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Review

Ecological non-monotonicity and its effects on complexity and stability of populations, communities and ecosystems

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ABSTRACT

In traditional ecological models, the effects of abiotic and biotic factors are often assumed to be monotonic, *i.e.* either positive, negative or neutral. However, there has been growing evidence that non-monotonic effects of environmental factors and both intra- and inter-specific interactions can significantly influence the dynamics and stability of populations, communities and ecosystems. In this paper, we present a review and synthesis on both theoretical and empirical studies on ecological non-monotonicity. There are various non-monotonic relations observed in populations, communities and ecosystems. The non-monotonic function of per capita population increase rate against intrinsic or extrinsic factors is a significant driving force in determining the complexity and stability of biological systems. There are several mechanisms such as the law of tolerance, adaptive behaviors, or opposing dual or pathway effects which may result in non-monotonic functions. Ecological non-monotonic functions are often closely related to spatial and temporal scale processes which may explain why ecosystems are often highly variable and unpredictable in both space and time. Recognizing ecological non-monotonicity would greatly change our conventional monotonic views on the effects of environmental factors and species interactions on ecosystems. We appeal for more effort to study ecological non-monotonicity and re-think our strategies to manage ecosystems under accelerated global change.

Contents

1. Introduction

In Chinese philosophy, *Yin* and *Yang*, which often represent the negative or positive aspects of thing are two opposite driving forces in governing the universe and human society, and they can be transformed into each other at certain conditions. About 2500 years ago, Lao Zi, the founder of Chinese philosophy of Daoism, first proposed the non-monotonic idea that things must develop in the opposite direction when they become extreme (wù jí bì fǎn in Chinese). In fact, this idea can be traced back to the Eight Diagrams proposed by Fu Xi about 6000 years ago.

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Monotonicity and non-monotonicity are two important relationships in nature and human society. In mathematics, a monotonic function $y = f(x)$ against x is defined as either entirely increasing or entirely decreasing, while a non-monotonic function is defined as one with both increasing and decreasing sectors (Fig. 1). In calculus, the 1st order derivative of monotonic function is either entirely positive or entirely negative, while that of a non-monotonic function has both positive and negative sectors. In physics, for example, non-monotonicity is equivalent to the concept of phase change in which matter changes its quality (*e.g.* solid, liquid and gas) when an environmental factor (temperature) reaches a threshold. In human society, non-monotonicity can refer to boom and bust market crises in economics or to the rise and fall of dynasties. The non-monotonicity in logic or reasoning has attracted very much attention in social and computer sciences (Bidoit and Hull, 1989; Donini et al., 1990).

There are various types of non-monotonic relations reported in the ecological literature. For example, the population abundances of prey and predators can show periodic cycles in time (Vik et al., 2008). The harvest rate is often a humped curve when plotted against the population density of the harvested species (Gotelli, 2008; Milner-Gulland and Mace, 1998). Moderate grazing can increase the productivity and biodiversity of grassland ecosystems (Luo et al., 2012; McNaughton, 1979; Schuman et al., 1999), while overgrazing can reduce productivity and biodiversity. Wang et al. (2014) found a bell-shaped relationship between total soil nitrogen concentration and an aridity index in China. The intermediate disturbance hypothesis predicts that diversity becomes maximized at the intermediate disturbance level when both r- and k-selected species can coexist (Connell, 1978; Wilkinson, 1999). Li and Chen (2014) reported that rising temperatures had a positive effect on vegetation cover but continued warming resulted in a decline of vegetation cover in arid regions of northwest China. Although a positive monotonic relationship between the diversity and productivity of ecosystems is often found (Naeem et al., 1994; Tilman, 1996), a hump-shaped relation is also frequent (Grime, 1998; Mittelbach et al., 2001; Schmid, 2002; Waide et al., 1999).

The various non-monotonic relations observed at different levels of ecological systems are likely driven by the non-monotonic response of the population's increase rate. In this study, we defined the ecological non-monotonicity as the non-monotonic function $f(x)$ of per capita population's increase rate (r) of organisms against their intrinsic or extrinsic factors (x). In mathematics, the ecological non-monotonic function is defined as:

$$r = \frac{dN}{Ndt} = f(x)$$

where N is population density. For the monotonic function $f(x)$, the first order derivative:

$r' = f'(x) > 0$, or, $r' = f'(x) < 0$

If $f'(x) > 0$, the function is monotonically increasing, if $f'(x) < 0$, the function is monotonically decreasing. For the non-monotonic function $f(x)$, its first order derivative:

$$f'(x) > 0 \quad \text{when} \quad x \in X_1$$

$$f'(x) < 0 \quad \text{when} \quad x \in X_2$$

$$f'(x) = 0 \quad \text{when} \quad x \in X_3$$

X_1, X_2 and X_3 represent a range of x. In the discrete-time model, $r_t = f(\mathrm{N}_t) = \ln(N_{t+1}/N_t)$. It is obvious that if $f'(x) > 0$, the effect of x on r is positive, if $f'(x) < 0$, the effect of x on r is negative, and if $f'(x) = 0$, the effect of x on r is neutral. The change of sign (*i.e.* positive, negative and neutral) of the effect of x on r is the fundamental features of ecological non-monotoncity which we will address in this paper.

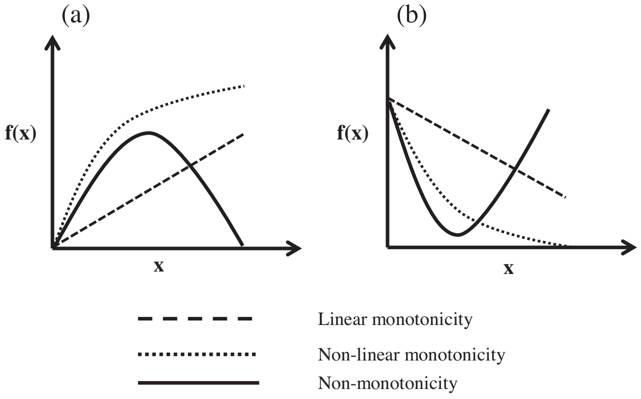

Fig. 1. Illustration of linear monotonicity (broken lines), non-linear monotonicity (dashed lines) and non-monotonicity (solid lines). Non-monotonicity includes a hump-shaped non-monotonic function (a) and a U-shaped non-monotonic function (b).

Non-monotonicity should be an important driving force in ecological systems because environmental factors are highly variable in both space and time, and organisms are strongly affected by extreme environmental changes. There may be several mechanisms which could result in non-monotonic response. First, organism would not survive when an ecological factor is insufficient or in excess as indicated by the law of tolerance (Shelford, 1931). As shown in Fig. 2a, the fitness of many organisms as measured by reproduction and survival (which will determine the population's increase rate) is often maximal in the middle of an environment gradient (*e.g.* temperature, salinity, rainfall). Fitness would decrease when the environment gradient they live in approaches an extreme value. This non-monotonic response of organism is obviously caused by the limitation imposed by environmental factors or resources, and can be used to explain or predict species distribution in space (Elith et al., 2006). Second, organisms can adapt in both physiology and behavior to changing environments. Their interactions with abiotic and biotic factors are not always fixed, but changeable under certain conditions. Organism can adopt opposite strategies based on a change of environments. For example, in the game of the Prisoner's dilemma, people can shift their behavior between cooperation and defection (Fig. 2b) (Hilbe et al., 2013). In repeated trials, the tit-for-tat strategy in which one starts by cooperating and then mimics the other player's performances is shown to be a good strategy (Boyd, 1989). The kind of adaptive behavior can result in non-monotonic responses in population's growth rate of organisms through changing competition or cooperation strength. Third, some organisms have opposing dual effects (both positive and negative) on the other organisms. For example, in a plant–animal system, animals may harm plants by consuming them, but also benefit them by providing services of seed dispersal or nutritional cycling. Finally, environmental factors often have opposing pathway effects which may produce non-monotonic response on population's increase rate of organisms.

If the opposing positive and negative effects change in the same order or scale, their net effect will be additive and the function of population's increase rate of organisms to population density or environmental factors would be monotonic. However, if the positive and negative effects change in different orders or scales, their net effect will not be additive and the function will be non-monotonic. The non-additive effect of positive and negative effect is illustrated in Fig. 2c. Let $r_p = a_1 + b_1x$, $r_n = a_2 - b_2x^2$, r_p represents the positive effect, r_n represents negative effect, all $a_1, a_2, b_1, b_2, > 0$. It is obvious that the negative effect r_n grows more quickly in the power of 2 against x, while the positive effect r_p grow slowly in the power of 1. The net effect is $r = r_p + r_n = a_1 + a_2 + b_1x - b_2x^2 = a + bx - cx^2$

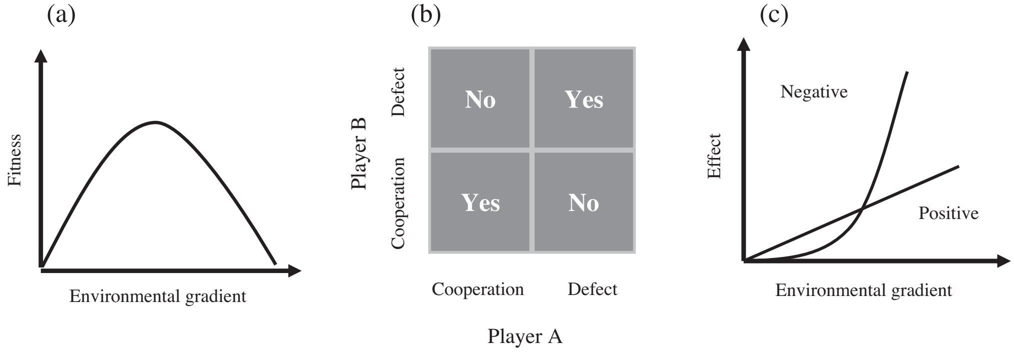

Fig. 2. Mechanisms of non-monotonic interaction effects or functions. (a) The law of tolerance, (b) the tit-for-tat strategy in the prisoner's dilemma, (c) allometric growth of opposing positive and negative effects.

($a = a_1 + a_2$, $b = b_1$, $c = b_2$). This is a non-monotonic function which is similar to a parabolic curve in Fig. 1a. Similarly, if we let $r_p = a_1 - b_1x$, $r_n = a_2 + b_2x^2$ (all a_1, a_2, b_1, b_2, >0), we will have a non-monotonic parabolic curve in Fig. 1b. Thus, the allometric growth of opposing positive and negative effects with different powers or scales can result in non-monotonic function.

In general, ecological non-monotonicity has been largely ignored in previous studies of population, community and ecosystem dynamics. For simplification, ecological interactions are often assumed to be monotonic, *i.e.* either positive, negative or neutral. But in nature, non-monotonic interactions are commonly seen at the individual, population, community and ecosystem levels. The over-simplification of biological complexity has been criticized by many ecologists (Devin et al., 2014; Steudel et al., 2012). In time series analysis, the Self-Exciting Threshold AutoRegressive (SETAR) models was proposed to allow for higher degree of flexibility in model parameters through a regime switching behavior, depending on the past values of the time series (Chan and Tong, 1986; Tong and Lim, 1980). The SETAR models have been used to explain and predict the cycles of many systems including Canadian lynx (Stenseth et al., 1998; Tong, 1982). There are several models (*e.g.* theta-logistic model, predator–prey model with Holling's type III function response) which describe a non-linear function of population' increase rate on population density. Sibly et al. (2005) demonstrated a strongly concave relation between population increase rate and population density in mammals, birds, fish and insects. Rosenzweig and MacArthur (1963) proposed a humped prey isocline in a graphical predator and prey models with a vertical predator isocline which result in a paradox of enrichment of prey. The prey isoclines may turn upwards due to refuge effect, immigration effect or Type III functional responses and then attribute to the stability of prey-predator system (Gotelli, 2008). Hernandez (1998) defined a nonlinear interaction alpha-function which may undergo transitions from one type of interaction to another in a two species model.

The ecological consequences of non-monotonicity was first discussed in a study of a competition and mutualism model in which the interaction between two competing species shifts from competition to mutualism at their lower densities (Zhang, 2003). It was found that shift between positive and negative interaction can increase competitive capacity and coexistence of two competing species. This shift of species interaction was then extended to ecological network models in which six kinds of non-monotonic interactions were defined, and four of them can promote persistence of models and then increase biodiversity (Yan and Zhang, 2014). During past decades, studies related to ecological non-monotonicity have begun to increase. In this paper, we present a brief review and synthesis of studies on ecological non-monotonicity in population and community dynamics, and to discuss its perspectives and possible future research directions.

2. Non-monotonic effect of climate

Climatic factors have long been suggested to affect the population dynamics of organisms. Traditional climate hypotheses typically assume that the effect of climate is monotonic. However, the effects of climate on biological populations are likely non-monotonic. The direct and indirect pathway effects of climate may be different, or even opposite. Climate may affect a biological population directly or indirectly through another climatic factor or *via* another species. If the direct and indirect effects are opposite and non-additive, a non-monotonic function of climatic factor on population's increase rate will appear. In addition, climate may have two opposing effects on the population's rate of increase which may result in a non-monotonic function.

Traditionally, the direct effects of increasing temperature are thought to benefit insect populations (Zhang et al., 2012). During past decades with continued global warming, many pest insects have shown higher winter survival and have more generations per year due to faster development rates, and their geographic range boundaries have moved further poleward. Thus, it is widely believed that global warming will cause more pest problems (IPCC, 2007). But a recent study indicated that the indirect effects of climate warming do not necessarily favor pest insects. By compiling and using historical data of 1910-y-long time series of outbreaks of Oriental migratory locusts (*Locusta migratoria manilensis*, Meyen 1835) in ancient China, the occurrences of locust plagues and drought/floods were found to be positively associated with low temperatures (Stige et al., 2007; Tian et al., 2011), contradicting previous shorter-time scale studies suggesting that warm temperatures benefit the locust directly by increasing winter survival and the development rate (Ma et al., 1965). But in a longer-time scale, the frequency of drought/flood was positively associated with cold phases in China. Drought/flood benefits the locusts by providing favorable breeding habitats (Ma, 1958). This study revealed that an indirect negative effect of temperature through precipitation at long-time scales was opposite to that of direct positive effect of temperature in short-time scales (Fig. 3a), which resulted in a non-monotonic function of climate on populations. This observation suggests that climate may have opposing direct and indirect pathway effects which depend on the time scale.

Studies on lynx populations have also indicated that temperature has opposite pathway effects (Fig. 3b). Previous studies have indicated that high temperature has positive effect on survival of adult and first litter young snowshoe hares but high rainfall showed negative effects on second litter hare survival (Meslow and Keith,

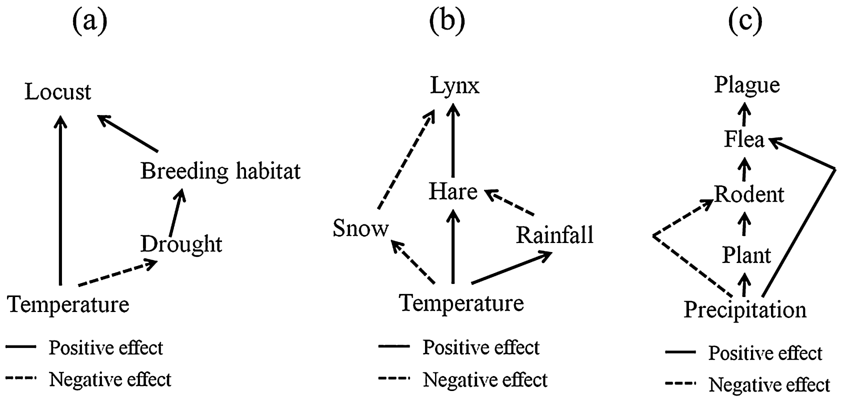

Fig. 3. Examples showing the non-monotonic effects of climate on biological populations. (a) Opposing pathway effects of temperature on locust populations in China. Direct positive and indirect negative effect were found in short-time and long-time scale, respectively. (b) Opposing pathway effects of temperature on Canadian lynx populations. Positive and negative effects were found in several pathways. (c) Opposing pathway effects of precipitation on rodent-borne plague. Positive and negative effects were found in different regions with different precipitation levels.

1971), thus affecting hare's predator lynx. In a recent study using nearly 100 years of data, increase of northern hemisphere air temperature was found to reduce snow cover but increase rainfall in Canada (Yan et al., 2013a). The decline of lynx during past decades was found to be closely associated with high rainfall which was associated with global warming (Yan et al., 2013a). Reduced snow cover under global warming conditions may benefit lynx because deep winter snow may limit the hunting efficiency of hares by lynx (Stenseth et al., 1999). Thus, high temperature not only has positive effects on lynx, but also has negative effects (positive through hare and snow, while negative through rainfall). Again, this observation indicates that climate may have opposing pathway effects on organisms.

It was found that precipitation showed opposing pathway effects on human plague (Fig. 3c). Traditional plague theory suggests that occurrences of rodent-borne plague are associated with warm and wet weather because high precipitation increases the primary production of plants and this increases the abundance of rodents (Parmenter et al., 1999). In addition, wet weather also favors plague by benefiting fleas (Krasnov et al., 2002). However, using the spatial and temporal human plague records in China from 1850 to 1964, Xu et al. (2011) found that plague occurrences were positively related to precipitation last year in northern and dry regions but negatively related to precipitation last year in southern and wet regions of China, contradicting the conventional view that wet weather always benefits plague occurrences. In south China, precipitation is usually high. It was proposed that more precipitation in high-precipitation region would reduce rodent density through flooding and then not favor plague occurrences. This observation suggests that the opposing pathway effects of climate on organisms may be related to spatial difference in environmental factors.

Chen et al. (2015) found population growth rates of Daurian pikas (*Ochotona Dauurica*) showed a humped relationship between their population's growth rate and precipitation in the Inner Mongolia grassland, China. In the semi-arid grassland, precipitation would improve plant growth and thus promote reproduction and survival of *O. dauurica*. But, excess rainfall, particularly in summer, may be detrimental to them by flooding their burrows. This observation suggests that climate may have an opposing dual effect depending on the quantity of the climatic variable like rainfall.

These examples indicate that climate may have opposing effects which may depend upon variation of climatic variables on both temporal and spatial scales. The positive and negative effects of climate on organisms may occur directly or indirectly or through different pathways.

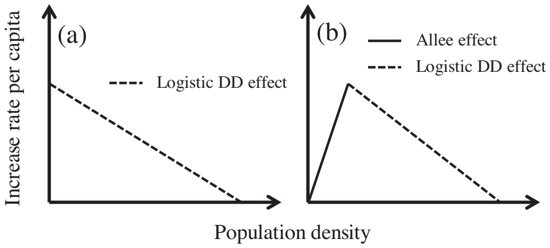

Fig. 4. Illustration of density dependent (DD) effects in the traditional logistic model (a) and the non-monotonic model by integrating the Allee effect at low density with the traditional logistic model (b).

3. Non-monotonicity within species

At the intra-specific level, individuals are often competitors because they share similar resources. Thus, traditional theory often assumes intra-specific population regulation is a monotonic and negative density dependent function (Lotka, 1925; Volterra, 1926). However, many previous studies on behaviors of animals or people have demonstrated that cooperation could benefit the population (Holland, 1975; Koella, 2000; Langton, 1989; Lloyd, 1995), and thus it may play a significant role in shaping the social structure of animals or people (Alcock, 1989). It is well recognized that group defense by prey against predators can effectively increase prey survival, while cooperation among groups can increase working efficiency. In these models, *e.g.* prisoner's dilemma (Fig. 2b), the behavior of individuals is adaptive, but depends upon the performance of their counterparts.

Intra-specific competition is a very important factor in population regulation. With increase of population density, resource becomes limited, and thus the growth rate of the population will decrease. In most ecological models, density dependent effects are assumed to be linearly monotonic and negative (Fig. 4a). But at low density, density dependence may be positive when cooperation is essential for population reproduction and survival. The Allee effect was first defined by Allee et al. (1949) and refers to a positive association between the per capita rate of population increase and population density (Courchamp et al., 1999; Stephens and Sutherland, 1999). There are several mechanisms that can result in an Allee effect, including a failure of reproduction or cooperative foraging, inbreeding, or excessive predation (Courchamp et al., 1999; Stephens and Sutherland, 1999). The Allee effect may help to explain population declines or extinction of endangered species (Lande, 1998) or the successful establishment of alien species (Liebhold and Bascompte, 2003). Inbreeding or genetic

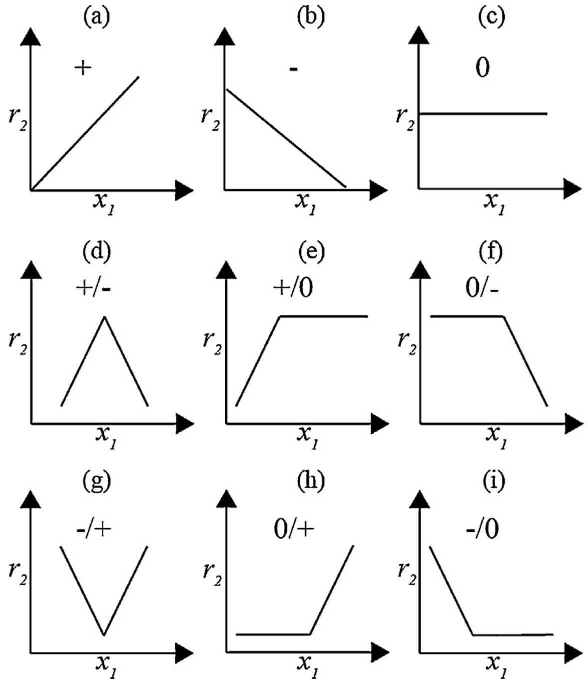

Fig. 5. Illustration of three monotonic functions (a–c) and six non-monotonic functions (d–i). r_2 indicate the per capita population increase rate of species 2. x_1 indicate the population density of species 1. These relations are equal to the zero growth lines of species 2 against species 1 in which r_2 is replaced with x_2 (see Zhang, 2003, Yan and Zhang, 2014). For simplification, the non-monotonic function is shown with two linear lines changing signs between positive, negative and neutral functions. In reality, these non-monotonic functions can be shown in smooth curves. (a) a positive function (+), (b) a negative function (−), (c) a neutral function (0), (d) a hump-shaped function (+/−), (e) a satiation function (+/0), (f) a sliding-down function (0/−), (g) a U-shaped function (−/+), (h) an emerging function (0/+), (i) a sheltering function (−/0).

bottlenecks at low density may slow down population recovery (Dong et al., 2010; Xu et al., 2013).

By integrating the Allee effect with the traditional logistic model, the density dependence function for a population would become non-monotonic; *i.e.* the association of population's increase rate is positively related to population density at low density but negatively related at high density (Fig. 4b). In Fig. 5 and the following figures, the non-monotonic function is represented by positive and negative linear lines for simplifications. In reality, the non-monotonic function can be a curve, *e.g.* a humped- or U-shaped curve. The empirical examples of the intra-specific non-monotonic are still rare. Liebhold and Bascompte (2003) have demonstrated population's increase rate of alien species showed positive association with small foundering populations in the colonized regions although it may have a negative association with their large population in their native places. In the classic Rosenzweig-MacArthur model, predator isocline is a vertical line, while the prey isocline is actually a humped non-monotonic function of the prey density. When predators are limited only by prey abundance and not by other factors, stable equilibria or limit cycles of prey and predator can be obtained, but an increase of prey would destabilize the predator's population which is named as "paradox of enrichment" (Krebs, 1994; Rosenzweig, 1971; Rosenzweig and MacArthur, 1963).

4. Non-monotonicity between species

In many traditional models, species interaction functions are assumed to be monotonic, *i.e.* either positive (+), negative (−) or neutral (0) (Fig. 5a–c) with change of population density. In these models, interaction signs are always fixed, not changeable. In theory, the three monotonic functions (M) can produce a total of six kinds of species interactions: competition (−, −), mutualism (+, +), predation/parasitism (+, −), commensalism (+, 0), amensalism (−, 0) and neutralism (0, 0) (Fig. 6c).

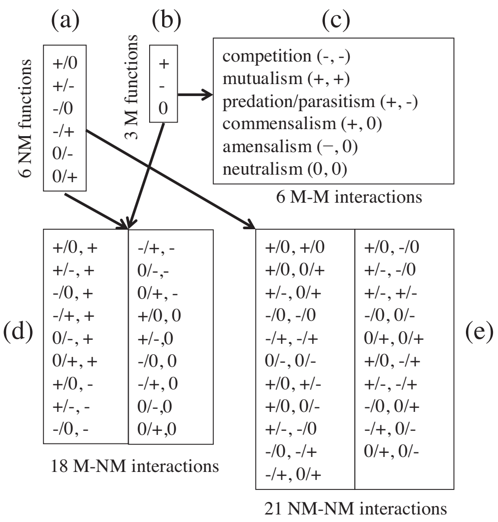

Fig. 6. Species interaction types under combinations of 3 monotonic functions (M) (a) and 6 non-monotonic functions (NM) (b) which produce 6 types of purely monotonic interactions (M-M) (c), 18 monotonic and non-monotonic mixed interactions (M-NM) (d) and 21 purely non-monotonic interactions (NM-NM) (e). Arrows indicate the results of interactions types due to combination of the monotonic or/and non-monotonic functions between two species.

In the non-monotonic models, Yan and Zhang (2014) defined 6 non-monotonic functions (NM) (+/0, +/−, −/0, −/+, 0/−, 0/+) in which interaction signs change between positive, negative and neutral with change of population density (Fig. 5d–i). +/− represents interaction shift from positive to negative (Fig. 5d, defined as a hump-shaped function). +/0 represents interaction shift from positive to neutral (Fig. 5e, defined as a satiation function). 0/− represents interaction shift from neutral to negative (Fig. 5f, defined as a sliding-down function). −/+ represents interaction shift from negative to positive (Fig. 5g, defined a U-shaped function). 0/+ represents interaction shift from neutral to positive (Fig. 5h, defined as an emerging function). −/0 represents interaction shift from negative to neutral (Fig. 5i, defined as a sheltering function). In theory, the 6 NM functions and 3 M functions can produce 18 species interactions containing M and NM functions (Fig. 6d), and 6 NM functions can produce 21 species NM interactions between two species (Fig. 6e).

The interactive shifts among signs of positive, negative and neutral relationships between species impose a great challenge to traditional models (*e.g.* Lotka–Volterra models and their variations). Hernandez (1998) demonstrated that transitions of two species interactions can result in multiple equilibrium points. Zhang (2003) demonstrated that mutualism at low density and competition (or predation/parasitism) at high density (*i.e.* shifting from positive to negative) promoted the carrying capacity and coexistence of two species. Similarly, Wang and Deangelis (2012) showed that mutualism at low density and parasitism at high density improved the stability of the system. In the non-monotonic models with two interacting species, Zhang (2003) defined 11 possible equilibrium points. As compared to monotonic models, non-monotonic functions can increase species coexistences by producing stable equilibrium or reducing unstable equilibrium (Yan and Zhang, 2014, also see below).

For two species competing for similar resources, it is generally believed that they are negatively affected by each other. But in

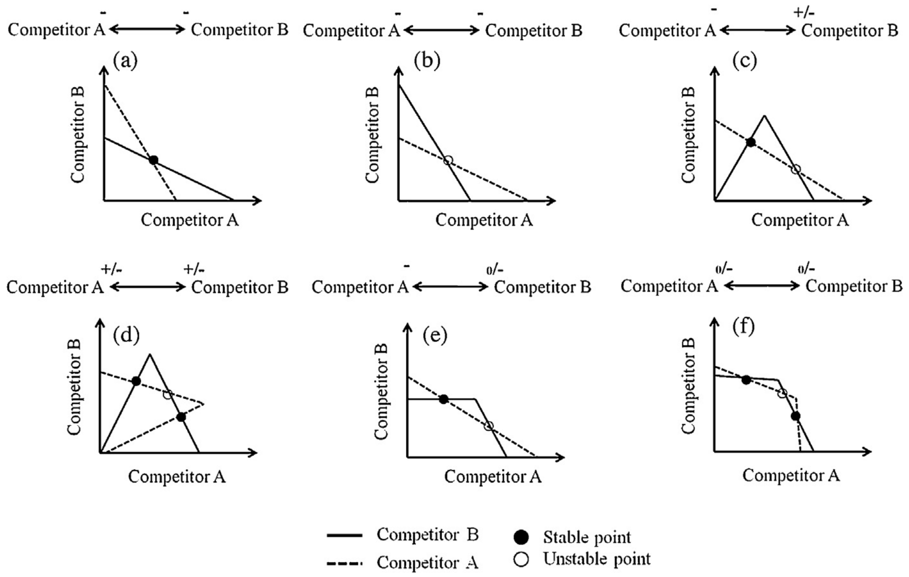

Fig. 7. Competition models which consist of purely monotonic functions (a and b), monotonic and non-monotonic mixed functions when interaction shift from negative at high density to positive at low population density (c and d) or from negative at high density to neutral at low population density (e and f) between species A and B. The monotonic or non-monotonic lines represent their zero growth isoclines of the two species. "−" represents negative effect of one species to the other (a–c and e). "+/−" represents shift of negative effect of species A to B (c) or both (d) at high density to positive at low density. "0/−" represents shift of negative effect of species A to B (e) or both (f) at high density to neutral effects at low density. In these models, density-dependency of both species is assumed.

nature, there are many examples of positive interactions among competitors. For example, leguminous or mycorrhizal plants benefit their neighboring plants by providing nitrogen or minerals and thus increase plant diversity or primary production (Bergelson, 1988; Bertness and Leonard, 1997; Díaz and Cabido, 2001; Fridley, 2001; Loreau et al., 2001; Tilman et al., 2001). Interaction between two seaweed flies, *Coelopa frigida* and *C. pilipes*, can change between acting as competitors or as amensalists (Phillips et al., 1995). As shown in Fig. 7, two competitors can coexist in one situation in Fig. 7a, but not in the other situation (Fig. 7b). If mutualism (Fig. 7c and d) or neutralism (Fig. 7e and f) occurs at low density, this can change the unstable situation in Fig. 7b into stable situations in Fig. 7c–f by producing a stable equilibrium point and then allows the coexistence of two competing species.

As illustrated in Fig. 8, two mutualists can coexist in one situation (Fig. 8a), but not in the other situation (Fig. 8b). If competition occurs at high density (Fig. 8c and d) or neutralism occurs at high density (Fig. 8e and f), this can change the unstable situation in Fig. 8b into stable situations in Fig. 8c–f by producing stable equilibrium points and then promotes the coexistence of two mutualistic species. Results of both Fig. 7 and 8 suggest that interaction functions shifting among positive, negative and neutral can be important in promoting species coexistence of two species. Cushman and Addicott (1991) reported that interactions between some ant and aphid species can shift from positive at low aphid densities to negative or neutral at high density.

In predator–prey systems with density-dependent effects of both predator and prey, mutualisms between prey and predators at low predator density likely increase the abundance of both prey and predators. As shown in Fig. 9, if the response of prey to predators is monotonic, the abundances of both prey and predator at the stable equilibrium point are low (Fig. 9a). However, if predator shows a positive effect at low density to prey, that is, the response of prey to predator is non-monotonic (a humped function against predator), then their abundances would increase significantly (Fig. 9d contrasting with Fig. 9a). Introduction of non-monotonic function shifting from positive to negative or from positive to neutral would produce various equilibrium points. These function shifts correspond well to the saturation effect (Fig. 9b), shelter effect (Fig. 9c) and mutualism effect (Fig. 9d) observed in natural predator–prey systems. For example, mutualism occurs commonly in plant–animal systems. In grassland ecosystems, herbivores show negative effect on plants by eating them, but also show positive effects by providing plants with nitrogen (Davidson et al., 2012; Zhang et al., 2003). It has been reported that mutualistic arbuscular mycorrhizal fungi can increase the competitive ability of plants that host them (Bever, 1999, 2002; Urcelay and Diaz, 2003). In forest ecosystems, small rodents and birds impose negative effects on tree species by eating seeds, but they also show positive effects by facilitating seedling regeneration through dispersing and buying seeds (Herrera, 1995; Xiao et al., 2013). At low density of seed-dispersers or in masting years, seed-dispersers would have positive effects; but at high density of seed dispersers or non-masting years, they would have negative effects (Li and Zhang, 2007; Zhang, 2003).

Empirical observations show that refuges that shift interactions from negative at high density of prey to neutral at low density can protect prey from over-consumption by predators, which stabilizes predator–prey interactions (Křivan, 1998; Utne et al., 1993). Predator satiation can also protect prey from excessive predation by predators and thus contribute to coexistence of prey and predator (Williams and Martinez, 2004). Xiao et al. (2013) found seed masting of tea tree *Camellia oleifera* (Theaceae) in a subtropical forest was positively associated with pre-dispersal survival of oil tea seeds, supporting the predator satiation hypothesis. Examples of prey showing negative effects on their predators are very rare, but Loladze et al. (2000) showed that indirect competition between a producer (plant) and a grazer (beetle) for phosphorus can shift predation to competition interaction between predator and prey. In the Inner Mongolia grasslands of China, the response of Brandt's voles to grass vegetation was found to be bell-shaped (Zhang et al., 2003). If the grass is too sparse, there is no enough food and shelter; but if the grass is too dense or too high, it prevents social interactions and predator alerting (Zhong et al., 1999). These two examples indicate that when prey is too abundant, the prey likely shifts its positive effect into a negative effect on predators (Fig. 9e).

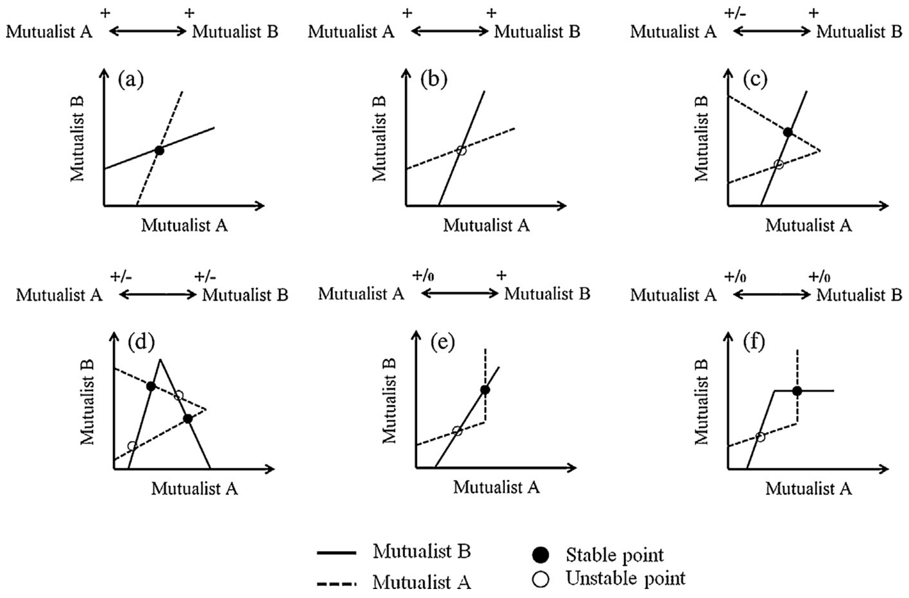

Fig. 8. Mutualism models which consist of purely monotonic functions (a and b), monotonic and non-monotonic mixed functions when interaction shift from positive to negative (c and d) or from neutral to negative (e and f). The monotonic or non-monotonic lines represent their zero growth isoclines of the two species. "+" represents positive effect of one species to the other. "+/−", "+/0" represents shift of positive effect of one species to the other at low density to negative or neutral effects at high density. "+" represents positive effect of one species to the other (a–c and e). "+/−" represents shift of positive effect of species B to A (c) or both (d) at low density to negative at high density. "+/0" represents shift of positive effect of species B to A (e) or both (f) at low density to neutral at high density. In these models, density-dependency of both species is assumed.

It is notable that in the models illustrated in Figs. 7–9, density dependent effects of both interacting species are assumed. But in the traditional Lotka–Volterra predator–prey model without density dependent effects, the zero isoclines of both prey and predator are vertical which can result in a limit cycle. In the Rosenzweig and MacArthur model, the prey has a humped isocline while the predator has a vertical isocline which results in a stable equibrium at low density of prey but unstable

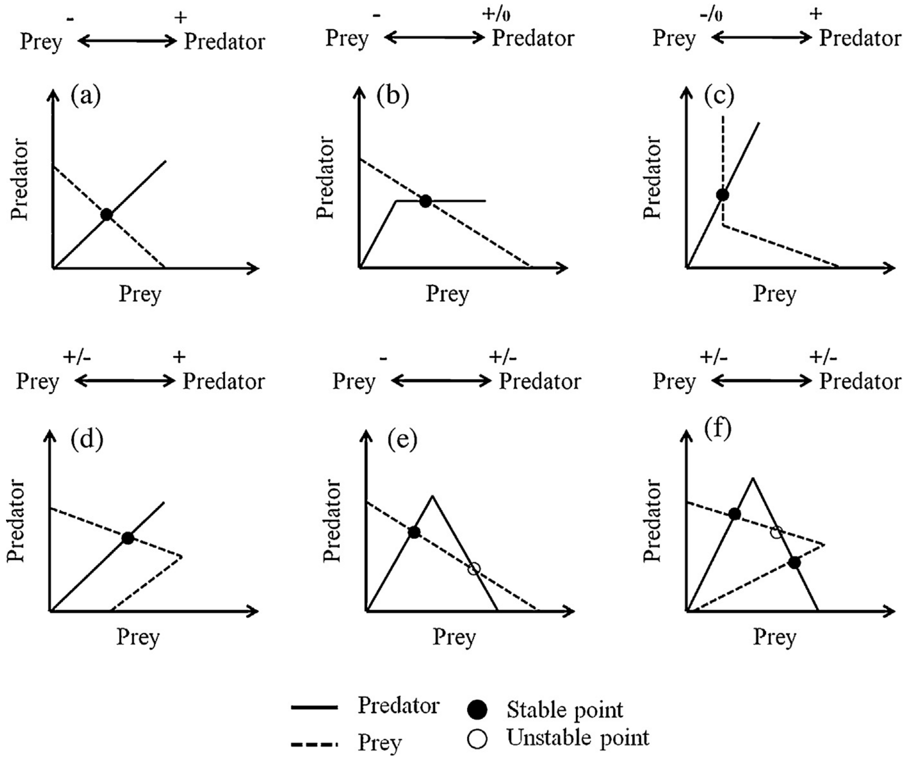

Fig. 9. Predation models which consist of purely monotonic functions (a), and monotonic and non-monotonic mixed functions shifting from positive to neutral (b, saturation effects), from negative to neutral (c, shelter effects), from positive to negative (d, e, f; mutualistic effects). The monotonic or non-monotonic lines represent their zero growth isoclines of the two species. "+" represents positive effect of prey to predator. "−" represents negative effect of predator to prey (a–f). "+/0" represents shift of positive effect of prey to predator at low density to neutral at high density (b). "−/0" represents shift of negative effect of predator on prey at low density to neutral at high density (c). "+/−" represent shift of negative effect of predator on prey at high density to positive at low density (d) or shift of positive effect of prey on predator at low density to negative at high density (e) or both (f). In these models, density-dependency of both species is assumed.

equilibrium at high density of prey (paradox of enrichment of prey).

5. Non-monotonicity in ecosystems

In traditional ecological network models, species interactions are also assumed to be monotonic. Theoretical analysis indicate that stability decreases with an increase in the number of species and their connectance (Allesina and Tang, 2012; May, 1972), which contrasts with the empirical observation that stability is positively associated with biodiversity (Elton, 2000; MacArthur, 1955; McCann, 2000). Recently studies indicate that some mechanisms can improve the stability of monotonically connected networks. For example, compartmentalization and nestedness have been found to promote stability (Thébault and Fontaine, 2010). A moderate mixture of antagonistic and mutualistic interactions also stabilizes a community (Mougi and Kondoh, 2012). Allesina and Tang (2012) found that predator–prey interactions increase stability, but mutualistic and competitive interactions destabilize stability. Omnivory is also found to stabilize food webs (McCann and Hastings, 1997). Weak interactions are important in maintaining the stability of an ecosystem (Berlow, 1999; McCann et al., 1998; Rooney and McCann, 2012). A non-random pattern of interaction strengths also increases the stability of networks (Neutel et al., 2002, 2007). All of these studies are based on monotonic models.

By introducing the six non-monotonic functions into the conventional models (Fig. 5d–i), Yan and Zhang (2014) investigated the persistence of three classic networks (*i.e.* randomly connected networks, cascade prey–predator networks and bipartite mutualistic networks). The non-monotonic model is shown as follows:

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

where x_i is the population abundance of a species i, r_i is the intrinsic rate of increase, a_i is the density dependent coefficient, S is the number of species influencing species, b_{ij} is the interspecific interaction from species j. $b'_{ij} = f(x_j)b_{ij}$, and $f(x_j)$ is used to change the sign (+, − or 0) of b_{ij}, depending on x_j.

Through simulation, Yan and Zhang (2014) found that four kinds of non-monotonic functions, shifting signs to negative or neutral interactions at high population density (Fig. 5d–f and i) increases persistence of ecological networks. Two non-monotonic interactions that changed signs to positive (Fig. 5g and h) were found to destabilize the networks. Further analysis indicates that the four non-monotonic interactions stabilize the network by avoiding unbounded population growth or decline, which also provides a good explanation why unbounded mutualism often destabilizes the network. It is notable that although non-monotonic functions increase persistence (in term of species survival) of the network, they likely increase the amplitude of population fluctuations of each species. Thus a high level of species coexistence in an ecological network can be achieved through dynamic stability of each species in the non-monotonic models. This study revealed a novel network stabilizing mechanism caused by specific non-monotonic interactions.

The non-monotonic interaction function shifting sign from positive to negative (+/−) corresponds to observations on mutualism–competition (Cushman and Addicott, 1991; Zhang, 2003), mutualism–predation (Thompson, 1988; Thompson and Uttley, 1982) and mutualism–parasitism (Neuhauser and Fargione, 2004) interactions in natural conditions. The non-monotonic interaction function that shifts sign from positive to neutral (+/0) corresponds well to the observation of a predator satiation effect in predator–prey system (Williams and Martinez, 2004). The non-monotonic interaction function shifting from negative to neutral (−/0) corresponds well to observations on the refuge effect (Křivan, 1998; Miller and Carefoot, 1989; Sih, 1987; Srinivasu and Gayatri, 2005; Utne et al., 1993). The non-monotonic interaction function shifting from neutral to negative (0/−) corresponds well to observation on the emerging effect (*e.g.* epidemic threshold of infectious diseases or pests). The two destabilizing non-monotonic interactions shifting to positive (−/+, 0/+) are rarely seen in nature.

For the four stabilizing non-monotonic interactions, the biological meaning of b'_{ij} is obvious. It works as a stabilizing regulator which prevents too strong or too weak interspecific interaction, reducing the probability of population explosion or extinction. The two destabilizing non-monotonic interactions (−/+, 0/+), b'_{ij} do not stabilize a network because there are unbounded positive effects which often result in population explosions (Yan and Zhang, 2014).

6. Perspective and outlook

In contrast with previous studies in which ecological effects are often assumed to be monotonic (mostly linear), our review indicates that ecological non-monotonic responses are common in nature. Driven by the three possible mechanisms of ecological non-monotonicity mentioned above (*i.e.* the law of tolerance, adaptive behaviors, or opposing dual or pathway effects), interactions of organisms with biotic or abiotic factors are able to change signs among positive, negative and neutral at certain conditions. Many studies have demonstrated that the effects of some climatic factors cause non-monotonic relationships (Tian et al., 2011; Xu et al., 2011; Yan et al., 2013a), and some species interactions are non-monotonic (Křivan, 1998; Loladze et al., 2000; Utne et al., 1993; Williams and Martinez, 2004); these non-monotonic functions can produce significant impacts on ecological complexity and stability (Yan and Zhang, 2014; Zhang, 2003). Thus, ecological non-monotonicity should be an important driving force for species coexistence and the stability of ecosystems, and it should be closely evaluated in future ecological studies.

To understand the significance of non-monotonicity in ecological patterns and processes, it is necessary to investigate the proportion of non-monotonic interactions in natural ecosystems so as to assess their significance in maintaining biodiversity and ecosystem functions. Unfortunately, direct estimation of non-monotonic interaction strength is still rare. Both long-term temporal or short-term spatial community data are often essential in estimating the non-monotonic interaction strength of organisms with abiotic and biotic factors.

Traditionally monotonic or linear models are not able to detect non-monotonic variations. There is a need to integrate non-monotonic interactions into ecological modeling studies. To reveal non-monotonic effects of interactions, it is necessary to use or develop non-monotonic statistical methods and models. It is difficult to discover non-monotonic functions or interactions by using linear models. But it is possible to use a linear model by introducing piecewise functions if the threshold can be determined. Generalized additive models (GAMs) are very useful tools for revealing non-monotonic interactions (Xu et al., 2011; Yan et al., 2013a,b). Indeed, application of GAMs significantly increased the fitting performance of the models. However, GAMs have some limitations. First, results of GAMs are only presented in the way of curve changes, not in forms of mathematical equations. Second, the model results are often sensitive to model parameters. Third, some non-monotonic results (*e.g.* with U-shaped relation) are hard to explain and are often ignored or even dropped by ecologists. As discussed above, non-monotonic functions may be caused by spatial, temporal or scale factors. The observed non-monotonic relations which are difficult to explain should be examined further to find the biological or ecological mechanisms behind the unexpected relations. For example, pooling data of many sites of a large region or a long-time period can easily produce non-monotonic relationships because the response of organisms in different sites or time domains would be different. Separate analysis is necessary to reveal the underlying mechanism behind non-monotonic relationships.

It is necessary to develop non-monotonic models with mathematic equations. To reflect the non-monotonic relation (with parabolic curves) as demonstrated in Fig. 1, the non-monotonic model can be shown as follows:

$$\frac{dx_i}{x_i dt} = r_i + a_i x_i + \sum_{j=1, i \neq j}^{S} (\mathrm{b}_{ij} + c_{ij} x_j + d_{ij} x_j^2) + \sum_{k=1}^{K} (e_{ik} + f_{ik} y_k + g_{ik} y_k^2)$$

where r_i is the intrinsic rate of increase, a_i is the density dependence coefficient, S is the number of species influencing species i; b_{ij}, c_{ij}, d_{ij}, e_{ik}, f_{ik}, g_{ik} are constants; x_i, x_j are population density of species i and j; y_k is the environmental variable k; K is the number of environmental variables influencing species i. The model is extended from the non-monotonic model from Yan and Zhang (2014) by including effects of environmental variables.

Ecological non-monotonicity would greatly change our conventional view of policies for managing biodiversity. Traditionally, the positive effects of organism interactions (*e.g.* cooperation, altruism, mutualism) are favored, while the significance of negative effects (*e.g.* parasitism, diseases, pests) is often ignored. From non-monotonic point of view, organisms may have both positive and negative effects on other organisms and these two opposing effects need to be integrated with each other. Non-monotonic functions can be important in maintaining a healthy and stable ecosystem. For example, rodents often cause damage to grasslands or forests when their population density is high, but they also benefit grassland or forest through facilitating nutrient cycling or seed regeneration when their population density is low or moderate. Therefore, we should re-think these “good” or “bad” effects involved in managing ecosystems.

Ecological non-monotonicity may also change our popular view on global change. The earth is facing accelerated climate warming and human disturbance, and the ecological effects on species may change signs if the trends do not stop. This will increase the complexity of predictions of future trends in population and community dynamics. Climate warming may benefit some animal species on a local scale, but on a regional or global scale, the temperature-induced precipitation changes may have a negative effect on the same species. Thus, continued global change would likely cause population declines when the negative indirect effects overwhelm the direct positive effects. There have been reports that cycling patterns of some small mammals in the northern hemisphere have been reduced or have even disappeared with increased global warming and human disturbance (Kausrud et al., 2008; Yan et al., 2013a,b). Therefore, we call for further investigation on the non-monotonic effects of climate change in possibly causing population declines on a global scale.

In summary, there are various kinds of non-monotonic relations in nature. Ecological non-monotonicity, which is defined as a non-monotonic relationship of the per capita rate of population increase to intrinsic or extrinsic factors, is a driving force in shaping the complexity and stability of ecological systems. Adaptive behaviors, the law of tolerance, and opposing dual or pathway effects may result in non-monotonic functions. The non-monotonic functions of climatic factors or species interactions are often related to the spatial and temporal scale or to population density. There are six kinds of non-monotonic functions between two species which can produce more diversified interaction types than those of the three monotonic functions. Specific non-monotonic functions can increase complexity and stability of ecological systems. Ecological non-monotonicity would change our conventional monotonic views. We appeal for a shift of paradigms from monotonic to non-monotonic point of view in studying population dynamics, species interactions, and ecosystem functioning.

7. Conclusions

(1) There is growing evidence that the effects of both biotic and abiotic factors on a population’s rate of increase are non-monotonic under conditions of different spatial and temporal scales or population density. In contrast with many descriptions of monotonic relations, the type and proportion of non-monotonic relations at population, community and ecosystem levels are largely unknown. More effort is needed to estimate the non-monotonic relations across large spatial-temporal scales and environmental gradients.

(2) In contrast with traditional modeling studies, recent theoretical studies indicate that specific non-monotonic functions can promote species coexistence and affect productivity. Therefore, ecological non-monotonicity could play a significant role in maintaining ecosystem stability and functioning. It is necessary to consider non-monotonic relationships in future modeling studies.

(3) Given the potential significance of ecological non-monotonicity, it is necessary to change our conventional thinking in future ecological studies and policy making for ecosystem management. This is particularly important because accelerated global change could result in abrupt ecological shifts which need to be anticipated in our research programs.

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