Integrative Zoology 2020; 0: 1–13 doi: 10.1111/1749-4877.12487

REVIEW

Mutualism between antagonists: its ecological and evolutionary implications

Zhibin ZHANG,[1,2] Chuan YAN[3] and Hongmao ZHANG[4]

[1]State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, Beijing, China, [2]CAS Center for Excellence in Biotic Interactions, University of Chinese Academy of Sciences, Beijing, China, [3]State Key Laboratory of Grassland Agro-ecosystem, Institute of Innovation Ecology & College of Life Sciences, Lanzhou University, Lanzhou, China and [4]School of Life Sciences, Institute of Evolution and Ecology, Central China Normal University, Wuhan, China

Abstract

Mutualism or antagonism between species is often investigated within the framework of monotonic interactions of either mutualism or antagonism, but studies on transition from mutualism to antagonism (within the context of nonmonotonic interactions) have been largely ignored. In this paper, through a brief review and synthesis, we highlighted the role of mutualism between antagonists in regulating the ecological and evolutionary processes, as well as maintaining the stability and complexity of ecosystems. Mutualism between antagonistic species represents the density-dependent transition between mutualism and antagonism, which is beneficial to species coexistence and stability of complex ecosystems; thus, it should be favored by natural selection. Species may face selection of conflicting pressure on functional traits in co-balancing mutualism and antagonism, which may result in evolution of the dual character of species with moderate mutualistic or antagonistic traits. Coevolution and co-balance of these traits are driving forces in shaping mutualism–antagonism systems. Rewards for mutualists, punishment for exploiters, and competition of meta-communities are essential in stabilizing mutualism between antagonists. We appeal for more studies on mutualism between antagonists and its ecological and evolutionary implications by expanding the conventional ecological studies from monotonic to nonmonotonic regimes.

Key words: antagonism, biodiversity and stability, coevolution, ecological nonmonotonicity, mutualism

INTRODUCTION

Revealing the spatial-temporal dynamics of abundance and diversity of species is one of the important missions of population and community ecology (Krebs 2015). This largely relies on understanding the role of species interactions as the driving force in the maintenance of stability and complexity of various ecosystems. There are 3 basic ecological effects on the population increase rate of one species on the other species, that is, the positive, negative, and neutral effect. They produce 6 basic species interactions: mutualism, competition, predation/parasitism, commensalism, amensalism, and neutralism (Zhang 2003; Yan & Zhang 2014).

Understanding species coexistence is a fundamental goal in ecology (Yan *et al*. 2016). For 2 competitors, niche

Correspondence: Zhibin Zhang, Chinese Academy of Sciences, Institute of Zoology, Beijing 100101, China.
Email: zhangzb@ioz.ac.cn

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

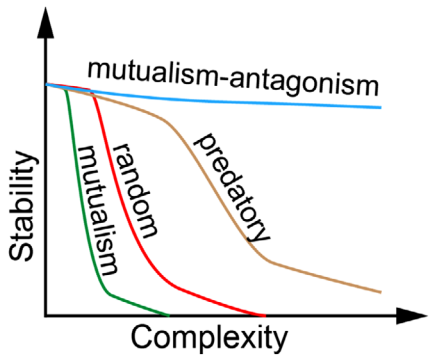

Figure 1 Illustrations on the relation between stability (the proportion of survived species) and complexity (i.e. species number, connectance and interaction strength) in different networks. For the random network, species are randomly connected by either mutualism (++), competition (−−), predation or parasitism (+−), commensalism (+0), amensalism (−0), and neutralism (00). For predatory network, species are only connected by predation (+−). For the mutualism–antagonism network, species are connected by a dome-shaped function (i.e. mutualism at low density but antagonism at high density). For details, see: Yan and Zhang (2014).

theory and Gause's competitive exclusion principle predict that 2 species sharing the same or similar niche cannot coexist within an environment. This prediction was well modeled in the Lotka–Volterra competition models (LV models hereafter) for 2 species: Only weak competition with smaller competition coefficients (i.e. sharing dissimilar niche) could produce stable coexistence of 2 competing species, while strong competition with larger competition coefficients (i.e. sharing similar niche) would result in non-coexistence (Zhang 2003; Zhang *et al*. 2015). Similarly, for mutualists, strong mutualism would result in non-coexistence, while weak mutualism would result in stable coexistence. At the community or ecosystem level, the conventional LV models result in the 2 most well-known complexity–diversity paradoxes in ecology. The first paradox is that more species and higher connectance between species would result in less stability of an ecosystem (May 1972; McCann 2000; Allesina & Tang 2012), which is contradictory to the empirical observations that higher biodiversity benefits stability (MacArthur 1955; Elton 1977). The second paradox is that mutualism would result in instability due to its unbound population growths (May 1973), which is also contradictory to the empirical observations that mutualism prevails in real ecosystems (Bascompte & Jordano 2007). As shown in Fig. 1, the ecological networks with connectance of only mutualism between species (mutualism network) or random connectance of either mutualism, competition, predation/parasitism, commensalism, amensalism, and neutralism between species which consists of linear species interaction are not able to produce a stable and complex ecosystem. Predatory networks with connectance of only predation are relatively robust. To solve the complexity-diversity paradox, many hypotheses have been proposed including modularity (Yodzis 1981), weak interaction (Berlow 1999; Neutel *et al*. 2002), nestedness (Bascompte & Jordano 2007; Rohr *et al*. 2014), and mixture of interactions (Allesina & Tang 2012; Mougi & Kondoh 2012). These hypotheses largely rely on the mechanisms of weak interactions between species in explaining the stability of a complex ecosystem. Recent studies report that specific nonmonotonic interactions are able to stabilize ecosystems (Zhang 2003; Yan & Zhang 2014) and increase the biomass or productivity of ecosystem (Yan & Zhang 2018), suggesting that the ecological nonmonotonicity would play a significant role in maintaining the biodiversity and stability of ecosystems (see below).

This work aims to highlight the role of mutualism between antagonists in maintaining the stability and complexity of ecosystems, and to appeal for more investigations on evolutionary and ecological process of transitions between mutualism and antagonism. We focus this review on transition between mutualism and antagonism and its ecological and evolutionary implications. In this synthesis, we illustrated several important concepts by using the seed–rodent system, which has been previously investigated in the context of ecological nonmonotonicity (see glossary on Table S1, Supporting Information, for facilitating understanding the technical terms of this paper). In this study, species having an interaction of mutualism are defined as a mutualist to each other, while species having an interaction of antagonism such as predation, parasitism, or competition are defined as an antagonist to each other. The stability of an ecosystem is often measured by 2 indicators: variation of population abundance or biomass and species coexistence or persistence (i.e. proportion of survived species) (Yan & Zhang 2014). In this study, stability is referred to the species coexistence or persistence of ecosystem.

ECOLOGICAL NONMONOTONICITY

It is obvious that in the LV models with monotonic interactions with either positive, negative, or neutral function or effect, higher biodiversity is maintained at the sacrifice of species interaction strength or connectance. However, weak interaction or small connectance would

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

limit energy or matter flow between species, and then the biomass of an ecosystem (Yan & Zhang 2018). Recently, the role of nonmonotonic interaction allowing transition between positive, negative, and neutral effect in maintaining stability and complexity of an ecosystem has been realized (Yan & Zhang 2014; Zhang *et al*. 2015). The nonmonotonic interactions mean that transition of species interaction would occur with the change of population density. The nonmonotonic interaction was studied in earlier predator–prey models such as those by Holling (1965) and Tanner (1975). Dome-shaped species interactions could produce 2 stable equilibria in a 2-species system (Vandermeer 1973; Hernandez 1998; Zhang 2003; Wang & Deangelis 2011, 2012; Wang *et al*. 2011, 2013). Zhang (2003) proposed a nonmonotonic model (NM model hereafter) by changing the linear zero-growth isocline (nullcline) in LV models into a parabolic curve (a type of dome-shaped functions), which means transition from mutualism at low population densities to competition at high population densities. In the LV models of 2 competitors or mutualists, only 1 of 2 possible intersection points is stable, but in the NM model, 9 of 11 possible intersection points are stable, indicating that the parabolic interaction could increase probability of coexistence of 2 competing or mutualistic species. Zhang (2003) defined the positive, neutral, or negative effect of a species on population increase rate of the other species based on the positive, neutral, and negative association of zero-growth isoclines with population density in the NM model (Fig. 2). Thus, the 11 possible intersections could produce 6 interaction types, including mutualism, competition, predation/parasitism, commensalism, amensalism, and neutralism (Zhang 2003; Yan & Zhang 2018). Besides, Zhang (2003) also found population size of both interaction species at equilibrium points can be larger than the carrying capacity in the NM models with moderate parabolic functions, while in the LV models, the population size at equilibrium points was always lower than the carrying capacity, which explains why the dome-shaped interaction could increase total biomass of an ecosystem (Yan & Zhang 2018).

It is notable that mutualism or antagonism defined by Zhang (2003) in the NM models is different from those in the LV models, and also different from the conventional concepts based on absolute positive or negative effect (see below). In the LV models, mutualism or antagonism between 2 species are fixed, regardless of changes of their population density of interacting species, but in the NM models, the mutualism or antagonism between species could change with population density of the interacting species. In the NM models, mutualism or antagonism

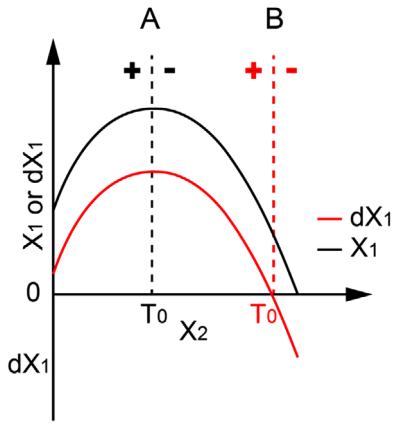

Figure 2 Illustrations of a positive or negative effect of species 2 with population density of x_2 on species 1 in the nonmonotonic models (NM models). Line A shows a transition from positive to negative effect of species 2 on species 1 based on the association between increase rate (or zero-growth isocline) of population density of species 1 (x_1) and population density (x_2) of species 2. Line B shows a transition of absolute positive to negative effect of species 2 on the increase rate of species 1. x_1 is the zero-growth isocline of species 1 in the NM models. dx_1 is the effect of species 2 on the increase rate of species 1. The stability of coexistence of species 1 and 2 is determined by the zero-growth isoclines of the two species in NM models. "+" and "−" represents the transition between positive and negative effects across the dashed line A, B. T_0 represents the threshold at which a transition occurs.

is defined as the positive or negative association of zero-growth isoclines with population density of the interacting species as defined by Zhang (2003). As shown in Fig. 2, mutualism or antagonism between 2 species in the NM models is not determined by the absolute positive or negative effect of population density of species 2 (x_2) on the increase rate (dx_1) of species 1, instead by the positive or negative association of zero-growth isocline (x_1) or increase rate with population density of species 2 (x_2) (Fig. 2). The intersection of zero-growth isoclines, not the absolute interacting effects, determines stability or complexity of species coexistence (Zhang 2003; Zhang *et al*. 2015). Because the association of the population increase rate (dx_1) of species 1 with population density of species 2 (x_2) is similar to that of the zero-growth isoclines (x_1) (Fig. 2), density-dependent change of population increase rate can be used to determine the transition between mutualism and antagonism. This transition would result in mutualism between antagonists (i.e. competitors or prey/predator or host/pathogen), that is, the population increase rates of 2 species were positively associated with population densities of the interacting species at the

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

low population density phase, but negatively associated at the high population density phase (for details, see Zhang 2003; Zhang *et al*. 2015). To avoid confusion, the conventional mutualism or antagonism is defined as the absolute mutualism or antagonism, while mutualism or antagonism in our NM models is defined as the relative mutualism or antagonism.

From the 3 types of monotonic ecological effects in the LV models, Yan and Zhang (2014) defined 6 types of nonmonotonic ecological effects and 39 types of species interactions in the NM models. In the NM models, the positive, negative, or neutral effect of one species on the other is changeable depending on the population density, resulting in transition from mutualism at low densities to antagonism at high densities.

Although the properties of some monotonic functions have been investigated in 2-species systems, their roles in maintaining complexity and stability in ecological networks have only been investigated recently. Yan and Zhang (2014) found 4 of the 6 nonmonotonic functions showing transitions from positive to neutral or negative, from negative to neutral, and from neutral to negative could stabilize ecological networks. Yan and Zhang (2018) further demonstrated that both dome-shaped (i.e. transition from positive to negative effect) and saturation function (i.e. transition from positive to neutral effect) could increase stability of ecological networks; however, only the dome-shaped function could increase both stability and "biomass" of ecological networks. The dome-shaped function represents mutualism between antagonists at low-density, but antagonism at high-density. The other 2 functions showing transition from negative to positive and from neutral to positive effect destabilize ecological networks because their effects are not bounded with an increase in population density. These results indicate that the ecological nonmonotonicity may play a significant role in formation of mutualism or cooperation, and in maintaining biodiversity and stability of ecosystems (Zhang *et al*. 2015).

DUAL CHARACTER OF SPECIES

If the dome-shaped function benefits complexity and stability of ecosystems as revealed in previous studies (Yan & Zhang 2014, 2018), the role of a species in the ecosystem should be dual in nature as both a mutualist and an antagonist to the other species. At an individual level, organisms often possess both defensive and attractive traits, which lay the basis of mutualism between antagonists. For example, seeds of plants produce nutritious food to animals for getting ecosystem services of pollination or seed dispersal from animals, but they also possess physical structures or chemical compounds to prevent over-predation. At the population level, the net positive or negative effect of a species possessing this dual character would cause density-dependent transition from mutualism at low density to antagonism at high density.

The density-dependent transition from mutualism to antagonism has been reported in a few earlier studies. For example, interactions can be both positive and negative depending on the population density for ants and aphids (Addicott 1979; Cushman & Addicott 1991), seaweed and animals (Wahl & Hay 1995), seaweed flies (*Coelopa frigida* and *C. pilipes*) (Phillips *et al*. 1995; Hodge & Arthur 1997), and Mullerian mimics (Gilbert 1983). The ant–aphid system is a classic example of mutualism between species, where aphids provide honey to ants, and ants provide protection to aphids. At low densities of aphids, ants tending to aphids promote aphid population growth, but the beneficial relationship of ants to aphids would disappear or even be detrimental when population densities of aphids are high (Addicott 1979).

Traditionally, flowers and bees are thought to be mutualists to each other in a flower–pollinator system. Flowers provide nectar to bees, and bees help flowers by pollination, but they are also exploiters (antagonists) to each other. Flowers exploit bees for pollination, and bees exploit flowers for food. Dedej and Delaplane (2003) found the pollination efficiency of honey bee (Hymenoptera: Apidae) on rabbiteye blueberry (*Vaccinium asshei* var) is pollinator density-dependent, with the highest proportion of fruit occurring when bee density was moderate. The pollination efficiency in fig–wasp system increased initially but decreased with an increase in the number of founder wasps in fig flower (Wang *et al*. 2011). Similarly, Elliott and Irwin (2009) found seed production per flower of *Delphinium barbeyi* (Ranunculaceae) showed a dome-shaped association with flowering plant density. These studies demonstrated a transition of mutualist to exploiter for bees or flowering plant with increases in their population density.

In a plant–herbivore system, plants may impose conflicting impacts on small herbivores with respect to both food and shelter. For example, with an increase of vegetation cover of plants, the reproductive rate of Brandt's voles (*Microtus brandti*) in the Inner Mongolia grassland increased initially (due to food effects) but decreased (due to shelter effects) because they favor open habitats for preventing predation (Zhang *et al*. 2003). Similarly, small herbivores may impose positive effects on plants by providing nutrients or prohibiting their competitors and negative effects by consuming them. A

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

stem parasitic plant (*Cuscuta australis*) could transfer herbivory-induced signals among plants, and therefore help their host plants to counter predation by herbivores (Hettenhausen *et al*. 2017).

In a seed–animal system, animals (such as rodents, birds) impose both positive and negative effects on plants as seed dispersers and predators. Natural regeneration of many plant species heavily depends on seed dispersal and caching by animals. However, over-abundant predators would prohibit natural regeneration of plants due to heavy predation pressure on plant seeds (Li & Zhang 2003, 2007). Yi *et al*. (2019) found the proportion of seed caching (good for seeding regeneration) showed a dome-shaped association with population density of rodents. Zeng *et al*. (2020) found the seed dispersal effectiveness of an oak tree species (*Quercus serrata*) showed a dome-shaped response with per capita seed availability of rodents in a subtropical forest (in this issue). By referring to the definition of mutualism and antagonism in the NM models (Zhang 2003; Zhang *et al*. 2015), Zeng *et al*. (2020) proposed a graphical model showing the transition of mutualistic or predatory interaction between seed and rodents based on the positive or negative association between the proportion of seedling recruitment and per capita rodent abundance. These definitions on mutualistic or predatory relationships are different from the conventional definitions which are evaluated by the absolute positive or negative effect of rodent on plants by comparing the difference of seedling recruitment in the presence and absence of rodents (Jansen & Forget 2001; Theimer 2005; Zwolak & Crone 2012; Lichti *et al*. 2014; Bogdziewicz *et al*. 2020). According to the conventional definitions, if the seedling recruitment rate of seeds in the presence of rodents was higher than that in the absence of rodents (Fig. 3a), the seed–rodent relationship was defined as mutualistic; otherwise, it was defined as predatory (Fig. 3c). If the relation between seedling recruitment rates and rodent abundance is a dome-shaped, the relationship is mutualistic (++) when population density of rodents was smaller than the threshold (x_0), but it is predatory when the population density is larger than the threshold (Fig. 3b). However, according to the definitions of relative mutualism or antagonism in the NM models (Zhang 2003; Zhang *et al*. 2015), the mutualism (++) was transformed to predation (+−) when population density reached the threshold (x_0) (Fig. 3d).

Species not only has dual effects on the other species directly, but also shows indirect effect via a third species. Parasite may have a direct negative effect on its host, but it may prevent invasion of the competitor of its host which is vulnerable to the endemic parasites. Symbiotic microbes could help invasion of a species into a new region (Lu *et al*. 2016). For example, bacterial microbiota (*Leptographium procerum*) can help an invasive bark beetle (*Dendroctonus valens*) by decomposing defensive chemical compounds produced by the pine tree (Cheng *et al*. 2018). Yang *et al*. (2019) found rodents are able to mediate apparent mutualism, competition or predation between sympatric tree species through interspecific synchrony of seed rain. If the direct and indirect dual effects are nonlinear, nonmonotonic associations could arise between species (Zhang *et al*. 2015). Many plant species could release volatiles attracting natural enemies of herbivores (Hare 2011). For example, spider mites (*Tetranychus urticae*) feed on bean plants (*Phaseolus vulgaris*),

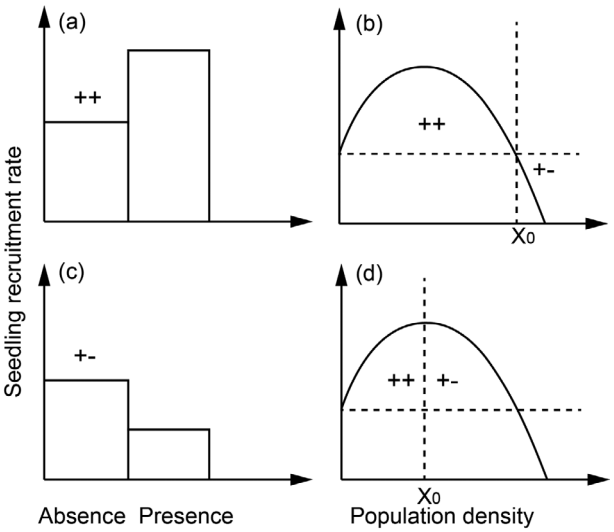

Figure 3 Illustrations of different definitions of mutualism or predation in seed–rodent system. (a,c) Conventional definition of absolute mutualism (++) and predation (+−) evaluated by the differences of seedling recruitment rate between the absence and presence of rodents; (b) the transition from mutualism (++) to predation (+−) with increase of population density of rodents based on the conventional definition; and (d) the transition from relative mutualism (++) to predation (+−) with increase of population density of rodents based on positive or negative association between seedling recruitment rate and population density of rodents as defined in nonmonotonic models. Vertical dashed lines indicate the transition threshold of population density (x_0). Horizontal dashed line indicates the seedling recruitment rate lower than that in the absence of rodents. This illustration is also applicable to other systems showing transition from mutualism to antagonism. (a,c) for details, see Jansen and Forget (2001), Theimer (2005), Zwolak and Crone (2012), Lichti *et al*. (2014), Bogdziewicz *et al*. (2020). (b,d) for details, see Zhang (2003).

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

but bean plants can also attract natural enemies of spider mites by emitting volatiles induced by the mycorrhizal fungus *Glomus mosseae* (Schausberger *et al*. 2012), indicating bean plants act as both a mutualist (providing food) and an antagonist (attracting predator) to spider mites. These studies imply that one species may show a dual effect on the other species through a third species. Therefore, indirect interactions should be considered in examining the dual character of species.

COEVOLUTION AND CO-BALANCE UNDER CONFLICTING SELECTION PRESSURE

The observed mutualism or antagonism is likely the results of coevolution under natural selection. Coevolution of matching traits between antagonists (such as prey and predators) has been well recognized. There are many examples of arms races between predator and prey. For example, seeds of some plant species germinate quickly to avoid over-predation by rodents, while rodents developed the strategy of removing the embryo or radicle of seeds (Cao *et al*. 2011). The matching morphology of flower and pollinator's proboscis are good examples of coevolution of mutualism between plants and insects or honeyeater birds. The matching trait would guarantee reciprocal cooperation between species, which is a significant criterion for identifying the co-evolutionary mutualism. There is also evidence of co-evolutionary mutualisms in seed–animal systems (Steele *et al*. 2018; Wang 2020). Seed with weak odor are more likely scatter-hoarded by rodents to avoid pilferage by other competitors, which is beneficial for natural regeneration of plants (Yi *et al*. 2016b; Cao *et al*. 2018). The rodents showing scatter-hoarding behavior often possess strong spatial memory in order to retrieve the cached seeds, and specifically, rodents can invest more on memorizing the location of seeds with weak odors (Yi *et al*. 2016b; Li *et al*. 2018).

In contrast to the absolute mutualism or antagonism systems, coevolution of relative mutualism between antagonists faces conflicting pressure of selection. The matching traits for both mutualism and antagonism must be well balanced in a certain ratio; otherwise, they are not able to produce the maximum fitness for both species, resulting in collapse of mutualism. Take the seed–rodent system as an example (Fig. 4). Seeds have developed resistant traits (e.g. thick and hard seed coat, sharp spines, smooth skin, early germination, weak odor) or chemical traits (toxicants) to defend over-predation by rodents,

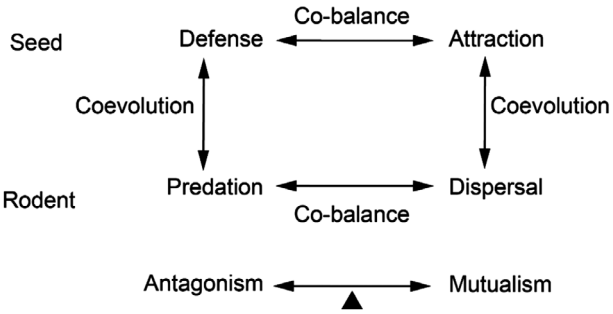

Figure 4 Illustrations of coevolution and co-balance of function traits between plants and rodents under conflicting selection pressure for both mutualism and antagonism. Coevolution may occur for both antagonism and mutualism between species, but the strength between antagonism and mutualism needs to be co-balanced for maximizing the individual fitness. The 2 coevolutionary and 2 co-balancing forces are important in maintaining mutualism–antagonism relation between two interacting species. This illustration is also applicable to other systems showing transition from mutualism to antagonism. For details, see Zhang *et al*. (2007).

while at the same time, they contain nutritional matter such as protein, starch, sugar, and fat to attract dispersal by rodents (Zhang & Zhang 2008; Zhang *et al*. 2016a,b; Xiao & Huang 2020). Over-defense would result in failure of seed dispersal because rodents would show no interest of hoarding them, while over-attraction would result in failure of seed survival because rodents would consume all of them (Zhang *et al*. 2016a,b, 2017). Thus, balance between defensive and attractive traits is essential in realizing the maximum fitness of seeds (Zhang *et al*. 2016a). Rodents have developed strong jaws and skills to open the thick and hard seed coat, or capacity of decomposing toxicants, or behavior of removing embryo or cutting the radicles to stop early seed germination (Zhang & Zhang 2008; Xiao *et al*. 2009; Yi *et al*. 2012, 2014, 2019). At the same time, rodents have evolved caching behavior with strong spatial memory for scatter hoarding and retrieving seeds (Yi *et al*. 2016b). Similarly, over-consumption by rodents on seeds would destroy their future food resources by causing failure of tree regeneration, while over-caching would increase risk of food pilferage by their competitors or causing inadequate food intake for themselves (Zhang *et al*. 2016b). It is obvious that selection of mutualistic and antagonistic traits is conflicting for both seeds and rodents (Zhang *et al*. 2016a; Steele *et al*. 2018). Therefore, in the mutualism–antagonism system like in the seed-rodent system, there are 2 co-evolutionary forces between predation and anti-predation for antagonism, and between attraction and dispersal for mutualism;

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

2 co-balancing forces between defense and attraction, and between predation and dispersal. Co-balancing is essential to maintain the equilibrium between mutualism and antagonism between species. The co-balance was often realized through evolution or ecological adaptation of defensive and attractive traits at the individual level, or through density-dependent transition between mutualism and antagonism at the population level.

At the individual level within mutualism and antagonism systems, it is predicted that the relevant traits of seeds or rodents should be selected toward a moderate state. A recent study indicates that medium-sized seeds have highest dispersal fitness under predation of rodents because small-sized seeds are more likely eaten in the early seed dispersal stage, while large-sized seeds are more pilfered by rodents in the later seed dispersal stage (Zhang *et al*. 2008; Cao *et al*. 2016). Over-defense of seeds may reduce scatter hoarding intensity of seeds by rodents, and thus, suffer a low seedling recruitment rate in field (Zhang *et al*. 2016a,b). For example, wild apricot (*Armeniaca sibirica*) and wild peach (*Amygdalus davidiana*) are 2 sympatric trees in temperate forests. The ratio of seed coat thickness/caloric value per seed for wild peach was 4 times high as that for wild apricot (Zhang & Zhang 2008). As compared to wild apricot, wild peach has a low seedling recruitment rate because its seeds have very thick and hard woody coats relative to the caloric value per seed, which prevent rodents from dispersing the seeds (Zhang *et al*. 2016b). However, over-attraction may also result in high level of predation. For example, as compared to the nuts of wild walnut (*Juglans mandshurica*), those of cultivated walnuts (*J. regia*) contain high nutritional kernels but possess thin seed coats under artificial selection; the ratio of seed coat thickness/caloric value per seed for cultivated walnuts was 9 times lower than that for wild walnuts, resulting in much higher loss of nuts of cultivated walnuts than those of wild walnuts under the predation of rodents in the field (Zhang & Zhang 2008; Zhang *et al*. 2017).

Antagonism may enhance mutualism between antagonists. For example, rodents prefer to eat seeds with a soft seed coat or low-tannin content, while they prefer to hoard seeds with high-tannin content (Hadj-Chikh *et al*. 1996; Xiao *et al*. 2008; Wang & Chen 2008; Sundaram *et al*. 2018) or a thick seed coat (Jacobs 1992; Xiao *et al*. 2006; Zhang & Zhang 2008). Early germination of nondormant seeds could help to minimize predation of rodents (Hadj-Chikh *et al*. 1996; Steele *et al*. 2001; Smallwood *et al*. 2001; Sundaram *et al*. 2020), but rodents are able to cut the radicles of germinated seeds (Cao *et al*. 2011). Interestingly, a study showed that the pruned seeds by rodents could have higher seedling recruitment rate (Cao *et al*. 2011), indicating the arms race of antagonism between seeds and rodents can enhance the mutualism between them.

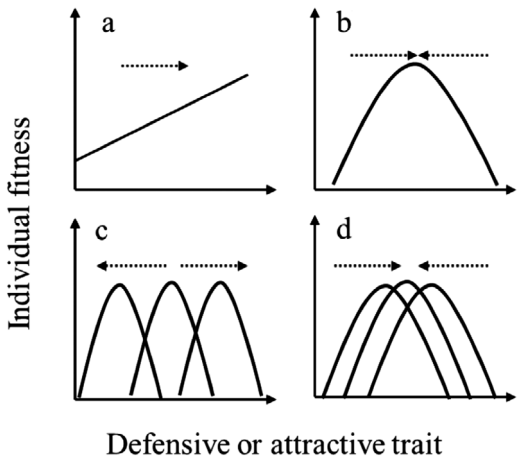

Figure 5 Illustrations of evolution of defensive or attractive traits of species under circumstances of monotonic (a,c) and nonmonotonic (b,d) interactions between species. For either mutualistic or antagonistic systems with monotonic interaction, the functional defensive or attractive traits would evolve toward the maximum values within a population (a), which would result in niche differentiation among sympatric species (c). For a mutualism–antagonism system with nonmonotonic interaction, the functional defensive or attractive traits would evolve toward the moderate values within a population under conflicting selecting pressure (b), which would result in niche convergence among sympatric species which promotes species coexistence of function groups (d).

Functional traits are important in determining species interactions. There are large variations of functional traits of species, which provide the opportunity of detecting the micro-evolution process of mutualism and antagonism. Under the circumstance of monotonic interactions, defensive or attractive traits should be maximized for realizing highest fitness of individuals (Fig. 5a). Meanwhile, under the conflicting selection pressures of both mutualism and antagonism shown in Fig. 4, the moderate defensive or attractive traits should be favored by natural selection (Fig. 5b). Coevolution of mutualism or antagonism would cause niche differentiation among species, which would benefit species coexistences (Fig. 5c). However, apparent mutualism (see above) would promote convergent evolution of defensive or attractive traits of sympatric antagonists (Fig. 5d), which may partially explain why closely related species tend to occur together in an environment (Yan *et al*. 2016).

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

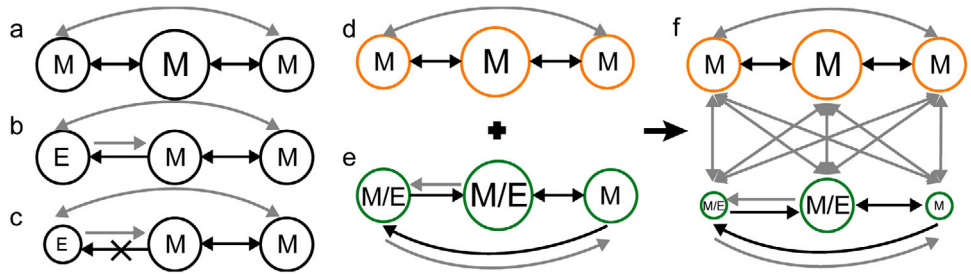

Figure 6 Illustrations of impacts of reciprocal cooperation and punishment on abundance of species which show cooperation (i.e. mutualist, M) and no cooperation (i.e. exploiters, E). Left panel: (a) Reciprocal cooperation increases abundances of both mutualists; (b) exploiters or cheaters without rewards also have a high abundance; (c) punishment to exploiter can reduce the abundance of the exploiter. Right panel: two independent communities (d,e) are connected to form a meta-community by dispersal of individuals; (f) the merged community. The circles with two letters (M/E) indicate that one species can be an exploiter to a second species and a cooperator to a third species. The size of the circle indicates abundance of mutualists or exploiters. The black lines with double arrows indicate the reciprocal cooperation (cooperation with reward) between species; the black lines with single arrow indicate the cooperation without reward; the grey lines with double arrows indicate competition; the grey lines with single arrow indicate exploitation. X indicates punishment on the exploiter. For details, see Yan and Zhang (2019).

REWARD, PUNISHMENT AND META-COMMUNITY FOR STABILIZING THE MUTUALISM

The origin of cooperation or altruism has long been a puzzle to biologists (Axelrod & Hamilton 1981). If an individual cooperates with its conspecific individuals (often competitors), its fitness will be lower than that of its partners and thus will not be selected by nature, but why does cooperation prevail in the world? Several theories such as kin-selection, group selection, social punishment, and reciprocal cooperation have been proposed to explain the emergence of cooperation or altruism among selfish competitors (Nowak 2006; Nowak *et al*. 2010). The kin-selection and group selection hypotheses emphasize the common interests of the closely-related individuals. The social punishment hypothesis emphasizes the common interests of less genetically related individuals. The reciprocal cooperation hypothesis emphasizes the direct free-trade mechanism of cooperation among non-genetically related individuals (direct reciprocal cooperation). Punishment to cheaters is important to stabilize mutualism between 2 species. Yan and Zhang (2019) demonstrated that, in a 3-species system, reciprocal cooperation would increase abundance of both mutualists (Fig. 6a); however, exploiters or cheaters without punishment also prevails (Fig. 6b). There are 2 ways of suppressing exploiters. First, punishment to exploiter would likely reduce abundance of the exploiter (Fig. 6c). Second, competition at the meta-community level through dispersal of individuals would help to promote cooperation but depress cheating (Yan & Zhang 2019). For instance, if a community like that shown in Fig. 6d (with more reciprocal cooperation but less exploitation) is connected with a community like that shown in Fig. 6e (with less reciprocal cooperation but more exploitation) though dispersal of individuals, the community shown in Fig. 6d could dominate in the merged meta-community like that in Fig. 6f (for details, see Yan *et al*. 2019). Yan and Zhang (2019) found a community with indirect cooperation via a third parter could outweigh a community with pure competition, suggesting competition between meta-communities may help explain prevalence of altrusim or cooperation without direct reward. For example, plants provide foods to herbivores. Herbivores produce dung which serve as food to beetles. Beetles bury dung balls into soil which is beneficial to plants. This is defined as a circulating mutualism between every two species via a mutualist loop (Fig. S1a). Two direct mutualisms could result in apparent mutualism, another kind of indirect mutualism (e.g. Fig. 6a, Fig. S1b). For example, plants are beneficial to many animal species by providing food. Different animal species provide various services to plants through pollination, seed dispersal, and nutrients; thus, apparent mutualism appears among different animal species. Through competition of meta-communities, communities with more direct or indirect mutualisms would outweigh those with fewer ones. Therefore, cooperation with either direct or indirect rewards should be favored by natural selection. Thus, we predicted that in a close community, reciprocal cooperation and punishment to cheaters would be more popular, while indirect mutualism (without punishment

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

to "cheater") would be more popular in meta-community system (e.g. island or fragmented habitats).

During the process of cooperation, cheating may occur when the partner receiving the benefits does not reward its cooperator. Thus, mutualism could collapse, being converted into antagonism (Boyd 1989; Yan & Zhang 2018). Because cheating would reduce fitness of its cooperator, the cooperator must be able to identify the cheater or cooperator. As predicted by game theory, a cheater or cooperator will lose, while *Tit for Tat* strategy will prevail (Boyd 1989). *Tit for Tat* of an individual employs both punishment and reward strategies to its interacting partners, depending on its amount of net income. For example, mycorrhiza transports water to tree roots which could provide nutrition to them (Muhsin & Zwiazek 2002; Lehto & Zwiazek 2011). Flowers could increase nectar sugar concentration to facilitate pollination based on the sound frequency of the pollinators (Veits *et al*. 2019). The nectar chemical components of plants can be altered for attracting pollinators (mutualists) and repelling nectar robbers (exploiters) (González-Teuber & Heil 2009). Rodents tended to eat germinated seeds, but scatter-hoarded dormant seeds (Xiao *et al*. 2008). Plants suffering attack from herbivores can emit herbivory-induced volatiles in order to attract natural enemies of these herbivores (de Boer *et al*. 2008).

As predicted by the zero-sum game theory, the income of one partner will result in the loss of the other, with the net income or loss being zero. Similarly, in the monotonic interaction models, for antagonists, the resource supporting them is limited; the higher abundance of one species means the lower abundance of its counterpart species. The mutualism between antagonists is a kind of positive-sum game, which will produce extra resources as compared to the condition without cooperation. As predicted by the dome-shaped curve, to realize the large benefit for antagonists, it is important to reach a large population density where transition from mutualism to antagonism occurs so as to delay the appearance of antagonism.

CONCLUSION AND OUTLOOK

Through this brief review and synthesis, we wanted to highlight the significance of ecological nonmonotonicity (e.g. transition from mutualism to antagonism) in the understanding of evolution and stability and complexity of the biological world. The ecological processes have long been studied within the frame work of the monotonic domain. In fact, the signs of species interaction are not fixed, but changeable in time and space. Species often face the dilemma of having to select between 2 conflicting pressures which could result in nonmonotonic interactions between species and the dual characters of species as both mutualists and antagonists. The relative mutualism or antagonism defined in the NM models is different from those in the LV models and the conventional concepts based on absolute positive or negative effects. Therefore, we need a nonmonotonic way of thinking in studying ecology.

Because the nonmonotonic interactions play a significant role in maintaining diversity and stability of an ecosystem, there should be more density-dependent transition of interactive strength or function traits of the species which need to be discovered. Revealing the nonmonotonic interactions between species not only requires extensive surveys in both time and space covering a large gradient of population densities, but also novel technologies of quantifying the interactive strength. Under natural conditions, high-density years or habitats are rare; thus, it is difficult to detect the density-dependent nonmonotonic interactions. Therefore, manipulative experiments are necessary to simulate the density-dependent effects. Besides, islands or fragmented habitats with large variation of population abundance may provide a good chance of detecting nonmonotonic interactions (e.g. Zeng *et al*. 2019, 2020).

Individual-level studies are needed for understanding the evolutionary and ecological processes of mutualism and antagonism. Technologies that identify the fitness of individuals need to be developed, such as using stable isotopes to track seedlings of each individual tree (Carlo *et al*. 2009), and or to study the seed-rodent interactions using seed tagging and camera tracking method (Gu *et al*. 2017). Under selection of conflicting pressure for both mutualism and antagonism, it is worthwhile to examine fitness of defensive and attractive traits of interacting species, so as to better understand how mutualism and antagonism is balanced for maximizing the individual fitness of interacting species. We predict that the evolutionary directions of the defensive and attractive traits within the species should be opposite to those among species. Reward, punishment and meta-community are essential in stabilizing mutualism between antagonists. Therefore, individuals should possess the capacity to identify the cooperator and exploiter to maximize their fitness.

In summary, a better understanding of ecological nonmonotonicity would likely expand and enrich the traditional theory of ecology which is mainly established on the basis of monotonic interactions. We call for more efforts to investigate the roles of ecological nonmonotonicity in the origin of mutualisms among antagonists, and its role in the maintenance of biodiversity and stability of ecosystems.

© 2020 International Society of Zoological Sciences, Institute of Zoology/
Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

AUTHOR CONTRIBUTIONS

Z.Z., C.Y., and H.Z. contributed to the writing and revising.

ACKNOWLEDGMENTS

This study was supported by the National Key R&D Program of China (2017YFC0503802), and the Information Fund of the Chinese Academy of Sciences (XXH13506–201). C.Y. was supported by the Young Elite Scientist Sponsorship Program by the China Association of Science and Technology (2017QNRC001). H.Z. was supported by the National Natural Science Foundation of China (3177247).

REFERENCES

Addicott JF (1979). A multispecies aphid-ant association: Density dependence and species-specific effects. *Canadian Journal of Zoology* **57**, 558–69.

Allesina S, Tang S (2012). Stability criteria for complex ecosystems. *Nature* **483**, 205–8.

Axelrod R, Hamilton W (1981). The evolution of cooperation. *Science* **211**, 1390–6.

Bascompte J, Jordano P (2007). Plant–animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **38**, 567–93.

Berlow EL (1999). Strong effects of weak interactions in ecological communities. *Nature* **398**, 330–4.

Bogdziewicz M, Crone EE, Zwolak R (2020). Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. *Journal of Ecology* **108**, 1009–18.

Boyd R (1989). Mistakes allow evolutionary stability in the repeated prisoner's dilemma game. *Journal of Theoretical Biology* **136**, 47–56.

Cao L, Wang B, Yan C *et al*. (2018). Risk of cache pilferage determines hoarding behavior of rodents and seed fate. *Behavioral Ecology* **29**, 984–91.

Cao L, Wang Z, Yan C, Chen J, Guo C, Zhang Z (2016). Differential foraging preferences on seed size by rodents result in higher dispersal success of medium-sized seeds. *Ecology* **97**, 3070–8.

Cao L, Xiao Z, Wang Z, Guo C, Chen J, Zhang Z (2011). High regeneration capacity helps tropical seeds to counter rodent predation. *Oecologia* **166**, 997–1007.

Carlo T, Tewksbury J, Río C (2009). A new method to track seed dispersal and recruitment using ^{15}N isotope enrichment. *Ecology* **90**, 3516–25.

Cheng C, Wickham J, Chen L, Xu D, Lu M, Sun J (2018). Bacterial microbiota protect an invasive bark beetle from a pine defensive compound. *Microbiome* **6**, 132–47.

Cushman JH, Addicott JF (1991). Conditional interactions in ant-plant-herbivore mutualisms. In: Huxley CR, Cutler DF, eds. *Ant–Plant Interactions*. Oxford University Press, Oxford, UK, pp. 92–103.

de Boer JG, Hordijk CA, Posthumus MA, Dicke M (2008). Prey and non-prey arthropods sharing a host plant: effects on induced volatile emission and predator attraction. *Journal of Chemical Ecology* **34**, 281–90.

Dedej S, Delaplane KS (2003). Honey bee (Hymenoptera: Apidae) pollination of rabbiteye blueberry *Vaccinium ashei* var. 'Climax' is pollinator density-dependent. *Journal of Economic Entomology* **96**, 1215–20.

Elliott S, Irwin R (2009). Effect of flowering plant density on pollinator visitation, pollen receipt and seed production in *Delphinium barbeyi* (Ranunculaceae). *American Journal of Botany* **96**, 912–9.

Elton CS (1977). *The Ecology of Invasions by Animals and Plants*. University of Chicago Press, Chicago, IL.

Gilbert LE (1983). Coevolution and Mimicry. In: Futuyma DJ, Slatkin M, eds. *Coevolution*. Sinauer Associates, Sunderland, MA, pp. 263–81.

González-Teuber M, Heil M (2009). Nectar chemistry is tailored for both attraction of mutualists and protection from exploiters. *Plant Signaling & Behavior* **4**, 809–13.

Gu H, Zhao Q, Zhang Z (2017). Does scatter-hoarding of seeds benefit cache owners or pilferers? *Integrative Zoology* **12**, 477–88.

Hadj-Chikh LZ, Steele MA, Smallwood PD (1996). Caching decisions by grey squirrels: A test of the handing time and perishability hypotheses. *Animal Behaviour* **52**, 941–8.

Hare JD (2011). Ecological role of volatiles produced by plants in response to damage by herbivorous insects. *Annual Review of Entomology* **56**, 161–80.

Hernandez MJ (1998). Dynamics of transitions between population interactions: A nonlinear interaction alpha-function defined. *Proceedings of the Royal Society B: Biological Sciences* **265**, 1433–40.

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

Hettenhausen C, Li J, Zhuang H *et al*. (2017). Stem parasitic plant *Cuscuta australis* (dodder) transfers herbivory-induced signals among plants. *PNAS* **114**, E6703–9.

Hodge S, Arthur W (1997). Asymmetric interactions between species of seaweed fly. *Journal of Animal Ecology* **66**, 743–54.

Holland JN, Deangelis DL (2009). Consumer-resource theory predicts dynamic transitions between outcomes of interspecific interactions. *Ecology Letters* **12**, 1357–66.

Holling CS (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* **45**, 3–60.

Jacobs LF (1992). The effect of handling time on the decision to cache by grey squirrels. *Animal Behaviour* **43**, 522–4.

Jansen PA, Forget P-M (2001). Scatterhoarding rodents and tree regeneration. In: Bongers F, Charles-Dominique P, Forget P-M, Théry M, eds. *Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest*. Springer, Dordrecht, Netherlands, pp. 275–88.

Krebs CJ (2015). One hundred years of population ecology: Successes, failures and the road ahead. *Integrative Zoology* **10**, 233–40.

Lehto T, Zwiazek JJ (2011). Ectomycorrhizas and water relations of trees: A review. *Mycorrhiza* **21**, 71–90.

Li H, Zhang Z (2003). Effect of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz.). *Forest Ecology and Management* **176**, 387–96.

Li H, Zhang Z (2007). Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). *Forest Ecology and Management* **242**, 511–7.

Li Y, Zhang D, Zhang H, Wang Z, Yi X (2018). Scatterhoarding animal places more memory on caches with weak odor. *Behavioral Ecology and Sociobiology* **72**, 53.

Lichti NI, Steele MA, Zhang H, Swihart RK (2014). Mast species composition alters seed fate in North American rodent-dispersed hardwoods. *Ecology* **95**, 1746–58.

Lu M, Hulcr J, Sun J (2016). The role of symbiotic microbes in insect invasions. *Annual Review of Ecology, Evolution and Systematics* **47**, 487–505.

MacArthur R (1955). Fluctuations of animal populations and a measure of community stability. *Ecology* **36**, 533–6.

May RM (1972). Will a large complex system be stable? *Nature* **238**, 413–4.

May RM (1973). *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, NJ.

McCann KS (2000). The diversity-stability debate. *Nature* **405**, 228–33.

Michael MA, Yi X, Zhang H (2018). Plant-animal interactions: Patterns and mechanisms in terrestrial ecosystems. *Integrative Zoology* **13**, 225–7.

Mougi A, Kondoh M (2012). Diversity of interaction types and ecological community stability. *Science* **337**, 349–51.

Muhsin TM, Zwiazek JJ (2002). Ectomycorrhizas increase apoplastic water transport and root hydraulic conductivity in *Ulmus americana* seedlings. *New Phytologist* **153**, 153–8.

Neutel AM, Heesterbeek JA, de Ruiter PC (2002). Stability in real food webs: Weak links in long loops. *Science* **296**, 1120–3.

Nowak MA (2006). Five rules for the evolution of cooperation. *Science* **314**, 1560–3.

Nowak MA, Tarnita CE, Wilson EO (2010). The evolution of eusociality. *Nature* **466**, 1057.

Phillips DS, Legget M, Wilcockson R, Day TH, Arthur W (1995). Coexistence of competing species of seaweed flies: The role of temperature. *Ecological Entomology* **20**, 65–74.

Rohr RP, Saavedra S, Bascompte J (2014). On the structural stability of mutualistic systems. *Science* **345**, 1253497.

Schausberger P, Peneder S, Jurschik S, Hoffmann D (2012). Mycorrhiza changes plant volatiles to attract spider mite enemies. *Functional Ecology* **26**, 441–9.

Smallwood PD, Steele MA, Faeth SH (2001). The ultimate basis of the caching preferences of rodents, and the oak-dispersal syndrome: Tannins, insects, and seed germination. *American Zoologist* **41**, 840–51.

Steele MA, Smallwood PD, Spunar A, Nelsen E (2001). The proximate basis of the oak dispersal syndrome: Detection of seed dormancy by rodents. *American Zoologist* **41**, 852–64.

Steele MA, Yi X, Zhang H (2018). Plant-animal interactions: Patterns and mechanisms in terrestrial ecosystems. *Integrative Zoology* **13**, 225–7.

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

Sundaram M, Higdon AE, Wood KV, Bonham CC, Swihart RK (2020). Mechanisms underlying detection of seed dormancy by a scatter-hoarding rodent. *Integrative Zoology* **15**, 89–102.

Sundaram M, Lichti NI, Olynk Widmar NJ, Swihart RK (2018). Eastern gray squirrels are consistent shoppers of seed traits: Insights from discrete choice experiments. *Integrative Zoology* **13**, 280–96.

Tanner JT (1975). The stability and the intrinsic growth rates of prey and predator populations. *Ecology* **56**, 855–67.

Theimer TC (2005). Rodents scatterhoarders as conditional mutualists. In: Forget PM, Lambert JE, Hulme PE, Vander Wall SB, eds. Seed Fate: Seed Predation, Seed Dispersal and Seedling Establishment. CABI, Wallingford, UK, pp. 283–95.

Vandermeer JH (1973). Generalized models of two species interactions: A graphical analysis. *Ecology* **54**, 809–18.

Veits M, Khait I, Obolski U *et al*. (2019). Flowers respond to pollinator sound within minutes by increasing nectar sugar concentration. *Ecology Letters* **22**, 1483–92.

Wahl M, Hay ME (1995). Associational resistance and shared doom: Effects of epibiosis on herbivory. *Oecologia* **102**, 329–40.

Wang B (2020). Seed density affects post-dispersal seed predation: Evidence from a seed removal experiment of 62 species. *Integrative Zoology* **15**, 135–43.

Wang B, Chen J (2008) Tannin concentration enhances seed caching by scatter-hoarding rodents: An experiment using artificial 'seeds'. *Acta Oecologica* **34**, 379–85.

Wang R, Sun B, Zheng Q, Shi L, Zhu L (2011). Asymmetric interaction and indeterminate fitness correlation between cooperative partners in the fig-fig wasp mutualism. *Journal of the Royal Society Interface* **8**, 1487–96.

Wang Y, Deangelis DL (2011). Transitions of interaction outcomes in a unidirectional consumer-resource system. *Journal of Theoretical Biology* **280**, 43–9.

Wang Y, Deangelis DL (2012). A mutualism-parasitism system modeling host and parasite with mutualism at low density. *Mathematical Biosciences and Engineering* **9**, 431–44.

Wang Y, Wu H, Wang S (2013). A predator–prey model characterizing negative effect of prey on its predator. *Applied Mathematics and Computation* **219**, 9992–9.

Xiao Z, Chang G, Zhang Z (2008). Testing the high tannin hypothesis with scatter-hoarding rodents: Experimental and field evidence. *Animal Behaviour* **75**, 1235–41.

Xiao Z, Gao X, Jiang M, Zhang Z (2009). Behavioral adaptation of Pallas's squirrels to germination schedule and tannins in acorns. *Behavioral Ecology* **20**,1050–5.

Xiao Z, Huang X (2020). How seed defense and seed abundance predict dispersal and survival patterns in *Camellia*. *Integrative Zoology* **15**, 103–14.

Xiao Z, Wang Y, Zhang Z (2006). Spatial and temporal variation of seed predation and removal of sympatric large-seeded species in relation to innate seed traits in a subtropical forest, Southwest China. *Forest Ecology and Management* **222**, 46–54.

Xiao Z, Zhang Z (2016). Contrasting patterns of short-term indirect seed–seed interactions mediated by scatter-hoarding rodents. *Journal of Animal Ecology* **85**, 1370–7.

Yan C, Xie Y, Li X, Holyoak M, Zhang Z (2016). Species co-occurrence and phylogenetic structure of terrestrial vertebrates at regional scales. *Global Ecology and Biogeography* **25**, 455–63.

Yan C, Zhang Z (2014). Specific non-monotonous interactions increase stability of ecological networks. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20132797.

Yan C, Zhang Z (2018). Dome-shaped transition between positive and negative interactions maintains higher persistence and biomass in more complex ecological networks. *Ecological Modelling* **370**, 14–21.

Yan C, Zhang Z (2019). Meta-community selection favours reciprocal cooperation but depresses exploitation between competitors. *Ecological Complexity* **37**, 55–62.

Yang X, Yan C, Gu H, Zhang Z (2019). Interspecific synchrony of seed rain shapes rodent-mediated indirect seed-seed interactions of sympatric tree species in a subtropical forest. *Ecology Letters* **23**, 45–54.

Yi X, Bartlow AW, Curtis R, Agosta SJ, Steele MA (2019). Responses of seedling growth and survival to post-germination cotyledon removal: An investigation among seven oak species. *Journal of Ecology* **107**, 1817–27.

Yi X, Steele MA, Stratford JA, Wang Z, Yang Y (2016b). The use of spatial memory for cache management by scatter-hoarding rodent. *Behavioral Ecology and Sociobiology* **70**, 1527–34.

Yi X, Steele MA, Zhang Z (2012). Acorn pericarp removal as a cache management strategy of the

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.

Siberian Chipmunk, *Tamias sibiricus*. *Ethology* **118**, 87–94.

Yi X, Wang Y, Zhang H, Zhang Z (2016a). Weak olfaction increases seed scatter-hoarding by Siberian chipmunks: Implication in shaping plant-animal interactions. *Oikos* **125**, 1712–8.

Yi X, Zhang M, Bartlow AW, Dong Z (2014). Incorporating cache management behavior into seed dispersal: The effect of pericarp removal on acorn germination. *PLoS ONE* **9**, e92544.

Yodzis P (1981). The stability of real ecosystems. *Nature* **289**, 674–6.

Zeng D, Jin T, Zhao Y, Yan C, Zhang Z, Ding P (2020). Density-dependent switch of mutualism and predation between an oak species (*Quercus serrata*) and rodents in a subtropical island forest. *Integrative Zoology* (in press).

Zeng D, Swihart RK, Zhao Y, Si X, Ding P (2019). Cascading effects of forested area and isolation on seed dispersal effectiveness of rodents on subtropical islands. *Journal of Ecology* **107**, 1506–17.

Zhang H, Chen Y, Zhang Z (2008). Differences of dispersal fitness of large and small acorns of Liaodong oak (*Quercus liaotungensis*) before and after seed caching by small rodents in a warm temperate forest, China. *Forest Ecology and Management* **255**, 1243–50.

Zhang H, Chu W, Zhang Z, Wang W (2017). Cultivated walnut trees showed earlier but not final advantage over its wild relatives in competing for seed dispersers. *Integrative Zoology* **12**, 12–25.

Zhang H, Yan C, Chang G, Zhang Z (2016b). Seed trait-mediated selection by rodents affects mutualistic interactions and seedling recruitment of co-occurring tree species. *Oecologia* **180**, 475–84.

Zhang H, Zhang Z (2008). Endocarp thickness affects seed removal speed by small rodents in a warm-temperate broad-leafed deciduous forest, China. *Acta Oecologica* **34**, 285–93.

Zhang Z (2003). Mutualism or cooperation among competitors promotes coexistence and competitive ability. *Ecological Modelling* **164**, 271–82.

Zhang Z, Li H, Xiao Z, Lu J, Cheng J (2007). Impacts of animals on seed fates of plants. In: Wu J, ed. *Lectures on Modern Ecology (III): Advances of Disciplines and Frontier Topics*. High Education Press, Beijing, China, pp. 63–91. (In Chinese with English abstract.)

Zhang Z, Pech R, Davis S, Shi D, Wan X, Zhong W (2003). Extrinsic and intrinsic factors determine the eruptive dynamics of Brandt's voles *Microtus brandti* in Inner Mongolia, China. *Oikos* **100**, 299–310.

Zhang Z, Wang Z, Chang G *et al*. (2016a). Trade-off between seed defensive traits and impacts on interaction patterns between seeds and rodents in forest ecosystems. *Plant Ecology* **217**, 253–65.

Zhang Z, Yan C, Krebs CJ, Stenseth NC (2015). Ecological non-monotonicity and its effects on complexity and stability of populations, communities and ecosystems. *Ecological Modelling* **312**, 374–84.

Zwolak R, Crone EE (2012). Quantifying the outcome of plant-granivore interactions. *Oikos* **121**, 20–7.

SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 List of glossaries of some important terms.

Figure S1 Illustration of two kinds of indirect mutualism showing indirect cooperation without direct rewards.

Cite this article as:

Zhang Z, Yan C, Zhang H (2020). Mutualism between antagonists: its ecological and evolutionary implications. *Integrative Zoology* **00,** 1–13.

© 2020 International Society of Zoological Sciences, Institute of Zoology/ Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd.