

Dome-shaped transition between positive and negative interactions maintains higher persistence and biomass in more complex ecological networks

Chuan Yan, Zhibin Zhang*

State Key Laboratory of Integrated Management on Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101, China



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ABSTRACT

Positive relationship between diversity and biomass was often observed by empirical experiments at the community level, but the effects of species interactions on community total biomass have been rarely explored from a network perspective. Weak interaction and specific non-monotonic interactions have been proposed to be stabilizing mechanisms in maintaining persistence in more complex ecosystems, but it is unclear how they contribute to the high level of biomass or productivity of these systems. In this study, we examined the effects of various interactions, specifically dome-shaped (shifting from positive to negative effect with increase of density) and satiated interactions, on biomass and biomass flow with the increase of complexity in theoretical networks. Our results indicated that, as compared to linear or satiated interactions, dome-shaped interactions maintained both higher persistence and biomass or biomass flow in more complex networks, but resulted in larger variations of species biomass. However, variation of network biomass was much smaller than that of species biomass. Our results suggest that species interaction shifting between mutualism at low density and competition or predation at high density could be a driving force for maintaining high levels of persistence, diversity, biomass and biomass flow in natural ecosystems.

1. Introduction

Diversity-stability debate has been a long-standing topic in ecology. Empirical observation leads early ecologists to conclude that complex ecosystems should be more stable than simpler ones (MacArthur, 1955), but theoretical network analysis led to the opposite conclusion (May, 1972). This paradox has stimulated tremendous studies to investigate key factors in determining the diversity-stability relationship. Several hypotheses on the stabilizing mechanisms of ecological networks have been proposed, such as modularity (sometime called compartmentation), nestedness, omnivory, diversity of interaction types, weak interaction hypothesis, and so on (Bascompte et al., 2003; McCann, 2000; Mougi and Kondoh, 2012). For theoretical linear ecological networks, the local stability (that measures the tendency of the system to return to equilibrium after perturbations) decreases abruptly with increase of complexity that is composed of number of species, number of interaction links and interaction strength (Allesina and Tang, 2012; May, 1972; McCann et al., 1998; Neutel et al., 2002), thus weak interaction (less connectance or interaction strength) is often speculated to be necessary to maintain stable ecological networks with more species. Yan

and Zhang (2014) proposed an alternative stabilizing mechanism for complex ecological networks that some specific non-monotonic interactions, such as shifting signs from positive to negative (dome-shaped function) or to neutral (satiated function) with increase of density, could significantly increase the persistence of ecological networks. The underlying stabilizing mechanism of these non-monotonic interactions might be that they can increase probability of species coexistence by producing more stable equilibrium points, and by reducing the chance of unbounded mutualistic feedbacks which are often observed in traditional linear models (Yan and Zhang, 2014; Zhang, 2003; Zhang et al., 2015).

Besides the diversity-stability paradox, the relationship between diversity and biomass is another hot topic in ecological literature. Community total biomass, i.e., the mass of all species, is an important aspect of natural ecosystems by representing the ecosystem function or productivity. For a long time, ecologists have focused on testing the relationships between species richness and community biomass in natural communities (mostly in plant communities). Both empirical and experimental evidence suggest that there is usually a positive species richness-biomass (productivity) relationship (Grime, 1973; Michalet

* Corresponding author.

E-mail address: zhangzb@ioz.ac.cn (Z. Zhang).

et al., 2006; Mittelbach et al., 2001). The theoretical exploration on this relationship has led to two major hypotheses: (1) functional niche complementarity (the complementarity effect) stresses that niche differentiation or facilitation increases the performance of communities above that expected from the performance of individual species, and (2) selective processes, such as interspecific competition, can cause dominance of species with very high biomass (Loreau, 2000; Loreau and Hector, 2001). However, the relationship between biomass and species interactions has rarely been investigated, probably due to the difficulty of simultaneously quantifying species interactions and community biomass in natural ecosystems. This issue is also rarely explored in a multi-species context by using theoretical models. In random linear models of ecological networks, weak interaction is essential in maintaining a stable complex network, but its effects on biomass or biomass flow are largely unknown. By using a theoretical model of two species, Zhang (2003) suggested that dome-shaped interaction, i.e., mutualism at low density but competition at high density, would not only increase probability of species coexistence but also the carrying capacity of the two competitors. Therefore, non-monotonic interactions are likely to promote both persistence and biomass of ecological networks, but this has never been studied in the context of ecological networks.

In nature, there have been growing evidences of dome-shaped or satiated interactions between species. For instance, in rodent-seed interactions, some rodent species show positive effects on seed tree species by scatter-hoarding seeds at low-density levels, but showed negative effects by over-consuming seeds at high-density levels (Li and Zhang, 2007). Other examples were seen in ant-aphid interactions (Addicott, 1951), pollinator-mediated plants (Thompson, 1988), and plant-mycorrhizae interaction (Neuhauser and Fargione, 2004). The purpose of this study emphasized their effects on persistence, biomass and biomass flow of theoretical ecological networks with the increase of complexity, as compared to the linear interactions.

2. Method

2.1. Interaction functions

Following the classical Lotka-Volterra equations, we defined signed interaction strength a as the per capita effect of one species on another species. We applied four types of functions to interaction strength a . The first one was derived from a linear function in which the interaction strength a was independent of population density (L function, Fig. 1a). The second one was derived from the Holling’s type 2 functional response, defined as the satiated function in this study, assuming the strength was satiated by the density (N) of prey or resource species (here named as the H function, Fig. 1b), where h controls the satiation

rate, which was set to be 1. The third one was a simplified dome-shaped non-monotonic function provided in the work by Yan and Zhang (2014), i.e., shifting interaction from positive to negative effect when population density was higher than a threshold value (N_t), but the magnitude of strength is fixed (hereafter named as the NM1 function, Fig. 1c). The fourth one was a dome-shaped non-monotonic function, shifting interaction from positive to negative effect smoothly when the population density was higher than a threshold value (N_t) and the magnitude of strength was weakest around threshold density (hereafter named as the NM2 function, Fig. 1d), where b controlled the shifting rate of strength, which was set to be 0.8.

The interaction functions representing the changes of interaction strength against N_j were shown below:

$$L(a) = a$$

$$H(a, h, N) = \frac{a}{1 + hN}$$

$$NM1(a, N, N_t) = \begin{cases} |a|, & N < N_t \\ 0, & N = N_t \\ -|a|, & N > N_t \end{cases}$$

$$NM2(a, b, N, N_t) = |a| \frac{1 - e^{b(N-N_t)}}{1 + e^{b(N-N_t)}}$$

2.2. Network construction

Following May’s model (May, 1972), we constructed the randomly-connected networks based on an interaction matrix M of size $S \times S$ (the number of species, $S = 10, 20, 40, 60$ or 80). We defined connectance ($C = 0.2, 0.4, 0.6$ or 0.8) as the proportion of realized interaction links in the off-diagonal elements of M . The values of interaction strengths were drawn from a normal distribution (mean = 0 and standard deviation = 0.0625, 0.125, 0.25 or 0.5), and we used standard deviation to represent the magnitude of interaction strength (IS). To test the effects of non-monotonic interactions on various properties of networks, we introduced a certain proportion (20%, 50% and 80%) of non-monotonic interactions into the connected elements respectively by replacing the L or H interactions functions. These resulted in six kinds of networks containing different interaction functions or their combinations: “L”, “L+NM1”, “L+NM2”, “H”, “H+NM1” and “H+NM2”. Similarly, we introduced non-monotonic interactions into 26 networks with empirical food web structure established by Thompson and Townsend (2003), downloaded from an online Interaction Web Data-Base (www.nceas.ucsb.edu/interactionweb/). We have conducted 200 replicates of random networks for each combination of species number, connectance and interaction strength magnitude, and 50 replicates of

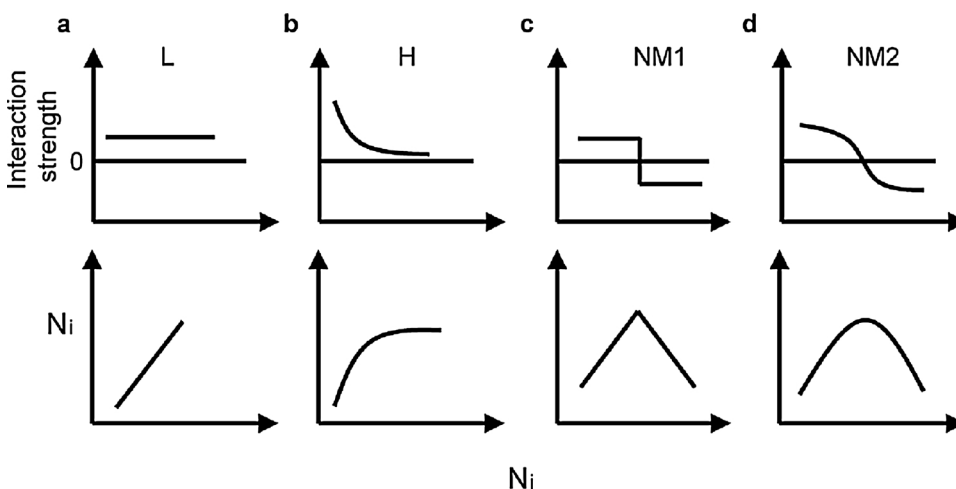


Fig. 1. The four types of interaction functions describing the change of interaction strength of N_j on N_i (upper panels) and the corresponding zero-growth isoclines of N_j (lower panels).

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