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Viewing the effects of species loss in complex ecological networks

Lei Zhao, Huayong Zhang*, Wang Tian, Ran Li, Xiang Xu

Research Center for Engineering Ecology and Nonlinear Science, North China Electric Power University, Beijing, 102206, China

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ABSTRACT

Species loss is becoming a major threat to ecosystems. An urgent task in ecology is to predict the consequence of species loss which requires an extending of our traditional study of the topology of network structure to the population dynamic analyses in complex food webs. Here, via numerical simulations of the model combining structural networks with nonlinear bioenergetic models of population dynamics, we analyzed the secondary effects of species removal on biomass distribution and population stability, as well as the factors influencing these effects. We found that the biomass of target species, the nutrient supply, and the trophic level of target species were the three most significant determiners for the effects of species loss. Species loss had large negative effect on the biomass of the species with small biomass or intermediate trophic levels, especially in infertile environment. The population stability of the species with large biomass or low trophic level is easily to be influenced especially in nutrient-rich environment. Our findings indicate the species which are easily to be affected by species loss in food webs, which may help ecologists to outline a better conservation policy.

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1. Introduction

There exists little doubt that most of the earth's ecosystems are experiencing losses of biological diversity [1], which has been one of the most pervasive environmental changes of our time [2]. These high rates of species extinction put ecosystems under enormous stress, making it critical to understand how the loss of biodiversity influences the stability and function of the ecosystems we rely on [3]. In the past 20 years, accelerating rates of species extinction have prompted an increasing number of studies towards understanding how the loss of species affects the functioning of ecosystems, including the biomass distribution, secondary extinctions and so on, via both experimental and theoretical methods [4].

In empirical researches, researchers have conducted field experiments to quantify the effects of species loss by removing a species [5]. This removed species can be dominant plants [6] or consumers including insects and mammals [7]. These empirical researches have revealed some patterns mostly about how the biomass of the other species changes after the removal under the top-down or bottom-up effects [8]. Yet since most of the empirical studies have been short term, and have typically examined the effects of one species in local communities, we urgently need a comprehensive theoretical analysis to get the general results.

Most theoretical researches about the species removal effects use topological analysis of natural [1,9] or artificial [10] food webs. Though there is much strength, the topological approach has also weakness. It just records the secondary extinctions caused by bottom-up effects [11], and ignores the effects of top-down and competition [12]. Besides, the topological approach underestimates the effects of species loss and overestimates the stability of food webs [13]. As the dynamics of ecological communities is not taken into account, the topological approach cannot records the change of population stability or the redistribution of biomass, which are the most important indicators to detect the effects of species loss in empirical researches [14]. Thus, the dynamical approach appears particularly important, especially in analyzing species removal effects on biomass and population stability.

Here we use a dynamic model that synthesizes the structure of complex food webs, predator-prey interactions and nutrient-dependent growth of the producer species [15,16] to simulate the biomass change of each species before and after species removal. The effects of species loss on both biomass and population stability were investigated, with the aim of detecting the major determiners for the effects of species loss.

2. Materials and methods

The species removal effects (SRE) on biomass distribution and population stability of the survival species were analyzed in 1000 artificial ecological networks. The process was divided into three steps: (1) the food web structure was created by the niche model

* Corresponding author.

E-mail address: rceens@ncepu.edu.cn (H. Zhang).

[17], (2) the population dynamics before and after the removal of a randomly chosen species was recorded from numerical simulation of the bioenergetics model [16] and the SRE were calculated, and (3) the major factors (including resource supply, community properties and species properties) influencing the SRE were detected using classification and regression tree (CART) analyses [18].

2.1. The niche model and community structure

The structures of the food webs were determined by the niche model [17], which has been used widely in theoretical researches involving complex ecological networks [16,19]. Following the guidance of the prior study [16], the two input parameters, species richness S and directed connectance C , were assigned to follow normal distribution, with $S \sim N(25, 5^2)$ and $C \sim N(0.15, 0.025^2)$. In the niche model, each species is assigned a niche value which is generated randomly from 0 to 1, which retains the ordering of species in one dimension. All the species whose niche values within a certain range would be consumed by a given species. The size of this niche range is assigned by a beta function whose expected value is $2C$, and the center of the niche range is less than the consumer's niche value. In this way all the trophic links would be determined, and a virtual community is built up.

2.2. Bioenergetic model and population dynamics

We used a nonlinear bioenergetics consumer-resource model [15,16,20] to depict the population dynamics within the food webs. The model is given as follows:

$$\frac{dN_l}{dt} = D(S_l - N_l) - \sum_{i=\text{producers}} c_{li}\mu_i P_i \quad (1a)$$

$$\frac{dP_i}{dt} = \mu_i P_i - \sum_{j=\text{consumers}} x_{ji} y_j B_j F_{ji} / e_{ji} - x_i P_i \quad (1b)$$

$$\frac{dB_j}{dt} = \sum_{i=\text{preys}} x_{ij} y_j B_j F_{ji} - \sum_{i=\text{predators}} x_{ij} y_j B_i F_{ij} / e_{ij} - x_j B_j \quad (1c)$$

Here N_l , P_i , and B_j respectively denotes the concentration of nutrient l and the biomass of producer i and consumer j . Two limiting nutrients are involved and the numbers of producer and consumer species are determined by the food web structures generated from the previous step.

Eq. (1a) describes the dynamics of the nutrient availabilities which depend on both the rates of nutrient supply and the amount of nutrients consumed by the producer species. Nutrients are exchanged at a turnover rate D with a supply concentration S_l . D is kept constant to 0.25. S_1 , the supply concentration of nutrient 1, varies randomly from 0 to 4 while S_2 is always fixed to 4. c_{li} is the content of nutrient l in producer species i . For all the producer species, the content of nutrient 1 c_{1i} is 1 and the content of nutrient 2 c_{2i} is 0.5, which makes sure that the first nutrient is the one most needed by all the producer species as it has the highest content in their biomasses. $\mu_i(N_1, N_2)$ 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

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

where r_i is the maximum mass-specific growth rate of species i , K_{ji} is the half-saturation constant for resource j of species i , and the 'min' is the minimum operator. r_i is set to be 1, and K varies randomly from 0.1 to 0.2. This growth rate model has been widely used [16,21,22] and successfully evaluated in experiments [23].

Eqs. (1b) and (1c) describe changes in biomass densities of primary producer and consumer species respectively. In these equations, x_i is i 's mass-specific metabolic rate; y is the maximum consumption rate of the consumers relative to their metabolic rate; and e_{ji} is j 's assimilation efficiency when consuming population i . Following the setting of previous works [15,16], bioenergetic parameters are selected as $y=10$, and $e=0.85$ for carnivores and $e=0.45$ for herbivores. The metabolic rate is calculated as below:

$$x = \frac{a_x}{a_r} \left[Z^{\frac{1}{4}} \right]^{TL-1} \quad (3)$$

where a_x and a_r are allometric constants for metabolic rate and production rate. a_x/a_r is 0.138 for producers and 0.314 for consumers [16,24]. Z is prey-predator body size ratio selected as 0.1 here, which is consistent with empirical data [25]. TL is the species' prey-averaged trophic level [26]. The functional response, F_{ij} , describes the realized fraction of i 's maximum rate of consumption achieved when consuming species j .

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_0^h + \sum_{k=\text{resources}} \omega_{ik} B_k^h} \quad (4)$$

where ω_{ij} is the proportion of i 's maximum consumption rate targeted to consuming j ; B_0 is the half-saturation density of species i ; h is the Hill exponent that regulates the shape of the curve. B_0 is fixed to 0.5. We use uniform preference which means $\omega_{ij} = 1/n$ (n is the number of prey species of i). Hill exponent h is kept to 1.2, i.e. a modified 'type II.2' functional response [27] is used. This response is close to a type II response and providing much of the stability of type III response [28].

2.3. Numerical simulations

1000 communities were generated from the niche model with S and C following the normal distribution, $S \sim N(25, 5^2)$, and $C \sim N(0.15, 0.025^2)$. The supply of nutrient 1 follows the uniform distribution, $Supp \sim U(0, 4)$. In each community one species is designed to be removed and it is picked up randomly (see Fig. 1a). The SRE on each of the other species were recorded. Every individual simulation started with random initial biomass densities following $U(0.05, 1)$ and ran 20,000 steps. The species removal occurs at $t=10,000$. The time series are divided into 4 stages, 2 before the species removal and 2 after (Fig. 1b). The period of stage 1 (between $t=1$ and $t=5000$) and stage 3 (between $t=10,001$ and $t=15,000$) is set to allow transient dynamics caused by initial effects and species removal to settle down. The values of the biomass densities on stage 2 (between $t=5001$ and $t=10,000$) and stage 4 (between $t=15,001$ and $t=20,000$) are used to calculate the SRE.

2.4. Measurement of effects

The log response ratio (LRR), one of the most commonly used effect metrics in ecological meta-analysis [8,29,30], is used as the size ratio metric of the species removal effects (SRE). The SRE on each species in a community is characterized by two aspects: effects on biomass and effects on population stability. Biomass is depicted by the mean value of the population dynamics during a given period, while population stability is depicted by the coefficient of variation (CoVar) [31,32]. CoVar is defined as the ratio of the standard deviation to the mean. The effect metrics for each species are the log ratio of mean biomass and CoVar after and before species removal.

$$SRE_{\text{biomass}} = \log(B_{\text{after}}/B_{\text{before}}) \quad (5a)$$

$$SRE_{\text{stability}} = \log(\text{CoVar}_{\text{after}}/\text{CoVar}_{\text{before}}) \quad (5b)$$

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