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Specific non-monotonous interactions increase persistence of ecological networks

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The relationship between stability and biodiversity has long been debated in ecology due to opposing empirical observations and theoretical predictions. Species interaction strength is often assumed to be monotonically related to population density, but the effects on stability of ecological networks of non-monotonous interactions that change signs have not been investigated previously. We demonstrate that for four kinds of non-monotonous interactions, shifting signs to negative or neutral interactions at high population density increases persistence (a measure of stability) of ecological networks, while for the other two kinds of non-monotonous interactions shifting signs to positive interactions at high population density decreases persistence of networks. Our results reveal a novel mechanism of network stabilization caused by specific non-monotonous interaction types through either increasing stable equilibrium points or reducing unstable equilibrium points (or both). These specific non-monotonous interactions may be important in maintaining stable and complex ecological networks, as well as other networks such as genes, neurons, the internet and human societies.

1. Introduction

There has been a long-standing paradox about the relationship between biodiversity and stability in ecology. Based on empirical observations, many ecologists believe that complex communities are more stable than simple ones [1–3]. However, theoretical studies indicate that diversity tends to destabilize community dynamics in a randomly connected ecological network [4], and such findings have been confirmed in many other types of ecological networks [5]. Various mechanisms have been proposed to maintain the community or network stability, including compartmentalization [6], nestedness [7], mixture of interactions [5,8], omnivory [9], weak interaction [10], pattern of interaction strength [11,12] and saturated functional responses [13].

All the previous studies on ecological networks have assumed that the sign of species interactions is fixed. However, in natural ecosystems, such as in seed–animal and plant–herbivore systems [14–17], the interaction between species is often non-monotonous and changing population density of interacting species (or environments) changes the sign of interactions. The effects of non-monotonous interactions on stability have been evaluated in two-species systems [18–20], but the network-level evaluation is lacking and should exert more general significance.

There are several kinds of stabilities in ecological studies, such as coefficients of variation (CV), resilience, persistence and so on, depending on the purpose of the study [1,21]. CV measures population variation of a species within a period of time. Resilience measures the returning time of populations to equilibrium after disturbance. Persistence measures the proportion of number of species survived as compared with the initial number of species within a period of time [22,23]. In this study, we are mainly interested in the relationship between number of species and complexity, thus we use ‘persistence’ as the measure of stability of ecological networks.

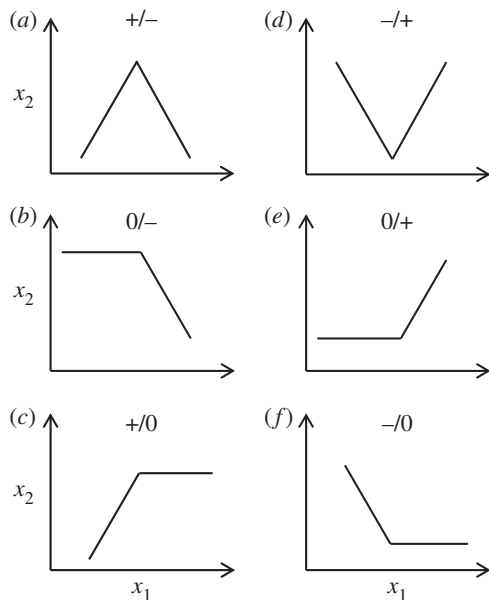


Figure 1. (a–f) Zero-growth isoclines of species x_2 against population density of species x_1 showing six non-monotonous interaction types shifting signs among positive (+), negative (–) and neutral (0) interactions.

The purpose of this study is to explore the effects of non-monotonous interactions (figure 1) on persistence of randomly connected, cascade prey–predator and bipartite mutualistic networks, as well as the underlying mechanism (see electronic supplementary material, figure S1). We hypothesize that specific non-monotonous interactions such as we observed in nature may be important in maintaining persistence of ecological networks.

2. Material and methods

(a) Networks construction

To understand the effects of non-monotonous interaction, we conducted our modelling analyses based on three classic theoretical networks. Following May's model [4], the randomly connected network is constructed based on an interaction matrix M of size $S \times S$ (S is the number of species; electronic supplementary material, figure S1A). We define C as the proportion of realized interaction links in the off-diagonal elements of M . The interaction coefficients are drawn from a normal distribution $N(0, \sigma^2)$. We define P as the probability of non-monotonous interactions in the connected elements. Following May [4], K is defined as the complexity of the network: $K = \sigma\sqrt{SC}$.

The cascade prey–predator and bipartite mutualistic networks are constructed by following Allesina & Tang [5]. In the cascade prey–predator network, species are ordered and only higher-ranked species can consume lower-ranked species (see electronic supplementary material, figure S1B). To construct the cascade prey–predator matrix M , paired off-diagonal elements M_{ij} and M_{ji} ($i < j$) are randomly selected with a total proportion of C . M_{ij} is drawn from $|N(0, \sigma^2)|$ and M_{ji} from $-|N(0, \sigma^2)|$ (here, i, j are species codes). Otherwise, 0 is assigned to both elements. All diagonal elements M_{ii} are assigned to be -1 .

In the bipartite mutualistic network, interactions only occur between different trophic levels (see electronic supplementary material, figure S1C). To construct the bipartite mutualistic matrix M , M is divided into two groups. For each M_{ij} where species i belongs to the first group and species j to the second, M_{ij} and M_{ji} are drawn from a half-normal distribution $|N(0, \sigma^2)|$. Otherwise, 0 is assigned to other off-diagonal elements. All diagonal elements M_{ii} are assigned to be -1 .

(b) Population dynamic model with non-monotonous interaction

We constructed non-monotonous population dynamic models by following a traditional model with a linear functional response [8], but with some modifications. The population abundance of a species i (x_i) is determined by its intrinsic increase rate (r_i), density dependence (a_i , diagonal elements in M) and interspecific interaction (b'_{ij}) of species j ; thus, we have the non-monotonous model as follows:

$$\frac{dx_i}{dt} = x_i \left(r_i + a_i x_i + \sum_{i=1, j \neq i}^S b'_{ij} x_j \right), \quad (1)$$

where $(b'_{ij}) = f(x_j)b_{ij}$, and $f(x_j)$ is used to change the sign (+, – or 0) of b_{ij} (or M_{ij}) in M , that is, the non-monotonous interaction. The six non-monotonous interactions are illustrated in figure 1 (also see the electronic supplementary material, table S1).

(c) Simulation and stability analysis

The persistence of an ecological network is calculated as the proportion of survived species by the end of simulation. By the end of simulation, if the population size $x > 10^{-6}$, the species is thought to be survived; otherwise, it is thought to be extinct. If the simulation collapses owing to population explosion (infinite growth) of some species, persistence is set to zero (i.e. no species survived the simulation).

To see how non-monotonous interactions affect CV and its links with persistence, we also calculate the average CV of all species in different kinds of ecological networks after excluding species becoming extinct or exploding. For simplification, CV is calculated as $(100 \times \text{s.d.}/\text{mean})$ of population abundances of the last 10 time-points which are sampled at an interval of 1000 time units for a survived population, and the CV of a network is calculated by averaging the CVs of all survived populations.

In order to evaluate the effects of non-monotonous interactions on network persistence, we set S and C at several levels by fixing σ at 0.5. The proportion of non-monotonous interactions (P) is set at three levels (i.e. 0.1, 0.3 and 0.5). The maximum intrinsic increase rate (r) and initial population density (x_0) are drawn from uniform distribution. The simulation parameters are listed in the electronic supplementary material, table S2. The simulation of population dynamics was integrated by the fourth-order Runge–Kutta method for 25 000 time units with a step of 0.01, implemented by *deSolve* package in R v. 2.15.2 [24,25].

(d) Phase-plane analysis

Phase-plane analysis using quadrantal diagrams was applied to identify equilibrium points of two interacting species [19,26] so as to infer the potential mechanism of stability of ecological networks related to non-monotonous interactions. Zero-growth isoclines of species i on j are drawn in two dimensions when $dx_i/dt = 0$. Any point above the zero-growth isoclines of species i will move down towards the zero-growth isoclines because $dx_i/dt < 0$, and vice versa. The crossing points of zero-growth isoclines of two species are defined as equilibrium points. If the changing directions (denoted as arrows) of both species in all four quadrants points towards the equilibrium point, this point is defined as a stable equilibrium point; otherwise, it is defined as an unstable equilibrium point. There are two kinds of unstable equilibrium points: extinctive unstable equilibrium point and explosive unstable equilibrium point.

3. Results

We found that four kinds of non-monotonous interactions increase the persistence of the randomly connected

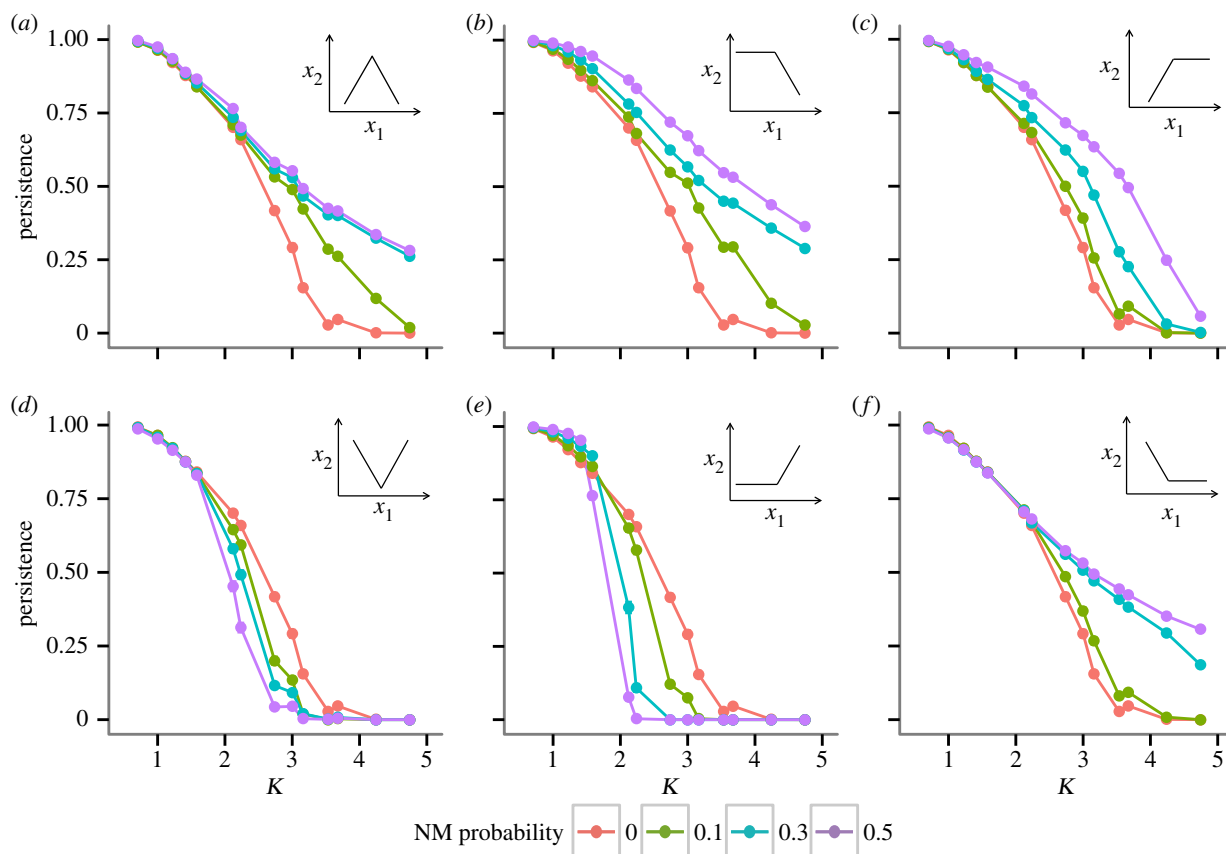


Figure 2. (a–f) The effects of non-monotonous (NM) interactions with different probabilities on the persistence of the randomly connected networks. The non-monotonous interaction type is shown in the corner of each plot. Each data point represents the mean and standard error calculated from 500 matrices. The probability of non-monotonous interaction (P) is set at 0, 0.1, 0.3 and 0.5, respectively. K is the complexity of the network.

networks (figure 2a–c,f). Conversely, the other two types of non-monotonous interactions decrease the persistence (figure 2d,e). This indicates that non-monotonous interactions that shift signs to negative or neutral at high population density of the interacting species (+/–, 0/–, +/0 and –/0) increase persistence of networks, while those shifting signs to positive (–/+ and 0/+) at high population density decrease persistence of networks. The results from cascade prey–predator and bipartite mutualistic networks are similar, but the influential amplitude of non-monotonous interactions on network persistence show some differences (figures 3 and 4). In the cascade prey–predator models, non-monotonous interactions shifting signs to positive cause obvious decrease of network persistence (figure 3d,e), whereas non-monotonous interactions shifting signs to negative or neutral cause small increase of network persistence (figure 3a–c,f). In the bipartite models, non-monotonous interactions shifting signs to positive cause little change of network persistence (figure 4d,e), whereas non-monotonous interactions shifting signs to negative or neutral cause obvious increase of network persistence (figure 4a–c,f).

Figure 5 shows a tendency of persistence of \wedge type (or +/– type; shifting sign from positive to negative) network > cascade prey–predator network > randomly connected network > \vee type (or –/+ type; shifting sign from negative to positive) network > bipartite mutualistic network. This indicates that networks with interactions shifting signs to positive at high population density (i.e. bipartite mutualistic and \vee type networks) tend to have low persistence. High persistence can be achieved in a \wedge type network even when complexity (K) is high (figures 2 and 5).

Phase-plane analyses of two interacting species show two kinds of unstable equilibrium points: extinctive unstable equilibrium points (resulting in species extinction) and explosive unstable equilibrium points (resulting in population explosion owing to unbounded population growth). For monotonous interactions, strong mutualism results in an explosive unstable equilibrium point (see electronic supplementary material, figure S2D), whereas strong competition results in an extinctive unstable equilibrium point (see electronic supplementary material, figure S2B). Simulations also indicate that a high proportion of mutualistic interactions destabilize the randomly connected network (see electronic supplementary material, figure S3). Although non-monotonous interactions can produce both stable and unstable equilibrium points, only \vee and 0/+ interactions produce explosive unstable equilibrium points similar to those produced by strong mutualism (see electronic supplementary material, figure S4). Simulations confirm that \vee and 0/+ interactions increase the probability of population explosion that contributes to observed instability of the randomly connected and cascade prey–predator networks (see electronic supplementary material, figures S5–S7), which explains why they destabilize the networks (figures 2 and 3). For the other four kinds of non-monotonous interactions, simulations indicate that they reduce probability of population explosions either through removing the unstable explosive equilibrium points or through producing extra stable equilibrium points (see electronic supplementary material, figure S4). Particularly, non-monotonous interaction shifting signs from positive to negative (+/–) removes the unstable explosive equilibrium point, and produces a stable equilibrium point and an unstable extinctive equilibrium

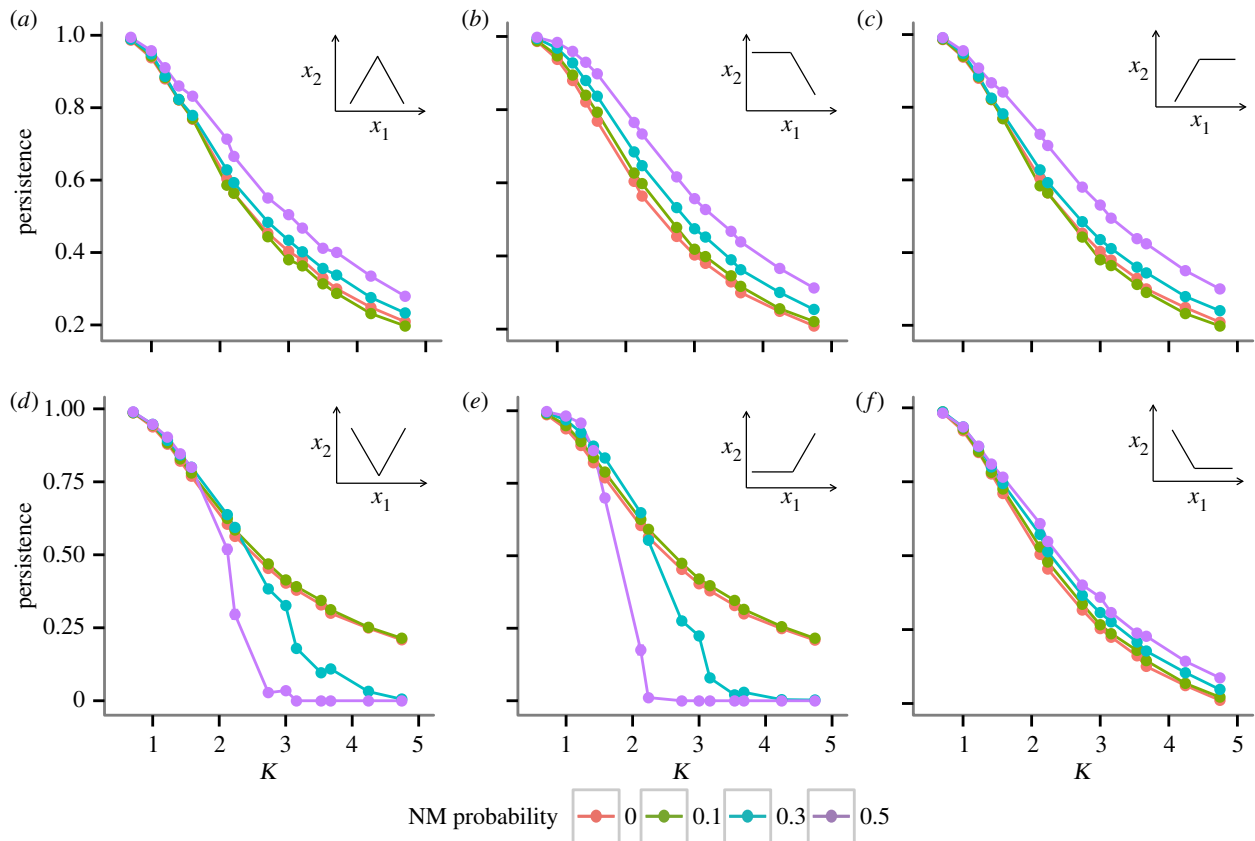


Figure 3. (a–f) The effects of non-monotonous interactions with different probabilities on the persistence of the cascade prey–predator networks. The non-monotonous interaction type is shown in the corner of each plot. Each data point represents the mean and standard error calculated from 500 matrices. The probability of non-monotonous interaction (P) is set at 0, 0.1, 0.3 and 0.5, respectively. K is the complexity of the network.

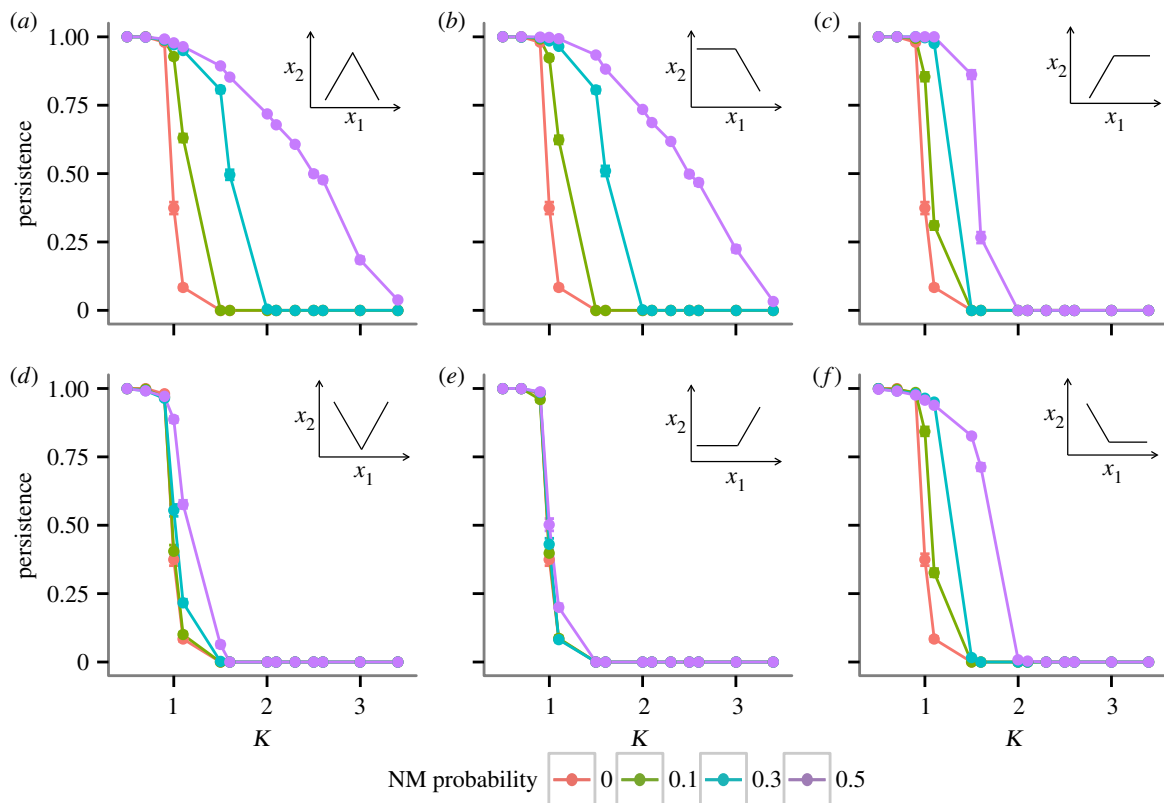


Figure 4. (a–f) The effects of non-monotonous interactions with different probabilities on the persistence of the bipartite mutualistic networks. The non-monotonous interaction type is shown in the corner of each plot. Each data point represents the mean and standard error calculated from 500 matrices. The probability of non-monotonous interaction (P) is set at 0, 0.1, 0.3 and 0.5, respectively. K is the complexity of the network.

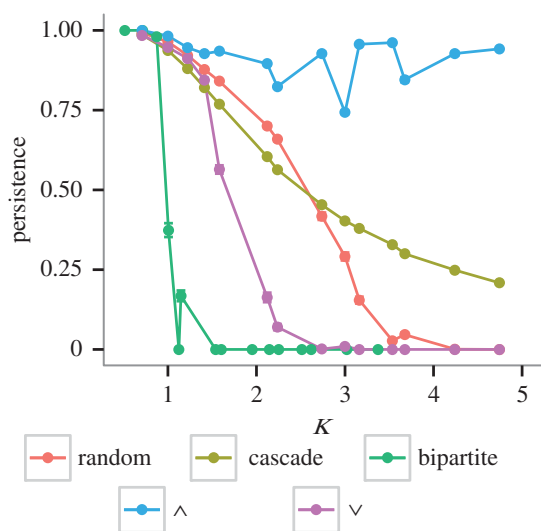


Figure 5. Comparisons of persistence among the randomly connected networks, cascade prey–predator networks, bipartite mutualistic networks, \wedge type (shifting sign from positive to negative) networks and \vee type (shifting sign from negative to positive) networks. The randomly connected networks contain mutualism ($++$), competition ($--$), predation or parasitism ($+ -$), commensalism ($+0$) or amensalism (-0) interactions. The cascade prey–predator networks contain only predation or parasitism ($+ -$) interactions. The bipartite mutualistic networks contain only mutualism ($++$) interactions. Both \wedge type and \vee type networks contain mutualism ($++$), competition ($--$), predation or parasitism ($+ -$) interactions.

point (see electronic supplementary material, figure S4A), thereby increasing the probability of network stability (figures 2a, 3a and 4a). Similarly to the $+/-$ interaction, a non-monotonous interaction shifting sign from positive to neutral at high population density ($+/0$) stabilizes the network by removing the unstable explosive equilibrium point, and producing a stable equilibrium point and an unstable extinctive equilibrium point (see electronic supplementary material, figure S4K). Non-monotonous interaction shifting sign from negative to neutral ($-/0$) at high population density can produce extra stable equilibrium points in two conditions (see electronic supplementary material, figure S4S,T). Similarly, non-monotonous interaction shifting signs from neutral to negative ($0/-$) at low population density can also produce extra stable equilibrium points in two conditions (see electronic supplementary material, figure S4O,P).

Analysis of CV of survived populations (excluding extinct and explosive populations) indicates that non-monotonous interactions significantly increase CV of the randomly connected networks, and slightly increase CV of cascade prey–predator network (but non-monotonous interactions of $0/-$, $+/0$ and $0/+$ decrease CV) and bipartite mutualistic networks (see electronic supplementary material, figures S8–S11).

4. Discussion

In previous studies on network models, species interaction is often assumed to be monotonous against population density of interacting species. In these models, the stability (as measured by species coexistence or persistence) decreases rapidly with increase of complexity (as measured by number of species, connectance or interaction strength) [4,5]. In this study, we first investigated the effects of non-monotonous

interactions on persistence of ecological networks, and found that non-monotonous interactions shifting signs to positive at high population density decrease persistence of ecological networks, while interactions shifting to negative or neutral increase the persistence. For the three classic networks of randomly connected network, cascade prey–predator network and bipartite mutualistic network, persistence shows steady decline (figure 5). But for the non-monotonous networks, sustained high level of persistence can be realized regardless of increase of complexity (figure 5), which is consistent with empirical observations in nature. Our study provides a novel alternative mechanism of species coexistence and network stability caused by specific non-monotonous interactions.

In natural ecosystems, there are many realistic examples of stability-enhancing non-monotonous interactions similar to those described in our study. Many complex interactions similar to non-monotonous interactions shifting sign from positive to negative ($+/-$) have been reported, such as mutualism–competition [16,19], mutualism–predation [14,27] and mutualism–parasitism [28] interactions. For example, herbivores usually impose negative effects on grass, but moderate browsing often benefits grass growth by enhancing nutrition cycling [14]. Grasses are found to exhibit a hump-shaped effect on Brant’s voles in grassland because of a trade-off between food supply and habitat preference of voles [29]. Some animals, acting as seed eaters and seed dispersers in forests simultaneously, show both negative and positive effects on plants [27,30–32]. Interactions between some ant and aphid species can be shifted from positive at low aphid densities to negative or neutral at high density [16]. The non-monotonous interaction shifting sign from positive to neutral ($+/0$) is similar to the Holling type II functional response and Holling type I functional response with a saturation effect in prey–predator system, which stabilize communities and food webs [13,33]. The non-monotonous interaction shifting sign from negative to neutral ($-/0$) is similar to the refuge effect in nature. Empirical observations show that refuges can protect prey from over-consumption by predators and allow some prey to survive, which stabilizes predator–prey interactions [34,35]. The non-monotonous interaction shifting sign from neutral to negative ($0/-$) is also logical. The negative effect of one species on the other may be negligible at its low population density, but obvious at high population density (e.g. effects of infectious diseases or out-breaking pests or predators; here we define it as the ‘emerging effect’). Indeed, predators only exhibit a detrimental effect on prey at high density, especially for some cooperative-hunting predators such as lions and wild dogs. Ruesink [36] also found that the predation effects of hermit crabs on diatoms apparently crossed a threshold from weak to strong when consumption exceeded resource production, similar to $0/-$ interaction.

Although interaction strength in some communities or ecological networks has been widely investigated [37,38], estimations of nonlinear interaction strength at network level are still rare [37,39,40], particularly for non-monotonous interactions, which often need long-term dynamic community data (but see [29,36,41,42]). At present, it is still not clear how large the proportion of non-monotonous interactions is in real ecological networks. However, given that the observed non-monotonous interactions (e.g. mutualism–competition, mutualism–predation, mutualism–parasitism, predator saturation effect, refuge effect and emerging effect) in literature are significant components of real ecosystems,

the non-monotonous interactions should be pervasive in real networks, and they should play significant roles in maintaining diversity and stability of ecological networks such as we simulated in this study.

Mutualism has been widely observed in nature [38], but theoretical analysis indicates that mutualism destabilizes the network owing to unbounded positive feedback [43]. The findings of two non-monotonous interactions (i.e. $+/-$ and $+/0$) stabilizing the network indicate that mutualism may occur in non-monotonous interactions at low population density. It is notable that the two destabilizing non-monotonous interactions (i.e. $-/+$ and $0/+$) are also rarely observed in nature.

Previous studies have shown that the distribution of interaction strength over the food-web links is highly patterned, and that this pattern has a strong link with stability of the food web [11]. For simplification and comparison with previous models, we selected interaction strengths randomly from a normal distribution without considering the position of an interaction in the network. In the future, there is a need to consider the effects of patterns of interaction strength on network stability influenced by non-monotonous interactions.

It is interesting that although specific non-monotonous interactions increase network stability as measured by persistence, non-monotonous interactions obviously increase population variations in most cases. Traditionally, large CV is often linked to instability of natural populations [1,21]. But we believe large CV does not necessarily mean instability of a community. A population may reach a static stable condition by approaching or staying at an equilibrium (with zero or small CV), or may reach a dynamic stable condition by periodically or chaotically cycling around the equilibrium (with large CV) [4,33]. Previous studies have shown that populations of many species can persist with periodical [44–47] or chaotic fluctuations [48,49]. Population becomes unstable when it becomes extinct or explodes (far away from the equilibrium). Thus, we should be cautious in interpreting the biological meanings of CV, which represent both static and dynamic stability. In our results, the effects of non-monotonous interaction are variable. Some non-monotonous interactions are able to increase CV to a great extent in the randomly connected networks, and to a lesser extent in the

cascade prey–predator and bipartite mutualistic networks. But some non-monotonous interactions decrease CV in the cascade prey–predator networks. Increase of CV by non-monotonous interactions does not necessarily mean decrease of stability of networks because populations are dynamically stable. We argue that CV should be restricted to reflect the static stability of a community or ecological network. In modelling studies, CV of extinctive and explosive populations is not likely to be measured. Besides, in our study, CV of survived populations is not exactly associated with persistence (see electronic supplementary material, figures S8–S10). For example, two non-monotonous interactions (i.e. $-/+$ and $0/+$) decrease persistence but increase CV of the randomly connected networks, while the other four non-monotonous interactions increase both persistence and CV of the networks (figure 2; electronic supplementary material, figure S8).

Networks are important features of diverse systems, including ecosystems, genes, neurons, the internet and human societies. It is therefore critical to fields as diverse as science, engineering and medicine that we understand how network stability and reliability arise and can be manipulated. About 2500 years ago, Lao Zi, a famous Chinese philosopher, first developed the idea ‘When things reach one extreme, a reversal to the other extreme takes place’ (*wu ji bi fan* in Chinese), which is thought to be an important driving force in maintaining social and natural harmony [50, p. 89]. We suggest that specific non-monotonous interactions of changing signs are critical to network stability of many complex systems, such as gene, neuron, internet and social networks. Future studies should focus on measuring non-monotonous interaction strength and its distribution patterns in real networks, and testing the modelling predictions of the network stability.

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