

Effects of Nutrient Enrichment on the Stability of Producer Species Under the Pressure of Predation

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Keywords: nutrient enrichment, population dynamics, stability, generalist predation.

Abstract. Nutrient enrichment has a great influence on the stability of producer species. However, in the presence of predators, its influence has not yet been studied. In this research, we build a food web model which coupled a classic nutrient competition model with a bio-energetic predator-prey model, and a trade-off between competitive abilities of producers is considered. We considered the generalist predation and explored the effect of nutrient enrichment on the stability of producer species under the pressure of predation. The results showed increasing with the nutrient supplement, the biomass of the producers increased and the stability of producer was broken. It turned out that eutrophication destroyed the stability of producer species. Results in this research will be helpful in understanding the influence of nutrient enrichment under the pressure of predation and providing theoretical guidance for ecosystem and biodiversity conservation.

Introduction

The stability of producer species is important in maintaining the functions of an ecosystem. Nutrient enrichment by human activities is one of the greatest threats to global ecosystems and it has great influence on the stability of producer species [1]. As a result, species extinction or even breakdown of ecosystem is often happen. Knowing the effects of nutrient enrichment is an important and wide discussed subject in both theoretical and applied ecology [2].

Ecologists have researched the influence of nutrient enrichment on stability of producers for a long time. Early in 1971, Rosenzweig demonstrated that with the increase of resource supply, species abundance will oscillate more intensively, the minimum values of the population abundance decrease and finally drop below a local extinction threshold [3]. This so called ‘paradox of enrichment’ is analyzed in a simple consumer-resource model [3-6]. Then many ecologists tried to test this idea through theoretical and experimental approach. For example, Simple models of predator-prey dynamics predict a “paradox of enrichment”, where enriching the prey causes population cycles that increase in amplitude with further enrichment [3,7-9]. In a classic laboratory experiment conducted by Huffaker et al. (1963), increasing the supply of food to herbivorous mites destabilized their interaction with predatory mites and resulted in the extinction of both species. The dynamics of a protozoan predator-prey system was also destabilized by enriching the prey [10]. However, these analyses are based on two trophic levels. The influence of nutrient enrichment on the stability of producer species under the pressure of predation has not been analyzed.

In this research, the food web model is constructed by adding two specialist consumer species to a well-known resource competition model [11-13], in which two producer species are competing for two essential nutrients. A bio-energetic model with allometric coefficients [8,17-21] is employed to depict the producer-consumer interactions, and then we added a generalist predator into the system. The influences of nutrient enrichment on the stability of producer species in this model are examined via analyzing the standard deviation of the producer species. Through theoretical analysis, the results show that with generalist predation nutrient enrichment destroys the stability of producer species, which provide a theoretical support to protect the diversity of species under the condition of eutrophication.

Methods

The Model. The food web model is constructed by two producer species competing for two limiting nutrients, and a generalist predator. In the research, the effects of nutrient enrichment are analyzed following two scenarios: 1) the supply concentration of nutrient 1 increase linearly while the concentration of nutrient 2 keeps constant; 2) the supply concentration of nutrient 1 increases and the concentration of nutrient 2 decreases, while the total amount of these two nutrients remains constant. The standard deviation of producers' abundance in the food web is analyzed to explore the stability of producers under nutrient enrichment.

The food web model is given as follows:

$$\frac{dN_j}{dt} = D(S_j - N_j) - \sum_{i=1}^2 c_{ji} \mu_i(N_1, N_2) P_i \quad j=1,2 \quad (1a)$$

$$\frac{dP_i}{dt} = P_i [\mu_i(N_1, N_2) - x_{Pi}] - x_{Ci} y_i f_i(P_i) C_i / e_i \quad i=1,2 \quad (1b)$$

$$\frac{dC_i}{dt} = x_{Ci} y_i f_i(P_i) C_i - x_{Ci} C_i \quad i=1,2 \quad (1c)$$

Here N_j denotes the abundance of nutrient j , P_i denotes the biomass of producer i , and C_i denotes the biomass of consumer i which only feeds on producer i .

In the Equation (1a) D is the system's turnover rate; S_j is the supply concentration of nutrient j , c_{ji} is the content of resource j in species i . We assume that the specific growth rates follow the Monod equation:

$$\mu_i(N_1, N_2) = \min\left(\frac{r_i N_1}{K_{1i} + N_1}, \frac{r_i N_2}{K_{2i} + N_2}\right) \quad (2)$$

where r_i is the maximum specific growth rate of species i , K_{ji} is the half-saturation constant for resource j of species i , and the 'min' refers to the minimum function.

In the Equation (1b) x_{Pi} and x_{Ci} denote the mass-specific metabolic rate of producer i and consumer i respectively; y_i is the maximum consumption rate of consumer i relative to its metabolic rate; e_i is the biomass conversion efficiency of the consumer i ingesting producer i .

Equation (1c) is the time derivative of the consumers' biomasses. Here the functional response f_i describes the realized fraction of the consumer's maximum rate of consumption:

$$f_i(P_i) = \frac{P_i}{K_{Ci} + P_i} \quad (3)$$

where K_{Ci} is the half saturation density. This response is the Holling type II response [22], also it is the widely used functional response.

Parameters. The reference parameter values for the nutrient-producer interactions have already been used by Huisman and other authors [11,12,14-16]. According to the references, $D=0.25 \text{ day}^{-1}$ is employed here for all nutrients, and $r_i=1 \text{ day}^{-1}$ for all producers. The values of K and c are given in the matrixes below:

$$K = \begin{bmatrix} 0.15 & 0.1 \\ 0.1 & 0.2 \end{bmatrix} \quad c = \begin{bmatrix} 1.0 & 0.5 \\ 0.5 & 1.0 \end{bmatrix}$$

Different columns represent different consumers, and different rows represent different resources. $y=6$, $e_i=0.45$ and $K_{Ci}=0.5$ [8,20,21,23]. The metabolic rate is calculated as below:

$$x = \frac{a_x}{a_r} \left[L^{0.25} \right]^{l-1} \quad (4)$$

where a_x/a_r is 0.138 for producers and 0.314 for consumers [2,17,19,24], l is the species' trophic level and L is producer-consumer body size ratio selected as 0.1 here [21]. x_{Pi} and x_{Ci} are calculated to be 0.138 and 0.162 respectively.

Results

Fig. 1 shows the stability of the two producer species with one generalist predator under different nutrients supply. Through the figure we can conclude that under low concentration of nutrients 1 and 2, the standard deviation of the two producer species is zero, since the producer species can not survive under the pressure of low nutrients and predation. This is a stable point of the system but with less ecological significance. Then with the increase of nutrient concentration, the standard deviation of the two producer species is increasing and the stability of the two producer species is decreasing. When the nutrients supply is sufficient, the standard deviation of the two producer species changed slowly. These kinds of phenomenon can be seen through both 3D and contour figures.

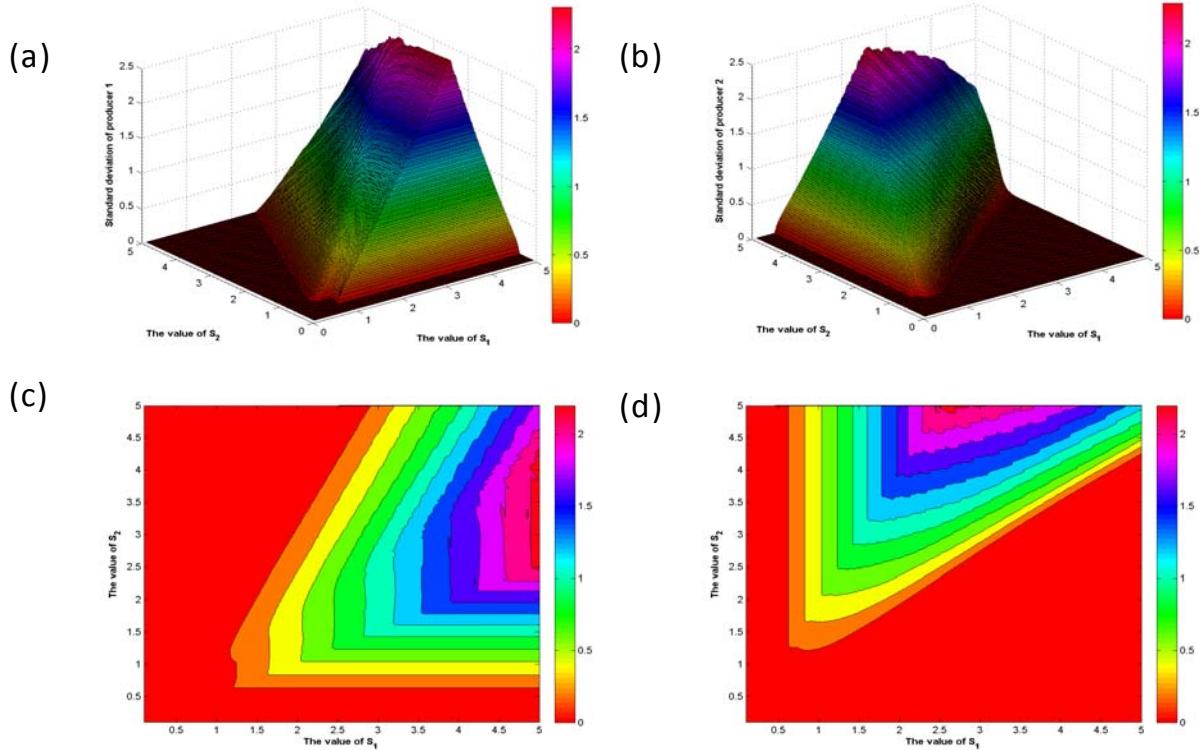


Fig. 1. Standard deviation of the two producer species in the food web with generalist predation. (a) and (b) are 3D figures of producer 1 and producer 2, while (c) and (d) are contour figures of producer 1 and producer 2.

To analyze the stability of producers under generalist predation further, the bifurcation diagram (fig. 2a and 2c) and the mean biomass (fig. 2b and 2d) of producer species have been researched along the supplement of nutrient 1 in two scenarios. In scenario 1 S_2 keeps constant at 2, while in scenario 2 the sum of S_1 and S_2 remains at 4.

In the upper left zone, nutrient 1 is the limiting resource, thus producer 2, which is the better competitor for nutrient 1, will win the competition and exclude producer 1. With the increasing of supplement of nutrient 1, at first the producer biomass is too little to sustain the predator and the biomass of producer 2 keeps rising. When the producer biomass is big enough, the predator population can survive. Meanwhile, the flows of increasing nutrients move along the food chain to the upper trophic level, which causing the producer biomass keeps constant. This is completely coherent with the ‘trophic cascade’ theory [25,26]. After that, the population of producer 2 begins to oscillate, with the amplitude and mean value increasing with the nutrient supplement, and the ‘enrichment paradox’ emerges [3].

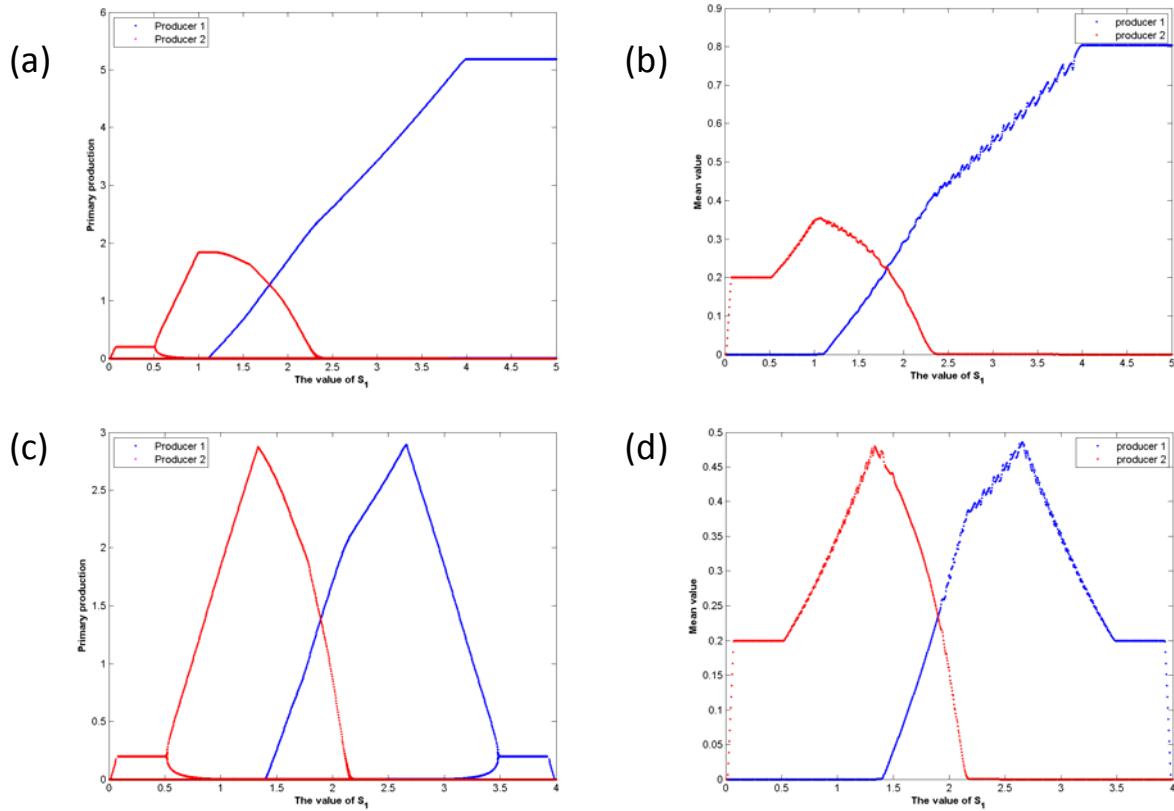


Fig. 2. Bifurcation diagram (plotting the local maximum and minimum values during the time series at each supplement) and mean biomass of producer species in scenario 1 (a and b) and scenario 2 (c and d) with generalist predation. Blue points indicate biomass of producer 1 while red ones indicate producer 2. In scenario 1 S_2 keep constant while in scenario 2 the sum of S_1 and S_2 keeps constant. The mean biomasses and bifurcation diagrams are calculated and plotted for the period from 1000 to 2000 days to avoid initial influences.

In the middle zone, both of the two nutrients are the limiting resources and the two producer species can coexist because ‘each species consumes most of the resource for which it has the highest requirement’ [13] and the predator species give the same top-down pressure to these two producer species. This is the process of the old winner being replaced gradually by the new dominators because of the changing of the nutrient supplements. This is coherent with the ordinary attitude that generalist predation imposes apparent competition [27] between prey species.

In the lower right zone, nutrient 2 is the limiting resource and producer 1 is the better competitor of nutrient 2 and will win the competition. In scenario 1 the primary biomass keeps constant because the growth of producer 2 is limited by nutrient 2. In scenario 2, things are nearly the same as those in the upper left zone, except that the leading actor is producer 2.

Conclusions

In this work, we explored the responses of the stability of producer species to the nutrient enrichment with a generalist consumer. Generalist predators impose apparent competition and eventually lead to competitive exclusion. We found that the biomass of the producer increases with enriched nutrient concentrations, and the stability of producer species is broken.

Acknowledgements

This work was supported by the National Science and Technology Support Project (2006BAC10B0

3) and the National Water Special Project (No. 2009ZX07210-009, No. 2015ZX07203-011, No. 2015ZX07204-007) and Ecological Safety Survey and Assessment of Nansi Lake (2012-2015) and Ecological Riverway Artificial Strengthen Key Technology Research and Demonstration Project of Shandong Province (SDHBPJ-ZB-08).

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