

Akihiko Mougi · Michio Kondoh

Adaptation in a hybrid world with multiple interaction types: a new mechanism for species coexistence

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Abstract In ecological communities, numerous species coexist and affect each others' population levels via various types of interspecific interactions. Previous ecological theory explaining multispecies coexistence tended to focus on a single interaction type, such as antagonism, competition, or mutualism, and its consequences on population dynamics. Hence, it remains unclear what, if any, contribution multiple coexisting interaction types have on the multispecies coexistence. Here, we show that the coexistence of multiple interaction types can be essential for multispecies coexistence. We present a simple model in which the exploiter and mutualist adaptively switch between two competing resource species. An adaptive mutualist, which favors the more abundant species, provides a mechanism of majority-advantage and, thus, potentially inhibits the coexistence of resource species. In the absence of an exploiter, an adaptive mutualist leads to competitive exclusion at the resource species level. However, the coexistence of an adaptive exploiter and a mutualist allows the coexistence of all species in the community, because the mutualist-mediated “winner” tends to be suppressed by the adaptive exploiter. The mutualist indirectly increases the abundance of the exploiter through mutualistic interactions, thereby indirectly supporting this coexistence

mechanism. In fact, coexistence may occur even if the exploiter or mutualist alone cannot mediate the coexistence of two resources. We conclude that the coexistence of mutualism and antagonism may be the key to the persistence of the four-species module in the presence of adaptive switching.

Keywords Community persistence · Antagonism · Mutualism · Competition · Adaptation

Introduction

Understanding what maintains the coexistence of multiple species in nature is a central issue in ecology (Elton 1958; May 1973; Pimm 1991). According to ecological theory, interactions between species, the network structure of these interactions, and their effects on population dynamics, are keys to understanding the mechanisms by which biodiversity is maintained (May 1973; Bascompte et al. 2003). Previous studies have primarily focused on a single interaction type, antagonism (predator–prey or host–parasite), competition, or mutualism, despite the fact that various interactions coexist in nature. The implication of coexistence of the multiple interaction types on the maintenance of ecological community is a relatively new issue, and related questions have been left unanswered (Fontaine et al. 2011; Allesina and Tang 2012; Mougi and Kondoh 2012).

One such unexplored issue is of how adaptation and the variety of interaction types interactively affect species coexistence. Adaptation alters species interactions, thereby affecting population dynamics and community maintenance (Fussmann et al. 2007). An adaptive switch of interaction partners has been shown to occur in both antagonistic (Murdoch 1969; Staniczenko et al. 2010) and mutualistic interactions (Basilio et al. 2006; Fortuna and Bascompte 2006; Olesen et al. 2008; Petanidou et al. 2008). Theory has shown that adaptive switching of the antagonist or mutualist can shape the network structures of communities and may promote species

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A. Mougi (✉)
Department of Biological Science, Faculty of Life and Environmental Science, Shimane University,
1060 Nishikawatsu-cho, Matsue 690-8504, Japan
E-mail: amougi@gmail.com
Tel.: +81-852-326430

M. Kondoh
Department of Environmental Solution Technology, Faculty of Science and Technology, Ryukoku University,
1-5 Yokoya, Seta Oe-cho, Otsu 520-2194, Japan

coexistence (Kondoh 2003; Staniczenko et al. 2010; Kaiser-Bunbury et al. 2010; Zhang et al. 2011). However, earlier studies tended to deal with communities that were comprised of a single type of interaction. Thus, it remains unexplored how adaptation works in a community with multiple interaction types, or how the mixing of different interaction types affects community dynamics in the presence of adaptation.

A widespread example of a community module in which exploiters and mutualists share interacting species is that of terrestrial plant and animal species. The animal species may be a mutualist, such as a pollinator and seed disperser, or an exploiter, such as an herbivore, seed feeder, and leaf miner. There is evidence that animal exploiters and mutualists adaptively switch between resource plants (Egas and Sabelis 2001; Whittall and Hodges 2007). The module, consisting of a resource, its mutualist, and an exploiter, is the simplest building block of community in terrestrial ecosystems. The exploration of community modules would enhance our understanding of how biodiversity is maintained in natural ecosystems.

Here, we present a mathematical model of a basic community module consisting of two competitive resource species, their adaptive consumer, and an adaptive mutualist. Using this model, we demonstrate how the major types of interspecific interactions (antagonism, competition, and mutualism) support each other to maintain the whole system in the presence of adaptation. More specifically, adaptive mutualists and adaptive exploiters tend to promote and prevent, respectively, the competitive exclusion of competing resource species. However, when the adaptive exploiter and adaptive mutualist coexist, the mutualist indirectly increases the abundance of the exploiter through an indirect effect mediated by the resource species, which, in turn, may support the coexistence of the resource species. Therefore, even if the subsystems of two resources-exploiter and -mutualist cannot persist in isolation, their combination can allow the coexistence of all four species.

Model

We consider two competing resource species, superior (X_1) and inferior competitors (X_2), that cannot coexist on their own because the former always excludes the latter. Using a mathematical model, we analyze the effects of the presence of an adaptive exploiter species (Y) and/or an adaptive mutualist species (Z) on the competitive outcome and persistence of the whole system. For adaptation, the interaction effort is allocated between potential resources, as was assumed in earlier studies (Kondoh 2003; Staniczenko et al. 2010; Kaiser-Bunbury et al. 2010; Zhang et al. 2011). We analyze the conditions for species coexistence for various community compositions and adaptation speeds.

We utilized the simplest model setting that allows the stable coexistence of either a resource-mutualist or a

resource-exploiter subsystem. More specifically, we assumed a type I functional response in the antagonistic interaction and a type II functional response in the mutualistic interaction. We did not utilize the type I functional response for the mutualistic interaction, because this assumption can lead to unrealistic, unbounded population growth (Thébault and Fontaine 2010; Okuyama and Holland 2008). Using the type II functional response for the antagonistic interaction does not qualitatively alter the results (data not shown).

The population dynamics in the community can be described as follows:

$$\dot{X}_1 = \{r_X - X_1 - \alpha X_2 - Aa_1Y + Mu_1b_1Z/(h_1 + b_1Z)\}X_1, \quad (1a)$$

$$\dot{X}_2 = \{r_X - X_2 - \beta X_1 - Aa_2Y + Mu_2b_2Z/(h_2 + b_2Z)\}X_2, \quad (1b)$$

$$\dot{Y} = \{A(ga_1X_1 + ga_2X_2) - d\}Y, \quad (1c)$$

$$\dot{Z} = \{r_Z - \varepsilon_Z Z + M(v_1b_1X_1 + v_2b_2X_2)/(h_3 + b_1X_1 + b_2X_2)\}Z, \quad (1d)$$

where X_i ($i \in 1, 2$), Y , and Z are the abundances of the resource species (superior and inferior competitor for $i = 1$ and 2 , respectively), exploiter, and mutualist, respectively. r_X is the intrinsic growth rate of the competitors. α and β are the competition coefficients, which are defined as the relative strength of interspecific competition to intraspecific competition (we implicitly assume that competition coefficients are normalized by the strength of self-regulation assumed to be one). a_i is the foraging effort of the exploiter on the resource species i ($\sum_i a_i = 1$). g is the conversion efficiency. d is the death rate of the exploiter. r_Z is the intrinsic growth rate in the mutualist (the results qualitatively do not change even if $r_Z > 0$). ε_Z is the strength of self-regulation for the mutualist. Mu_i (Mv_i) is the maximum benefit of the resource species i due to the mutualist (the maximum benefit of the mutualist due to resource species i) when the population size of the interaction partner is very large. b_i is the interaction effort of the mutualist on the resource species i ($\sum_i b_i = 1$). Finally, h_i is the half-saturation density when all foraging efforts are allocated to a resource. For the simplicity, we assume $h_i = h$.

A and M are the absolute interaction strengths of the antagonistic and mutualistic interactions, respectively. M is set to 1, although relaxing this assumption does not change the qualitative result (see Figs. S1, S2). In the absence of an exploiter or mutualist, the competitors never coexist, as the inferior competitor is always excluded ($\alpha < 1 < \beta$). The dynamics of the allocation of the exploiter's foraging efforts to two resource species and the mutualist's interaction efforts to two resource species are given by:

$$\dot{a}_i = G_Y a_i \left(\frac{\partial F_Y}{\partial a_i} - \sum_j a_j \frac{\partial F_Y}{\partial a_j} \right), \quad (2a)$$

$$\dot{b}_i = G_Z b_i \left(\frac{\partial F_Z}{\partial b_i} - \sum_j b_j \frac{\partial F_Z}{\partial b_j} \right), \quad (2b)$$

where F_i is the per-capita growth rate of the exploiter or mutualist (dY/dtY or dZ/dtZ) and G_i is the adaptation rate, which is higher when the adaptation is phenotypic plasticity or behavior and lower when it is evolutionary change (Matsuda et al. 1996). These equations represent an adaptive interaction effort allocation that the interaction effort among resource species are re-allocated among interacting partners in a way that increases fitness based on a constraint that efforts sum to unity. This is achieved by increasing (or decreasing) the interaction effort allocations to the resource species that gives energy gain per unit effort more (or less) than the average.

We calculated the population and trait dynamics by direct simulation. The mean abundances and trait values of each species were calculated after the dynamics had reached an asymptotic state. The values of the initial abundances, traits, and parameters did not affect the results qualitatively.

Results

The species composition at equilibrium depends on the strength of the antagonistic interactions relative to the mutualistic interactions ($S = A/M$) and can be classified into phases I, II, and III (Figs. 1, 2).

When S is small (phase I), the exploiter does not persist, and the mutualist chooses the superior competitor (or more abundant species) as its partner. Superiority of the superior competitor is enhanced, and competitive exclusion is inevitable in the competitive community (Fig. 1a, phase I in Fig. 2). This mutualist-driven competitive exclusion can be derived analytically as well, as shown in the SI Appendix.

When S is larger (phase II), the inferior competitor is again excluded, but the other species (mutualist, exploiter, and superior competitor) coexist (Fig. 1b, phase II in Fig. 2). This phase is divided into two subphases (phase IIa and IIb). As shown in Fig. 2, in phase IIa, the mutualist is necessary for the exploiter to be feasible. Exploiter abundance tends to increase with increasing S . In phase IIb, the exploiter is feasible even without the mutualist, and the exploiter abundance tends to decrease with increasing S (SI Appendix). Abundances of species other than the exploiter always decrease as S increases in phase II (SI Appendix).

When S is even larger (phase III), all species (mutualist, exploiter, superior competitor, and inferior competitor) coexist (Fig. 1c–e, phase III in Fig. 2). This phase consists of three subphases (phase IIIa, IIIb, and IIIc). In phase IIIa, both the exploiter and mutualist interact with only the superior competitor (Fig. 1c). The abundances of all species, except the inferior competitor, decrease as S increases (SI Appendix). Whether the inclusion of the interspecific competition stabilizes or destabilizes the system depends on the strength of interspecific competition. When the interspecific competition

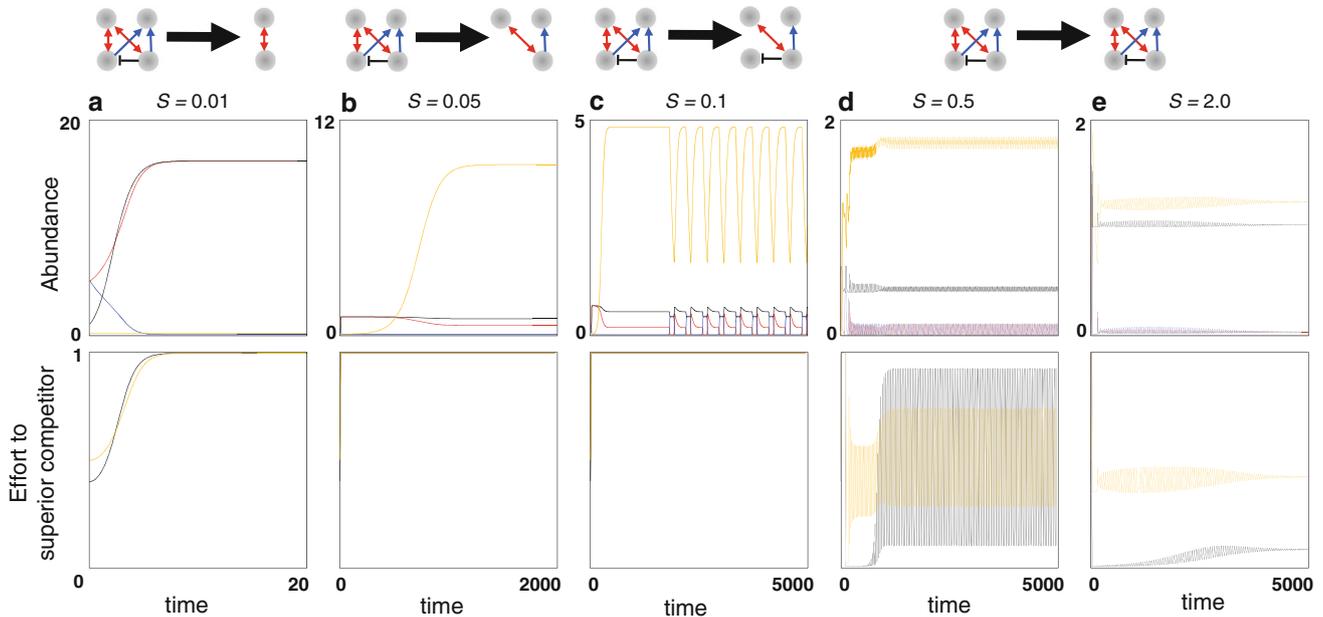


Fig. 1 Dynamics of population sizes and trait values. Illustrations along the upper side of the panels indicate changes in the community structures over time. Blue and red arrows indicate antagonistic and mutualistic interactions, respectively. Black lines indicate competitive interactions. Different colors of population dynamics and trait

dynamics indicate different species (red superior competitor, blue inferior competitor, orange exploiter, black mutualist). **a** $S = 0.01$. **b** $S = 0.05$. **c** $S = 0.1$. **d** $S = 0.5$. **e** $S = 2$. Parameter values: $r_X = 1$, $\alpha = 0.8$, $\beta = 1.8$, $g = 0.25$, $d = 0.01$, $r_Z = 1$, $\varepsilon_Z = 1$, $u_i = 1$, $v_i = 1$, $h = 1$, $G_Y = 3$, and $G_Z = 2$ (color figure online)

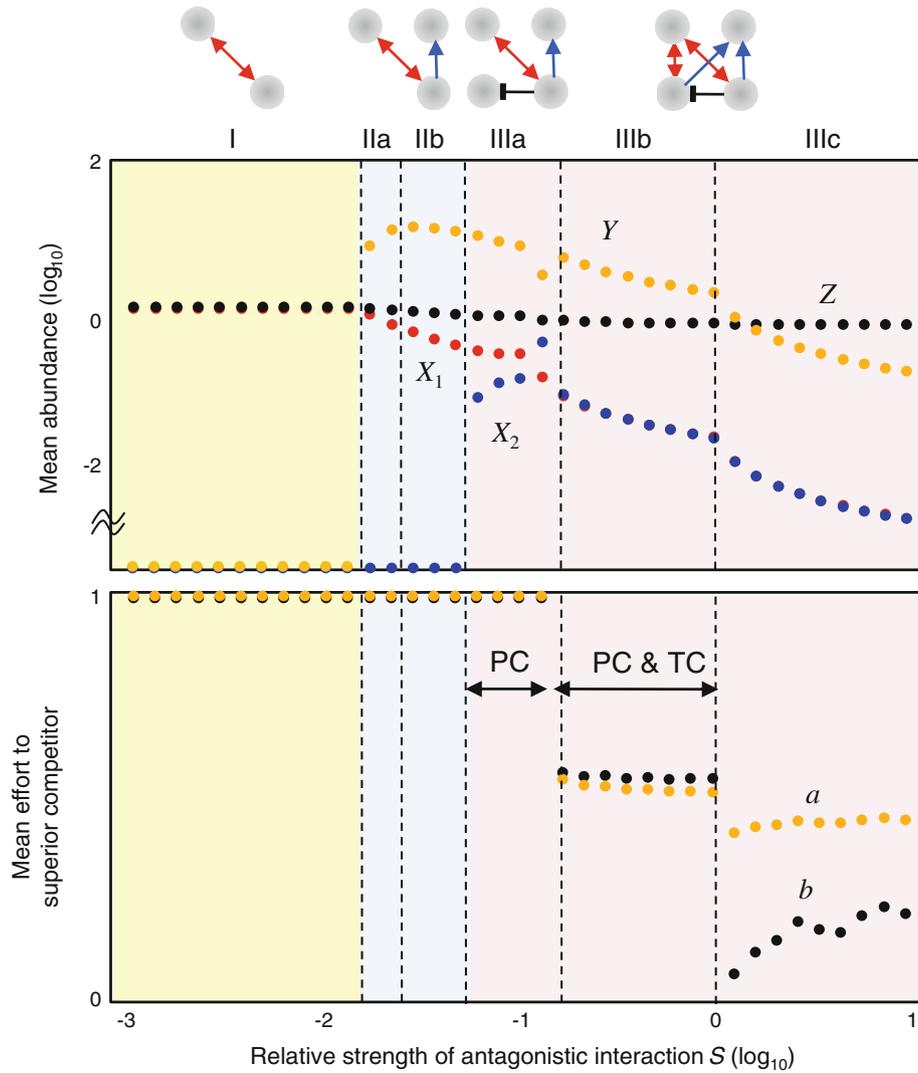


Fig. 2 Parameter dependence of dynamic regime in the community. We assume strong interspecific competition [$\alpha\beta > 1$ ($\alpha = 0.8$ and $\beta = 1.8$)]. Horizontal axes are the strengths of the antagonistic interaction relative to the mutualistic interaction S . Vertical axes (upper panels) are the mean abundances of each species within the community or (lower panels) the mean interaction efforts to the superior competitor by the mutualist and the exploiter. We calculated the mean values of population and trait dynamics after the dynamics approach to the asymptotic behaviors. *Differently*

colored circles indicate different species. Arabic numerals above the upper panels indicate different phases (see text). Illustrations are the community structures corresponding to each phase. Colors in the panels indicate three phases, in which the numbers of coexisting species are different. In phase IIIa, the population cycles (PC) occur (Fig. 1c). In phase IIIb, both population cycles and trait cycles (TC) occur (Fig. 1d). Parameter values are same as those in Fig. 1 (color figure online)

is weaker than the intraspecific competition, the system is stable; otherwise, it is unstable (Figs. 2, S3). In phase IIIb, when the interspecific competition is weaker than intraspecific competition ($\alpha\beta < 1$), the mutualist interacts with only the superior competitor, and the exploiter interacts with two competitors (Fig. S3). When interspecific competition is greater than intraspecific competition ($\alpha\beta > 1$), trait cycles occur and the interacting partners of the exploiter and mutualist change over time (Figs. 1d, 2). In phase IIIc, the strength of the antagonistic interaction is greater than that of the mutualistic interaction. Thus, both the exploiter and mutualist interact with the two competitors at steady

state (Fig. 1e, and phase IIIc in Fig. 2). Whether sub-phase IIIb or IIIc occurs depends on the speed of adaptation. Subphase IIIb is likely to appear when the adaptation speeds of the species are similar; otherwise, subphase IIIc is more likely (Fig. 3).

Taken together, the results suggest that larger S is necessary for the four species to coexist. This is because adaptive switching of the exploiter effectively regulates the instability caused by adaptive mutualist when the exploitation is strong. However, this does not mean that mutualism is not necessary for the coexistence. On the contrary, there is a case in which the mutualist greatly contributes to community persistence. This situation

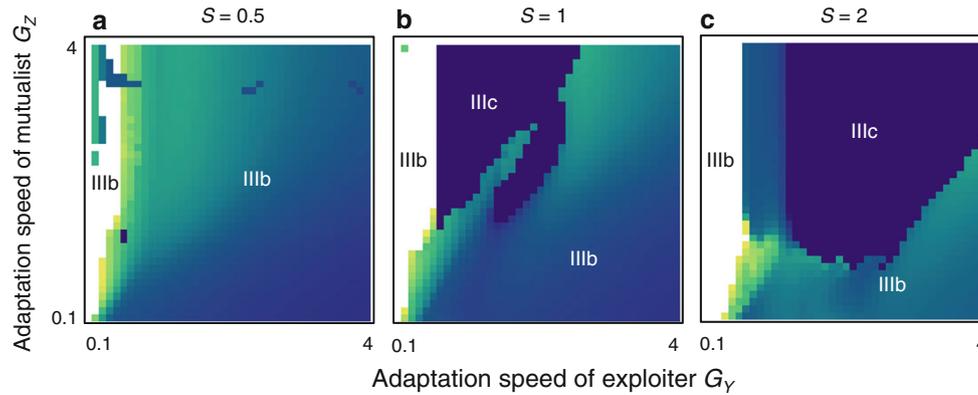


Fig. 3 Relationship between speed of adaptation and stability. **a** $S = 0.5$, **b** $S = 1$, **c** $S = 2$. Horizontal and vertical axes are the adaptation speeds of the exploiter (G_Y) and mutualist (G_Z), respectively. Contours indicate the magnitudes of the amplitudes of population dynamics. Lighter colors indicate larger magnitudes.

We used the dynamics of the mutualist. The tendency in the panels does not depend on the species used. *IIIb* and *IIIc* in the panels indicate the phases shown in Fig. 2. Parameter values are same as those in Fig. 1 (color figure online)

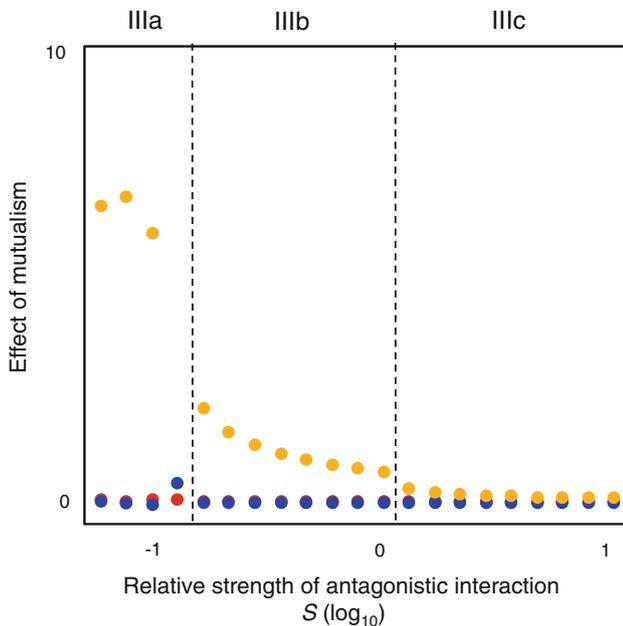


Fig. 4 Effects of mutualism on the abundance of other species. Horizontal axes are the relative strengths of the antagonistic interaction S . Vertical axes are the effects of mutualism, defined as the difference between the mean abundance of each species with and without the mutualist. Differently colored circles indicate different species (see Fig. 2). Phases shown in the upper side of the panels correspond to those in Fig. 2. Strong interspecific competition [$\alpha\beta > 1$ ($\alpha = 0.8$ and $\beta = 1.8$)]. Parameter values are same as those in Fig. 2 (color figure online)

stems from the positive indirect effect of the mutualist on the exploiter [Eq. (7) in SI Appendix, Figs. 4, S4]. This indirect effect may also allow non-persistent subsystem comprised of weak exploiter and two resources (inferior resource goes extinct) in the absence of mutualist to persist, when the strength of mutualistic and antagonistic interactions are relatively strong and weak, respectively, and the adaptation speed of mutualist and

exploiter are relatively slow and fast, respectively (Figs. 5, S5).

Discussion

Adaptive antagonism and adaptive mutualism can interactively support multispecies coexistence. Adaptive antagonism potentially enhances the coexistence of competing resources; yet, the interaction strength should be strong enough for this predator-mediated coexistence mechanism to work. Thus, a community of two competing species and an adaptive exploiter with weak interactions cannot persist. However, this non-persistent community comprising two resource species and an adaptive exploiter can be made persistent by adding an adaptive mutualist, which potentially inhibits resource coexistence in the absence of an adaptive exploiter. This pattern demonstrates the critical role of the coexistence of multiple interaction types for community maintenance.

Species coexistence mediated by the antagonism–mutualism coexistence can be explained as follows. The adaptive exploiter favors more abundant resource species and provides a disadvantage to the more abundant resource. Thus, its presence tends to prevent competitive exclusion at the resource level. For the same reason, a “weak” exploiter cannot make competing resource species coexist. This predator-mediated coexistence mechanism can be enhanced by the existence of a mutualist. Specifically, adaptive mutualism effectively supports the adaptive exploiter via a positive indirect effect mediated by the resource species. This indirect effect strengthens the exploitation, which can regulate the superior competitor, and enhances coexistence.

Adaptation has an important effect to the community persistence. The coexistence of four species could be achieved without adaptation (Fig. S6). However, this is possible only within a small parameter space of interaction strength (Fig. S6), suggesting that, even if the

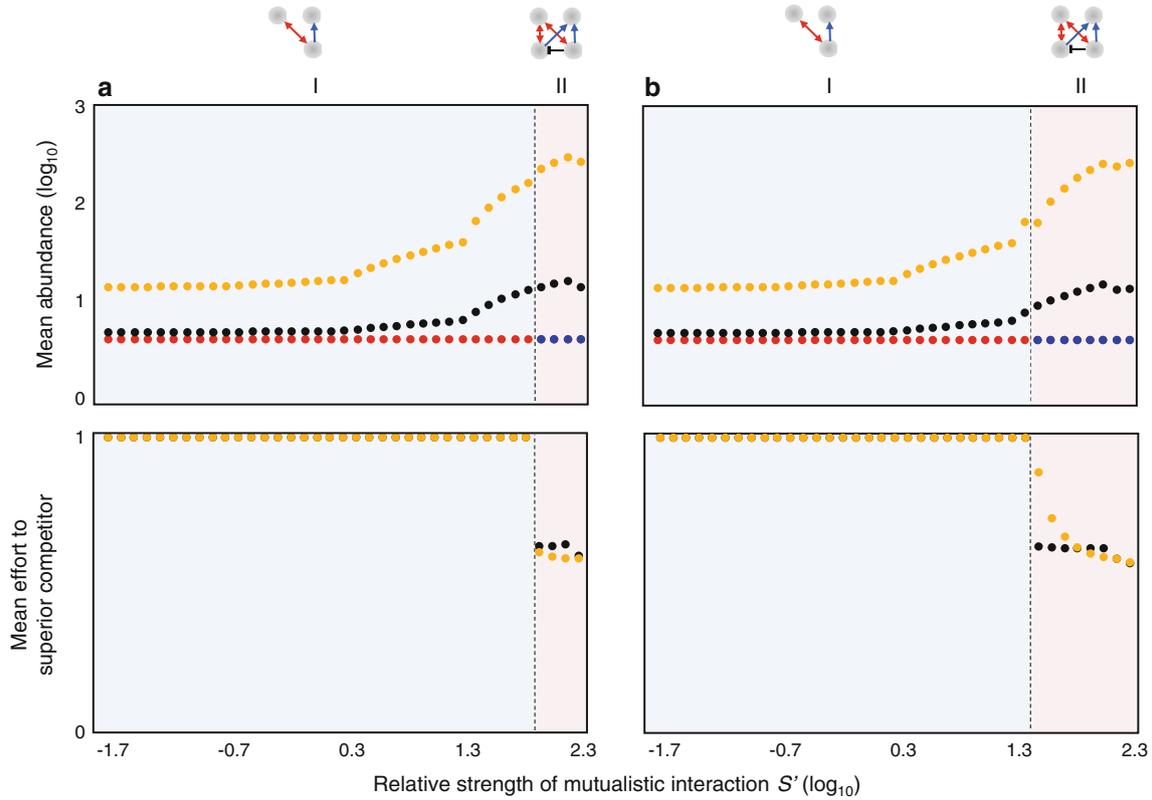


Fig. 5 Parameter dependence of the dynamic regime in the community. *Horizontal axes* are the strengths of the mutualistic interaction relative to the antagonistic interaction, S' . We assume strong interspecific competition [$\alpha\beta > 1$ ($\alpha = 0.8$ and $\beta = 1.8$)]. We set $A = 0.05$ and $G_Y = 0.05$ to prevent the subsystem of

exploiter-two resources (inferior competitor does not persist). In this setting, the subsystem of mutualist-two resources also does not persist (inferior competitor does not persist). **a** Faster adaptation of mutualist ($G_Z = 0.01$). **b** Slower adaptation of mutualist ($G_Z = 0.001$). Other information is the same as in Fig. 2

coexistence is achieved at some time point, a small change of interaction strength may easily destroy the system. In contrast, if the organisms adaptively change the interaction efforts, the coexistence is easily achieved and maintained, because adaptive dynamics brings the system to the parameter region that allows the all species to persist. Furthermore, when the interspecific competition is strong, adaptation, especially quick ones, has a critical role of stabilizing the community dynamics (Fig. 3). In addition, when the strength of antagonistic interaction is stronger, the adaptation of mutualistic interaction more greatly stabilizes the system. Our results suggest that the adaptation and interaction types synergistically contribute to the community persistence.

Does adaptation alter community stability? Our study shows that the answer to this question depends on whether and how multiple interaction types are mixed in the community (Fig. 3). Adaptation tends to enhance species coexistence in resource-exploiter systems (Kondoh 2003), whereas it inhibits species coexistence in mutualistic systems. When the mutualistic interaction is relatively strong or when the antagonistic interaction is relatively weak, then the effects are unchanged: adaptations in antagonism and mutualism enhance and inhibit coexistence, respectively, even in a mixed

community. However, when the mutualistic interaction is relatively weak, the adaptation effects can be reversed. Faster adaptation of the mutualist enhances species coexistence by stabilizing the community dynamics. In contrast, faster adaptation of the exploiter may enhance or prevent coexistence, depending on the speed of mutualist adaptation. We cannot determine whether adaptation will promote or inhibit species coexistence without knowing the relative interaction strength and adaptation speed of different interaction types.

In nature, there exist the adaptive partner choices in mutualistic interactions (Basilio et al. 2006; Fortuna and Bascompte 2006; Whittall and Hodges 2007; Olesen et al. 2008; Petanidou et al. 2008). Our model, however, predicts that an adaptive mutualism tends to cause competitive exclusion and, thus, is destabilizing. This discrepancy between observation and theory poses a new question of what allows the persistence of multiple competing species and their adaptive mutualist in nature. Our study suggests a possible role of adaptive exploiters for the coexistence of multiple resources and their adaptive mutualists. Above-ground exploiters, such as parasitic pollinators and herbivores (Genini et al. 2010; Evison et al. 2012), may be essential for the coexistence of plant species and mutualists, such as

pollinators and seed dispersers. Similarly, parasitic fungi may be necessary for the coexistence of plants and mutualistic mycorrhizal fungi in underground ecosystems (Smith and Smith 1996; Johnson et al. 1997).

There is an important extension to be made in future works. In the present study, we assume that a nonresource species (e.g., animals) plays only a single role of either exploiter or mutualist. Yet, in nature, organismal species can play multiple roles (Johnson et al. 1997). An earlier study showed that the coexistence of multiple interaction types may promote community persistence when a species can take more than two ecological roles in the community (Mougi and Kondoh 2012). It is unclear how the species-level mixing and adaptive changes of such interaction types affect the dynamics and maintenance of communities. Other questions that remain to be answered include how different interaction types are embedded into natural communities; whether the coexistence of different ecological roles (e.g., mutualist, prey, and predator) in a single population affects the community dynamics; and whether the way that different interactions are arranged in a community network affects the stability of the community dynamics.

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References

- Allesina S, Tang S (2012) Stability criteria for complex ecosystems. *Nature* 483:205–208
- Bascompte J, Jordano P, Merián CJ, Olesen JM (2003) The nested assembly of plant–animal mutualistic networks. *Proc Natl Acad Sci USA* 100:9383–9387
- Basilio AM, Medan D, Torretta JP, Bartoloni NJ (2006) A year-long plant–pollinator network. *Austral Ecol* 31:975–983
- Egas M, Sabelis MW (2001) Adaptive learning of host preference in a herbivorous arthropod. *Ecol Lett* 4:190–195
- Elton CS (1958) *The ecology of invasions by animals and plants*. Methuen, London
- Evison SEF, Roberts KE, Laurenson L, Pietravalle S, Hui J, Biesmeijer JC, Smith JE, Budge G, Hughes WHO (2012) Pervasiveness of parasites in pollinators. *PLoS One* 7:e30541
- Fontaine C, Guimarães PR Jr, Kéfi S, Loeuille N, Memmott J, van der Putten WH, van Veen FJF, Thébault E (2011) The ecological and evolutionary implications of merging different types of networks. *Ecol Lett* 14:1170–1181
- Fortuna MA, Bascompte J (2006) Habitat loss and the structure of plant–animal mutualistic networks. *Ecol Lett* 9:278–283
- Fussmann GF, Loreau M, Abrams PA (2007) Eco-evolutionary dynamics of communities and ecosystems. *Funct Ecol* 21:465–477
- Genini J, Morellato LPC, Guimarães PR Jr, Olesen JM (2010) Cheater in mutualistic networks. *Biol Lett* 6:494–497
- Johnson NC, Graham JH, Smith FA (1997) Functioning and mycorrhizal associations along the mutualism–parasitism continuum. *New Phytol* 135:575–586
- Kaiser-Bunbury CN, Muff S, Memmott J, Müller CB, Calfisch A (2010) The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol Lett* 13:442–452
- Kondoh M (2003) Foraging adaptation and the relationship between food–web complexity and stability. *Science* 299:1388–1391
- Matsuda H, Hori M, Abrams PA (1996) Effects of predator-specific defence on biodiversity and community complexity in two-trophic-level communities. *Evol Ecol* 10:13–28
- May RM (1973) *Stability and complexity in model ecosystems*. Princeton University Press, Princeton
- Mougi A, Kondoh M (2012) Diversity of interaction types and ecological community stability. *Science* 337:349–351
- Murdoch WW (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol Monogr* 39:335–354
- Okuyama T, Holland JN (2008) Network structural properties mediate the stability of mutualistic communities. *Ecol Lett* 11:208–216
- Olesen JM, Bascompte J, Elberling H, Jordano P (2008) Temporal dynamics in a pollination network. *Ecology* 89:1573–1582
- Petanidou T, Kallimanis AS, Tzanopoulos J, Sgardelis SP, Pantis JD (2008) Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecol Lett* 11:564–575
- Pimm S (1991) *The balance of nature? Ecological issues in the conservation of species and communities*. University of Chicago Press, Chicago
- Smith FA, Smith EE (1996) Mutualism and parasitism: diversity in function and structure in the “arbuscular” (VA) mycorrhizal symbiosis. In: Callow JA (ed) *Advances in botanical research*. Academic Press, London, pp 1–43
- Staniczenko PPA, Lewis OT, Jones NS, Reed-Tsochas F (2010) Structural dynamics and robustness of food webs. *Ecol Lett* 13:891–899
- Thébault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853–856
- Whittall JB, Hodges SA (2007) Pollinator shifts drive increasingly long nectar spurs in columbine flowers. *Nature* 447:706–709
- Zhang F, Hui C, Terblanche JS (2011) An interaction switch predicts the nested architecture of mutualistic networks. *Ecol Lett* 14:797–803