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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, $r_t = f(N_t) = \ln(N_{t+1}/N_t)$. 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-monotonicty which we will address in this paper.

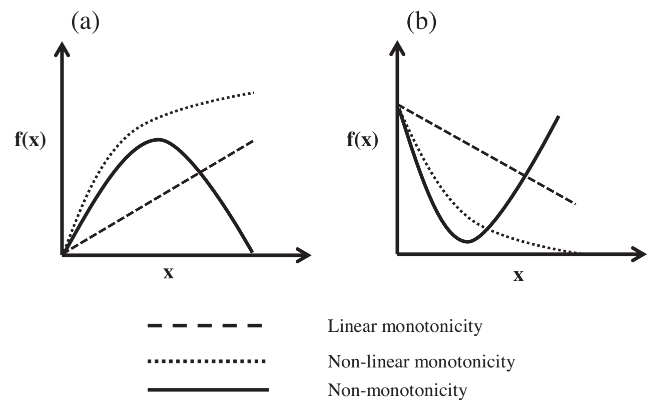

Fig. 1. Illustration of linear monotonicity (broken lines), non-linear monotonicity (dashed lines) and non-monotonicity (solid lines). Non-monotonicity includes a hump-shaped non-monotonic function (a) and a U-shaped non-monotonic function (b).

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 $r_p = a_1 + b_1 x$, $r_n = a_2 - b_2 x^2$, 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 $r = r_p + r_n = a_1 + a_2 + b_1 x - b_2 x^2 = a + bx - cx^2$