

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

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ARTICLE INFO

Keywords:

Non-monotonic interaction
Complexity
Diversity-stability
Persistence
Biomass
Ecological network

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

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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

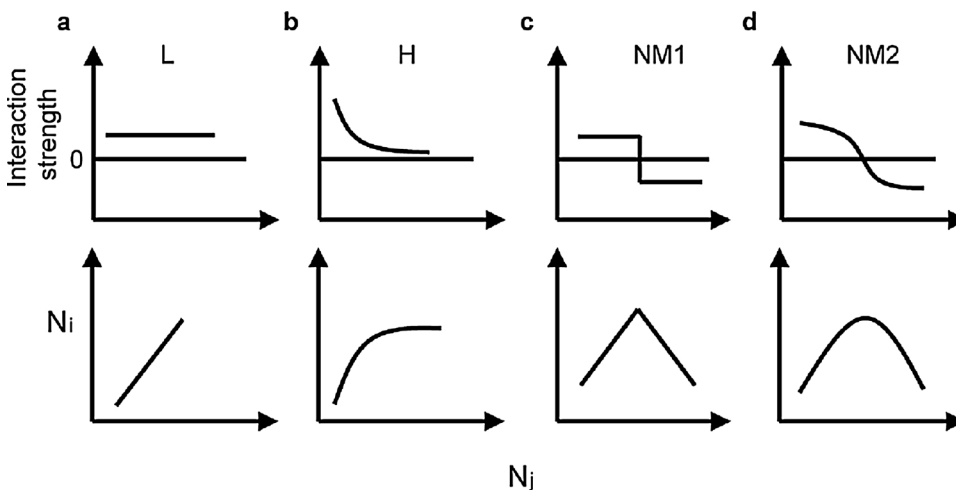


Fig. 1. The four types of interaction functions describing the change of interaction strength of N_j on N_i (upper panels) and the corresponding zero-growth isoclines of N_j (lower panels).

each food web with empirical structure for each level of interaction strength. All the parameters of our simulations were summarized in Table A.1.

2.3. Community dynamics simulations

The community dynamics was applied by using a set of multi-species differential equations. Eq. (1a) and Eq. (2a) described community dynamics with only L or H functions of interaction strength, as shown below:

$$\frac{dN_i}{dt} = N_i \left(r_i - N_i + \sum_{j=1, j \neq i}^S a_{ij} N_j \right) \quad (1a)$$

$$\frac{dN_i}{dt} = N_i \left(r_i - N_i + \sum_{l=1, l \neq i}^L \frac{a_{il}^+ N_l}{1 + N_l} + \sum_{k=1, k \neq i}^K \frac{a_{ik}^- N_k}{1 + N_i} \right) \quad (2a)$$

Where N_i is population density of species i , r_i is the intrinsic growth rate, a_{ij} is the interaction effect of species j on species i in Eq. (1a), a_{il}^+ is the positive effect of the species l on species i in Eq. (2a), and a_{ik}^- is the negative effect of the species k on species i in Eq. (2a). In Eq. (2a), L and K indicate the number of species that show positive and negative effects on species i respectively.

Eqs. (1b) and (1c) described the community dynamics when non-monotonic interactions were introduced into networks with linear interactions (L+NM1, L+NM2), and Eqs. (2b) and (2c) described the community dynamics when non-monotonic interactions were introduced into networks with satiated interaction function (H+NM1, H+NM2), as shown below:

$$\frac{dN_i}{dt} = N_i \left(r_i - N_i + \sum_{j=1, j \neq i}^J a_{ij} N_j + \sum_{m=1, m \neq i}^M NM1(a_{im}, N_m, N_i) N_m \right) \quad (1b)$$

$$\frac{dN_i}{dt} = N_i \left(r_i - N_i + \sum_{j=1, j \neq i}^J a_{ij} N_j + \sum_{m=1, m \neq i}^M NM2(a_{im}, N_m, N_i) N_m \right) \quad (1c)$$

$$\frac{dN_i}{dt} = N_i \left(r_i - N_i + \sum_{l=1, l \neq i}^L \frac{a_{il}^+ N_l}{1 + N_l} + \sum_{k=1, k \neq i}^K \frac{a_{ik}^- N_k}{1 + N_i} + \sum_{m=1, m \neq i}^M NM1(a_{im}, N_m, N_i) N_m \right) \quad (2b)$$

$$\frac{dN_i}{dt} = N_i \left(r_i - N_i + \sum_{l=1, l \neq i}^L \frac{a_{il}^+ N_l}{1 + N_l} + \sum_{k=1, k \neq i}^K \frac{a_{ik}^- N_k}{1 + N_i} + \sum_{m=1, m \neq i}^M NM2(a_{im}, N_m, N_i) N_m \right) \quad (2c)$$

Where, the NM1 and NM2 are the non-monotonic functions, a_{im} represents the original interaction strength of species m on species i , N_m is the species m showing a non-monotonic effect on species i , and N_t is the threshold density where the species m shifting between positive and negative effects. In above equations, J indicates the number of species that have linear interactions with species i ; L and K indicate the number of species that show positive and negative effects on species i respectively; M indicates the number of species that have non-monotonic interactions (NM1 or NM2) with species i .

Because multiple nonlinear equations can hardly be solved analytically, we adopted simulation methods to study population dynamics of above models in six kinds of networks (“L”, “L+NM1”, “L+NM2”, “H”, “H+NM1” and “H+NM2” networks). Following previous study (Yan and Zhang, 2014), the simulation of population dynamics was integrated by 4th order Runge-Kutta method for 25,000 time units, implemented by *deSolve* package in R version 3.4 (Karline Soetaert et al., 2010; R Development Core Team, 2010). Initial population

density was randomly drawn from uniform distribution [1,10]. The parameters (summarized in Table A.1) used in simulations followed previous study (Yan and Zhang, 2014).

2.4. Network statistics

The complexity of an ecological network was measured by number of species, connectance (number of realized interaction links) and interaction strength (see above in *network construction*) (May, 1972). Persistence representing network stability of an ecological network was calculated as the number of survived (population density $> 10^{-6}$) species/initial number of species (S) at the end (the 25000th time step) of each numerical simulation (Yan and Zhang, 2014). Previous studies showed that intrinsic growth rate (r) has a close relationship with species body mass (Hennemann, 1983; Niklas and Enquist, 2001; Van M. Savage et al., 2004). We have set a narrow range (0.8–1.1) of the parameter r in our study, and the difference of biomass between species was assumed to be negligible, which allowed us to use the population density to represent biomass. Thus, we used the sum of population density of survived species at the end of each numerical simulation to represent the network biomass. In this study, we defined the biomass flow as biomass increase or decrease rates of one species caused by (not necessarily transferred from) the other species, which represents the net turnover rate of biomass of a species caused by interspecific interactions. This definition is different from energy or matter flow between species in food webs of ecosystems in which either input or output flow is calculated (they are equivalent). Because such positive and negative biomass flow are often asymmetric and not equivalent (e.g. between competitors or mutualists), both positive and negative biomass flow were summarized. Thus, the network biomass flow was calculated by summing the absolute values of input (positive) and output (negative) biomass flow of all species, i.e., absolute value of interaction strength multiplied by the biomass for each species at the end of each numerical simulation. The per capita biomass flow, which would represent the per capita biomass flow efficiency of a network at the end of simulation, was calculated by the criteria: network biomass flow/network biomass, which is a relative efficiency adjusted by community total biomass (1/time unit). For each survived species, we could calculate coefficient of variation (CV, standard deviation/mean) for the last 5000 time steps (time window of 20000th–25000th). Population-level (or species-level) biomass variation (PCV) was calculated as the mean value of the CVs of all survived species for the last 5000 time steps, while the network-level biomass variation (NCV) was calculated as the CV of network biomass for the last 5000 time steps. For random networks, each data point of network statistic is summarized as mean and standard error (SE, very small at most cases due to large sample size) from 3200, 4000 and 4000 simulated networks at each level of species number, connectance and interaction strength respectively; for food webs, each data point was summarized from 1300 simulations. To test the robustness of our results, we also estimated the persistence, network biomass, and (per capita) biomass flow at the 22000th, 23000th or 24000th time step, and to estimate the PCV and NCV by using at the time windows of from 20000th to 22000th, from 20000th to 23000th, or 20000th to 24000th step. The additional analyses indicated that the results were similar by using different time steps or time windows, suggesting our results were robust.

3. Results

3.1. Random networks

Because introducing 50% (Figs. 2–6), 20% (Fig. A.1) and 80% (Fig. A.2) of non-monotonic interactions into our simulated ecological networks produced similar results, here we only presented the results with a proportion of 50% non-monotonic interactions.

For the random networks, the persistence of all networks showed a

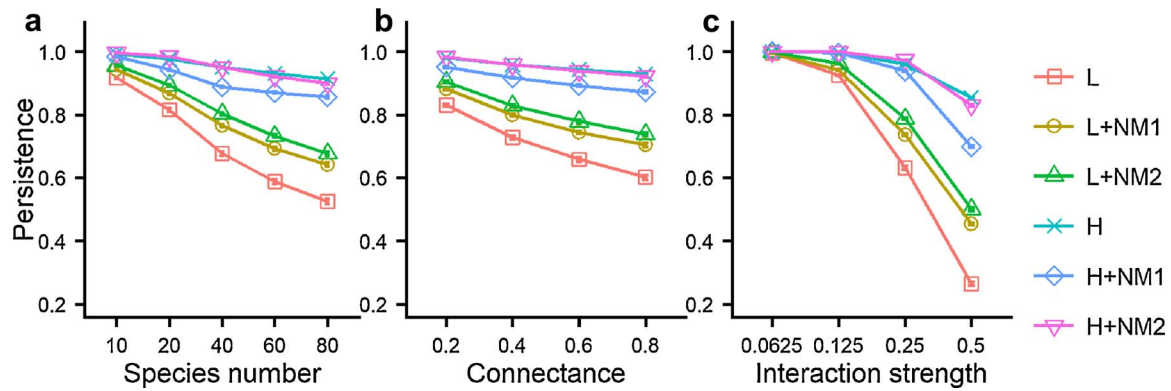


Fig. 2. The effects of interaction functions on the persistence (mean \pm SE) of random networks with different species number, connectance and interaction strength. Each data point represents the mean and standard error (very small at most cases due to large sample size) calculated from all the simulated networks for each parameter set.

decrease with increase of network complexity (i.e., species number, connectance and magnitude of interaction strength), more rapidly in “L” networks, but more slowly in “H” networks (Fig. 2). At high levels of complexity, the “L+NM1” and “L+NM2” networks showed a much higher persistence than “L” networks, but lower persistence than “H”, “H+NM1” and “H+NM2” networks, and the difference was much larger when network complexity was high, indicating satiated interaction or combination of satiated and dome-shaped interactions performed better in maintaining a higher network persistence in more complex networks (i.e., with higher network complexity).

The total network biomass all showed a positive relationship with species number and connectance (except “L” networks showing a dome-shaped response), but a dome-shaped relationship with the magnitude of interaction strength except “H” networks (Fig. 3). In general, the order of network biomass was shown as: “H+NM1” and “H+NM2” networks > “L+NM1” and “L+NM2” network > “L” and “H” networks, and the difference was much larger when network complexity was high, indicating that dome-shaped interaction or combination of satiated and dome-shaped interactions performed better in maintaining higher network biomass in more complex networks. Satiated interaction alone produced low network biomass, even lower than “L” networks at many cases.

As shown in Fig. 4, the biomass flow and per capita biomass flow of all networks showed an increase with the increase of species number, connectance and magnitude of interaction strength, except that “L” networks showed a decrease when connectance and magnitude of strength reached a certain threshold (0.4 and 0.2, respectively). In general, “L+NM1”, “L+NM2”, “H+NM1” and “H+NM2” networks had a higher biomass flow or per capita biomass flow than “H” networks and the difference was much larger when network complexity was high, suggesting that dome-shaped interactions performed better in

maintaining higher biomass flow or per capita biomass flow in more complex networks. Satiated interactions showed lower biomass flow or per capita biomass flow.

The PCV and NCV of all networks showed an increase with the increase of species number, connectance and magnitude of interaction strength (Fig. 5). In general, the order of both PCV and NCV was shown as: “L+NM1” and “H+NM1” > “L+NM2” and “H+NM2” > “L” and “H” networks and the difference was much larger when network complexity was high, indicating that dome-shaped interactions increased variations of both population- and network-level biomass. The values of NCV were much lower than those of PCV in all networks. These results showed that dome-shaped interactions tended to increase PCV and NCV, but NCV was much smaller than PCV, indicating asynchronous oscillations within community.

In general, in more complex random networks, satiated interaction performed better in maintaining high persistence but poorly in maintaining biomass or biomass flow. Dome-shaped interaction performed better in maintaining both high persistence and biomass or biomass flow. A combination of dome-shaped and satiated interactions would benefit network biomass. Dome-shaped interaction would cause large variation of both species and network biomass, but the latter was much smaller than the former. Additional analyses suggest the results were similar by using different time steps or time windows (Fig. A.3 -A.5).

3.2. Food webs

For the food webs with empirical structure, similar results to those of the random networks were obtained, but with some slight differences (Fig. 6). The persistence of all food webs showed a decrease with increase of the magnitude of IS. The order of persistence is “H+NM2” > “H+NM1” > “H” > “L+NM2” > “L+NM1” > “L”

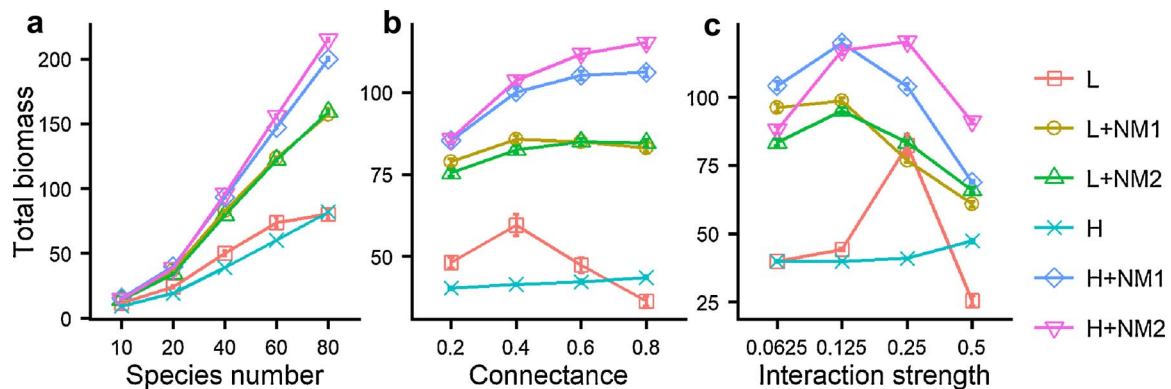


Fig. 3. The effects of interaction functions on the network total biomass (mean \pm SE) of random networks with different species number, connectance and interaction strength. Each data point represents the mean and standard error calculated from all the simulated networks for each parameter set.

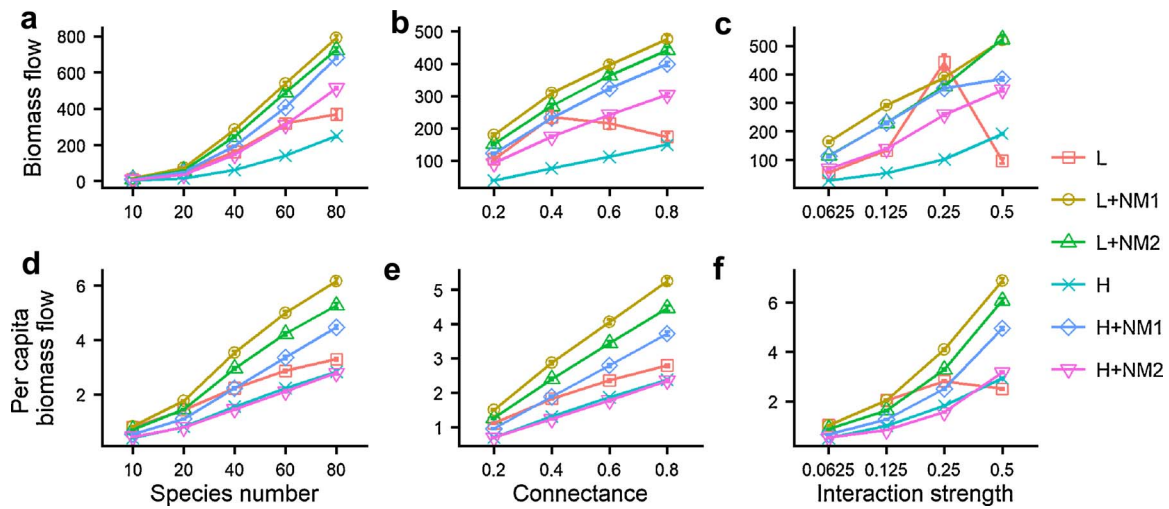


Fig. 4. The effects of interaction functions on the biomass flow (a-c) and per capita biomass flow (d-f, mean \pm SE) in the random networks with different species number, connectance and interaction strength. Each data point represents the mean and standard error calculated from all the simulated networks for each parameter set.

food webs and the difference was much larger when network complexity was high, suggesting combination of satiated and dome-shaped interactions performed better in maintaining high persistence than other interactions, in particular than the L- or H-interactions.

The network biomass in food webs decreased with the increase of the magnitude of IS in “L” and “H” food webs, but increased with the magnitude of IS in “L+NM1”, “L+NM2”, “H+NM1” and “H+NM2” food webs. The order of network biomass is “H+NM1” > “H+NM2” > “L+NM1” > “L+NM2” > “H” > “L” food webs and the difference was much larger when network complexity was high, suggesting dome-shaped interactions performed better in maintaining high biomass of networks.

The biomass flow and per capita biomass flow of all food webs showed an increase with the increase of the magnitude of IS. The order of biomass flow is “L+NM1” > “L+NM2” and “H+NM1” > “H+NM2” > “L” > “H” food webs. The order of per capita biomass flow is “L+NM1” > “L+NM2” > “L” > “H+NM1” > “H+NM2” and “H” food webs and the difference was much larger when network complexity was high. These results suggested that dome-shaped interactions performed better in maintaining high biomass and per capita biomass of networks.

The PCV and NCV of food webs showed little change with the increase of the magnitude of IS, except that “L+NM1” and “H+NM1”

food webs showed an increasing trend. The PCV and NCV values of “L+NM1” and “H+NM1” food webs were larger than other types of food webs when the magnitude of IS reached a high level. For “L+NM1” and “H+NM1” food webs, NCV was much lower than PCV. These results indicated that dome-shaped interaction would result in larger variations of both species and network biomass in more complex networks; the variation of network biomass was much smaller than that of species biomass.

In general, in the food-web networks, dome-shaped interaction also performed better in maintaining both high diversity and biomass or biomass flow, but it would increase variation of species and network biomass.

4. Discussion

We have theoretically studied the effects of specific non-monotonic interactions on both persistence and biomass. Our simulation results indicated that, as compared to the linear or satiated interactions, the dome-shaped interaction (shifting positive to negative interaction with increase of density) maintained higher persistence, biomass, and biomass flow in more complex ecological networks, but it resulted in larger variations of both species and network biomass. These results were consistent with the empirical observations in natural conditions,

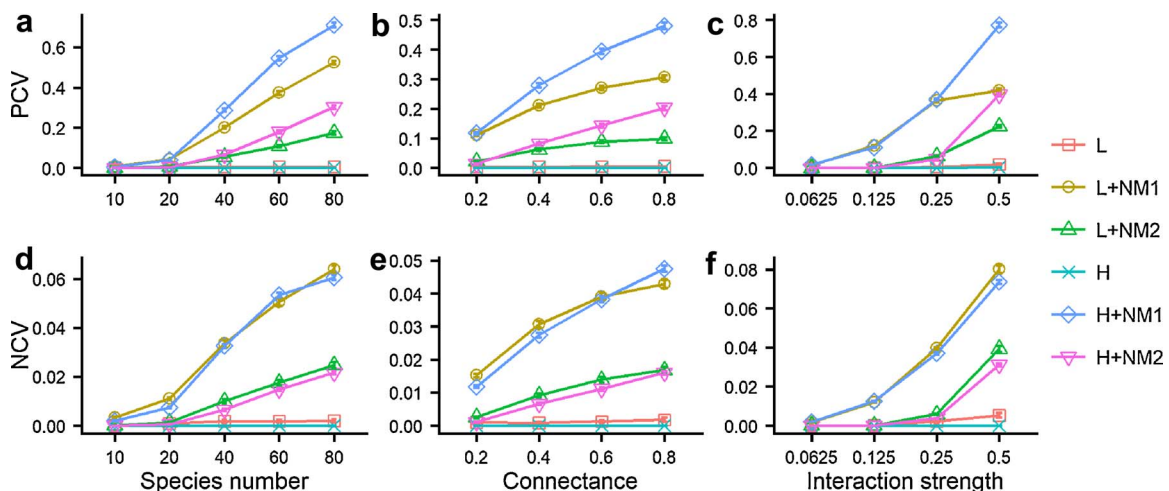


Fig. 5. The effects of interaction functions on the population-level (PCV, a-c) and network-level (NCV, d-f) temporal variations (represented by coefficients of variation, CV) in the random networks with different species number, connectance and interaction strength. Each data point represents the mean and standard error calculated from all the simulated networks for each parameter set.

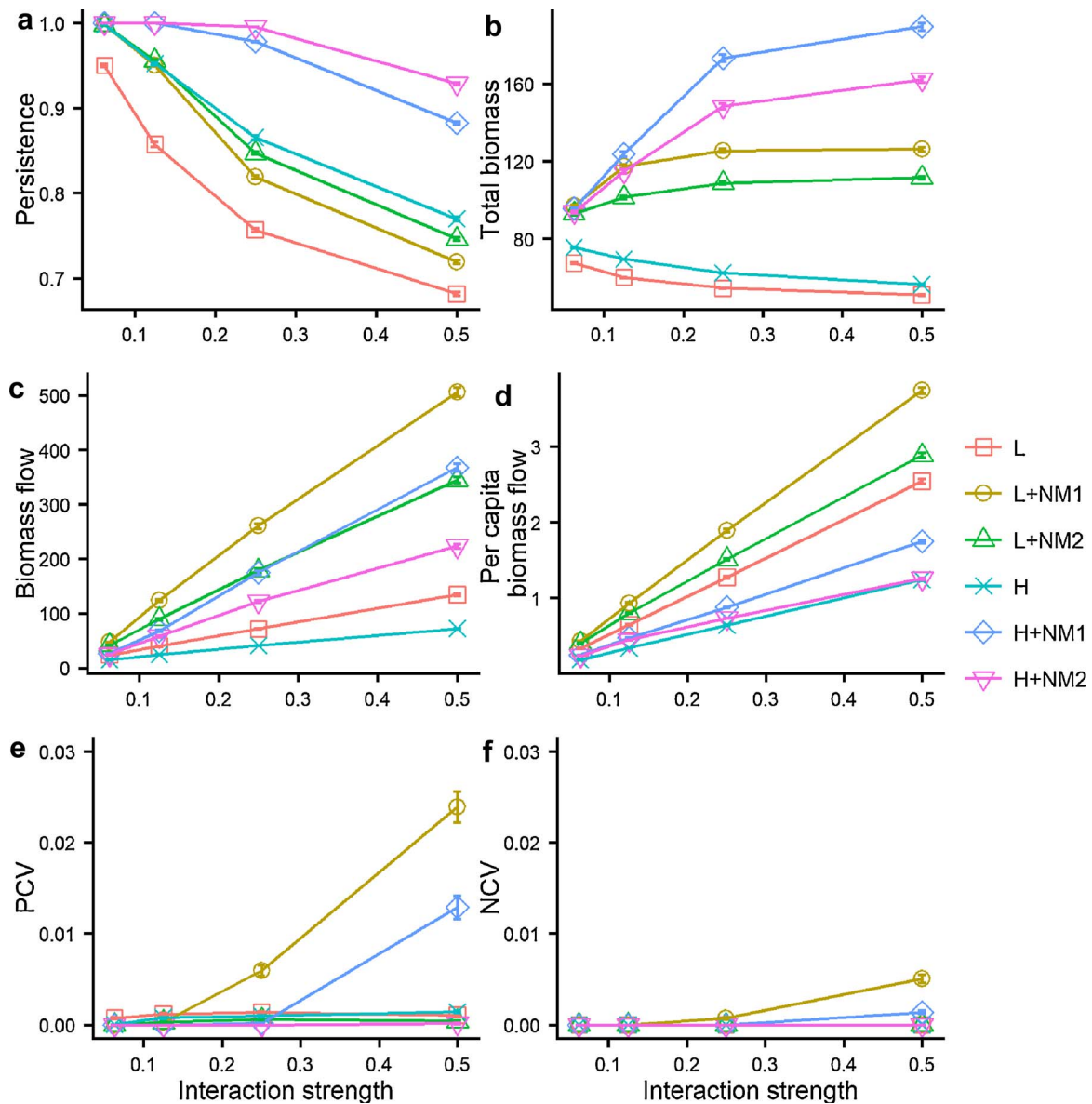


Fig. 6. The effects of interaction functions on the persistence (a), total biomass (b) biomass flow (c), per capita biomass flow (d), population-level biomass variation (PCV, e) and network-level biomass variation (NCV, f) of empirical food webs with increase of magnitude of interaction strength. Each data point represents the mean and standard error calculated from all the simulated networks for each parameter set.

highlighting the significant role of transition between positive and negative interaction in maintaining biodiversity and stability of ecosystems. Therefore, it is necessary to make further investigation on dome-shaped interactions in future studies.

Previous theoretical studies have shown that as the species number and their interactions increase, the interaction strength, precisely the magnitude of interaction strength, must become weak so as to maintain a higher stability in more complex ecological networks (Allesina and Tang, 2012; May, 1972; McCann et al., 1998; Neutel et al., 2002). The weak interaction can also be achieved by introducing the Holling's type 2 or 3 functional response (Holland et al., 2006), which is a way to satiate the per capita interaction strength when prey (or resource species) population increases (Soria-Díaz et al., 2017). Weak interaction strength, either by static weak strength or functional satiation, could increase persistence of ecological communities. Weak interaction has been one of dominant hypotheses in solving the diversity-stability debate (McCann, 2000). Alternatively, previous theoretical exploration of non-monotonic interaction in two-species systems suggested the dome-shaped interaction might serve as an alternative mechanism for

persistence of ecological networks (Zhang, 2003). Yan and Zhang (2014) reported specific non-monotonic interactions (e.g. dome-shaped function) increased persistence of ecological networks. Similarly, in this study, we showed that introduction of dome-shaped interactions (NM1 and NM2) could increase persistence of networks. But the NM2 interaction showed a stronger effect in promoting persistence than NM1 interaction functions in the L-networks, while in H-networks, both dome-shaped interactions showed similar effects on persistence. The difference between NM1 and NM2 interactions indicated that the satiation of interaction strength and non-monotonicity are both important stabilizing forces.

Previous studies on the relationship between diversity and biomass have been mainly conducted in natural communities (mostly in plant communities), such as positive species richness-biomass (productivity) relationships (Grime, 1973; Michalet et al., 2006; Mittelbach et al., 2001). However, the relationship between community biomass and species interactions is rarely explored. Consistent to some natural observations, we found the network biomass increased with species number of networks for all types of interactions. The network biomass

showed a minor increase with connectance (except in L-networks) and a mainly dome-shaped relationship with interaction strength (except in H-networks). These results suggested that network biomass depended on not only species number but also species interactions. The dome-shaped relationship of biomass with connectance in L-networks and with interaction strength in most types of networks was probably due to reduced number of survived species when connectance and interaction strength were too high. At different levels of species number, connectance and interaction strength, we observed that introduction of dome-shaped non-monotonic interaction into either L- or H-networks could increase the network biomass. It is notable that although the satiated interaction performed best in maintaining a high persistence in more complex networks, it resulted in a very low network biomass, suggesting that weak interaction may increase network persistence at the cost of biomass reduction, which is not consistent with empirical observations. Nonetheless, dome-shaped non-monotonic interactions performed better than the other interactions in maintaining both high persistence and biomass in more complex networks, which is consistent with empirical observations.

It has been a long-standing view to see natural ecosystems as energy-flow systems (Odum, 1968). Energy-matter flow is related to activity and efficiency of input energy for ecosystems (Finn, 1976). In this study, we used the sum of input and output biomass of all species, which was the multiplication of interaction strength and species' biomass, representing the net biomass turn over in the networks. Therefore, it was reasonable that the network biomass flow would increase with increase of species number, links, and interaction strength. The decrease of biomass flow in more complex L-networks (i.e. with higher levels of species number, links, and interaction strength) was due to the lower number of survived species (i.e. lower persistence). The dome-shaped non-monotonic interactions showed higher levels of both biomass flow and per capita biomass flow, while the H-functions showed the lowest biomass flow. A higher level of biomass flow for a system indicates a more efficient usage of input energy or matter. Therefore, dome-shaped interaction would benefit the ecological efficiency of an ecosystem.

On the temporal variation of biomass, it is widely recognized that high diversity reduces the variation of the total biomass of communities (Gross et al., 2014; Hector et al., 2010), but there is still debate on the relationship between species richness and population-level biomass (Jiang and Pu, 2009). In our modeling framework, the temporal variation of biomass at population- and network-level was zero or quite low in L- and H- networks because population dynamics reached stable equilibriums, which is not consistent with empirical observations. As suggested in our previous studies, dome-shaped non-monotonic interaction could increase temporal variation of single populations (Yan and Zhang, 2014). In this study, we found the population- and network-level temporal variation increased with species number, connectance and interaction strength. The dome-shaped non-monotonic functions assumed that the signs of interaction were density-dependent, which made the population dynamics more difficult to reach equilibriums in more complex networks, and then resulted in larger variation of single populations and also higher biomass. Within a study using the classical Rosenzweig-MacArthur model, biomass and productivity were also found to be higher at complex dynamic regimes (with chaotic and possibly greater oscillations) (De feo and Rinaldi, 1997). However, we found the network-level biomass variations were much lower than those of population-level variations in models with dome-shaped interactions. These results indicate that in networks with dome-shaped interactions, more species would help to reduce network biomass variation due to compensation effects among these fluctuating populations or asynchronous oscillation.

Traditionally, the mutualistic interaction is believed to be unstable in ecological models because of unbounded population growth caused by inherent positive feedback (May, 2001). Recent studies demonstrated that mutualistic interactions might be stabilizing when they are

mixed with antagonistic interactions (Mougi and Kondoh, 2012; Sauve et al., 2014). In fact, facilitation effects in plant community have also been extensively reported (Brooker et al., 2008). Zhang and Yan (2014) discussed the effects of different forms of non-monotonic interactions on species coexistence and network persistence. Among the six non-monotonic interactions, the density-dependent shifting from positive to negative interaction (i.e. dome-shaped function) has been reported to occur in natural ecosystems, such as rodent-seed interactions (Li and Zhang, 2007), ant-aphid interactions (Addicott, 1951), pollinator-mediated plants (Thompson, 1988), plant-mycorrhizae interaction (Neuhauser and Fargione, 2004). From our analyses, we demonstrated that the dome-shaped non-monotonic interaction was important in maintaining not only high persistence but also high biomass in more complex ecosystems. Our results suggest that positive interactions at low density benefit biomass accumulation, while negative interactions at high density benefit persistence. Species adjusting strategies between mutualisms at low density and competition or predation at high density would be selected by nature at community and network levels. This implies the dome-shaped interaction may be an alternative mechanism in the evolution of mutualism and in shaping the structure and function of ecosystems. We thus appeal for more efforts to study the non-monotonic interactions and their roles in maintaining biodiversity, persistence and productivity of ecosystems in future studies.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (31500347, 31330013), Strategic Priority Research Program of the Chinese Academy of Sciences (XDB11050300) and Information Fund of Chinese Academy of Sciences (XXH13506-201). We are grateful to Dr. Marcel Holyoak from University of California (Davis) for his valuable suggestions on this manuscript. We also thank the two anonymous reviewers and the editor for their valuable comments and suggestions on our manuscript. The authors declare no conflict of interest.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2018.01.003.

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