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Effects of Nutrient Enrichment on Producers in A Simple Food Web

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ABSTRACT *' Paradox of enrichment' has been generally verified in simple models containing biotic resources, and here we explore whether this paradox can last in more realistic models. A simple food web with two producer species and two specialist predators was analyzed. The influences of nutrient enrichment on producers in the food web models are explored via analyzing the change of producers' mean biomass and population stability. The results showed that the enrichment of one nutrient would not alter the biomass or population stability of producer species. However, the enrichment of both nutrients would increase the producer biomass and at the same time decrease the population stability. Our findings extend the traditional paradox of enrichment into simple food webs.*

KEYWORDS : nutrients enrichment; food webs; population dynamics

INTRODUCTION

Nutrient enrichment by human activities is one of the greatest threats to global ecosystems (Davis *et al.* 2010), and particularly eutrophication resulting from excessive nutrient enrichment has become the primary problem for most surface waters in the world (Smith & Schindler 2009). It is believed that global cycles of nitrogen and phosphorus have been amplified by about 100% and about 400% respectively by postindustrial human activities (Falkowski *et al.* 2000; Elser *et al.* 2007), which should be responsible for widespread aquatic eutrophication (Carpenter *et al.* 1998; Gruner *et al.* 2008).

Simple consumer-resource models have predicted that enrichment of resource increases the average biomass of the species, but reduces population stability because of accelerated oscillations (Rosenzweig 1971; Boukal *et al.* 2007), which is named as the 'paradox of enrichment'. However, if this paradox still exists in more realistic food webs has been rarely studied. Here we built up a simple food web with two producer species and two specialist predators. In analyzing the effects of nutrient enrichment on the biomass and the population stability of producer species, we are trying to see how the paradox of enrichment changes.

MATERIALS AND METHODS

The food web model is constructed by adding two specialist consumer species to a well-known resource competition model (Huisman & Weissing 2001a, b), in which two producer species are competing for two limiting nutrients. A bioenergetic model with allometric coefficients (Brose *et al.* 2005) is employed to depict the producer–consumer interactions. The model is given as follows:

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

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

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

The coupled ordinary differential equations depict that two producers compete for two limiting nutrients and each producer species is consumed by a specialist consumer. Here N_j, P_i, and C_i respectively denotes the abundance or biomass of nutrient *j*, producer *i*, and consumer *i* which only feeds on producer *i*. *D* is the turnover rate, 0.25 day^{-1}; S_j is the supply concentration for nutrient *j*, which varying from 0 to 5 mmol L^{-1}; c_{ji} is the content of resource *j* in species *i*, with c_{11} = c_{11} = 1 and $c_{12} = c_{21}$ = 0.5; $m_i(N_1,N_2)$ is the specific growth rate of species *i*, which is assumed to follow the Monod equation and to be determined by the most limiting resource:

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

where r_i is the maximum specific growth rate of species *i*, 1 day^{-1}; K_{ji} is the half-saturation constant for resource *j* of species *i* with K_{11} = 0.15, $K_{12} = K_{21}$ = 0.1, and K_{22} = 0.2; and the 'min' refers to the minimum function.

x_{Pi} and x_{Ci} denote the mass-specific metabolic rate of producer *i* and consumer *i* respectively, which are calculated based on their trophic level (Brose *et al.* 2005); y_i is the maximum consumption rate of consumer *i* relative to its metabolic rate, fixed to 6; and e_i is the biomass conversion efficiency of the consumer *i* ingesting producer *i*, fixed to 0.45. The functional response f_i describes the realized fraction of the consumer's maximum rate of consumption:

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

where K_{Ci} is the half saturation density, fixed to 0.5.

Numerical simulations are based on a fourth-order Runge-Kutta method with a fixed time step of 0.01 day. Initial conditions are $P_i(0)$ = 0.1 for all producers, $C_i(0)$ = 0.1 for specialist predators, and $N_j(0)=S_j$ for all resources. Simulations run for 2000 days for each *S*. The mean biomasses and population stability are calculated and plotted for the period from 1000 to 2000 days to avoid initial influences. The population stability is indicated by the coefficient of variation (CoVar), as prior studies did (Brose *et al.* 2006; Rall *et al.* 2008). A higher CoVar value indicates higher magnitude of fluctuation and thus lower population stability.

RESULTS AND DISCUSSION

The producer biomass basically kept constant if the supply of the nutrient with high concentration increased and the supply of low-concentration nutrient kept constant (see Figure 1). This should be attributed to the Liebig's law of the minimum, i.e. only the concentration of the limiting nutrient determines the growth of producers. Once both nutrients had similar concentration, the producer biomass fluctuated with the increase of either nutrient. In this case, a trade-off emerge in which each species consumed most of the resource for which it had the highest requirement (Huisman & Weissing 2001a), and this facilitated the chaotic behaviors of the system which might lead to the fluctuations.

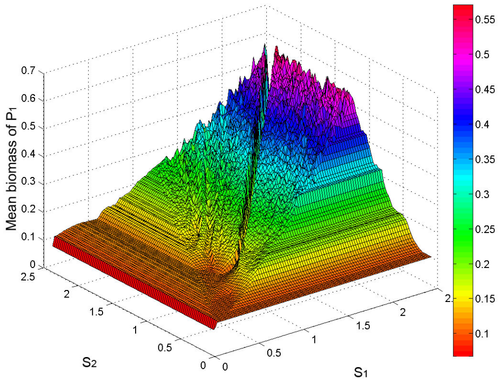

Figure 1 Relationship between the mean biomass of the producer species P_1 with the supply of the two nutrients.

The population stability (measured in 'CoVar') of the producer species performed similar pattern with biomass, except that the change was dramatic in infertile environment but gentle in fertile environment (Figure 2). The enrichment of only one nutrient would not cause the decrease of stability. But enrichment of both of them would again decrease the population stability of producer species. This conclusion would extend the traditional 'paradox of enrichment' (Rosenzweig & Schaffer 1978) into simple food webs.

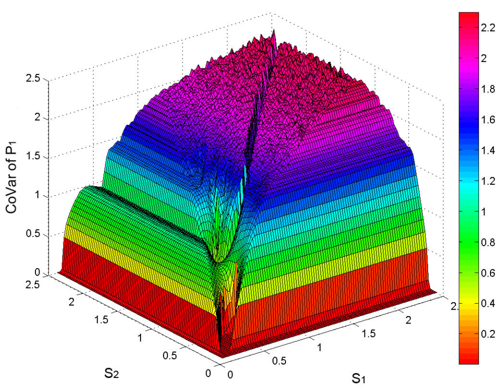

Figure 2 Relationship between the population stability of the producer species P_1 with the supply of the two nutrients.

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