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# Stability of competition–antagonism–mutualism hybrid community and the role of community network structure

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## HIGHLIGHTS

- Stabilizing effect of interaction mixture is a general feature of 'hybrid' communities.
- Positive complexity–stability relationship is a general feature of 'hybrid' communities.
- A realistic hierarchical structure in food web contributes to the maintenance of hybrid community.

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## ABSTRACT

Theory predicts that ecological communities of many interacting species are unstable, despite the fact that complex ecosystems persist in nature. A recent theoretical study hypothesised that coexistence of antagonism and mutualism can stabilise a community and even give rise to a positive complexity–stability relationship. Here, using a theoretical model, we extended the earlier hypothesis to include competition as a third major interaction type, and showed that interaction-type diversity generally enhances stability of complex communities. Furthermore, we report a new finding that the hierarchically structured antagonistic interaction network is important for the stabilizing effect of interaction type diversity to emerge in complex communities. The present study indicated that the complexities characterised by species number, connectance, species variation, and interaction type diversity synergistically contributed to maintaining communities, and posed an interesting question of how present complex communities emerged, and developed from simpler ecosystems.

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## 1. Introduction

Maintenance mechanism of ecological communities remains a central question in ecology. Theoretical studies (Gardner and Ashby, 1970; May, 1972; Pimm and Lawton, 1978), most notably May (1972), predicted that large and complex communities are inherently unstable, despite the coexistence among many interacting species being observed in nature. These incongruities between theory and observation have long inspired ecologists to identify what maintains natural ecological communities (Neutel et al., 2002; Bascompte et al., 2006; Brose et al., 2006; Martinez et al., 2006; Allesina et al., 2008; Okuyama and Holland, 2008). A number of theoretical studies have attributed this inconsistency to an unrealistic network structure assumed in earlier community models (Lawlor, 1978; Pimm, 1979), and have contributed to efforts demonstrating that a complex model community with realistic

topology or interaction strength can be stable (Lawlor, 1978; Pimm, 1979; Yodzis, 1981; Neutel et al., 2002; Emmerson and Raffaelli, 2004).

However, the variety of interspecific interaction types, a prominent feature of real communities (Fontaine et al., 2011; Poccock et al., 2012), has received little attention in the earlier studies. Most theoretical studies have addressed a specific community type, e.g. competitive, trophic, or mutualistic to model a “real” community. May’s model communities were generated by assigning random values to community matrices, and therefore may be interpreted as consisting of various interaction types. However, most theoretical studies that followed did not address the variety of interaction types (but see Ringel et al., 1996; Melián et al., 2009), and it was only recently that the complexity–stability effect was compared between communities with different types of interactions (Yoshino et al., 2007; Allesina and Tang, 2012). The studies confirmed that antagonistic interactions exhibited a more stabilising effect than competitive, mutualistic, or a combination of interaction types; and complex associations resulted in a destabilising effect on communities (Allesina and Tang, 2012).

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Community stability responds to a complexity of changes in relative frequencies of interaction types. Mougí and Kondoh (2012) were the first to systematically examine these relationships in antagonistic and mutualistic relationships. They presented a mathematical model of ‘hybrid’ community, where (i) mutualism and antagonism coexist in the same community network and (ii) each species allocate their interaction efforts of mutualism and antagonism separately to interacting species. With this model they showed that moderate mixing of the two interactions stabilised population dynamics, and generated a positive complexity–stability relationship. Their results suggested a potential contribution in interaction type richness or diversity to community maintenance. However, only two interaction types were considered (Mougí and Kondoh, 2012), therefore important questions remain unanswered. For example, what contribution do other interaction types and mixing have on stabilizing population and community dynamics and maintenance? What, if any, is the contribution of competition to system stability; a viable question, as competition is a well-studied interspecific interaction. Can the insights gained through an antagonism–mutualism mixture study be applicable to other interaction combinations? What are the interaction–mixing effects to community stability, and what are its relationships to complexity when more than three interactions are present?

Here, using a community model that incorporated antagonistic, competitive, and mutualistic interactions, we analysed the effects of interaction-type diversity and richness on community dynamics. Our purpose was threefold. First, we generalized our earlier hypothesis by showing that the stabilising effect of an interaction-type mixing, originally demonstrated by using the antagonism–mutualism model, was applicable to broader mixtures, such as competition–antagonism, competition–mutualism, and competition–antagonism–mutualism. Second, we clarified the variability in stability among communities of different interaction types. We showed that a hybrid community exhibiting competition and mutualism was relatively unstable compared to other hybrid communities. Finally, we demonstrated the key role of an interaction network structure on hybrid community maintenance. The model indicated that a positive complexity effect for stability was more prevalent in the presence of a hierarchical food web structure.

## 2. Model

Consider a community where  $N$  species may interact with each other through antagonism (prey–predator, host–parasitoid, or host–parasite interaction), competition, or mutualism. In the model, the competition represents direct competition such as interference competition. If a type I functional response is assumed, the population dynamics of species  $i$  is described as:

$$\frac{dX_i}{dt} = X_i \left( r_i - s_i X_i + \sum_{j=1, j \neq i}^N a_{ij} X_j \right), \quad (1)$$

where  $X_i$  is the abundance of species  $i$ ,  $r_i$  is the intrinsic rate of change in species  $i$ ,  $s_i$  is density-dependent self regulation, and  $a_{ij}$  is the interaction coefficient between species  $i$  and species  $j$ . We used two network types, random and cascade, for antagonistic networks. We choose the cascade as the simplest model, including an essential realistic network structure of trophic interaction (the cascade is not used for competition or mutualism). Trophic roles of resource and consumer were randomly assigned to two interacting species in a random model; in the cascade model, for each pair of species  $i, j, i = 1, \dots, n$  with  $i < j$ , species  $i$  never consumes species  $j$ , while species  $j$  might consume species  $i$ . Following our earlier study (Mougí and Kondoh, 2012), we defined the proportion of connected pairs  $P$  as the proportion of realized interaction links  $L$  in the possible maximum interaction links  $L_{max} (=N(N-1)/2)$  of

a given network model ( $L=PL_{max}$ ), and made an assumption that interaction strengths decreased with increased number of interactions between species and within interaction type, the critical assumption that may affect the stability patterns of hybrid communities (Mougí and Kondoh, 2012; Suweis et al., 2013). The latter assumption that for each species its total interacting effort is allocated separately in each interaction type might be appropriate, for example, when each interaction occur during different stages of life history or when the resource gained via one interaction is not substitutable with that gained via other interactions (e.g. a predator provided with shelter and food by mutualistic and antagonistic interactions, respectively). The interaction coefficients,  $a_{ij}$  ( $i \neq j$ ) are determined as  $a_{ij} = e_{ij} f_M A_{ij} / \sum_{k \in \text{resourceofmutualist}, k \neq i} A_{ik}$  and  $a_{ji} = e_{ji} f_M A_{ji} / \sum_{k \in \text{resourceofmutualist}, k \neq j} A_{jk}$  in a mutualistic interaction; and  $a_{ji} = u_{ji} f_C A_{ji} / \sum_{k \in \text{interactionpartnerofcompetitor}, k \neq j} A_{jk}$  in a competitive interaction;  $a_{ij} = g_{ij} f_A A_{ij} / \sum_{k \in \text{resourceofpredator}, k \neq i} A_{ik}$  and  $a_{ji} = -a_{ij} / g_{ij} = -f_A A_{ij} / \sum_{k \in \text{resourceofpredator}, k \neq i} A_{ik}$  in an antagonistic interaction between consumer  $i$  and resource  $j$ , where  $A_{ij}$  is the potential preference for the interaction partners in antagonistic and mutualistic interactions, the potential competition effect to the interaction partners in competitive interactions,  $f_A, f_C$ , and  $f_M$  are relative strengths of antagonistic, competitive, and mutualistic interactions, respectively (we assumed  $f_A=f_M=f_C=1$  in the simulations),  $e_{ij}$  and  $g_{ij}$  are the conversion efficiencies when species  $i$  utilizes species  $j$  in mutualistic and antagonistic interactions, respectively, and  $u_{ij}$  is the conversion coefficient of the competition effect of species  $j$  into the growth rate of species  $i$ . We also examined the types of functional responses in antagonistic and mutualistic interactions. For type II functional response we used

$$a_{ij} = n_{ij} f_l \left( A_{ij} / \sum_{k \in \text{resourceofsp.}, k \neq i} A_{ik} \right) / \left\{ 1 + \sum_k h_{ik} \left( A_{ij} / \sum_{k \in \text{resourceofsp.}, k \neq i} A_{ik} \right) X_k \right\},$$

where  $l$  is  $M$  or  $A$ ,  $n_{ij}$  is  $e_{ij}$  or  $g_{ij}$ , and  $h_{ij}$  is the handling time. Parameters,  $s_i, e_{ij}, u_{ij}, g_{ij}, A_{ij}$ , and  $h_{ij}$ , are randomly chosen from a uniform distribution between 0 and 1 (see Appendix B, Figs. B2–B10 for the cases relaxing this assumption), and there is no correlation between the pairwise parameters ( $A_{ij}$  and  $A_{ji}$ ,  $e_{ij}$  and  $e_{ji}$ ,  $u_{ij}$  and  $u_{ji}$ ,  $g_{ij}$  and  $g_{ji}$ ,  $h_{ij}$  and  $h_{ji}$ ). The intrinsic rate of change,  $r_i$ , is determined to hold  $dX_i/dt=0$  after imposing an equilibrium density of each species,  $X_i^*$ , from a uniform distribution between 0 and 1 (note that this assumption is not critical to the results because  $r$  does not affect the local stability in the systems). Thus,  $r_i$  of basal species with no mutualistic interactions should always be positive, while that of species with no predators should be negative. Stability analysis was based on a Jacobian community matrix following May’s approach (May, 1972). Stability was defined as the probability of local equilibrium stability, which was estimated as the frequency of locally stable systems across 1000 sample communities (Chen and Cohen, 2001).

## 3. Results

Model communities with a single interaction type, i.e. competition, antagonism, or mutualism differed in stability. Antagonistic communities ( $p_A=1$ ) were most stable, followed by competitive ( $p_C=1$ ) and mutualistic ( $p_M=1$ ) (Fig. 1).

The dynamic consequences of increasing complexity (high species richness  $[N]$ , more connected pairs  $[P]$ ) differed among community types. Stability of antagonistic webs tended not to be strongly affected by increased  $N$  or  $P$  (Fig. 1 and Fig. B1), yet the response depended on the network. More specifically, it is slightly destabilising for cascade food webs, while slightly stabilizing for random food webs (see also Fig. 2 and Online supporting information in Mougí and Kondoh, 2012 and Fig. 2B in Suweis et al., 2013).

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