



Original Research Article

Combined effects of intra- and inter-specific non-monotonic functions on the stability of a two-species system



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ABSTRACT

Although either interspecific or intraspecific non-monotonic functions have been found to influence stability of community and ecological networks, population models considering both interspecific and intraspecific non-monotonic functions have not been investigated. In this study, by using graphic stability analysis, we found a two-species model with both intra- and inter-specific non-monotonic functions could produce multiple equilibria; the probability of producing stable equilibrium points was larger than that using the models with only intraspecific non-monotonic functions, but lower than that using the models with only interspecific non-monotonic functions. Our results further confirmed that dome-shaped interspecific non-monotonic function was a stabilizing force, while dome-shaped intraspecific non-monotonic function was a destabilizing force; the former should be more favored by natural selection than the latter. Besides, limit cycles were also detected in this two-species system. We appeal for more efforts in studying the ecological non-monotonicity in both theoretical and empirical studies by considering multiple-species systems and various non-monotonic interaction forms.

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1. Introduction

For simplifications, the intra- or inter-specific interactions are often assumed to be linear or monotonic in ecological studies. Recently, ecological non-monotonicity, which allows transitions between positive, negative and neutral functions, has been recognized to play a significant role in affecting stability and persistence of population and community (Zhang et al., 2015). Therefore, it is necessary for further investigation on ecological non-monotonicity through both theoretical and experimental approaches.

In nature, interspecific non-monotonic interactions have been frequently reported. For example, positive interaction shifting to negative competition among birds were observed as the density of birds increased (Thompson, 2003). In rodent-seed interactions, at low density of rodent or in seed-masting years, rodents mainly show positive effects on trees by dispersing seeds to locations beneficial for germination, but when the density of rodents is too high or seeds were too few, rodents consume up almost all seeds, and thus show a negative effect on trees (Li and Zhang, 2007; Cao et al., 2017). In plant communities, the competition and facilitation

effects could shift with a gradient of environmental stress (Callaway, 2007). Other examples existed in ants-aphids (Addicott, 1951), seaweed flies (Phillips et al., 1995), seaweeds (Wahl and Hay, 1995). Theoretical models have been proposed to study the properties of these interspecific non-monotonic interactions. Comparing to linear models of two-species, strong nonlinear interactions would produce more stable equilibrium points. Vandermeer (1973) demonstrated that dome-shaped non-monotonic interspecific interactions in a two-species system could produce two stable equilibria for coexistence of the two species. Hernandez (1998) also indicated that alpha-function (a dome-shaped non-monotonic function) could produce two stable equilibria. In the traditional Lotka-Volterra competitive model, there are two possible intersections by zero-growth isoclines of the two species, but only one of them could be stable with a relatively weak interaction strength. By introducing a parabolic function into the Lotka-Volterra competition model, Zhang (2003) built a competition-mutualism model, and reported 9 of 11 possible intersections could be stable equilibrium points, showing a much larger probability than the linear models. This study suggested that mutualism at low density and competition at high density could promote stability and carrying capacity of two competitors. Introduction of non-monotonic interactions into Lotka-Volterra prey-predator model or consumer-resource model could produce mutualism-parasitism or mutualism-predation interactions

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(Wang and Deangelis, 2011, 2012; Wang et al., 2011, 2013). Recently, a study has shown that density-dependent shifts from positive to negative or neutral interaction could increase persistence in three kinds of ecological networks, but increase oscillations of population density at the species level (Yan and Zhang, 2014).

Within a species, negative density dependence is a well-documented phenomenon (Fowler, 1987; Li et al., 2016; Myers and Krebs, 1974) in natural and experimental systems. The negative density dependence is usually caused by intraspecific competition for food and space. Meanwhile, positive feedback of population density, usually called the Allee effect, is also widely acknowledged, which usually results from mate limitation or cooperation (Allee and Bowen, 1932; Kramer et al., 2009). Combination of Allee effect and negative density dependence would result in a dome-shaped non-monotonic function (Zhang et al., 2015). The graphical analyses by Vandermeer (1973) demonstrated a dome-shaped intraspecific non-monotonicity in two-species systems usually led to extinction of one species. Later studies also suggested the Allee effects was a destabilizing force in species coexistence (Wang et al., 1999; Zhou et al., 2005; Zu and Mimura, 2010), but see Scheuring (1999). For instance, Wang et al. (1999) found that introduction of the Allee effect into the competition models did not increase the number of stable equilibrium points, but sometimes decreased the number of stable equilibrium points. Zhou et al. (2005) introduced the Allee effect into the Lotka-Volterra predator-prey models, and found that the equilibrium point of the system could be changed from asymptotically stable to neutral stable or the system took much longer time to reach stable equilibria.

Although the non-monotonic functions have been introduced into intraspecific or interspecific density dependence separately in previous studies, to our knowledge, there is still no modeling study considering both intraspecific and interspecific non-monotonic density dependence. The aim of this study is to understand how both intraspecific and interspecific interactions would affect species coexistence of two species by using graphic stability analysis. By representing population dynamics of two interacting species with two differential equations, we focused on graphically analyzing the set of equations with non-monotonic functions nearby initial conditions. When neither of the two species' population is changing, population equilibrium is defined to occur in the models. The stability of our system in this study is defined as species coexistence in a two-species system when local stable equilibrium points or limit cycles are produced by intersecting the zero isoclines of two species. By evaluating the stable equilibriums of a two-species system, the combined effects of intra- and interspecific non-monotonic functions on a two-species system were explored.

2. Methods

We firstly considered a model with parabolic interspecies interaction function, derived from Lotka-Volterra competition model (Eqs. (1) and (2)). In this model, N_1 and N_2 are the population densities, $r_1, r_2 > 0$ are intrinsic growth rates, and $\omega_1, \omega_2, \beta_1, \beta_2, \gamma_1,$ and γ_2 are constants. When $N_2 < \gamma_1$ or $N_1 < \gamma_2$, the competitor's effect is positive, and when $N_2 > \gamma_1$ or $N_1 > \gamma_2$, the competitor's effect becomes negative.

$$\frac{dN_1}{dt} = r_1 N_1 (\omega_1 - N_1 - \beta_1 (N_2 - \gamma_1) N_2) \tag{1}$$

$$\frac{dN_2}{dt} = r_2 N_2 (\omega_2 - N_2 - \beta_2 (N_1 - \gamma_2) N_1) \tag{2}$$

For mathematical convenience, we modified Eqs. (1) and (2) to Eqs. (3) and (4), which are similar to the equations proposed by Zhang (2003). k_1, k_2, b_1, b_2, c_1 and c_2 are constants. The threshold value k in Eqs. (3) and (4) equals $\gamma/2$ in Eqs. (1) and (2), and their meanings are different. In this model for N_1 , when $N_2 < k_1$, the equilibrium density of N_1 increases with N_2 , and when $N_2 > k_1$, the equilibrium density of N_1 decreases with N_2 . The isoclines for this model are shown in Fig. 1 a&b, which are concave to the other species' density axes.

$$\frac{dN_1}{dt} = r_1 N_1 \left(c_1 - N_1 - \frac{(N_2 - k_1)^2}{b_1^2} \right) \tag{3}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(c_2 - N_2 - \frac{(N_1 - k_2)^2}{b_2^2} \right) \tag{4}$$

Similarly, if a parabolic function is introduced to represent intraspecific density dependence in a population model, the isoclines would be concave to the species' own density axes (Fig. 1c&d). Based on Eqs. (3) and (4), we built a model incorporating both intraspecific and interspecific non-

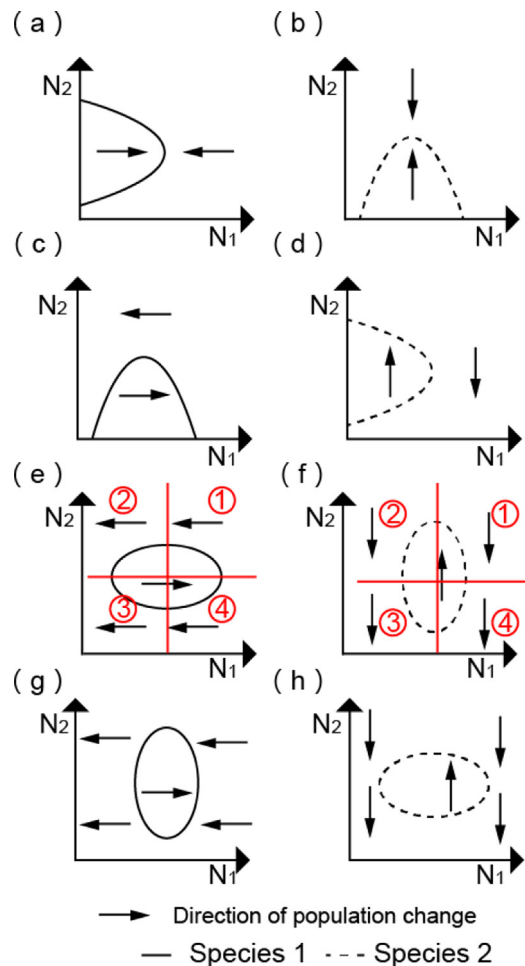


Fig. 1. The parabolic isoclines of interspecific non-monotonic function (a, b), intraspecific non-monotonic function (c, d), and ellipse isoclines in this study (e, f for Type 1: $a_1 = 4, a_2 = 4, b_1 = 2, b_2 = 2$; g, h for Type 2: $a_1 = 2, a_2 = 2, b_1 = 4, b_2 = 4$). The 1st, 2nd, 3rd and 4th quadrants of the isoclines are defined in Fig. 1e, f (divided by red lines). Any point along each specific isocline represents a combination of abundances of the two species where all species' population abundance does not increase or decrease. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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