

Productivity, nutrient imbalance and fragility in coupled producer–decomposer systems

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ABSTRACT

Ecosystem development is mediated by coupled synthesis–decomposition cycles that capture, store and release energy necessary for maintenance and growth. I present a minimal ecosystem model with explicit energy and matter conservation. Energy is captured and stored via synthesis and release through decomposition. This energy is used for biomass production and maintenance. I examine materially closed systems where growth is limited by nutrient availability. I present two key findings. First, maximum biomass production does not occur under conditions of equal nutrient concentrations. Instead, production is maximized when the initial environmental concentration of the energy carrying substrate is increased. Second, the system is characterized by an abrupt collapse when the concentration of the energy carrying substrate is increased above a threshold. This model indicates that in the region of maximum biomass production, ecosystems are fragile rather than resilient.

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1. Introduction

All ecosystems are organized around chemical cycles. The most fundamental of these is the coupled photosynthesis–respiration cycle that is the basis of energy flow in the majority of ecosystems. The extent to which synthesis exceeds decomposition, integrated over time, determines biomass accumulation, and is a measure of the thermodynamic work carried out in ecosystem development (Odum, E.P., 1969; Odum, H.T., 1983). Rates of synthesis and decomposition however depend on concentrations of chemical reactants, whose availabilities in turn depend on the net balance of their biochemical reactions through time (Loreau, 2010).

The inherent feedback between reaction rates that govern energy fluxes and availability of chemical nutrients sets up the possibility of strongly non-linear behavior and thresholds, particularly in materially closed systems where nutrient regeneration cannot rely on external sources. Although an extreme limiting case, materially closed ecosystems do have significance, for example in microcosm studies (Benton et al., 2007), and to first approximation the global biosphere, albeit on radically different time scales. Lessons from closed systems may also be applicable to sustainable design, where minimal external subsidy is an objective, and to engineering situations, such as remote space exploration, where external material inputs may be impossible.

Another factor limiting production and promoting non-linear dynamics is the stoichiometric balance of biochemical energy

pathways (Elser and Urabe, 1999; Elser, 2006; Cherif and Loreau, 2007; Hall, 2009). Because chemical elements combine in fixed ratios, an excess of one nutrient will not generally increase production. Rather, as von Liebig described in his “law of the minimum”, the least available nutrient typically regulates growth (de Baar, 1994). This leads to the interesting question of how ecosystem stoichiometry interacts with coupled synthesis and decomposition pathways to regulate production (Daufresne and Loreau, 2001; Kooijman et al., 2004; Kuijper et al., 2004; Iwabuchi and Urabe, 2012). Furthermore, the stoichiometric balance of ecosystems is of keen practical interest owing to increasing evidence for anthropogenic changes in global nutrient cycles (Vitousek et al., 1997a).

While nutrient-driven models abound in the literature (Loreau, 2010), explicit representations of biochemical reactions with strict material and energy conservation and stoichiometric balance are less common. I consider here a minimalist ecosystem model with the following properties: (1) all biomass production is driven by energy released through decomposition of stored molecular energy; (2) energy is captured by producers and used to synthesize energy-rich compounds; (3) some of the energy-rich compounds leak into the environment through mortality or other modes of tissue loss; (4) energy-rich compounds in the environment are consumed and metabolized by decomposers releasing inorganic compounds that are used in synthesis by producers; and (5) all energy transformations are modeled as explicit chemical reactions with stoichiometric balance of elements.

Using a chemically explicit producer–decomposer model (Fig. 1), I describe strongly non-linear behavior in the vicinity of maximum biomass accumulation and productivity. Nutrient

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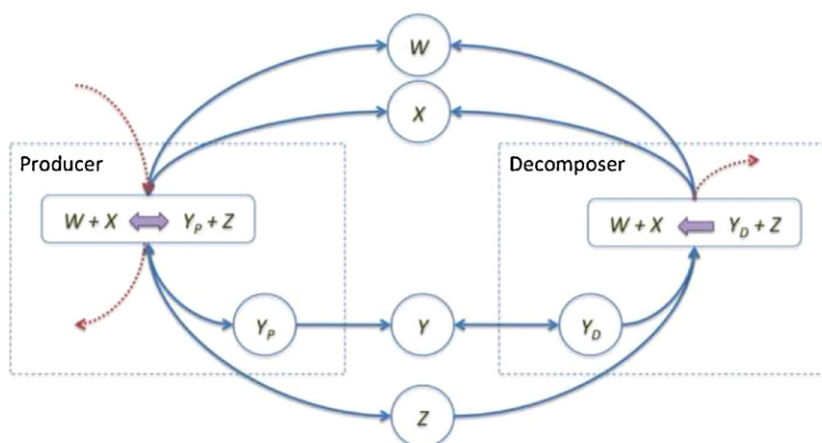


Fig. 1. System diagram showing material flows (solid blue arrows) and energy flux (dashed red arrows). Symbols represent reactants and products involved in synthesis–decomposition as explained in the main text.

conditions of maximum ecosystem productivity occur immediately adjacent to conditions of ecosystem collapse. Under these conditions, even slight changes in nutrient availability and model parameters shift the outcome from maximum ecosystem function to a virtual desert containing little or no biomass. These results strongly contrast a widely held view that productivity and function lend resilience to ecosystems (Tilman et al., 1996; Yu et al., 2010). The dynamics are mediated by a transient ecological response to increased concentration of an energy-carrying nutrient, resulting in a pulse of decomposition followed by depletion of a key reactant required for the exothermic reaction pathway. The result mimics the well-known “dead zone” effect in which oxygen levels are depleted following import of large quantities of biomass (Cloern, 2001; Vaquer-Sunyer and Duarte, 2008; Howarth et al., 2011), an environmental phenomenon of world-wide environmental and economic concern (Ryther and Dunstan, 1971; Vitousek et al., 1997b; Carpenter et al., 1998).

2. Modeling chemical reactions

I modeled energy acquisition and population growth as functions of rates of coupled synthesis–decomposition reactions (Fig. 1). These reaction pathways are specified abstractly, for example as



where it is assumed that the synthesis product AC always has greater chemical potential energy than the input nutrient AB . The isolated symbols A , B and C are assumed to be atomic and are always assigned zero chemical potential. I only consider cases where the each of the four reactants are distinct, and where element ratios are equivalent on right and left hand sides of the reaction. This arrangement was chosen because it permits more complicated models involving multiple, coupled pathways to be specified in a simple form (Keitt, unpublished).

It is convenient to abstract specific chemical species by introducing the generic symbols W , X , Y and Z , to represent the four reactants. I commit a small abuse of notation by letting these symbols also represent the concentration of the reactants rather than the more customary and busy approach of using square brackets to indicate concentration. I term reactants on the right hand side of Eq. (1) “endothermic reactants” (W , X) and those on the left hand side as “exothermic reactants” (Y , Z). Chemical species composed of more than one element are prefixed with “compound”, e.g., the “compound endothermic reactant” (W). Because the compound exothermic reactant Y is stored for metabolic use, it

is also referred to as the “energy-carrying substrate” or just “substrate”.

Modeled rates of synthesis and decomposition depend on internal and external concentration of nutrients, but not according to classical mean-field chemical kinetics. Numerous ecological studies have shown that rates of biomass accumulation scale with the concentration of the least abundant nutrient required for growth. This prompted Droop (1974) to model nutrient dependence by a minimum function; however, the sharp threshold in the Droop formulation complicates analysis. Kooijman (1998) derived as an alternative the “synthesizing unit” which behaves similarly to a minimum rule at low nutrient concentration, but is smooth in the region where nutrient concentrations are nearly equal. Proportion of maximum reaction flux is given by

$$J_{(W,X)} = \left[1 + \alpha \left(\frac{1}{W} + \frac{1}{X} - \frac{1}{W+X} \right) \right]^{-1} \quad (2)$$

where α determines how quickly the function saturates. More sophisticated elaborations on this basic scheme have been reported elsewhere (Kooijman et al., 2004; Poggiale et al., 2010; Sousa et al., 2010).

3. Biomass and substrate storage dynamics

The model includes two species: a producer whose biomass is denoted by P and a decomposer whose biomass is denoted by D . State variables and rate functions of the model are listed in Table 1. As a simplification, the physiology of producers and decomposers are considered identical, save for the mode of energy acquisition. Rate parameters shared between producers and consumers are therefore assumed to be equivalent. Parameter definitions and default values are given in Table 2. Drawing from the framework of dynamic energy budgets (Daufresne and Loreau, 2001; Nisbet et al., 2010), population growth of producers and decomposers is linked to the internal concentration Y_Q of the energy-carrying substrate by

$$Q' = G_{(Y_Q,Z)} Q \quad (3)$$

where Q represents biomass. The growth rate is given by $G_{(Y_Q,Z)} = \varepsilon g R_{(Y_Q,Z)} - \delta$, where ε is energy yield per unit reaction, g is the energy-to-biomass conversion ratio and δ is the biomass loss rate. The energy-releasing catabolic reaction rate is given by $R_{(Y_Q,Z)} = r_{\max} J_{(Y_Q,Z)}$, where r_{\max} is the maximum rate.

Table 1
State variables and rate functions.

Symbols	Description
Q	Biomass quantity of either producer (P) or decomposer (D).
Y_Q	Energy substrate storage per unit biomass.
W, X, Y, Z	Ambient nutrients and their concentrations.
$J_{(W,X)}$	Reaction rate expressed as proportion of maximum rate given concentrations W and X .
$G_{(Y_Q,Z)}$	Biomass growth rate (per unit biomass) given substrate storage Y_Q and reactant concentration Z .
$R_{(Y_Q,Z)}$	Scaled catabolic reaction rate (per unit biomass) given substrate storage Y_Q and reactant concentration Z .
$S_{(W,X,Y_P)}$	Scaled anabolic synthesis rate (per unit biomass) given concentrations W, X , and Y_P .
$U_{(Y,Y_D)}$	Decomposer substrate acquisition rate (per unit biomass) given ambient concentration Y and storage Y_D .
L_{Y_Q}	Loss rate (per unit biomass) of stored substrate Y_Q owing to mortality, exudation, shedding or other loss of biomass.
$\Pi_{(Y_Q,Z)}$	Dilution rate (per unit biomass) of stored substrate owing to changes in biomass $G_{(Y_Q,Z)}$.

Change equations for the internal substrate storage *per unit biomass* are

$$Y'_P = S_{(W,X,Y_P)} - L_{Y_P} - R_{(Y_P,Z)} - \Pi_{(Y_P,Z)} \quad (4)$$

$$Y'_D = U_{(Y,Y_D)} - L_{Y_D} - R_{(Y_D,Z)} - \Pi_{(Y_D,Z)}. \quad (5)$$

Here $S_{(W,X,Y_P)} = s_{\max} J_{(X,Y)} H_{Y_P}$ models the anabolic synthesis rate, where s_{\max} is the maximum rate and H_{Y_P} is the satiation function (see Eq. (6)). I assume energy driving synthesis is not limiting and therefore does not enter into the rate expression. The detritus uptake rate by the decomposer is given by $U_{(Y,Y_D)} = \gamma Y H_{Y_D}$, where γ is a rate constant and H_{Y_D} is satiation. Loss of substrate to the environment is given by $L_{Y_Q} = \delta Y_Q$, where δ is the biomass loss rate. The function $\Pi_{(Y_Q,Z)} = Y_Q G_{(Y_Q,Z)}$ accounts for storage dilution owing to changes in biomass.

Although it is common to model satiation indirectly using a Michaelis–Menten formulation (Holling, 1973), I took advantage of the explicit incorporation of energy storage in the model and modeled satiation directly as a function of storage. A sigmoid satiation function was defined by

$$H_{Y_Q} = \frac{1}{1 + (\mu Y_Q)^\phi} \quad (6)$$

where μ^{-1} is the half-satiation constant and ϕ determines how abruptly the function declines with increasing storage. The function modifies both synthesis and heterotrophic uptake rates, which are considered facultative depending on the degree of

Table 2
Model parameters and default values for simulations.

Symbol	Description	Default value
α	Shape parameter of synthesizing unit (dimensionless).	2.0
ε	Energy to biomass conversion factor (biomass per unit energy).	1.0
g	Energy yield per unit of substrate consumed in catabolism.	1.0
δ	Biomass loss rate constant (1/time).	1.0
r_{\max}	Maximum catabolic reaction rate (exothermic reaction).	19/6
s_{\max}	Maximum anabolic synthesis rate (endothermic reaction).	16
γ	Substrate acquisition rate per unit biomass.	4.0
μ	Inverse half-satiation constant.	1.0
ϕ	Satiation curve shape constant.	2.0

satiation. Because stored substrate is modeled proportionally (per unit biomass), the satiation function scales with total biomass such that total storage capacity increases with increasing biomass.

Changes in environmental nutrient concentrations are then given by

$$W' = X' = R_{(Y_P,Z)}P + R_{(Y_D,Z)}D - S_{(W,X,Y_P)}P, \quad (7)$$

$$Y' = L_{Y_P}P + L_{Y_D}D - U_{(Y,Y_D)}D \quad (8)$$

and

$$Z' = S_{(W,X,Y_P)}P - R_{(Y_P,Z)}P - R_{(Y_D,Z)}D. \quad (9)$$

Owing to conservation, it is possible to substitute one of the nutrient change equations with the conservation constraint yielding an equivalent differential-algebraic system if so desired.

4. Simulation scenarios

Default parameter values (listed in Table 2) were chosen to scale equilibrium biomasses to 1.0 in arbitrary mass units. I used a 50% rule to constrain rate parameter values such that 50% of autotrophic energy acquisition was allocated to biomass production. Numerical integrations were performed using the “deSolve” package (Soetaert et al., 2010) for the R statistical computing environment (R Development Core Team, 2011). The “runsteady” function of the R “rootSolve” package (Soetaert and Herman, 2009) was used to terminate integration once the rate of change, averaged across state variables, fell below one part in 10,000.

4.1. Sensitivity to initial nutrient concentrations

Simulations were run using default parameters and initial biomass and nutrient concentrations were set to their long-term steady state values ($P = D = Y_P = Y_D = 1.0$, $W = X = Z = 1.0$, $Z = 3.0$ in arbitrary units), except for the focal nutrient levels, which were varied as shown in Fig. 3. Quantities of non-focal nutrients were held constant. Thus the total nutrients varied across simulations. Simulations were run to steady-state as described previously.

4.2. Sensitivity to changing initial element ratios

Simulations were run using default parameters and a total nutrient concentration fixed at 16 units. Concentrations of W, X, Y and Z were randomly apportioned from a total of 16 units, and the proportion of each element subsequently computed as shown in Fig. 4. Simulation results from 10,000 initial conditions were used to interpolate a surface in the ternary space of elemental proportions. Note that while the nutrient concentrations changed through time, the elemental ratios, by construction, remained constant.

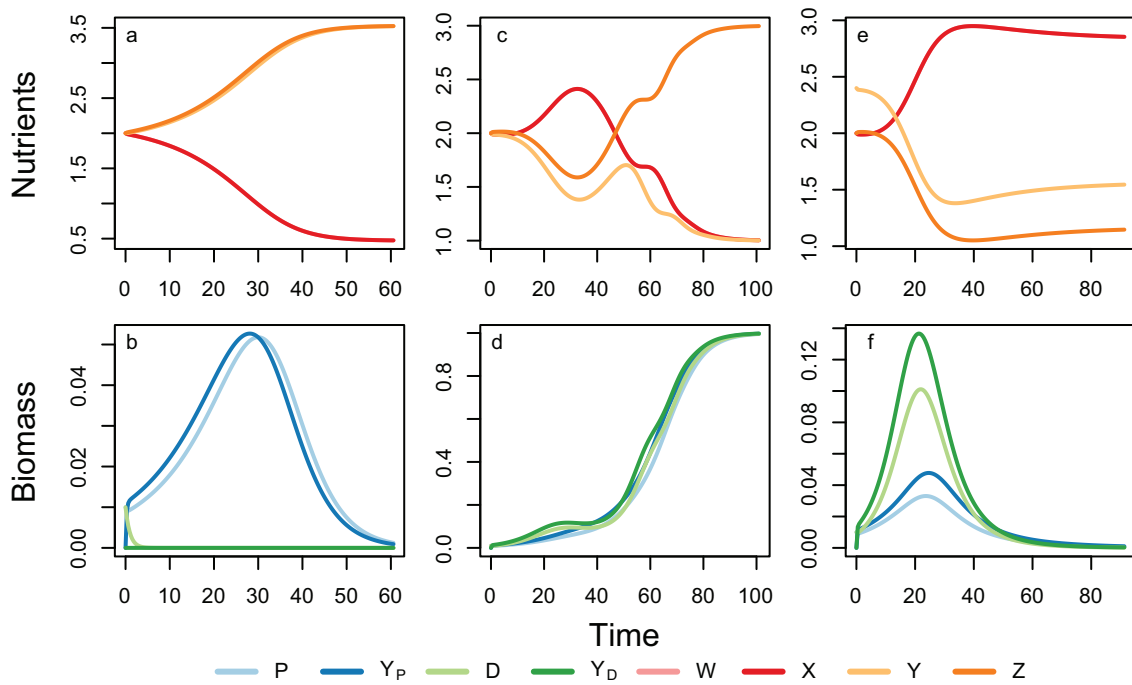


Fig. 2. Producer–decomposer dynamics simulated under three different scenarios. (a and b) In the absence of decomposer uptake ($\gamma = 0$) unprocessed resources accumulate and productivity halts. (c and d) With recycle, the producer and decomposer populations reach a steady-state where the rate of synthesis is equal to the rate of decomposition. (e and f) Starting from the same initial conditions as in (c and d), but with a slight (20%) increase in the initial concentration of substrate AC causes a pulse of decomposition followed by collapse.

4.3. Parameter sensitivity

As in the previous scenario, 10,000 simulations were run to steady-state with varying elemental proportions in the initial nutrient pools. With each simulation, the parameters were perturbed from their default values by multiplying each by a log-normal random deviate with log-mean = 0.0 and log-standard-deviation = 0.1. The outcome was an average random displacement of 10% around default parameter values. The mean and standard deviation of total biomass was estimated locally using a smoothing spline fit through the 10,000 simulation results as shown in Fig. 5.

5. Results and discussion

A fundamental result of the model is the importance of coupling decomposition to synthesis in the maintenance of ecological homeostasis. Time-series of nutrient concentrations and biomasses from three scenarios are shown in Fig. 2. In the first scenario, decomposer uptake is absent leading to starvation of both producer and decomposer. The second scenario includes nutrient recycle via the decomposition pathway and both populations grow to a steady-state determined by the quantity of nutrients available in the system. Nutrient dynamics show some evidence of transient oscillations during the growth pulse prior to reaching

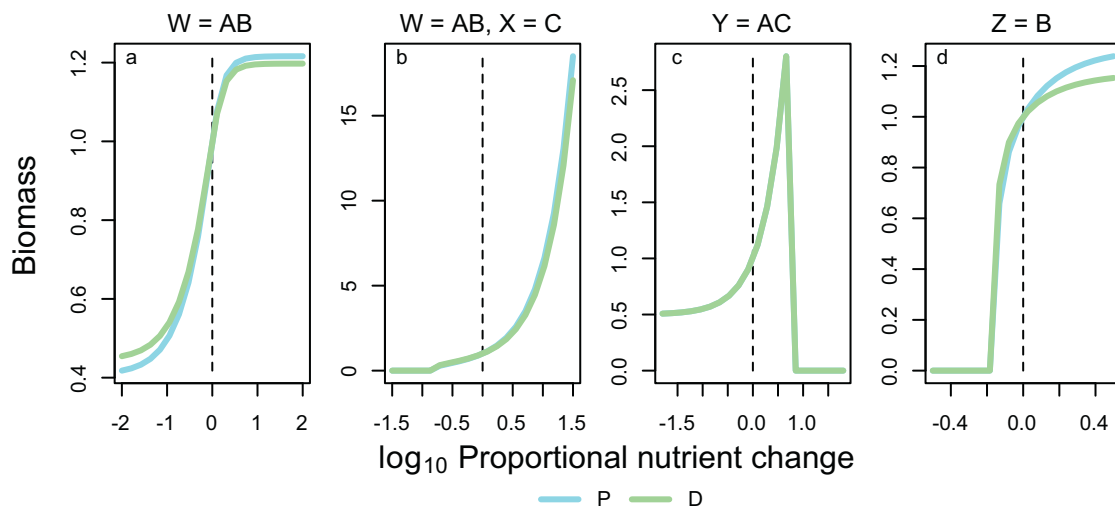


Fig. 3. Biomass sensitivity to changing initial nutrient concentrations. See Section 4 in the main text for detailed explanation. The nutrient manipulated is shown above each panel. The x-axis is the proportional change in the initial nutrient concentration on a log-scale. A value of 1.0 therefore represents a 10-fold increase, a value of -2.0 a 100-fold decrease, and so on. All changes are relative to the long-term steady-state nutrient concentrations shown in Fig. 2c.

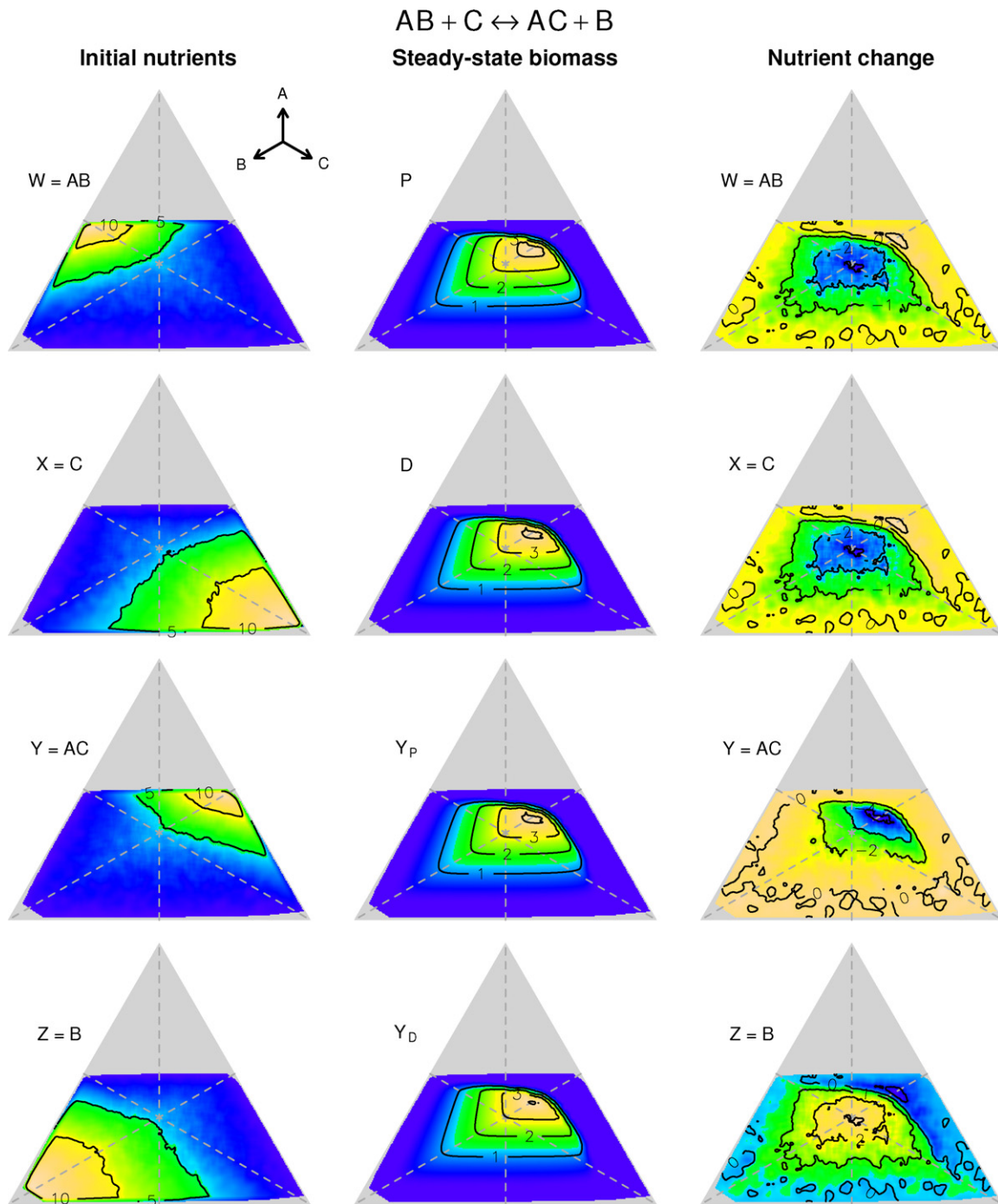


Fig. 4. Steady-state producer biomass as a function of relative proportions of constituent chemical elements A, B and C. Triangle corners represent 100% concentration of the corresponding element as indicated by the inset legend. Boundaries opposite the corners (connected by the dashed axes lines) correspond to a complete absence of that element. Note that because element A only appears in combinations with other elements, its proportion can never exceed 50%. The left-most column shows initial proportions of the endothermic and exothermic reactants. The second two columns show steady-state results obtained from numerical integrations with initial conditions as shown in the first column. The second column shows steady-state biomasses, whereas the third column shows the difference between steady-state nutrient concentrations and initial nutrient concentrations. Surface values are interpolated from 10,000 randomly generated initial elemental ratios distributed with constant probability throughout the heatmap colored region of the plot. A slight amount of surface smoothing (equivalent 0.035 units of axis length) was applied after interpolation to reduce contour complexity evident in the third column.

steady-state. These are caused by lags associated with movement of nutrient stocks between organic and inorganic phases. The third scenario is most interesting and illustrates the sensitivity of the closed producer–decomposer system. Starting from identical initial conditions illustrated in Fig. 2b, I increased the free energy substrate in the environment (Y) by 20%. The result was not an increase in production, but rather a catastrophic collapse of

productivity. The mechanism is the demand for the exothermic reactant Z necessary for decomposition of the substrate. The uptake and metabolic reaction of the substrate by the decomposer consumes sufficient Z to drive the producer population to extinction, which can no longer meet metabolic demands for energy because of the limited availability of the exothermic reactants. Ecologists will of course

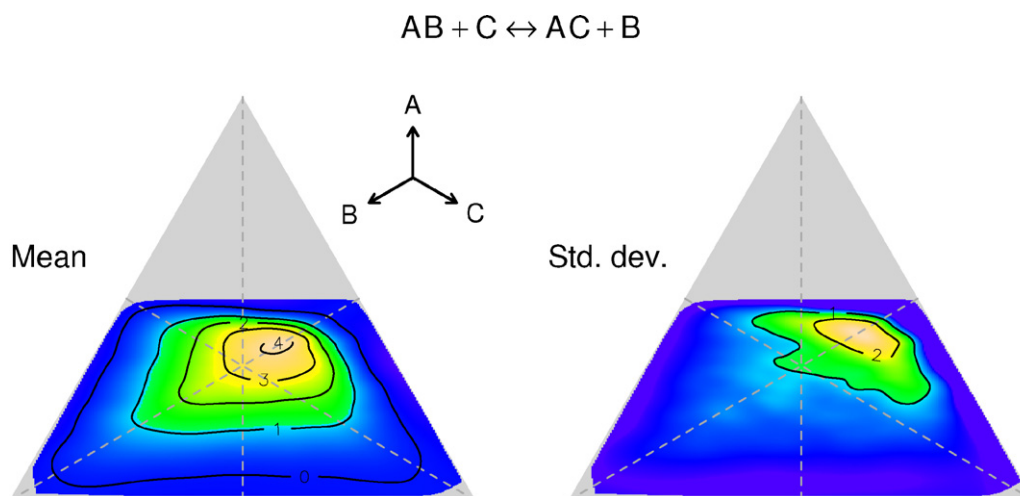


Fig. 5. Model sensitivity to stochastic parameter perturbations as a function of stoichiometric balance. The left-hand ternary plot shows estimated mean biomass and the right-hand plot, estimated standard deviation in biomass. Parameters were simultaneously varied around their default values with a coefficient of variation equal to 10%. Surfaces are smoothing spline fits of the mean biomass and square-root of the mean of the squared surface residuals. Surface tension was optimized using generalized cross-validation. Results are from 10,000 randomly generated stoichiometric combinations.

recognize this dynamic as a generalization of the concept of “biological oxygen demand” that can create hypoxic conditions and fish kills in estuarine and other aquatic ecosystems. While the importance of decomposition in homeostasis does not come as a surprise, it is only striking in the absence of such a key ecological concept in standard presentations of ecological theory, which have most often emphasized Lotka–Volterra formulations lacking explicit consideration of energy and material cycles.

Biomass sensitivity characteristics depended strongly on which nutrients concentrations were manipulated and whether changes were made singly or in concert. Fig. 3 shows changes in producer and decomposer biomasses with changes to initial nutrient concentrations. Manipulation of either endothermic reactant alone (Fig. 3a) had a relatively small influence on steady-state biomass as one or the other would become rapidly limiting. Reduction in the endothermic reactant concentrations (W, X) did not lead to collapse as their loss could be compensated for by their production in the reverse exothermic pathway. Under simultaneous increases or decreases, the endothermic reactants had a large impact on steady-state biomasses (Fig. 3b): simultaneous increase led to a dramatic increase in productivity; a sufficiently large decrease led eventually to extinction owing to insufficient nutrients.

Biomass responses to changes in initial quantities of the two exothermic reactants were strikingly different. Reductions in the energy-carrying substrate (Y) lead to a reduction in productivity, but not collapse as reduction in this nutrient was compensated for by production in the synthesis reaction (Fig. 3c). When the initial quantity of substrate in the environment was increased, there was a rapid increase in productivity until a threshold level, after which biomass production exhibited catastrophic decline. The explanation for this collapse is the system sensitivity to changes in the exothermic reactant Z , which declines sharply as the initial quantity of Y is increased (see Fig. 2e). As shown in Fig. 3d, when the quantity of Z declines sufficiently, biomass production ceases as maintenance energy demands cannot be met by the energy-releasing decomposition reaction pathway.

Environmental stoichiometry had a profound impact on modeled ecosystem growth (Fig. 4). Because the four reactants are composed of only three abstract “elements”, the entire space of possible elemental ratios can be projected into two dimensions. Fig. 4 illustrates two key results of the modeling. First, rather unexpectedly maximum biomass production did not occur under conditions of equal elemental ratios (*i.e.*, where the ternary

axes meet), a situation where one expects the least nutrient limitation. Rather, maximum production occurred when initial conditions favored elements A and C over the element B , *i.e.*, moving toward the upper right of the plots in Fig. 4. This result highlights a strong asymmetry in the influence of the exothermic reactants on productivity.

Because of the physical conservation of matter in the model, standing biomass is directly proportional to the degree to which nutrient concentrations are shifted away from equilibrium “toward the right” in Eq. (1), *i.e.*, the extent to which the total amount of synthesis dominates over decomposition while the system approaches steady-state (when the two rates must be equal). During this process the endothermic product Z becomes highly abundant whereas Y is bound up into organic storage for use in biomass growth. Hence, an increase in the amount of Y at the expense of Z , which in terms of elements means increasing A and C at the expense of B , initially has little effect on productivity because Z is abundant in the environment and its reduction does not limit the exothermic decomposition pathway. Further increase in Y however can reduce Z sufficiently that it become limiting to growth, which can no longer compensate for maintenance costs leading to collapse of productivity.

Although the abruptness of the transition is a surprise, the collapse of productivity with nutrient imbalance is relatively intuitive as we expect that at some point production will cease under server resource limitation. More interesting however is the sensitivity of the system near its transition point. Even small changes in parameter values near the threshold of collapse results in large changes in steady-state biomass (Fig. 5). The maximum coefficient of variation in model output was greater than 50% while the coefficient of variation in parameter values across trials was only 10%, indicating a high degree of sensitivity. Although the model is capable of supporting multiple equilibria (Keitt, unpublished), the mechanism at work here is not the classical “tipping-point” bifurcation of catastrophe theory (Scheffer et al., 2001) as all simulations were started with sufficient nutrients and biomass to avoid attraction to the zero-biomass solution. Rather, the large variation resulted from the sensitivity of the position of the threshold to changes in parameter values. Hence, unless parameters are known with high precision, it is difficult to predict whether one will encounter conditions of high productivity or ecological collapse under stoichiometric ratios found in the vicinity of maximum biomass production. The implication for ecosystem management is that if resiliency to change is

a desired end-point, then maximization of productivity should be discouraged.

All models are simplifications of the systems they attempt to emulate. While more complex than the most basic population models typically presented as the basis for population biology and evolutionary ecology, coupled nutrient-energy models have the potential to generating understanding of the essential role of physical process and conservation in explaining ecological organization and dynamics. Evolutionary theory often neglects resource constraints on growth, preferring to emphasize only positive exponential feedbacks related to differential fitness. Whereas ecological theory has a long history of linking resource concentrations to species coexistence, the vast majority of models are derived under constant nutrient flux boundary conditions and often neglect key ecological processes such as reciprocal resource transformation, exchange and physiochemical niche dynamics. The stoichiometric paradigm and the framework of dynamic energy budgets have made significant progress in the integration of coupled physical processes into ecological models. There is yet much work to be done in theoretical generalization and empirical validation of models. There exists great promise in simple and abstract formulations that explicitly integrate energy and material processing, and that can serve as simple building blocks for more complex and realistic ecosystem models.

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