Enhanced and constant productivity in impoverished and fluctuating environments

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Abstract

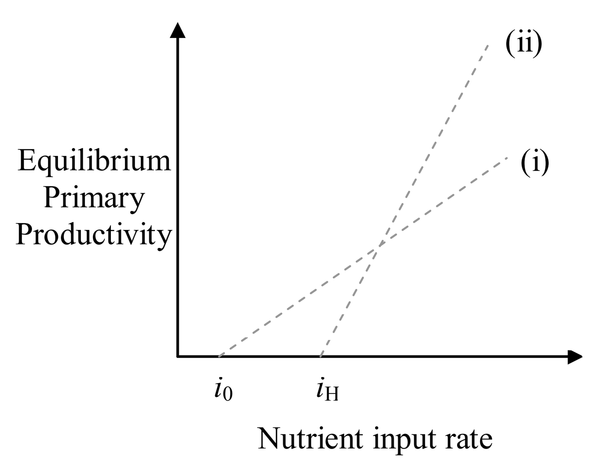
Many kinds of ecosystems can maintain stable, high levels of productivity despite scarce resources in a changing environment. We have analyzed theoretical models of nutrient cycling to clarify the mechanisms for maintaining this apparent paradox. Moreover, we confront the models with biological processes and data of the littoral community of Lake Tanganyika, an African Rift Valley lake. Our results suggest that the frequency of inputs, which can increase the variability of the stocks and flows, do not influence their average magnitude. However, the consumer was the main factor which can stabilize function, by decreasing variability. Enhanced productivity hinges on the efficacy of autotrophs to take up nutrient subsidies and of grazers to cycle nutrients, consistent with grazing optimization theory. The intensity of cycling between herbivores and primary producers is governed by a balance between grazing and recycling rates, which can trade-off in their effect on stability. In this context, maintenance of functioning, in terms of constancy and magnitude, depends on the intensity of coupling between consumers and the resource. For Lake Tanganyika, this suggests that climate warming and fishing will strongly affect long-term ecosystem functioning. Taken together, the results highlight the importance of feedbacks between ecosystem processes and the behaviours of biota for predicting ecological consequences of global change and exploitation.

Introduction

- Ecosystems with nutrient limitation can exhibit surprisingly high-levels of productivity, apparently breaking the barrier of resource scarcity or instability from extreme environmental conditions
- Several possible mechanisms may contribute to elevated and stable functioning in such a setting
- In grazing ecosystems with constant input, increases in total nutrient level and grazing optimization can lead to increases in productivity
- When inputs are periodic, the variability of trophic groups and productivity increases, potentially impacting ecosystem functioning and the abundance of trophic groups
- How does the process of pulsing and how do the mechanisms of recycling and resource consumption enhance or depress primary productivity and influence stability?

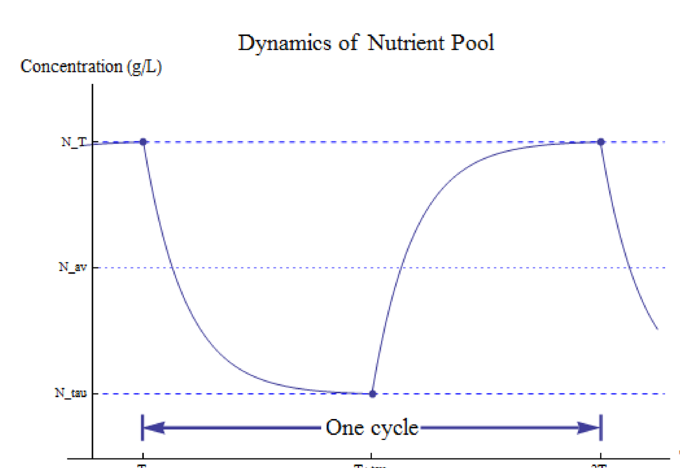
Hypotheses

- The presence of a herbivore can increase productivity by changing the relationship between autotroph and environment



Line (i) shows the relationship between nutrient input and equilibrium productivity in the absence of a herbivore; either the nutrient level is insufficient to maintain herbivores, or it is absent. Line (ii) depicts the relationship in the presence of herbivores. At input levels beyond the intersection of the two lines, the presence of the herbivore results in higher equilibrium productivity than when it is absent.

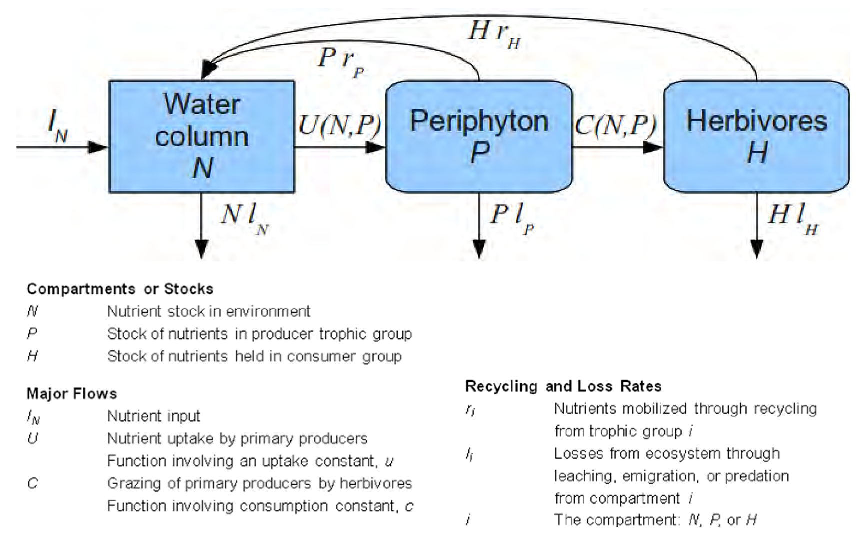
- Productivity will be higher or lower when stocks are changing drastically compared to a more continuous input, which tends to approach equilibrium steady state, when total rates of change are zero



Depending on the pulse regime, the trophic assemblages may not reach a stable steady state equilibrium because they are always responding to regular shifts in resource supply by changing biomass. Thus biotic interactions may change the patterns of growth and decline in a pulsing setting, changing the ex-

Objectives

- With simple grazing ecosystem models, assess the effect of several mechanisms, including:
  - o Pulsed inputs into the nutrient pool
  - o Losses out of the ecosystem through leaching and mortality
  - o Recycling from consumers
  - o Resource consumption by autotrophs and herbivores



Schematic of the grazing food chain with main parameters. Contrasting functions were used for uptake (U) and grazing (C), representing donor and recipient controlled consumption:

Functional response	Abbreviation	Primary Producer Uptake $U(N,P)$	Herbivore Consumption $C(P,H)$
Donor control	D	$u_1 N$	$c_1 P$
Recipient control	R	$u_2 N P$	$c_2 P H$

Main questions

- When does pulsing increase or depress productivity?
- Can herbivores still maintain or enhance productivity and does this effect interact with pulsing?
- What effect do autotrophs and herbivores have on the stability of functioning?

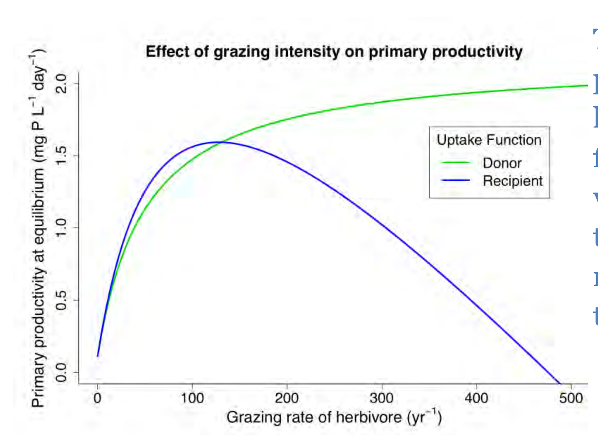
Methods

- Composition of food chain models with recycling
- Simulations comparing the effect of pulse regimes in different model types with biologically realistic parameters
- Mathematical analysis of the effect of pulsing
- Parameter estimation from Lake Tanganyika field data

Results

Productivity in the absence of pulsing

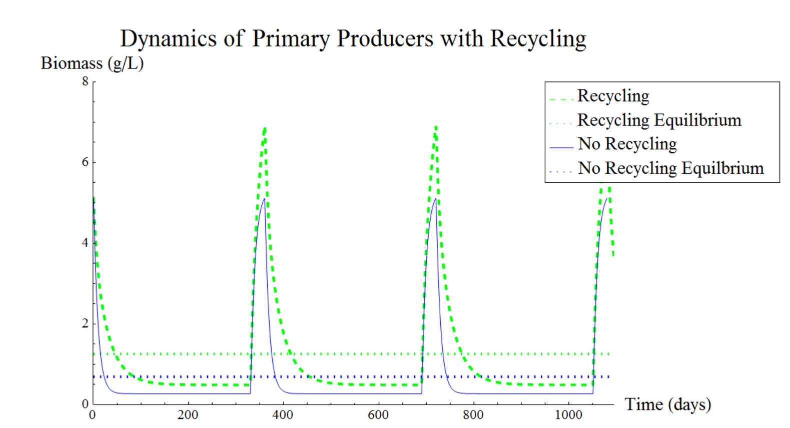
- Enrichment increases productivity, but for nutrients to remain limited there are constraints on the parameters depending on functional responses used
- This occurs when herbivores recycle a significant amount nutrients that are available to autotrophs rather than losing them out of the system directly or through leaching



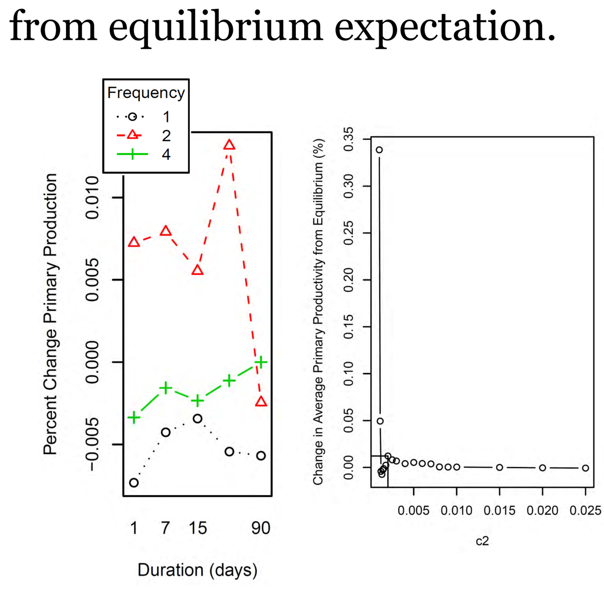
This potential shift in productivity due to the herbivore depends on functional response, which will determine the constraints on parameters which enable the mechanism

Productivity with pulsing

- Simple linear models show that pulsing has no effect on average magnitudes of productivity as well as stock sizes; recycling does not change the result
- Simulation of pulsing with alternate functional responses under different combinations of biotic parameters do not exhibit changes from equilibrium expectation.

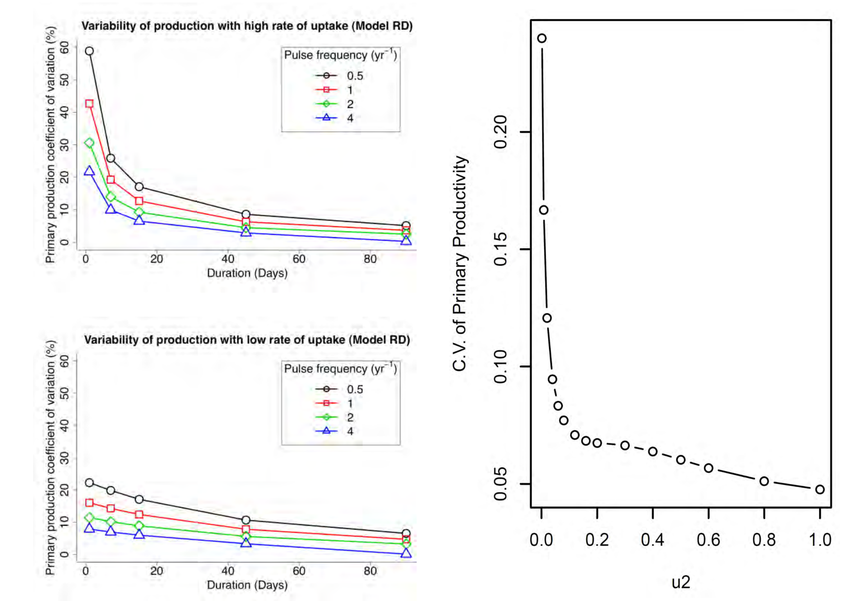


Linear models with pulsing have the same levels of biomass and productivity as predicted by equilibrium equations. This can be proven by taking the average amount of productivity, which is proportional to biomass, over a steady state cycle from pulses and comparing it to the equilibrium level. Recycling does not change this property, even though it increases the retention of nutrients and thus levels of biomass and productivity.



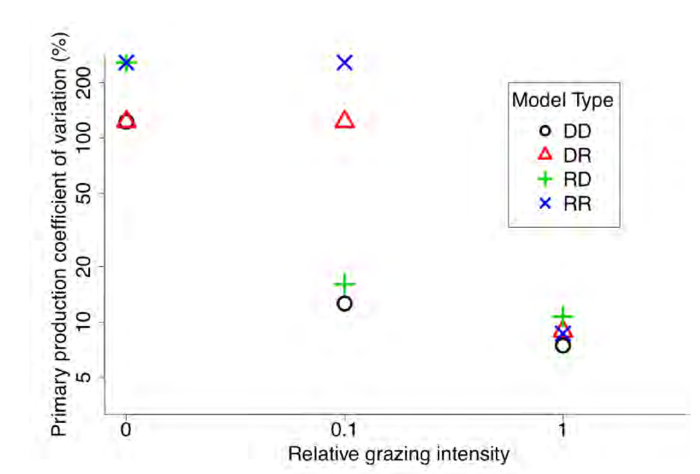
These results are for a recipient controlled. On the left, the percent change stays below the precision of numerical estimation. Changing various parameters such us grazing rate, also has no effect (right).

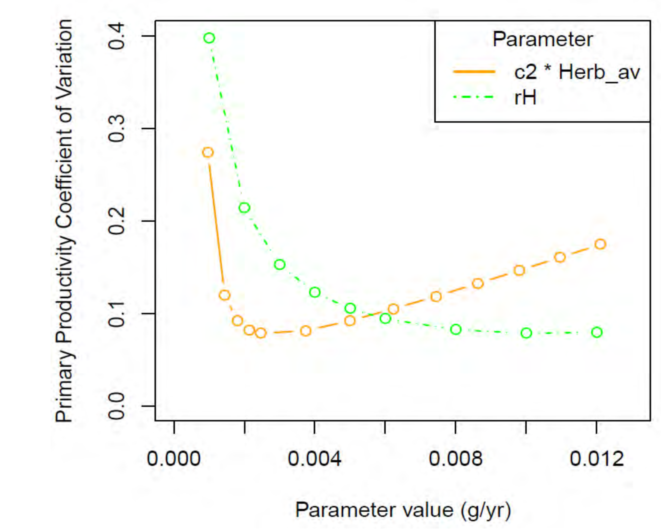
- Primary producers can stabilize production in the absence of the herbivore by decreasing the rate of uptake; however this relationship changes in the presence of the herbivore



The left panels show coefficient of variation of primary productive under different pulse regimes when the herbivore is absent for an autotroph with high uptake (upper left) and low uptake (lower left). The right panel shows the effect of changing uptake rate.

- The presence of grazers has a dramatic effect on the stability of primary production when pulses are extreme; when present, grazers stabilize productivity in an upwelling environment





The presence of herbivores quickly decreases the variability of productivity, no matter the functional responses (left). Note that the intermediate grazing intensities for the DR and RR model are insufficient to maintain herbivores. The grazing and recycling traits of herbivores then have opposing effects on stability of productivity (right).

Discussion

- When we consider a periodic steady state, there is no net change in growth, and productivity must balance between pulse and non-pulse phases, thus we observed means to be equal no matter the pulsing regime and were not different than the equilibrium value under equivalent constant input
- Because means are no different among pulse regimes, the effect of instability is solely due to the volatility of the pulse, rather than any interaction between pulsing and biotic processes
- Biotic processes did affect stability and could dampen variation induced by pulsing; important when variation affects the persistence or function of any trophic group
- Other impacts on productivity are independent of pulsing such as enhancement by recycling a limiting nutrient or increase in total amount of input
- The alternative that non-linear functional responses can be responsible for productivity to deviate from the levels when inputs are constant was not supported, but other types of functional responses must be scrutinized
- When uptake or consumption rates saturate at high resource levels, not as much resource may be taken and would be subject to greater loss compared to when inputs are at a lower albeit constant level; this would have a negative effect, decreasing average productivity
- If variability shifts productivity in a negative direction, the effect of herbivore on stabilizing primary producers by dampening variability, has direct implications for maintaining ecosystem functioning
- Thus future analysis will examine the behaviour of alternate consumer biology in response to pulses

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