Quasi-equilibrium reduction in a general class of stoichiometric producer–consumer models

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This article compares a general closed nutrient, stoichiometric producer–consumer model to a two-dimensional ‘quasi-equilibrium’ approximation. We demonstrate that the quasi-equilibrium system can be rigorously analysed, resulting in nullcline-based criteria for the local stability of system equilibria and for the non-existence of periodic orbits. These results are applied to a study of the dependence of the reduced system on nutrient and energy enrichment. When energy and nutrient enrichment are considered together, the associated bifurcation structures of the two models are seen to share the same essential qualitative characteristics. However, numerical simulations of the three-dimensional parent model show highly complex domains of the persistence and extinction that by Poincare–Bendixson theory are not possible for the two-dimensional reduction. This complexity demonstrates a major difference between the two models, and suggests potential challenges in the use of either model for predicting the long-term behaviour of real-world systems at specific nutrient and energy levels.

Keywords: producer–consumer models; stoichiometry; energy and nutrient enrichment

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1. Introduction

Stoichiometric producer–consumer population models take into account biomass creation and conversion processes which depend simultaneously on the carbon and nutrient requirements of both the prey and predator species. Systems in which the consumer’s biomass creation rate depends on the variable nutrient levels of the producer population were first considered in the works of Andersen [2] and Hessen and Bjerkeng [12]. Process-based stoichiometric models require a higher number of state variables than traditional population models, which only monitor species’ carbon densities. Although this does not significantly complicate the numerical simulation of solutions, general conclusions regarding the system persistence, the existence of co-existence states (constant, and otherwise), and the response of such systems to environmental change often rely on simplifying assumptions permitting the reduction of the original model to a system of lower dimensionality. See, for example, [5,25,28], and the references therein.
Of particular interest is the response of producer–consumer systems under energy and/or nutrient enrichment. Rosenzweig [24] considered a variation of the classical Lotka–Volterra model that assumes Holling II-like saturation of the consumer’s foraging rate. He observed that increasing the available energy/carbon for the producer destabilized the model’s co-existence state. In such non-stoichiometric models, the system then supports a unique, attracting, periodic co-existence state, whose amplitude increases with further energy enrichment.

Loladze et al. [19] observed that energy enrichment in nutrient-closed stoichiometric producer–consumer models can induce significantly different responses than for the non-stoichiometric case. In the ‘LKE’ model, the producer nutrient concentration is assumed to be a function of that portion of the nutrient pool that is not sequestered by the consumer. Numerical simulations of their model suggest that (as in the Rosenzweig model) with increasing energy enrichment, a system co-existence equilibrium can lose stability, resulting in a stable, attracting, periodic co-existence state. However, under further energy enrichment, the periodic state grows until at a critical energy level it is lost. In [28], the authors consider a three-dimensional model for which the LKE model can be viewed as an approximation. Based on numerical simulations, they conclude that their more mechanistic model and the LKE model share the same qualitative responses to energy enrichment.

Diehl [5] proposed an alternate, more mechanistic, producer–consumer model. Similar to the LKE model, Diehl makes a producer nutrient uptake assumption that permits a reduction of the model’s dimension. However, Diehl observed a system response to energy enrichment that is different from both the Rosenzweig and LKE models.

More recently, Stech et al. [25] have proposed a general producer–consumer model that generalizes both the LKE and Diehl models. This model is three-dimensional, with producer internal nutrient concentration included as a state variable, along with producer and consumer spatial carbon densities. However, this new model is analytically intractable. The goal of this article is to contribute to our understanding of that model by (1) deriving and analysing the dynamic properties of a simplified ‘quasi-equilibrium’ model, then (2) examining the commonality and differences between that simplified model and the general (parent) model. Section 2 presents the general stoichiometric producer–consumer model of [25] and derives the two-dimensional quasi-equilibrium approximation. Section 3 is devoted to a rigorous analysis of the quasi-equilibrium approximation, including an analysis of system nullclines, stability of equilibria, and a criterion for the non-existence of periodic solutions. Section 4 applies these results to a discussion of the response of the reduced system to energy enrichment. Section 5 compares the simplified and parent systems in the context of nutrient and energy enrichment, as well as the persistence/extinction of model solutions. We will present numerical bifurcation computations that indicate that the two systems support similar responses to simultaneous nutrient and energy enrichment. However, if compared in the context of energy enrichment under a fixed, total system nutrient level, then their respective bifurcation structures can be significantly different. This section also describes numerical simulations that demonstrate the potential for the parent system to possess highly complex domains of the persistence/extinction, a property that is ruled out by Poincare–Bendixson theory for its autonomous, two-dimensional quasi-equilibrium approximation. This complexity appears to arise because of global interactions between stable and unstable manifolds rather than from local properties of equilibrium points. Section 6 contains a discussion of results and concluding remarks. Technical details are found in an appendix.

2. Model derivations

Let $P = P(t)$ represent the spatial carbon density of a producer population, and $C = C(t)$ the analogous density for a consumer class. It is assumed that both populations compete for a fixed
total amount of nutrient $N_T$. The amount of nutrient sequestered by the consumer is assumed to be $q_c C$, with $q_c > 0$ denoting a constant nutrient: carbon ratio for the consumer class. In contrast, the amount of nutrient sequestered by the producer class is assumed dynamic, consisting of a structural component $q_p P$, $q_p \geq 0$ and a flexible nutrient reserve, $RP$ used for the production of new producer biomass. Because the system is assumed to be closed with respect to nutrients, the amount of (‘mineralized’) nutrient not sequestered in producer or consumer biomasses is given by $N_m = N_T - q_c C - q_p P - RP$.

The general stoichiometric, producer–consumer model derived in [25] is given by

\begin{align}
P' &= \frac{\delta_p \mu_p(l_p)g(P)P - d_p P - f(P)PC}{\text{primary productivity mortality predation losses}}, \\
C' &= \frac{\delta_c \mu_c(l_c)f(P)PC - d_c C}{\text{secondary productivity mortality}}, \\
R' &= g(P) \left[ h(N_T - q_c C - q_p P - RP) - \delta_p \mu_p \left( \frac{\epsilon_p}{\delta_p q_p} \right) (R + q_p) \right].
\end{align}

The terms $l_p = \epsilon_p R/\delta_p q_p$ and $l_c = \epsilon_c (q_p + R)/\delta_c q_c$ define, respectively, producer and consumer growth limitation indices, with $0 < \delta_p, \delta_c \leq 1$ ($0 < \epsilon_p, \epsilon_c \leq 1$) being carbon (nutrient) assimilation/respiration-related reduction factors. See [25] for details.

For the purpose of generality, we do not specify algebraic forms for the undefined functions on the right of Equations (1)–(3). Rather, we assume that they obey the following qualitative hypotheses:

$H_g$: The factor $g(P)$ represents the maximal (nutrient-unrestricted) specific growth rate for the producer. We assume $g(P)$ to be a non-negative and (when positive) a decreasing function of $P$.

$H_f$: The function $f(P)P$ represents the specific ingestion rate for the consumer. Its qualitative nature is motivated by Holling-II type predation. The product $f(P)P$ is increasing and concave downward in $P$ with $f''(P) < 0$ and maximum specific ingestion rate $f_{\text{max}} \equiv \lim_{P \to \infty} f(P)P < \infty$.

$H_\mu$: Nutrient biomass production factors $\mu(l) = \mu_c(l)$ and $\mu(l) = \mu_p(l)$ are assumed to be piecewise smooth, non-decreasing and to satisfy $l/(1 + l) \leq \mu(l) \leq \min(1, l)$. Moreover, both $\mu(l)/l$ and $\mu'(l)$ are assumed to be non-increasing in $l > 0$.

Technical conditions $H_g$ on the production factors $\mu_p(l), \mu_c(l)$ are consequences of a generalized version of the synthesizing unit concept of Kooijman [14]. For the special case when the producer’s growth is independent of nutrient availability, we take $q_p = 0$ and interpret $\mu_p(l_p) = 1$ in Equations (1) and (3). See [25] for a full discussion.

$H_h$: Producer nutrient uptake rate is assumed to be of the form $h(N_m)g(P)P$, that is, proportionate to the producer maximal growth rate. The factor $h = h(N_m)$ is assumed to be a smooth, non-negative, increasing function of non-sequestered nutrient. We assume that $h'(n)$ is non-increasing, so that $h(n) \leq h'(0)n = \beta n$ for some $\beta > 0$.

The associated monoculture system ($C \equiv 0$) is analysed in [25]. The full system is also parameterized for algae/Daphnia systems. In that study, a numerical bifurcation analysis demonstrates the dynamical changes supported by Equations (1)–(3) under energy enrichment (modelled as an increase in $g$) for a fixed total system nutrient, $N_T$, and how this bifurcation structure is affected by changes in $N_T$. As in that presentation, we intentionally do not scale the system variables, since this tends to obscure the biological interpretation of our results. (If $q_p > 0$, the scaling $x = q_p P/N_T$, $y = q_c C/N_T$, $z = R/q_p$ effectively eliminates three parameters.)
The quasi-equilibrium model associated with Equations (1)–(3) is based on the assumption that the producer’s internal nutrient state equilibrates, responding to changes in environmental nutrient levels much more quickly than producer and consumer population growth rates. We therefore assume \( R' \equiv 0 \) and replace Equation (3) with the algebraic constraint

\[
h(N_T - q_c C - q_p P + RP) = \delta_p \mu_p \left( \frac{e_p R}{\delta_p q_p} \right) (R + q_p).
\]

Many of the producer–consumer models with variable producer stoichiometry rely (perhaps implicitly) on a quasi-equilibrium assumption of the type considered here. Under the special assumptions, \( h(n) = \beta n \) (no saturation allowed for producer nutrient uptake) and \( q_p = 0, \mu_p = 1 \) (producer primary productivity is independent of producer nutrient reserves), the producer nutrient concentration can be computed from Equation (4) to be \( R = (N_T - q_c C)/(\delta_p/\beta + P) \). This is the form derived by quasi-equilibrium arguments in [16] (see also [27]). If one further assumes an immediate nutrient uptake (\( \beta \to \infty \)), one obtains the form used in the LKE model [19]. Similar observations are made in [28] for an extension of the LKE model to one in which producer nutrient uptake is not instantaneous. As a step towards understanding an intractable producer–consumer–sediment nutrient-reserve nutrient system, Diehl [5] also considers a simplified model based on immediate mineralization and instantaneous nutrient uptake by the producer.

Because the quasi-equilibrium approximation reduces the system to a planar one, it provides a clear technical advantage over the original, parent system. In the models of [2,15,19,22,23,26], the producer nutrient concentration is based on the assumption of an immediate recycling of system nutrients. In [5], a two-dimensional model is obtained from a four-dimensional producer–consumer model with explicit sediment class. Hall et al. [11] assumes instantaneous nutrient recycling in an open producer–consumer system with multiple nutrients. For those of these studies that consider the issue, the general observation is that the quasi-equilibrium system maintains many of the qualitative properties of the higher dimensional systems from which it is derived. However, we will show in Section 5 that under biologically reasonable parameter values, the producer, consumer, and the producer nutrient reserve model supports complicated dynamical behaviours that are not possible in the quasi-equilibrium approximation where the resource is assumed to be at steady state.

Equation (4) defines \( R \) implicitly. From the form of this equation, one can show that any solution can be viewed as having the structure \( R = R(N_T - q_c C - q_p P, P) \). In certain special cases, a closed-form expression for this ‘quasi-equilibrium surface’ can be obtained algebraically. For example, if \( \mu_p(l) = l/(l + 1) \) (Droop [7] producer biomass synthesis) and \( h(n) = (h_{max}^{-1} + (\beta n)^{-1})^{-1} \) (Monod-based producer nutrient uptake), then \( R \) can be computed as the root of a cubic polynomial. The surface is illustrated in Figure 1. The expression for \( R \) is computable with Mathematica [20], but is too long and opaque to be useful to our study.

Figure 2 illustrates the time-series profile for a typical asymptotically periodic solution of Equations (1)–(3). For this simulation, we specify the general model with the \( g(P) = \max(r(b - P/K), 0) \) (logistic producer growth rate), \( f(P)P = (f_{max}^{-1} + (\alpha P)^{-1})^{-1} = f_{max}^{-1}/(f_{1/2} + P) \) (Holling II predator functional response), and \( \mu_c(l) = (l^{-1} + 1 - (1 + l)^{-1})^{-1} \) (Poisson arrival time type consumer biomass synthesizing unit), and with \( \mu_p \) and \( h \) as above. Model parameter default values and ranges are given in Table 1. See [25] for a discussion of model parameterization and the supporting literature.

In addition to the computed producer nutrient concentration, \( R(t) \), we have plotted in Figure 2 the quasi-equilibrium approximation to this concentration as given by the solution of Equation (4). It is visually evident that both values are very similar, and this property is seen to hold for a wide range of parameter selections.

Lemma A.1 of the appendix shows that if the producer’s nutrient use efficiency is above its carbon use efficiency \( (\epsilon_p \geq \delta_p) \), then the quasi-equilibrium surface is defined and unique for all
Figure 1. The quasi-equilibrium surface in the case $\mu_p(l) = l/(l + 1)$ and $h(n) = (h_{\text{max}}^{-1} + (\beta n)^{-1})^{-1}$, with parameter selections $N_T = 0.02$, $\varepsilon_p = \delta_p = 1$, $q_p = 0.0045$, $q_c = 0.038$, $h_{\text{max}} = 0.01$, and $\beta = 15$. The surface is defined over the biologically feasible region $q_c C + q_p P \leq N_T$. See [25] for a discussion of parameter values and units.

Figure 2. The solid curves show a time-series plot of a typical solution of Equations (1)–(3). The system is essentially a periodic behaviour for $t \geq 100$ days. For the sake of clarity, producer (green) and consumer (red) coordinates are multiplied by factors of 10. Producer flexible nutrient pool (blue) is depicted in terms of its relation to producer structural nutrient, $R/q_p$ (a quantity that is closely related to the algae ‘nutrient storage capacity’ of [2]). The system was simulated with the default parameters of Table 1 [25] and with initial conditions $P(0) = 0.15\ \text{mg/l}$, $C(0) = 0.2\ \text{mg/l}$, and $R(0) = 0.04\ \text{mg}$ producer nutrient/mg producer carbon. The dashed curve represents the approximation of the producer flexible nutrient pool concentration as computed using the system’s quasi-equilibrium approximation $R(N_T - q_c C(t) - q_p P(t), P(t))$. 
selections of \( h \) and \( \mu_p \) (subject only to hypotheses \( H_h \) and \( H_\mu \)). This surface shares the essential qualitative characteristics as the surface of Figure 1. Specifically, \( R(N_T - q_c C - q_p P, P) \) is defined and is positive on the interior of the biologically feasible region \( 0 \leq q_c C + q_p P \leq N_T \). It is a non-increasing function of both \( P \) and \( C \), and \( R(N_T - q_c C - q_p P, P) = 0 \) when \( q_c C + q_p P = N_T \). By a straightforward calculation, the gradient \( (\partial R/\partial P, \partial R/\partial C) \) is proportionate to \( h'((N_T - q_c C - q_p P - RP)(q_p + R, q_c)) \). Therefore, the level curves \( R(N_T - q_c C - q_p P, P) = R_0 \) are straight lines with slopes \(- (q_p + R_0)/q_c\).

From Lemma A.1, we can draw specific conclusions regarding the dependence of the quasi-equilibrium surface on a total system nutrient, \( N_T \). We define \( h_{\max} = \lim_{n \to \infty} h(n) \). Then, for fixed \( P \) and \( C \), \( R(N_T - q_c C - q_p P, P) \) is a non-decreasing function of \( N_T \), and as \( N_T \to \infty \), \( R(N_T - q_c C - q_p P, P) \to R_{\max} \), with \( R_{\max} \) defined as the unique solution to

\[
h_{\max} = \delta_p \mu_p \left( \frac{\varepsilon_p R_{\max}}{\delta_p q_p} \right) (R_{\max} + q_p).
\]

This limit is uniform on regions of the form \( 0 \leq q_c C + q_p P \leq n < N_T \). By assumption \( H_\mu \), \( R_{\max} \) is finite if and only if \( h_{\max} \) is finite. Furthermore, if producer nutrient uptake can be fully saturated in the sense that \( h(n) = h_{\max} \) for some \( n > 0 \), then \( R = R(N_T - q_c C - q_p P, P) \) will also become fully saturated for large \( N_T \). That is, for each \( P, C \geq 0 \) in the feasible region, one has \( R(N_T - q_c C - q_p P, P) = R_{\max} \) for all sufficiently large \( N_T \). By Lemma A.1, a region of such saturation will be ‘triangular’ in shape \( q_c C + q_p P \leq n \). The nearly triangular ‘plateau’ observed in Figure 1 suggests being close to such saturation.

Additionally, Lemma A.1 provides upper and lower bounds on the quasi-equilibrium surface \( R(N_T - q_c C - q_p P, P) \), as well as its asymptotic approximation for \( q_c C + q_p P \approx N_T \). For example, we have the simple upper bound \( R(N_T - q_c C - q_p P, P) \leq (N_T - q_c C - q_p P)/P \), which conveys the interpretation that the concentration of the flexible nutrient pool can be no larger than that obtained by distributing all non-structurally sequestered nutrient uniformly across the producer population. If \( q_p > 0 \) and \( q_c C + q_p P \approx N_T \), then the quasi-equilibrium surface satisfies \( R(N_T - q_c C - q_p P, P) = (N_T - q_c C - q_p P)/(\varepsilon_p / \beta + P) + o((N_T - q_c C - q_p P)^2) \). These results will be used in the next section. It also follows from Lemma

| State variables | Units | Default and range |
|-----------------|-------|------------------|
| \( P \), producer | mg \( P \) carbon/l | 1.1, (1.0, 3.0) |
| \( C \), consumer | mg \( C \) carbon/l | 1.25, (0.25, 3.0) |
| \( R \), producer nutrient reserve | mg \( P \) nutrient/ mg \( P \) carbon | 0.05, (0.01, 0.1) |

| Parameters | Units | Default and range |
|------------|-------|------------------|
| Maximal producer specific growth rate, \( r \) | day\(^{-1} \) | 0.24, (0.02, 0.3) |
| Maximal producer carrying capacity, \( K \) | mgPcarbon/l | 0.8, (0.5, 1.0) |
| Producer specific natural mortality rate, \( d_p \) | day\(^{-1} \) | Unitless |
| Consumer specific mortality rate (no respiration), \( d_c \) | Unitless | 0.9, (0.5, 1.0) |
| Maximal producer carbon assimilation efficiency, \( q_p \) | Unitless | 0.8, (0.5, 1.0) |
| Maximal producer nutrient assimilation efficiency, \( \varepsilon_p \) | Unitless | 0.9, (0.5, 1.0) |
| Maximal consumer carbon assimilation efficiency, \( b_c \) | Unitless | 0.8, (0.5, 1.0) |
| Maximal consumer nutrient assimilation efficiency, \( \delta_c \) | Unitless | 0.9, (0.5, 1.0) |
| Maximal consumer specific predation rate, \( f_{\max} \) | day\(^{-1} \) | 1.0, (0.75, 1.0) |
| Consumer predation half-saturation constant, \( f_{1/2} \) | mg \( P \) carbon/l | 0.2, (0.12, 0.25) |
| Producer (‘structural’) nutrient: carbon ratio, \( q_p \) | mg \( P \) nutrient/ mg \( P \) carbon | 0.0045, (0.00085) |
| Consumer nutrient: carbon ratio, \( q_c \) | mg \( C \) nutrient/ mg \( C \) carbon | 0.0375, (0.01, 0.04) |
| Producer growth-specific nutrient uptake affinity, \( \beta \) | l/ \( mg \) nutrient | 6.0, (0.1, 25.0) |
| Producer maximal growth-specific nutrient uptake, \( h_{\max} \) | mg \( P \) nutrient/ \( mg \) \( P \) carbon | 0.1, (0.05, 1.0) |
| Total system nutrient, \( N_T \) | mg \( P \) nutrient/ \( l \) | 0.02, (0.0031, 0.031) |
| Energy enrichment factor, \( b \) | Unitless | 1, (0, 2) |
A.1 that the interior of the biologically feasible region is positively invariant for solutions of Equations (1), (2), (4).

3. Properties of the quasi-equilibrium model

In this section, we analyse Equations (1) and (2) with \( R = R(N_T - q_c C - q_p P, P) \) defined as the solution to Equation (4) in the previous section. Constituent functions \( g, f, h, \mu_p \) and \( \mu_c \) are not taken here to have any particular algebraic form, but must satisfy hypotheses \( H_g, H_f, H_h, \) and \( H_{\mu} \). Nullclines are described, and with these we derive graphical means of determining the stabilities of equilibria. The section concludes with a result that rules out the existence of periodic solutions of the quasi-equilibrium system in certain regions of the phase plane.

To motivate the discussion, we illustrate the nullclines and boundary line \( q_c C + q_p P = N_T \) in Figure 3 for the same function and parameter selections used for Figure 1. Also shown is the \( (P, C) \) projection of the solution in Figure 2.

![Figure 3](image-url)

Figure 3. Producer nullcline (shown in green), consumer nullcline (red), and boundary to the feasible region (blue) for the constituent function and model parameters for Figure 2. The projection of the solution trajectory (black) demonstrates a consistency of the solutions to Equations (1)-(3) with the quasi-equilibrium nullclines.
3.1. The producer nullcline

If \( q_p = 0 \) (\( \mu_p \equiv 1 \)), the producer nullcline \( P' = 0 \) is independent of total system nutrient, \( N_T \) and can be explicitly computed. Assuming \( q_p > 0 \), we first define the producer’s nutrient-saturated region

\[
\Sigma_p = \left\{ (P, C) \mid \mu_p \left( \frac{\varepsilon_p R(N_T - q_c C - q_p P, P)}{q_p} \right) = \mu_p \left( \frac{\varepsilon_p R_{\text{max}}}{q_p} \right) \right\},
\]

with \( R_{\text{max}} \) defined implicitly by Equation (5). If the producer’s nutrient uptake becomes fully saturated \( h(N_T) \equiv h_{\text{max}} \) for large \( N_T \), then by Lemma A.1 (iv), \( \Sigma_p \) will be nonempty for all large \( N_T \), and it will be triangular in shape \( q_c C + q_p P \leq n \), for some \( n \leq N_T \). Any portion of the producer nullcline within this region is given explicitly by \( C = (\delta_p \mu_p ((\varepsilon_p/\delta_p)R_{\text{max}}/q_p)g(P) - d_p)/(g(P) \right\} \), a formula that also includes in the limit the case \( q_p = 0 \).

By \( H_\mu \) and the properties of \( R(N_T - q_c C - q_p P, P) \), the curve \( C = (\delta_p \mu_p ((\varepsilon_p/\delta_p)R(N_T, 0)/q_p)g(P) - d_p)/(g(P) \right\} \) defines an upper bound on the location of the producer nullcline. The nullcline clearly must reside in the region where \( g(P) > 0 \). Thus, the nontrivial \( (P > 0) \) nullcline equation can be written implicitly as

\[
\delta_p \mu_p \left( \frac{\varepsilon_p R(N_T - q_c C - q_p P, P)}{q_p} \right) = \frac{d_p + f(P)C}{g(P)}.
\]

The expression on the left of Equation (6) defines a surface over the biologically feasible region \( 0 \leq q_c C + q_p P \leq N_T \). The qualitative shape of this surface is similar to that of \( R(N_T - q_c C - q_p P, P) \), since \( \mu_p \) is non-decreasing. In particular, it is a positive, non-increasing function of both \( P \) and \( C \) that vanishes at the boundary line \( q_c C + q_p P = N_T \).

The expression on the right of Equation (6) defines a surface over that region for which \( g(P) > 0 \). This surface is, for fixed \( P > 0 \) increasing in \( C > 0 \), and for \( C = 0 \), it is strictly increasing in \( P \). Therefore, there will be an intersection of the two surfaces in the biologically feasible region (and a producer nullcline in the positive quadrant) if and only if the maximum of the left side is larger than the minimum of the right side (both occurring at \( (P, C) = (0, 0) \)). That is, when \( \delta_p \mu_p ((\varepsilon_p/\delta_p)R(N_T, 0)/q_p) > d_p/g(0) \). This inequality can be interpreted to mean that the producer’s maximal reproductive number \( \delta_p \mu_p ((\varepsilon_p/\delta_p)R(N_T, 0)/q_p)g(0)/d_p \) is greater than one. By the discussion concerning Equation (5), this condition will hold for all large \( N_T \) if and only if \( \delta_p \mu_p ((\varepsilon_p/\delta_p)R_{\text{max}}/q_p)g(0)/d_p > d_p \).

Because \( P' = (-d_p - f(P)C)P < 0 \) along the boundary line \( q_c C + q_p P = N_T \), any producer nullcline must lie strictly within the biologically feasible region and will connect with the \( P \) axis at \( P = \hat{P}_m \), the producer monoculture equilibrium. This equilibrium satisfies \( \delta_p \mu_p ((\varepsilon_p/\delta_p)R(N_T - q_p P, P)/q_p)g(P) - d_p = 0 \), and is unique by \( H_\delta \) and since by Lemma A.1, the left side of this equation is a decreasing function of \( P \).

Using \( H_f \), \( H_\mu \) and the properties of \( R(N_T - q_c C - q_p P, P) \), one computes that \( \partial/\partial C (\delta_p \mu_p ((\varepsilon_p/\delta_p)R(q_p)/q_p)g(P) - d_c - f(P)C) \leq -f(P) < 0 \). The implicit function theorem then shows that the producer nullcline is described by a smooth function of \( P \) over the interval \( 0 \leq P \leq \hat{P}_m \).

3.2. The Consumer Nullcline

By analogy to the producer case, we define the consumer nutrient saturation region as

\[
\Sigma_c = \left\{ (P, C) \mid \mu_c \left( \frac{\varepsilon_c (R(N_T - q_c C - q_p P, P) + q_p)}{q_c} \right) = \mu_c \left( \frac{\varepsilon_c (R_{\text{max}} + q_p)}{q_c} \right) \right\},
\]
Figure 4. The dependence of the consumer nullcline on varying specific consumer mortality rates $d_c$. Consumer nullclines are computed from Equation (7) with $R$ computed from Equation (4). Constituent functions $\mu_p$, $f(P)$ and $h(n)$ are as in Figures 1 and 2, with parameters $\beta = 2.0$, $h_{\text{max}}^{-1} = 0$, $f_{1/2} = 0.2$, $f_{\text{max}} = 0.8888$, $\epsilon_c = \epsilon_p = 1.0$, $\delta_p = 0.8$, $\delta_c = 0.5$, $N_T = 0.02$, $q_p = 0.0075$, $q_c = 0.04$ and consumer biomass production using $\mu_c(l) = \min(1, l)$ (Liebig Law of the Minimum). The triangular consumer nutrient saturation region $\Sigma_c$ is shaded in blue. The domain of the consumer nullcline is shown in the case $d_c = 0.30$ with $I_{N_T} = (P_l^*, P_u^*)$ and $P_l^* = P_u^*$ as defined just prior to Theorem 3.1. For $d_c = 0.15$, the consumer nullcline intersects the boundary of the biologically feasible region at $(P_b^*, C_b^*)$ with $P_b^*$ defined in case (ii) of Theorem 3.1.

with $R_{\text{max}}$ defined implicitly as the solution to Equation (5). When nonempty, this region is triangular in shape, as illustrated in Figure 4. By the properties of $R(N,P)$ derived in Lemma A.1, points in $\Sigma_c$ can be characterized as satisfying $\mu_c^\prime(\frac{\epsilon_c}{\delta_c})(R(N_T - q_c C - q_p P, P) + q_p)/q_c)(\partial R/\partial N_T)(N_T - q_c C - q_p P, P) = 0$. The first factor being zero corresponds to the nutrient saturation of the consumer’s food source $\mu_c(\frac{\epsilon_c}{\delta_c})(R + q_p)/q_c) = 1$. By Lemma A.1, the second factor being zero corresponds to the saturation of the producer’s nutrient uptake mechanism: $h(N_T - q_c C - q_p P - R P) = h_{\text{max}}$.

The nontrivial ($C > 0$) consumer nullcline consists of those points for which

$$d_c = \frac{\gamma_c \mu_c \left( R(N_T - q_c C - q_p P, P) + q_p \right)}{q_c} = d_c/Pf(P).$$

(7)
However, for $q_p > 0$, it is clear that for all $N_T$ sufficiently small (or all $d_c$ sufficiently large), Equation (7) will not be solvable. Using $H_\mu$ and the fact that $P \leq N_T/q_p$, a computable sufficient condition for Equation (7) to be unsolvable in the positive quadrant is that $\delta_c(N_T/q_p)f(N_T/q_p) < d_c$. More precisely, the expression on left side of Equation (7) defines a surface that is non-increasing in both $P$ and $C$. The expression on the right defines a surface (independent of $C$) that is decreasing and concave upward in $P$. This surface is bounded from below by $d_c/f_{\text{max}}$ and is unbounded as $P \to 0^+$. If follows from $H_\mu$, $H_f$ and Lemma A.1 that Equation (7) will also never have a solution in the biologically feasible region if

$$\delta_c \mu_c \left( \frac{\varepsilon_c (R_{\text{max}} + q_p)}{q_c} \right) f_{\text{max}} < d_c. \quad (8)$$

That is to say, when at its largest possible predation rate and maximal food nutrient concentration the consumer’s basic reproductive number $\delta_c \mu_c ((\varepsilon_c/\delta_c)(R_{\text{max}} + q_p)/q_c)f_{\text{max}}/d_c$ is less than one. Moreover, under such a situation, Equation (2) easily shows that $C(t) \to 0$ for all solutions of Equations (1), (2), (4), as well as for the parent system (1)–(3).

Since by Lemma A.1, the left side of Equation (7) is a non-increasing function of $C$ that is zero on the boundary line $q_c C + q_p P = N_T$, the existence of a consumer nullcline $C^* = 0$ interior to the biologically feasible region is determined by the solvability of

$$\delta_c \mu_c \left( \frac{\varepsilon_c (R(N_T - q_p P, P) + q_p)}{q_c} \right) > d_c/P f(P) \quad (9)$$

on the interval $0 \leq P \leq N_T/q_p$. We define the $N_T$-dependent interval $I_{N_T} \equiv \{ P > 0|\delta_c \mu_c ((\varepsilon_c/\delta_c)(R(N_T - q_p P, P) + q_p)/q_c)P f(P) > d_c \}$ and set $P_i^* = \inf[P \in I_{N_T}]$ and $P_u^* = \sup[P \in I_{N_T}]$. By $H_\mu$, $H_f$ and the properties of $R$, the interval $I_{N_T}$ (when nonempty) will grow with increasing $N_T$ (or decreasing $d_c$.)

If $\Sigma_c \neq \emptyset$, any solution of $C = 0$ within $\Sigma_c$ must coincide with the (unique) solution $P = P_{\Sigma}$ of $\delta_c \mu_c ((\varepsilon_c/\delta_c)(R_{\text{max}} + q_p)/q_c)P \Sigma f(\Sigma) = d_c$. Outside of $\Sigma_c$, $\mu_c ((\varepsilon_c/\delta_c)(R + q_p)/q_c)\partial R/\partial N_T(N_T - q_c C - q_p P, P) > 0$, so the implicit function theorem guarantees that the consumer nullcline is described by the graph of a smooth function of $P$.

With increasing $P$, any consumer nullcline must either intersect the $P$ axis at $P = P_i^*$ or the boundary line $q_c C + q_p P = N_T$. With decreasing $P$, the nullcline will either intersect the $P$ axis at $P = P_i^*$ or terminate at a point $(P, C)$, where $\mu_c ((\varepsilon_c/\delta_c)(R + q_p)/q_c)\partial R/\partial N_T(N_T - q_c C - q_p P, P) = 0$; that is, on the boundary of $\Sigma_c$.

The following theorem shows that if the inequality (8) is reversed, then for all $N_T$ sufficiently large, there is a nontrivial $C^* = 0$ nullcline in the biologically feasible region. The two cases of the theorem correspond to having this nullcline terminate (with increasing $P$) at an intersection with the $P$ axis or at a point on the boundary line $q_c C + q_p P = N_T$.

**Theorem 3.1** Assume $\delta_c \mu_c ((\varepsilon_c/\delta_c)(R_{\text{max}} + q_p)/q_c)f_{\text{max}} > d_c$. Then, for all $N_T$ sufficiently large, the set $I_{N_T}$ is nonempty. Moreover, $P_{\Sigma} \leq P_i^* \leq (N_T/q_c) \varepsilon_c f_{\text{max}}/d_c$ and $\lim_{N_T \to \infty} P_i^* = P_{\Sigma}$. If, in addition, $q_p > 0$ : 

(i) If $\delta_c \mu_c ((\varepsilon_c/\delta_c)q_p/q_c)f_{\text{max}} < d_c$, then $P_u^* < N_T/q_p$.

(ii) If $\delta_c \mu_c ((\varepsilon_c/\delta_c)q_p/q_c)f_{\text{max}} > d_c$, then for all $N_T$ sufficiently large $P_u^* = N_T/q_p$, and the consumer nullcline intersects the boundary line $q_c C + q_p P = N_T$ at $(P, C) = (P_b^*, C_b^*)$, where $P_b^*$ is defined to be the unique solution of $\delta_c \mu_c ((\varepsilon_c/\delta_c)q_p/q_c)P_{f} f(P_b^*) = d_c$ and $C_b^* = (N_T - q_p P_b^*)/q_c$.

**Proof** Because $\mu_c(l) \leq l$, points on the consumer nullcline must satisfy $0 \leq \delta_c((\varepsilon_c/\delta_c)R(N_T - q_c C - q_p P, P)/q_c)f_{\text{max}} - d_c$, and (by Lemma A.1 (i)) $0 \leq (\varepsilon_c/q_c)(N_T - q_c C)/P f_{\text{max}} - d_c$. Thus,
any consumer nullcline must lie within the region \( C \leq N_T/q_c - d_c/\epsilon_c f_{\text{max}} P \). The upper bound on \( P^*_f \) follows. By \( H_f, Pf(P) \) is strictly increasing for \( P \geq 0 \). For fixed \( P \in (P_\Sigma, N_T/q_p) \),

\[
\lim_{N_T \to \infty} \frac{\delta_c \mu_c}{\delta_c} \left( \frac{\epsilon_c}{\epsilon_c} \frac{(R(N_T - q_p P, P) + q_p)}{q_p} \right) Pf(P) = \delta_c \mu_c \left( \frac{\epsilon_c}{\epsilon_c} \frac{(R_{\text{max}} + q_p)}{q_p} \right) Pf(P)
\]

by Lemma A.1 (v). Thus, \( P \in I_{N_T} \) for all \( N_T \) sufficiently large. On the other hand, for each \( P < P_\Sigma \) and all \( N_T \geq 0 \), we have \( P \notin I_{N_T} \) since

\[
\delta_c \mu_c \left( \frac{\epsilon_c}{\epsilon_c} \frac{(R(N_T - q_p P, P) + q_p)}{q_p} \right) Pf(P) < \delta_c \mu_c \left( \frac{\epsilon_c}{\epsilon_c} \frac{(R_{\text{max}} + q_p)}{q_p} \right) P_\Sigma f(P_\Sigma) = d_c.
\]

To show (i), we note that if \( \delta_c \mu_c ((\epsilon_c/\delta_c) q_p/q_c) f_{\text{max}} < d_c \), then along the boundary line \( q_c C + q_p P = N_T \), \( C' = [\delta_c \mu_c ((\epsilon_c/\delta_c) q_p/q_c) Pf(P) - d_c] C \leq [\delta_c \mu_c ((\epsilon_c/\delta_c) q_p/q_c) f_{\text{max}} - d_c] C < 0 \). Thus \( P^*_n < N_T/q_p \).

As for (ii), if \( \delta_c \mu_c ((\epsilon_c/\delta_c) q_p/q_c) f_{\text{max}} > d_c \), then \( C' = 0 \) is satisfied at \( P^*_n \) as defined above. Note that because \( Pf(P) \) is increasing in \( P \) and \( \mu_c \) is non-decreasing, it follows that the producer internal nutrient concentration \( R(N_T - q_c C - q_p P, P) \) will decrease along any consumer nullcline as \( P \) increases. Since \( R(N_T - q_c C_b - q_p P^*_b, P_b) = 0 \), the \( C' = 0 \) nullcline cannot re-enter the biologically feasible region for \( P > P^*_b \).

The inequality of case (i) can be interpreted to mean that the basic reproductive number of the consumer is less than one, assuming maximal predation on a food source possessing only of structurally bound producer nutrient. The opposite case (ii) applies to consumers that under maximal predation can persist on producer structural nutrient alone. See Figure 3 (and Figure 5 below) for situations where \( \Sigma_c \) is empty. In contrast, Figure 4 illustrates the possible consumer nullclines in a situation in which the consumer biomass conversion factor reaches saturation (\( \Sigma_c \neq \emptyset \)).

As Figure 4 demonstrates, by Lemma A.1 (iv), if consumer biomass conversion becomes fully nutrient saturated (in the sense that \( \mu_c ((\epsilon_c/\delta_c) (R(N_T, 0) + q_p) / q_c) = \mu_c ((\epsilon_c/\delta_c) (R_{\text{max}} + q_p) / q_c) \) for large \( N_T \), then \( P^*_f = P_\Sigma \) for all sufficiently large \( N_T \). The consumer nullcline includes that portion of the vertical line segment \( P = P_\Sigma \) that is contained in the saturation region \( \Sigma_c \). In the general case, \( \lim_{N_T \to \infty} \mu_c ((\epsilon_c/\delta_c) (R(N_T - q_c C - q_p P, P) + q_p) / q_c) = \mu_c ((\epsilon_c/\delta_c) (R_{\text{max}} + q_p) / q_c) \) uniformly on regions of the form \( 0 \leq q_c C + q_p P \leq N(\text{fixed}) < N_T \). Thus, the consumer nullcline approaches the vertical line segment \( P = P_\Sigma \) uniformly on regions of this type as \( N_T \to \infty \).

### 3.3. Stability of equilibria

Local stability of equilibria to Equations (1), (2), (4) can be determined using linearization arguments complicated by the generality of the constituent functions and the implicit definition of \( R \). For convenience, we write the quasi-equilibrium system as \( P' = F(P, C)P \) and \( C' = G(P, C)C \). Then, the Jacobian for the system reads

\[
J = \begin{pmatrix}
F + P \frac{\partial F}{\partial P} & P \frac{\partial F}{\partial C} \\
C \frac{\partial G}{\partial P} & G + C \frac{\partial G}{\partial C}
\end{pmatrix}
\]

(12)
Figure 5. Multiple co-existence equilibria $E_1 = (0.123, 0.107)$, $E_2 = (0.367, 0.135)$, $E_3 = (0.932, 0.0770)$, $E_4 = (1.464, 0.00957)$, and $E_m = (1.542, 0.0)$ for quasi-equilibrium system (1), (2), (4). Constituent functions are described in the text, with parameters $r = 1.0$, $\phi = 0.3$, $\kappa = 6.0$, $\beta = 1.2$, $f_{1/2} = 0.125$, $f_{\text{max}} = 0.8888$, $\epsilon_p = \epsilon_c = 1.0$, $\delta_p = 0.8$, $\delta_c = 0.6$, $d_p = 0.1$, $d_c = 0.12$, $N_T = 0.00949$, and $b = 0.721$. Both $\Sigma_p = \phi$ and $\Sigma_c = \phi$ for this set of parameter values. The trivial nullclines $P = 0$ and $C = 0$ are not shown.

\[ \frac{\partial F}{\partial P} = \delta_p \mu_p g'(P) - f'(P)C + \frac{\epsilon_p}{q_p} g(P) \left( -q_p \frac{\partial R}{\partial N} + \frac{\partial R}{\partial P} \right) \mu'_p, \]
\[ = \delta_p \mu_p g'(P) - f'(P)C \quad \text{for} \quad (P, C) \in \Sigma_p \]  \hspace{1cm} (13)

\[ \frac{\partial F}{\partial C} = -f(P) - \frac{q_c \epsilon_p}{q_p} g(P) \frac{\partial R}{\partial N} \mu'_p, \]
\[ = -f(P) \quad \text{for} \quad (P, C) \in \Sigma_p \]  \hspace{1cm} (14)

\[ \frac{\partial G}{\partial P} = \delta_c \mu_c \frac{d}{dP} (Pf(P)) + \frac{\epsilon_c}{q_c} Pf(P) \left( -q_p \frac{\partial R}{\partial N} + \frac{\partial R}{\partial P} \right) \mu'_c, \]
\[ = \delta_c \mu_c \frac{d}{dP} (Pf(P)) \quad \text{for} \quad (P, C) \in \Sigma_c \]  \hspace{1cm} (15)
The diagonal elements are the eigenvalues of $J$ with eigenvalues $\bar{\mu}$ corresponds to the creation of a system co-existence equilibrium via a transcritical bifurcation.

The trivial (no life) equilibrium $(P, C) = (0, 0)$ corresponds to the trivial nullclines $P = 0$ and $C = 0$. Here, one computes

$$J = \begin{bmatrix} F & 0 \\ 0 & G \end{bmatrix} = \begin{bmatrix} \delta_p \mu_p (\frac{\epsilon_p R(N_T, 0)}{\delta_p}) g(0) - d_p & 0 \\ 0 & -d_c \end{bmatrix}.$$  

The diagonal elements are the eigenvalues of $J$. Thus, $(0, 0)$ will be locally asymptotically stable (LAS) if $\delta_p \mu_p ((\epsilon_p / \delta_p) R(N_T, 0)/q_p) g(0) < d_p$. Moreover, under this inequality, $P' = [\delta_p \mu_p ((\epsilon_p / \delta_p) R/N_T, 0)/q_p) g(P) - d_p - f(P)C]P \leq [\delta_p \mu_p ((\epsilon_p / \delta_p) R(N_T, 0)/q_p) g(P) - d_p]P$ shows that $P \to 0$ for all solutions of Equations $(1), (2), (4)$, making $(0, 0)$ globally attracting. The origin will be an unstable saddle under the reversed inequality $\delta_p \mu_p ((\epsilon_p / \delta_p) R(N_T, 0)/q_p) g(0) - d_p > d_p$ (the same condition under which the positive producer monoculture, $\tilde{P}_m$ exists). A transition from one inequality to the other corresponds to the creation of a producer monoculture equilibrium via transcritical bifurcation.

At the monoculture equilibrium,

$$(P, C) = (\tilde{P}_m, 0), J = \begin{bmatrix} \tilde{P}_m \frac{\partial F}{\partial P} & \tilde{P}_m \frac{\partial F}{\partial C} \\ 0 & G \end{bmatrix}$$

with eigenvalues $\tilde{P}_m \partial F / \partial P(\tilde{P}_m, 0) \leq \delta_p \mu_p g'(\tilde{P}_m) \tilde{P}_m < 0$ (by $H_g$ and $H_f$) and $G(\tilde{P}_m, 0) = \delta_c \mu_c ((\epsilon_c / \delta_c)(R(N_T - q_p \tilde{P}_m, \tilde{P}_m) + q_p)/q_c) \tilde{P}_m f(\tilde{P}_m) - d_c$. Considering the discussion regarding the consumer nullcline, $(\tilde{P}_m, 0)$ will be unstable when $\tilde{P}_m$ is interior to $I_N$ (that is, lies below the consumer nullcline.) Equivalently, $(\tilde{P}_m, 0)$ will be unstable if at $P = \tilde{P}_m$, the consumer reproductive number $\delta_c \mu_c ((\epsilon_c / \delta_c)(R(N_T - q_p \tilde{P}_m, \tilde{P}_m) + q_p)/q_c) \tilde{P}_m f(\tilde{P}_m) - d_c$ is greater than one, and it will be LAS when this number is less than one. The transition from one case to the other corresponds to the creation of a system co-existence equilibrium via a transcritical bifurcation.

We remark that when phrased in terms of the producer and consumer reproductive numbers, the stability results for the trivial $(0, 0)$ and monoculture equilibrium $(\tilde{P}_m, 0)$ can be extended to the full, three-dimensional system $(1)-(3)$. Using the fact that the plane $C = 0$ is invariant for the system, the results can be proved without performing a complicated, three-dimensional Jacobian computation. Details are omitted.

Co-existence equilibria $(\bar{P}, \bar{C})$ correspond to intersection points of the producer and consumer nullclines interior to the biologically feasible region. Only in special cases are these nullclines explicitly computable since they are based on the implicitly define function $R$. Thus, we will derive graphical criteria for determining the stability types of co-existence equilibria. At any such equilibrium, one has

$$J = \begin{bmatrix} \tilde{P}_m \frac{\partial F}{\partial P} & \tilde{P}_m \frac{\partial F}{\partial C} \\ \bar{P} \frac{\partial G}{\partial P} & \bar{C} \frac{\partial G}{\partial C} \end{bmatrix}$$

with the characteristic polynomial

$$\lambda^2 - \left( \tilde{P}_m \frac{\partial F}{\partial P} + \bar{C} \frac{\partial G}{\partial C} \right) \lambda + \tilde{P}_m \bar{C} \left( \frac{\partial F}{\partial P} \frac{\partial G}{\partial C} - \frac{\partial F}{\partial C} \frac{\partial G}{\partial P} \right).$$  

(17)
By implicit differentiation, the slope of the producer nullcline $F(P, C) = 0$ can be computed as

$$\frac{dC}{dP} \Bigg|_{P=0} = -\frac{\partial F/\partial P}{\partial F/\partial C} \tag{18}$$

since (using $H_u$ and Lemma A.1 (ii)) $\partial F/\partial C \leq -f(P) < 0$.

If $(\bar{P}, \bar{C}) \in \Sigma_c$, then $\bar{P} = \bar{P}_\Sigma$ as defined just prior to Theorem 3.1. Using Equations (16) and (18), the characteristic polynomial (17) can be expressed as

$$\lambda^2 + \left( \bar{P} \frac{\partial F}{\partial C} \frac{dC}{dP} \bigg|_{P=0} \right) \lambda - \bar{P} \bar{C} \frac{\partial F}{\partial C} \frac{\partial G}{\partial P}.$$

Using Equation (15), we have $-\bar{P} \bar{C} (\partial F/\partial C)(\partial G/\partial P) = -\bar{P} \bar{C} (\partial F/\partial C)\delta_c \mu_c (d/dP)(Pf(P))|_{P=\bar{P}} \geq \bar{P} f(P) \bar{C} \delta_c \mu_c (d/dP)(Pf(P))|_{P=\bar{P}} > 0$. Thus, the stability of $(\bar{P}, \bar{C})$ is determined by the slope of the producer nullcline at $P = \bar{P}_\Sigma$. Specifically, within $\Sigma_c$, equilibria will be LAS if and only if the producer nullcline intersects the consumer nullcline $P = \bar{P}_\Sigma$ with negative slope.

If, in addition, $(\bar{P}, \bar{C})$ lies within the region of the producer nutrient saturation, $\Sigma_p$, then $\partial F/\partial C = -f(\bar{P})$ and this stability condition reduces to the classic one known for the (non-stoichiometric) Rosenzweig producer–consumer model, where a change in stability occurs when the peak of the producer nullcline intersects the (vertical) consumer nullcline.

If $(\bar{P}, \bar{C}) \notin \Sigma_c$, then the slope of the consumer nullcline obeys

$$\frac{dC}{dP} \Bigg|_{C=0} = -\frac{\partial G/\partial P}{\partial G/\partial C} \tag{19}$$

since by Equation (16) one has $\partial G/\partial C = -(q_c \epsilon_p/q_p) Pf(P) \partial R/\partial N \mu_c < 0$.

The characteristic polynomial (17) can be written as

$$\lambda^2 + \left( -\frac{\partial F}{\partial C} \left( \bar{C} \frac{\partial G/\partial C}{\partial F/\partial C} \bar{P} \frac{dC}{dP} \bigg|_{P=0} \right) \lambda + \bar{P} \bar{C} \frac{\partial F}{\partial C} \frac{\partial G}{\partial C} \left( \frac{dC}{dP} \bigg|_{C=0} - \frac{dC}{dP} \bigg|_{P=0} \right) \right)$$

with (as shown above) $-\partial F/\partial C > 0$ and $(\partial F/\partial C)\partial G/\partial C > 0$. Thus, $(\bar{P}, \bar{C})$ will be an unstable saddle if $dC/dP|_{C=0} < dC/dP|_{P=0}$ at the crossing of the nullclines – if the producer nullcline is more negative than the consumer nullcline slope. Conversely, if $dC/dP|_{C=0} > dC/dP|_{P=0}$, then $(\bar{P}, \bar{C})$ will be LAS if and only if

$$\frac{dC}{dP} \bigg|_{P=0} < \frac{\bar{C} (\partial G/\partial C)}{\bar{P} (\partial F/\partial C)}. \tag{20}$$

Because $\partial G/\partial C < 0$, the term on the right side of Equation (20) is always positive. Thus, if $dC/dP|_{C=0} > dC/dP|_{P=0}$ at the equilibrium, stability will be assured if the producer nullcline is non-increasing. Note that this includes all maximum and minimum points on the producer nullcline. In this, we see a difference from the non-stoichiometric case in that changes of stability will occur for Equations (1), (2), (4) on portions of the producer nullcline with a positive slope, rather than at maximum/minimum points. For given equilibria in the region $\Sigma_p$ (where the producer nullcline is given by $C = (\delta_c \mu_p (\epsilon_p/\delta_p) R_{\text{max}}/q_p) g(P - d_p)/f(P)$, condition (20) can be easily computed using Equations (14) and (16) if the quasi-equilibrium surface $R(N, P)$ is algebraically known. However, a simple nullcline-based interpretation of this condition in the general case is not clear.

The general shapes of producer and consumer nullclines permit a number of possible crossings. Figure 5 illustrates a situation with four co-existence equilibria. By the results of this section, equilibria $E_1$, $E_2$ and $E_4$ are unstable (the latter two being saddles), while $E_3$ and monoculture
The goal of this section is to examine the impact of energy enrichment on the dynamics of the quasi-equilibrium system. We will make use of this result in the next section.

**Theorem 3.2**  The quasi-equilibrium system (1), (2), (4) has no nontrivial periodic cycles wholly within the vertical strip within which the producer nullcline is decreasing: \( \frac{dC}{dP}|_{P=0} < 0 \).

**Proof**  As above, we write the system as \( P' = F(P, C)P \) and \( C' = G(P, C)C \) and apply Dulac’s Criteria [10] with multiplier \( 1/PC \). Using Equation (18), we compute

\[
\frac{\partial}{\partial P} \left[ \frac{1}{PC} P' \right] + \frac{\partial}{\partial C} \left[ \frac{1}{PC} C' \right] = \frac{1}{C} \frac{\partial F}{\partial P} + \frac{1}{P} \frac{\partial G}{\partial C} = \left( -\frac{1}{C} \frac{\partial F}{\partial C} \right) \frac{dC}{dP} |_{P=0} + \frac{1}{P} \frac{\partial G}{\partial C}
\]

with \((-1/C)\partial F/\partial C > 0\) and \((1/P)\partial G/\partial C \leq 0\). This expression will be negative in the region \( dC/dP|_{P=0} < 0 \), ruling out nontrivial periodic solutions.  

### 4. Energy enrichment and quasi-equilibrium system dynamics

The goal of this section is to examine the impact of energy enrichment on the dynamics of the quasi-equilibrium system. We will prove that for fixed nutrient \( N_T \), sufficiently high-energy enrichment drives all solutions of the quasi-equilibrium system to an equilibrium state. In the context of algae/Daphnia systems, this phenomenon was observed in the numerical experiments of [5,16,19] and elsewhere. This type of system response is in contrast to the enrichment-induced periodicity of the non-stoichiometric, Rosenzweig model.

By the previous section, we assume that \( \delta_p \mu_p ((\epsilon_p/\delta_p)R(N_T,q_c C - q_p P, P)/q_p)g(0) > d_p \), which is the necessary and sufficient condition for both the existence of a positive, monoculture equilibrium and a producer nullcline in the biologically feasible region.

The producer nullcline is the boundary of the set of points in the biologically feasible region that satisfy the inequality \( \delta_p \mu_p ((\epsilon_p/\delta_p)R(N_T - q_c C - q_p P, P)/q_p)g(P) - d_p \geq f(P)C \). In a set-theoretic sense, this region expands with increasing \( N_T \) since by Lemma A.1 \( R = R(N_T - q_c C - q_p P, P) \) is a non-decreasing function of \( N_T \). Thus, the producer nullcline tends to rise with the increasing total system nutrient, as well as with energy enrichment (increasing \( g(P) \)).

Similarly, the consumer nullcline is the boundary of the set of points in the biologically feasible region for which \( \delta_c \mu_c ((\epsilon_c/\delta_c)(R(N_T - q_c C - q_p P, P) + q_p)/q_c)g(P) \geq d_c \). This region expands with the increasing \( N_T \) along \( C' = 0 \) as long as \( \mu_c ((\epsilon_c/\delta_c)(R + q_p)/q_c)(\partial R/\partial N_T)(N_T - q_c C - q_p P, P) > 0 \). Thus, outside of the consumer’s nutrient saturation region \( \Sigma_c \), the consumer nullcline will rise with the increasing total system nutrient, but is unaffected by energy enrichment.

The case \( q_p = 0 \) (\( \mu_p \equiv 1 \)), corresponding to the situation where the producer is not nutrient-limited, is somewhat special, since the biologically feasible region is unbounded. Notice also that...
nutrient and energy enrichment effects decouple in this case, with nutrient levels affecting only the consumer nullcline, and the energy enrichment levels affecting only the producer nullcline. In this special case, the producer’s nutrient saturation region $\Sigma_p$ equals the entire biologically feasible region, and the producer nullcline is given explicitly by $C = (\delta_p g(P) - d_p)/f(P)$.

**Theorem 4.1** Assume $q_p = 0$ ($\mu_p \equiv 1$) and that $N_T > 0$ is fixed. Then, if $g(P)$ is sufficiently large on the interval $0 \leq P \leq (N_T/q_c)\varepsilon C_{\text{max}}/d_c$, system (1), (2), (4) has no interior equilibria (hence, no nontrivial periodic solutions), and the producer monoculture equilibrium is globally attracting.

**Proof** By Equation (7) and the properties assumed of $\mu_c$ and derived for $\delta$, the consumer nullcline must lie within the region $C \leq N_T/q_c - (d_c/\varepsilon C_{\text{max}})P$. Points on the producer nullcline satisfy $C \geq (\delta_p g(P) - d_p)/f(0)$; thus, will lie strictly above the consumer nullcline if $g(P)$ is sufficiently large on the interval $0 \leq P \leq (N_T/q_c)\varepsilon C_{\text{max}}/d_c$. The monoculture equilibrium is determined by $P = \bar{P}_m$, the unique solution of the equation $\delta_p g(P) = d_p$, which is independent of system nutrient levels. As discussed in Section 3, the monoculture equilibrium will be LAS. Global stability of that equilibrium then follows from Poincare–Bendixson theory.

The following result shows for $q_p > 0$ that under a fixed total system nutrient level and high-energy enrichment, the quasi-equilibrium system (1), (2), (4) supports no periodic solution and has at most one interior equilibrium (which will be globally attracting).

**Theorem 4.2** Assume $q_p > 0$ and that $N_T > 0$ is fixed.

(i) If the consumer nullcline does not intersect the boundary line $q_c C + q_p P = N_T$ then for all $g(P)$ sufficiently large on the interval $0 \leq P \leq N_T/q_p$, the system supports no co-existence equilibria, and the monoculture equilibrium $(\bar{P}_m, 0)$ is globally attracting.

(ii) If the consumer nullcline intersects the boundary line $q_c C + q_p P = N_T$ at some point $(P, C) = (P^*_b, C^*_b)$, $C^*_b = (N_T - q_c P^*_b)/q_c$, then for all $g(P)$ sufficiently large on the interval $0 \leq P \leq N_T/q_c$, the system (1), (2), (4) has exactly one interior equilibrium $(P, C)$. Moreover, $(P, C) \approx (P^*_b, C^*_b)$, and this equilibrium will be globally attracting.

**Proof** Consider the producer nullcline. Observe from Equation (6) that for $g$ sufficiently large on the interval $0 \leq P \leq N_T/q_p$, the quantity $\mu_p((\varepsilon_p/\delta_p)R(N_T - q_c C - q_p P, P)/q_p)$ can be made arbitrarily small. By the properties assumed of $\mu_p$, it follows that the producer nullcline must be restricted to a region, where $R(N_T - q_c C - q_p P, P)$ can be assumed arbitrarily small. By Lemma A.1 (i), the producer nullcline will then be made to be arbitrarily close to the boundary line $q_c C + q_p P = N_T$ for all $0 \leq P \leq N_T/q_p$.

Under assumption (i), the producer and consumer nullclines cannot intersect, and the monoculture equilibrium $\bar{P}_m \notin I_{N_T}$. The monoculture equilibrium can be shown to be globally attracting as in the proof of the previous theorem.

To show (ii), we again use the fact that the producer nullcline can under high-energy enrichment be made arbitrarily close to the boundary line $q_c C + q_p P = N_T$. By implicit differentiation, the slope of the producer nullcline can be computed from $\delta_p \mu_p ((\varepsilon_p/\delta_p)R(N_T, P)/q_p)g(P) - d_p - f(P)C = 0$ (with $N = N_T - q_c C - q_p P$) to be

$$\frac{dC}{dP} \bigg|_{P=0} = \frac{\delta_p \mu_p g' - f'C + \varepsilon_p((1/q_p)\partial R/\partial P - \partial R/\partial N)g\mu'_p}{f + \varepsilon_p(q_c/q_p)\partial R/\partial N}g\mu'_p$$

(For the sake of clarity, the arguments of the constituent functions are omitted.) Using the facts that $C \leq N_T/q_c$, $g' \leq 0$, $\mu'_p \approx 1$, $\partial R/\partial P \approx 0$ and $\partial R/\partial N \approx 1/(\varepsilon_p + P) \neq 0$ (see Lemma A.1 (vi) and (vii)), for all sufficiently large $g$, the quantity on the right is seen to be not larger than $-q_p/q_c$. 


Lemma A.1 (vii) permits the computation of the slope of the consumer nullcline as it intersects the boundary of the feasible region at \( P = P^*_b \). Specifically, outside of the consumer nutrient saturation region \( \Sigma_c \), implicit differentiation of Equation (7) results in

\[
\frac{dC}{dP} \bigg|_{C=0} = -\frac{q_p}{q_c} - \frac{(\varepsilon_p/\beta + P^*_b)}{\varepsilon_c \mu'_c((\varepsilon_c/\delta_c)q_p/q_c)} \left( \frac{d_c}{P_f(P)} \right) \bigg|_{P=P^*_b}
\]

This slope is bounded from below by \(-q_p/q_c\) (the slope of the boundary line \( q_c C + q_p P = N_T \)), is independent of \( N_T \), but is of indeterminate sign.

It follows that near \( P = P^*_b \), there will be exactly one intersection of the two nullclines. Theorem 3.2 and the fact that the producer nullcline is decreasing on the interval \( 0 \leq P \leq N_T/q_p \) combine to rule out the possibility of periodic cycles in the biologically feasible region. By the results of Section 3, the monoculture equilibrium is necessarily unstable since for all large \( g \), one has \( \bar{P}_m \in I_{N_T} \). Poincaré–Bendixson theory then shows that the unique interior equilibrium is globally attracting.

5. Comparison of the full- and quasi-equilibrium systems

Although we do not have rigorous results in this regard, numerical simulations of Equations (1)–(3) often suggest the existence of an attracting, two-dimensional, invariant manifold, and that this manifold is well-approximated by the quasi-equilibrium surface \( R = R(N_T - q_c C - q_p P, P) \). In support of this hypothesis, we note that for producers with saturating nutrient uptake \( (h(n) = h_{\text{max}} < \infty \text{ for all } n \text{ sufficiently large}) \), high system nutrient levels will saturate the producer nutrient content at \( R \equiv R_{\text{max}} \) for all \((P, C) \approx (0, 0)\), see Lemma A.1 (iv). This constant ‘plateau’ portion of the quasi-equilibrium surface is itself locally invariant with respect to the system.

As demonstrated in Figure 2, the loss of information in using the quasi-equilibrium approximation is often observed to be small, permitting the construction of hybrid phase-plane like diagrams for Equations (1)–(3), where \((P, C)\) projections of trajectories are plotted in relation to the nullclines for the associated two-dimensional quasi-equilibrium system. See Figure 3 and similar figures in [25]. By the nature of the quasi-equilibrium approximation, the parent and reduced systems share the same equilibria.

Beyond simple consideration of system simulations, we present here two alternate measures of comparison. The first examines the responses of the two systems to energy and nutrient enrichment. The second considers the domains of the persistence/extinction for the full system and its quasi-equilibrium approximation.

5.1. Enrichment responses

Figure 6 demonstrates the similarities of the enrichment-related bifurcation structures for the full system (1)–(3) and its two-dimensional approximation (1), (2), (4). This figure describes the bifurcations for the two systems under variation of the total system nutrient and energy levels. All constituent functions and model parameters are selected as for Figure 2, with the exception of \( N_T \) (total system nutrient) and \( b \), (fractional change in ambient energy levels) which are allowed to vary over \( 0 \leq N_T \leq 0.025 \) and \( 0 \leq b \leq 1.4 \).

The producer monoculture transcritical bifurcation (green) curve is computed algebraically by first solving Equation (A1) to obtain \( R(N_T, 0) \) as the root of a quadratic polynomial, then using this in Equation (6) with \((P, C) = (0, 0)\). For the above parameter selections, one can compute that \( \delta_c \mu_c((\varepsilon_c/\delta_c)q_p/q_c)f_{\text{max}}/d_c = 0.443 \), placing the system in case (i) of Theorem 3.1. The shape of the co-existence transcritical bifurcation curve (red) is consistent with Theorem 4.2 (i), which has
shown the monoculture equilibrium to be globally attracting for all $b$ sufficiently large. Because system (1)–(3) and its quasi-equilibrium approximation share the same equilibria, the transcritical and a saddle-node bifurcation curve (grey) for the two systems coincide.

For both systems, with adequate system nutrient, the co-existence equilibrium induced by energy enrichment is seen to destabilize to a periodic orbit (Hopf bifurcation.) Under intermediate nutrient levels, this family of periodic solutions terminates in a Hopf and/or homoclinic bifurcation. For both systems, the Hopf and homoclinic curves meet at Takens-Bogdanov points. Both homoclinic curves attach to a common saddle-node bifurcation curve at distinct non-central saddle-node/homoclinic points [18]. For high nutrient levels, periodic solutions to both systems are lost in central saddle node/homoclinic bifurcations. See [25] for a discussion of these possible energy-enrichment bifurcation scenarios and quasi-equilibrium phase planes for representative values of $b$ and $N_T$.

In Figure 6, relatively small changes are observed in the location of Hopf and homoclinic bifurcation curves for the two systems. In a general sense, both systems share a common response to simultaneous nutrient and energy enrichment. The relative locations of the Hopf bifurcation curves suggest that the quasi-equilibrium approximation tends to over-emphasize the destabilizing effects of energy enrichment on the co-existence equilibrium. The approximate system also exhibits homoclinic losses of periodic solutions at lower nutrient values than for the parent system.

While the two-parameter bifurcation diagrams for the two systems are qualitatively similar, they are quantitatively different. As a result, the systems can give significantly different predictions of system bifurcations for identical, total nutrient values, $N_T$. We illustrate this in Figure 7, which displays the one-parameter (energy-enrichment) diagrams for the two systems with $N_T = 0.019$. In terms of periodic solutions, the full system responds to energy enrichment in a manner similar to that reported by Diehl [5]. In contrast, under energy enrichment, the periodic co-existence
Figure 7. Energy enrichment bifurcation diagrams for Equations (1)–(3) (top row) and its quasi-equilibrium approximation (bottom row), with the producer described in the left column and the consumer in the right column. Monoculture equilibrium values are rendered in green, and co-existence equilibria are in red (solid = locally stable, dashed = unstable). Max/min values of periodic co-existence states are shown in blue; cycle averages are drawn in cyan. Transcritical bifurcation points are black diamonds. Homoclinic bifurcations are indicated with open circles. Saddle-node bifurcations of co-existence equilibria (not marked) correspond to vertical points on the co-existence equilibria curves. The curves of equilibria for the two systems are identical.

state for the quasi-equilibrium system terminates at a homoclinic bifurcation near $b = 0.998$, a phenomenon similar to the LKE model [19]. However, at $b = 1.088$, a periodic co-existence state arises at a homoclinic bifurcation, and closes to a Hopf bifurcation at $b = 1.100$. The observed non-existence of co-existence equilibria and periodic solutions for large $b$ is consistent with Theorem 4.2 (i).

5.2. Domains of the persistence/extinction

The results of Section 3 and 4 show that the quasi-equilibrium approximation to the parent system (1)–(3) is analytically tractable, leading to a rigorous understanding of how nutrient and energy enrichment can affect the existence and stability of system steady states. The previous discussion shows that while one can find nutrient levels where the two systems differ in their responses to energy enrichment, such differences should be understood in the broader context of simultaneous energy and nutrient enrichment. In particular, Figure 6 demonstrates common bifurcation structures for the two systems when nutrient and energy enrichment are varied together, and that over many intervals of nutrient values, the two systems will respond similar to energy enrichment.

Another advantage of the quasi-equilibrium system over the full system is the strong topological constraint imposed by planar vector fields. The Poincare–Bendixson theory often allows one to draw conclusions regarding the domains of attraction of system equilibria and periodic solutions. As illustrated in Figure 7, with adequate system nutrient, energy enrichment induces the creation of a co-existence equilibrium, which (under further energy enrichment) loses stability at a Hopf bifurcation. Solution trajectories initiated in a neighbourhood of the unstable
co-existence equilibrium either all tend to a surrounding orbitally asymptotically stable periodic cycle or (generically) all approach a common equilibrium state. See the numerical experiments and phase plane analyses of [3,5,19,25].

However, our numerical simulation experiments indicate that the domains of attraction for the parent system (1)–(3) can support features that by Poincare–Bendixson theory cannot be found in planar systems. To illustrate this, we specify the general model with the same constituent functions as in Figure 5: $g(P)P = (r/κ) \ln((φ + b)/(β + \epsilon e^{-κP}))$ (Huisman & Weissing type producer growth rate [5]), $h(n) = βn$ (linear producer nutrient uptake), $μ_c(l) = \min[1, l]$ (Liebig type consumer biomass conversion.), $μ_R(l) = l/(l + 1)$ (Monod producer biomass synthesis) and $f(P)P = f_{max}P/(f_{1/2} + P)$ (Holling II predator functional response). For our numerical experiments, we take $δ_c = 0.6$, $ε_c = 1.0$, $q_c = 0.03$, $f_{max} = 0.8$, $f_{1/2} = 0.125$, $d_c = 0.25$, $δ_p = 0.6$, $ε_p = 1.0$, $q_p = 0.0003$, $d_p = 0.05$, $β = 1.25$, $r = 0.9$, $φ = 0.35$, $κ = 6.0$, and $N_T = 0.25$. Near $b \approx 1.0$, the model supports a locally attracting periodic solution, a high food-quality co-existence equilibrium $E_1 = (P_1, C_1, R_1) \approx (0.14, 0.1, 0.035)$, one low food quality co-existence equilibrium $E_2 \approx (2.0, 0.03, 0.01)$ (both unstable), and a locally attracting monoculture equilibrium $E_m \approx (2.4, 0, 0.01)$.

In Figure 8(a) and (b), for three initial producer nutrient reserve concentrations $R(0) = R_0 (R_0 = 0.015, 0.0125, 0.010)$, a $100 \times 100$ grid of initial conditions $(P(0), C(0)) = (P_0, C_0)$ is colour-coded according to whether their associated solutions either approach a co-existence periodic orbit (red) or approach a locally stable monoculture equilibrium (green.) Only those initial conditions lying in the biologically feasible region $q_c C_0 + (R_0 + q_p) \leq N_T$ are shown. The enrichment parameter is $b = 1.000$ in Figure 8(a) and is $b = 1.019$ in Figure 8(b).

In Figure 8(a), where $b = 1.000$, the domain of attraction to the co-existence periodic orbit is ‘cylindrical’ in nature. The three horizontal slices are qualitatively similar, with initial conditions near the high food-quality co-existence state all approaching the periodic solution, similar to the behaviour of the Rosenzweig model. However, under slightly higher energy enrichment ($b = 1.019$), the domains of attraction depicted in Figure 8(b) become much more complicated, with the persistence/ extinction of the consumer population sensitively dependent on the initial producer nutrient reserve concentration, $R_0$.

The ‘variegated’ nature of the domains of attraction for the slices of Figure 8(b) can be understood in terms of the interactions of the stable and unstable manifolds for the system’s co-existence equilibria. Specifically, one can compute that when $b = 1.019$ that the high food quality equilibrium, $E_1$, has one negative eigenvalue and a complex conjugate pair of eigenvalues with positive real part. The low food quality equilibrium, $E_2$, has one positive and two negative eigenvalues.

Figure 9(a) depicts for $b = 1.019$ simulation-based approximations of the one-dimensional stable manifold, $W^S(E_1)$, and the two-dimensional unstable manifold, $W^U(E_1)$, for $E_1$. The stable manifold is approximated by solving Equations (1)–(3) in negative time, using as initial conditions small positive and negative perturbations along the eigenvector associated with the negative eigenvalue. The unstable manifold is estimated by solving the system for positive time using as initial conditions 90 perturbations (each equidistant from, and uniformly distributed around, $E_1$) within the two-dimensional plane defined by the complex eigenvectors of $E_1$. Trajectories in $W^U(E_1)$ are colour-coded as in Figure 8. Figure 9(b) details the family of simulations in a small neighbourhood of $E_1$; Figure 9(c) focuses on the behaviour of solutions near the unstable saddle $E_2$.

Our numerical experiments suggest that the associated two-dimensional stable manifold, $W^S(E_2)$, partitions small neighbourhoods of $E_2$ into regions of initial conditions that lead either to the monoculture equilibrium, $E_m$, or the periodic orbit. The red and green striations define two, distinct (open) domains of attraction within $W^U(E_1)$. Trajectories bounding these two domains of attraction approach $E_2$ as $t \to -\infty$.
Figure 8. Domains of attraction for Equations (1)–(3) for three fixed initial producer nutrient pool concentrations $R_0 = 0.015, 0.0125, 0.010$ and two energy enrichment levels $b = 1.000, 1.019$. The images in the right column are the projections to the $(P, C)$ plane of the images in the left column. Solutions with initial conditions in red are persistent, approaching a periodic co-existence cycle (drawn in black.) Solutions with initial conditions in green approach the system’s monoculture equilibrium (consumer extinction). All simulations where performed in *Mathematica* [20] using the NDSolve command with default integration methods.
Figure 8. Continued.
Figure 9. (a) Invariant manifolds for the high food-quality co-existence equilibrium of system (1)–(3). Stable manifold $W^S(E_1)$ is drawn in blue. Red trajectories within $W^U(E_1)$ approach the periodic co-existence cycle (Figure 8(b)); green trajectories approach the monoculture equilibrium, $E_m$. High food-quality equilibrium, $E_1$ and low food-quality equilibrium, $E_2$ are pictured, as well. Figure 9(b) and (c) detail the $(P, C)$ components of solution curves in small neighbourhoods of $E_1$ and $E_2$, respectively. In Figure 9(c), the orientations of the slow stable and unstable eigenvectors at $E_2$ are plotted, as well. See the text for parameter values.
intersections of $W^U(E_1)$ and $W^S(E_2)$. Figure 9(c) suggests the cleaving of $W^U(E_1)$ by $W^S(E_2)$ near $E_2$.

When they intersect, we expect (generically) $W^U(E_1)$ and $W^S(E_2)$ to intersect transversally. Thus, in all sufficiently small neighbourhoods of $E_1$, the two distinct open domains of the extinction/persistence will extend to points above and below $W^U(E_1)$. The geometry of the flow in a neighbourhood of $E_1$ is well understood [18]. The points of $W^S(E_2)$ near $E_1$ (but not on $W^U(E_1)$) will extend in negative time to define a scroll (‘Silnikov Snake’) that wraps around $W^S(E_1)$. This provides an explanation of the variegated scrolls seen in each of the slices of Figure 8(b) – distinct domains of attraction that spiral logarithmically around the points of the (transverse) intersection of these horizontal slices and $W^S(E_1)$.

Our numerical experiments indicate that the existence of variegation of this type depends on the selection of constituent functions and parameter selections for Equations (1)–(3). By the discussion above, a sufficient condition for variegation is the transverse intersection of $W^U(E_1)$ and $W^S(E_2)$. Such transverse intersections will persist over open regions of parameter space. However, such intersections are ruled out for parameter values near stable Hopf bifurcations at $E_1$. In fact, based on local centre manifold theory, it is known that at generic, stable Hopf bifurcations, all points in a neighbourhood of $E_1$ (with the exception of $W^S(E_2)$) will approach the small-amplitude periodic orbit.

6. Discussion and conclusions

This study continues the investigation of a general class of stoichiometric producer–consumer models derived in [25]. Motivated by simulation studies reported in that paper and numerical experiments reported for similar models, we have derived and rigorously analysed a related, two-dimensional producer–consumer ‘quasi-equilibrium’ model, where the producer internal nutrient pool is assumed to be at equilibrium because the size of this pool changes very quickly relative to producer and consumer growth/death rates. For the reduced system, nullcline-based criteria are derived regarding the stability of system equilibria, as well as for the non-existence of periodic orbits. With these results, we have rigorously shown that for a fixed total system nutrient, high-energy enrichment tends to drive the system to a globally attracting equilibrium state.

In the context of algae/Daphnia systems, high-energy enrichment has been reported to eliminate the possibility of a co-existence equilibrium state for similar two-dimensional models [5,9,16,17,19,27]. Our analysis suggests that this may be an attribute of systems in which the consumer nutrient: carbon ratio is significantly higher than that of the producer, that is, $q_c \gg q_p$. In fact, in situations in which the consumer can support itself on producer structural nutrient alone ($\delta_c (q_c q_p / q_c) f_{\text{max}} > d_c$), we have shown that high-energy enrichment may drive the system to a stable co-existence equilibrium, rather than to the monoculture state.

It is useful to consider our results in the context of global Hopf bifurcation theory [1]. This theory roughly states that for periodic solutions created via Hopf bifurcation, the parametric family of periodic orbits either (i) extends to infinity in the product space of bifurcation parameter (here, energy level $b$) and the system phase, (ii) terminates in another Hopf bifurcation, or (iii) along the parametric family, the period of the orbits approaches infinity, where (for examples) periodic solutions approach a homoclinic solution or a heteroclinic cycle. For the quasi-equilibrium models of this study, a fixed total system nutrient imposes a uniform bound on system solutions. By Theorems 4.1 and 4.2 (which rule out the existence of periodic cycles under high enrichment), the first alternative (i) is not possible. Thus, we have rigorously shown that energy enrichment results in either a subsequent Hopf bifurcation or an infinite-period bifurcation. In fact, Theorem 3.2 shows that the quasi-equilibrium system cannot support periodic solutions once (with sufficient energy enrichment) the producer nullcline becomes monotone decreasing.
The numerical bifurcation analysis of Section 5 indicates that for the quasi-equilibrium model, the variation in the total system nutrient itself can result in either case (ii) (as observed in the model of [5]) or case (iii) (as seen in [19]). Our numerical simulations illustrate that at a fixed nutrient level, energy enrichment can induce both a homoclinic loss of periodic orbits and a subsequent subcritical Hopf bifurcation that re-stabilizes at a co-existence equilibrium. Such behaviour was observed in the parent model in [25]. It should be pointed out that the numerical investigations described in Figure 7 do not rule out the existence of isolas of periodic solutions for parameters intermediate to the two observed homoclinic bifurcations or elsewhere.

Our numerical bifurcation studies indicate that generally, the parent and quasi-equilibrium models share similar bifurcation responses to nutrient and energy enrichment. But numerical simulations of the three-dimensional parent model demonstrate the potential for highly complex domains of the persistence/extinction for enrichment levels at which the model supports bistability consisting of both a locally attracting periodic co-existence state and a locally attracting equilibrium state. In particular, as demonstrated in Figure 8(b), our numerical experiments illustrate that the asymptotic behaviour of model solutions can depend sensitively on initial producer and consumer populations, as well as producer internal nutrient levels. These results demonstrate an inherent inability of the two-dimensional approximation to accurately capture the full dynamic complexity of the higher dimensional system. These observations point out the importance of going beyond model bifurcation analyses when comparing higher dimensional producer–consumer models to their quasi-equilibrium approximants. This study shows the need for examining through simulation experiments the domains of attraction in higher dimensional stoichiometric models. Our results demonstrate that a methodical, simulation-based, investigation of the limit sets on the system’s unstable manifolds is a useful first step in understanding the dynamic properties of such systems.

In summary, the model presented here provides a useful, unifying, framework for the study of simple stoichiometric producer–consumer models and identifies general dynamic trends associated with enrichment. Given the model’s generality, these results indicate that the energy enrichment-induced loss of periodic co-existence state reported in [3,5,16,17,25,27,28] is not an artifact of the algebraic details of those models.

However, our study raises important issues regarding the predictive capability of these (and even more complex) stoichiometric producer–consumer models at particular nutrient and/or energy levels. For the range of parameter values used in our study, none of our numerical experiments suggest that the parent model supports chaotic behaviour. Yet, the occurrence of highly complicated domains of attraction means that for certain parameter ranges, these models can share with chaotic systems unreliable predictive capabilities over long-time scales. Attempts to test stoichiometric producer–consumer models experimentally (as discussed in [3,8,21,23]) might rely on a perhaps unrealistically precise measurement of model parameters and initial conditions. Experimentalists in this area should recognize that even in the absence of chaos, the goal of reproducing experimental measurements of long-term producer–consumer interactions might be inconsistent with the intrinsic dynamical nature of the underlying systems.

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Appendix

The following lemma examines the properties of the implicitly defined quasi-equilibrium surface \( R(N_T - q_C - q_P, P) \).

**Lemma A.1** Assume \( \varepsilon_p \geq \delta_p \). For all \( P, N \geq 0 \), there is a unique solution \( R = R(N, P) \) to the equation

\[
h(N - PR) = \delta_p \mu_p ((\varepsilon_p/\delta_p)R/q_P)(R + q_P).
\]  \( \text{(A1)} \)
As a function of \((N, P)\), \(R(N, P)\) is piecewise smooth and satisfies the following properties:

(i) \(R(N, P) = 0\) if and only if \(N = 0\), and for \(N, P > 0, 0 < R(N, P) < N/P\).

(ii) \(\partial R/\partial N \geq 0\), and \(\partial R/\partial N = 0\) if and only if \(h'(N - PR) = 0\).

(iii) \(\partial R/\partial P \leq 0\), and \(\partial R/\partial P = 0\) if and only if \(h'(N - PR) = 0\).

(iv) \(h'(N - PR) = 0\) if and only if \(R = R_{\text{max}} \equiv \max_{N, P \geq 0}[R(N, P)],\) and \(R_{\text{max}}\) satisfies Equation (5).

(v) For all \(P > 0\), \(\lim_{N \to \infty} R(N, P) = R_{\text{max}}\).

(vi) For all \(N, P > 0, (1 - \delta_P q_P/h(N))/P + \delta_P/h(N) \leq R(N, P) \leq \min[h(N)/\delta_P, N/(\delta_P/\beta + P)]\).

(vii) If \(q_P > 0\), then \(R(N, P) = N/(\varepsilon_p/\beta + P) + o(N^2)\) for \(N \approx 0\).

Proof  Fix \(N, P \geq 0\) and define \(\eta(R) = \delta_P\mu_p((\varepsilon_p/\delta_P)R/q_P)(R + q_P)\), the right side of Equation (A1). If \(q_P = 0\), then \(\eta(R) = \delta_P R\). If \(q_P > 0\) then by assumption \(H_{\mu_p}\), it follows that \(\eta(0) = 0,\) \(\eta'(0) = \varepsilon_p,\) and \(\eta\) is a monotone increasing function with \(\eta(R) \leq \delta_P(R + q_P)\). Using the lower bound from \(H_{\mu_p}\) and \(\varepsilon_p \geq \delta_p\), one sees that

\[
\eta(R) \geq \delta_p R = \frac{1}{\delta_p \varepsilon_p q_P} (R + q_P)
\]

The solution of Equation (A1) represents the intersection of the graphs of the functions \(\eta(R)\) and \(h(N - PR)\), the latter being for \(P > 0\) a concave downward, non-increasing function of \(R\), with maximum value \(h(N)\) taken at \(R = 0\), and minimum value 0 when \(R = N/P\). The existence and uniqueness of \(R(N, P)\), and property (i) follow immediately. The piecewise smoothness of \(R(N, P)\) follows from the implicit function theorem. As for (ii), we differentiate Equation (A1) implicitly with respect to \(N\) to obtain \(h'(N - PR)(1 - (\partial R/\partial N)P) = (\partial \eta/\partial R)\partial R/\partial N\). The conclusions of (ii) follow using \(\partial \eta/\partial R > 0\). Assertion (iii) is proved similarly.

For (iv), observe that if \(h'(N - PR) > 0\), then Equation (A1) can be written as \(N = PR + h^{-1}(\eta(R))\), which rules out \((P, C)\) being an interior maximum of \(R(N, P)\). By hypothesis \(H_b\), \(h(N - PR)\) is a concave downward function of \(R\). Thus, if \(h(N - PR) = 0\) then \(h(N - PR) = h_{\text{max}},\) and \(R\) solves Equation (5). The limit (v) can be seen by considering the graphs of \(h(N - PR)\) and \(\eta(R)\) as functions of \(R\).

The upper bound of (vi) follows from the observation that \(R(N, P)\) is bounded from above by both the solutions of \(h(N) = \eta(R)\) and \(\beta(N - PR) = \eta(R)\), since both \(h(n) \leq h(N)\) and \(\beta(n) \leq \beta n\) hold on the interval \(0 \leq n \leq N\). The lower bound of (vi) holds because \(R(N, P)\) is bounded from below by the intersection of the graph of straight lines \(\delta_p(R + q_p)\) and \(h(N)[1 - (P/N)\beta]\) on the interval \(0 \leq R \leq N/P\). The final property follows from the rearrangement of Equation (A1)

\[
\beta(N - PR) + o((N - PR)^2) = \varepsilon_p R + o(R^2)
\]

and using \(R(0, P) = 0\). ■