

$$y' = y \left(\frac{k_1 \min(x_1, p_1) + \gamma k_2 \min(x_2, p_2)}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \right) = y \left(\frac{k_1 x_1 + \gamma k_2 x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \right).$$

Now, if we set $\frac{k_1}{\alpha_1} = \frac{\gamma k_2}{\alpha_2}$, then

$$\frac{k_1 x_1 + \gamma k_2 x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta = \frac{\gamma k_2}{\alpha_2} \left(\frac{x_1 + \frac{\alpha_2}{\alpha_1} x_2}{\frac{1}{\alpha_1} + \left(x_1 + \frac{\alpha_2}{\alpha_1} x_2\right)} \right) - \delta$$

upon setting $z = x_1 + \frac{\alpha_2}{\alpha_1} x_2$, we have

$$\frac{\gamma k_2}{\alpha_2} \left(\frac{x_1 + \frac{\alpha_2}{\alpha_1} x_2}{\frac{1}{\alpha_1} + \left(x_1 + \frac{\alpha_2}{\alpha_1} x_2\right)} \right) - \delta = \frac{\gamma k_2}{\alpha_2} \frac{z}{\frac{1}{\alpha_1} + z} - \delta = \frac{k_1}{\alpha_1} \frac{z}{\frac{1}{\alpha_1} + z} - \delta = \frac{k_1 z}{1 + \alpha_1 z} - \delta.$$

Now, define $v(z) = \frac{k_1 z}{1 + \alpha_1 z} - \delta$. For $(x_1, x_2) = (0, 0)$, $z = 0$. And, when $(x_1, x_2) = (1, 1)$, $z = 1 + \frac{\alpha_2}{\alpha_1}$. Thus, under the transformation $x_1 + \frac{\alpha_2}{\alpha_1} x_2 \rightarrow z$, the closed rectangle $[0, 1] \times [0, 1]$ is mapped onto the closed interval $[0, 1 + \frac{\alpha_2}{\alpha_1}]$. Clearly, $v'(z) = \frac{k_1}{(1 + \alpha_1 z)^2} > 0$. Therefore, since $v(z)$ is continuous on the closed interval $[0, 1 + \frac{\alpha_2}{\alpha_1}]$, the maximum value of $v(z)$ must occur at $\bar{z} = 1 + \frac{\alpha_2}{\alpha_1}$. Now,

$$v(\bar{z}) = \frac{k_1 \left(1 + \frac{\alpha_2}{\alpha_1}\right)}{1 + \alpha_1 \left(1 + \frac{\alpha_2}{\alpha_1}\right)} - \delta = \frac{k_1 + \gamma k_2}{1 + \alpha_1 + \alpha_2} - \delta.$$

Thus,

$$\frac{k_1 x_1 + \gamma k_2 x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \leq \frac{k_1 + \gamma k_2}{1 + \alpha_1 + \alpha_2} - \delta < 0.$$

This in turn implies that $y'(t) < 0$. The rest of the proof follows from proof of Theorem 6. \square

Appendix D

Proof of Proposition 1. Suppose that $p_1 \geq 1$ and $p_2 \geq 1$. Let $\bar{\sigma} = \max_{(x_1, x_2) \in [0, 1] \times [0, 1]} \left(\frac{k_1 x_1 + \gamma k_2 x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \right)$.

(i) If $k_1 + \alpha_2 k_1 - \alpha_1 \gamma k_2 < 0$ and $(1 + \alpha_1) \gamma k_2 > (1 + \alpha_2) k_1$ then $\bar{\sigma} = \frac{\gamma k_2}{1 + \alpha_2} - \delta$.

(ii) If $\gamma k_2 + \alpha_1 \gamma k_2 - \alpha_1 k_1 < 0$ and $(1 + \alpha_2) k_1 > (1 + \alpha_2) \gamma k_2$ then $\bar{\sigma} = \frac{k_1}{1 + \alpha_1} - \delta$.

Furthermore, if both (i) and (ii) fail to hold, then $\bar{\sigma} = \frac{k_1 + \gamma k_2}{1 + \alpha_1 + \alpha_2} - \delta$.

Proof. Define $\sigma(x_1, x_2) = \frac{k_1 x_1 + \gamma k_2 x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta$.

Now, since σ is a continuous function on the closed rectangle $[0, 1] \times [0, 1]$, then it attains its maximum on $[0, 1] \times [0, 1]$. Let $\bar{\sigma} = \max_{(x_1, x_2) \in [0, 1] \times [0, 1]} \left(\frac{k_1 x_1 + \gamma k_2 x_2}{1 + \alpha_1 x_1 + \alpha_2 x_2} - \delta \right)$. Now we make the following claim: *The maximum value, $\bar{\sigma}$, of σ on the closed rectangle $[0, 1] \times [0, 1]$ occurs at $(1, 0)$, $(0, 1)$, or $(1, 1)$.* To prove this, we apply the fundamentals of calculus. First of all, we observe that

$\frac{\partial \sigma}{\partial x_1} = \frac{k_1 + (\alpha_2 k_1 - \gamma \alpha_1 k_2) x_2}{(1 + \alpha_1 x_1 + \alpha_2 x_2)^2} = 0$ if and only if $x_2 = \frac{k_1}{\gamma \alpha_1 k_2 - \alpha_2 k_1}$. Now, for $x_2 > 0$ we require that $\gamma \alpha_1 k_2 - \alpha_2 k_1 > 0$. At the same time, we observe that $\frac{\partial \sigma}{\partial x_2} = \frac{\gamma k_2 + (\gamma \alpha_1 k_2 - \alpha_2 k_1) x_1}{(1 + \alpha_1 x_1 + \alpha_2 x_2)^2} > 0$ under the assumption that $\gamma \alpha_1 k_2 - \alpha_2 k_1 > 0$. Therefore the maximum value of σ cannot occur on the interior of $[0, 1] \times [0, 1]$ and must occur on its boundary. We will now investigate the values of σ on the boundary of $[0, 1] \times [0, 1]$. First, we will fix $x_1 = 0$. Then $\sigma(0, x_2) = \frac{\gamma k_2 x_2}{1 + \alpha_2 x_2}$. Now,

$\frac{d\sigma(0, x_2)}{dx_2} = \frac{\gamma k_2}{(1 + \alpha_2 x_2)^2} > 0$. Therefore, on the interval $\{0\} \times [0, 1]$ the extremum values of σ occur at $(0, 0)$ and $(0, 1)$. With $\sigma(0, 0) = -\delta$ and $\sigma(0, 1) = \frac{\gamma k_2}{1 + \alpha_2} - \delta$. Clearly, $\sigma(0, 1) = \frac{\gamma k_2}{1 + \alpha_2} - \delta$ is the maximum value of σ on this closed interval. We still need to investigate the other three sides of our boundary. Now, we will fix $x_1 = 1$. Then $\sigma(1, x_2) = \frac{k_1 + \gamma k_2 x_2}{1 + \alpha_1 + \alpha_2 x_2}$. Now, $\frac{d\sigma(1, x_2)}{dx_2} = \frac{\gamma k_2 + (\gamma \alpha_1 k_2 - \alpha_2 k_1)}{(1 + \alpha_1 + \alpha_2 x_2)^2}$ does not change sign on the interval $\{1\} \times [0, 1]$ the extremum values of σ occur at $(1, 0)$ and $(1, 1)$. And,

$\sigma(1, 0) = \frac{k_1}{1 + \alpha_1} - \delta$ and $\sigma(1, 1) = \frac{k_1 + \gamma k_2}{1 + \alpha_1 + \alpha_2} - \delta$. If we fix $x_2 = 0$, then $\sigma(x_1, 0) = \frac{k_1 x_1}{1 + \alpha_1 x_1}$. Now, $\frac{d\sigma(x_1, 0)}{dx_1} = \frac{k_1}{(1 + \alpha_1 x_1)^2} > 0$. Therefore, on the interval $[0, 1] \times \{0\}$ the extremum values of σ occur at $(0, 0)$ and $(1, 0)$. With $\sigma(0, 0) = -\delta$ and $\sigma(1, 0) = \frac{k_1}{1 + \alpha_1} - \delta$. Clearly, $\sigma(1, 0) = \frac{k_1}{1 + \alpha_1} - \delta$ is the maximum value of σ on this closed interval. Now, we will fix $x_2 = 1$. Then $\sigma(x_1, 1) = \frac{k_1 x_1 + \gamma k_2}{1 + \alpha_2 + \alpha_1 x_1}$. Now,

$\frac{d\sigma(x_1, 1)}{dx_1} = \frac{k_1 + (k_1 \alpha_2 - \gamma \alpha_1 k_2)}{(1 + \alpha_1 + \alpha_2 x_2)^2}$ does not change sign on the interval $[0, 1] \times \{1\}$ the extremum values of σ occur at $(0, 1)$ and $(1, 1)$. And, $\sigma(0, 1) = \frac{\gamma k_2}{1 + \alpha_2} - \delta$ and $\sigma(1, 1) = \frac{k_1 + \gamma k_2}{1 + \alpha_1 + \alpha_2} - \delta$. Of our four vertices, $(0, 0)$ is clearly not the location of the maximum of σ since $\sigma(0, 0) = -\delta$. If $(0, 1)$ is the maximum, then we require that $\sigma(0, 1) > \sigma(1, 0)$, $\sigma(0, 1) > \sigma(1, 1)$ and $\frac{d\sigma(x_1, 1)}{dx_1} < 0$. Now, $\frac{d\sigma(x_1, 1)}{dx_1} = \frac{k_1 + (k_1 \alpha_2 - \gamma \alpha_1 k_2)}{(1 + \alpha_1 + \alpha_2 x_2)^2} < 0$. This in turn requires that $k_1 + k_1 \alpha_2 - \gamma \alpha_1 k_2 < 0$. Also, if $\sigma(1, 0) > \sigma(1, 1)$, then $\sigma(1, 0) - \sigma(1, 1) > 0$. And, $\sigma(1, 0) - \sigma(1, 1) = -\left(\frac{k_1 + k_1 \alpha_2 - \gamma \alpha_1 k_2}{(1 + \alpha_2)(1 + \alpha_1 + \alpha_2)} \right) > 0$. Also, $\sigma(0, 1) - \sigma(1, 0) = \frac{\gamma k_2(1 + \alpha_1) - k_1(1 + \alpha_2)}{(1 + \alpha_2)(1 + \alpha_1)}$. Thus, if $k_1 + k_1 \alpha_2 - \gamma \alpha_1 k_2 < 0$, and $\gamma k_2(1 + \alpha_1) > k_1(1 + \alpha_2)$, then $(0, 1)$ is a global maximum. Similarly, if $(1, 0)$ is the maximum, then we require that $\sigma(1, 0) > \sigma(0, 0)$, $\sigma(1, 0) > \sigma(1, 1)$ and $\frac{d\sigma(1, x_2)}{dx_2} < 0$.

$\frac{d\sigma(1, x_2)}{dx_2} = \frac{\gamma k_2 + (\gamma \alpha_1 k_2 - \alpha_2 k_1)}{(1 + \alpha_1 + \alpha_2 x_2)^2} < 0$. This in turn requires that $\gamma k_2 + \gamma \alpha_1 k_2 - \alpha_2 k_1 < 0$. Also, if $\sigma(1, 0) > \sigma(1, 1)$, then $\sigma(1, 0) - \sigma(1, 1) > 0$. And, $\sigma(1, 0) - \sigma(1, 1) = -\left(\frac{\gamma k_2 + \alpha_1 \gamma k_2 - \alpha_2 k_1}{(1 + \alpha_1)(1 + \alpha_1 + \alpha_2)} \right) > 0$. Also, $\sigma(1, 0) - \sigma(0, 1) = \frac{k_1(1 + \alpha_2) - \gamma k_2(1 + \alpha_1)}{(1 + \alpha_2)(1 + \alpha_1)}$. Thus, if $\gamma k_2 + \gamma \alpha_1 k_2 - \alpha_2 k_1 < 0$, and $k_1(1 + \alpha_2) > \gamma k_2(1 + \alpha_1)$, then $(1, 0)$ is a global maximum. Obviously, if $(1, 0)$ and $(0, 1)$ are not maximums, then $(1, 1)$ must be the global maximum. \square

Appendix E

Proof of $A_3 > 0$ if and only if $x_i^* > 0$, $\chi > 0$, and $y^* > 0$ in the case where $p_i > 1$ with $\chi = \gamma(\gamma k_2 - \alpha_2 \delta) + \beta(k_1 - \alpha_1 \delta)$.

Proof. First, we observe that

$$A_3 = m_{31}m_{13}m_{22} + m_{23}m_{32}m_{11} - m_{13}m_{21}m_{32} - m_{23}m_{31}m_{12}.$$

From (6.7)–(6.14) we have

$$\begin{aligned} A_3 &= y^*(k_1 + \omega x_2^*(D^*)^2)(-x_1^*D^*)\beta x_2^*D^*(\alpha_2(1 - x_2^*) - (D^*)^{-1}) \\ &\quad + (-\gamma x_2^*D^*y^*)(\gamma k_2 - \omega x_1^*)(D^*)^2 x_1^*D^*\alpha_1(1 - x_1^*)(D^*)^{-1} \\ &\quad - (-x_1^*D^*)(\alpha_1\gamma y^*x_2^*(D^*)^2)(y^*(D^*)^2)(\gamma k_2 - \omega x_1^*) - (-\gamma x_2^*D^*)(y^*(D^*)^2)(k_1 + \omega x_2^*)(\alpha_2 y^*x_1^*(D^*)^2) \\ &= (x_1^*x_2^*y^*(D^*)^3)(\gamma^2 k_2 + \beta k_1 + \omega(\beta x_2^* - \gamma x_1^*)) \\ &= x_1^*x_2^*y^*(D^*)^3((\gamma^2 k_2 + \beta k_1 + \omega(\beta - \gamma))) \end{aligned}$$

since $\gamma x_1^* = (\gamma - \beta) + \beta x_2^*$.

Now, if we replace ω with $\omega = k_1\alpha_2 - k_2\alpha_1\gamma$, then, $A_3 = (x_1^*x_2^*y^*(D^*)^2)\chi$. Therefore, $A_3 > 0$ if and only if $x_i^* > 0$, $y^* > 0$ and $\chi > 0$. \square

Appendix F

Proof of $A_3 < 0$ if and only if $x_i^* > 0$ and $y^* > 0$ in the case where $p_i < 1$.

Proof. Once again, we have

$$A_3 = m_{31}m_{13}m_{22} + m_{23}m_{32}m_{11} - m_{13}m_{21}m_{32} - m_{23}m_{31}m_{12}$$

with m_{11} , m_{12} , m_{13} , m_{21} , m_{22} , and m_{23} given by (6.7)–(6.12), with

$$m_{31} = -\alpha_1 y^*((k_1 p_1 + \gamma k_2 p_2)(D^*)^2) \quad \text{and} \quad m_{32} = -\alpha_2 y^*((k_1 p_1 + \gamma k_2 p_2)(D^*)^2).$$

To simplify notation, we define $p = k_1 p_1 + \gamma k_2 p_2$.

Then,

$$\begin{aligned} A_3 &= y^*(-\alpha_1 p y^*)(D^*)^2(-x_1^*D^*)(\beta x_2^*D^*)(\alpha_2(1 - x_2^*) - (D^*)^{-1}) \\ &\quad + (-\gamma x_2^*D^*)y^*(-\alpha_2 p y^*(D^*)^2)(x_1^*D^*)(\alpha_1(1 - x_1^*) - (D^*)^{-1}) \\ &\quad - (-x_1^*D^*)(\alpha_1\gamma y^*x_2^*(D^*)^2)(y^*(D^*)^2)(-\alpha_2 p) \\ &\quad - (-\gamma x_2^*D^*)(y^*(D^*)^2)(-\alpha_1 p)(\alpha_2 y^*x_1^*(D^*)^2) \\ &= (x_1^*x_2^*y^*p(D^*)^4)(\alpha_1\beta(\alpha_2(1 - x_2^*) - (D^*)^{-1}) + \alpha_2\gamma(\alpha_1(1 - x_1^*) - (D^*)^{-1}) \\ &\quad - \alpha_1\alpha_2\gamma(1 - x_1^*) - \alpha_1\alpha_2\beta(1 - x_2^*)) \\ &= -\left(\frac{x_1^*x_2^*y^*p}{g^3}\right)(\alpha_1\beta + \alpha_1\gamma) < 0 \end{aligned}$$

since D^* , p , x_1^* , x_2^* , and $y^* > 0$. Therefore, $A_3 < 0$ if and only if $x_i^* > 0$ and $y^* > 0$ in the case that $p_i < 1$. \square

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