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.

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; Pocock 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. Mougi 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 (Mougi 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:

$$\frac{dX_i}{dt} = X_i \left(r_i - s_i X_i + \sum_{j=1, j \neq i}^{N} a_{ij} X_j \right),$$ (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 $i, j=1,…, n$ with $i < j$, species i never consumes species j, while species j might consume species i. Following our earlier study (Mougi 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 (Mougi 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 $a_{ij} = e_{ij} f_M A_{ij} / \sum_{k \in \text{resourceofmutualist}i, k \neq i} A_{ik}$ and $a_{ji} = e_{ji} f_M A_{ji} / \sum_{k \in \text{resourceofmutualist}j, k \neq j} A_{jk}$ in a mutualistic interaction; and $a_{ji} = u_{ij} f_C A_{ji} / \sum_{k \in \text{interactionpartnerofcompetitor}j, k \neq j} A_{jk}$ in a competitive interaction; $a_{ij} = g_{ij} f_A A_{ij} / \sum_{k \in \text{resourceofpredator}i, k \neq i} A_{ik}$ and $a_{ji} = -a_{ij} / g_{ij} = -f_A A_{ij} / \sum_{k \in \text{resourceofpredator}i, k \neq i} A_{ik}$ 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

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

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 Mougi and Kondoh, 2012 and Fig. 2B in Suweis et al., 2013).

Competitive webs were weakly destabilised by increased N (Fig. 1), while strongly stabilised by increases in P (Fig. B1, see also Rozdilsky and Stone, 2001 for similar results). Increased N or P destabilised mutualistic webs (see also Fig. 2 in Mougi and Kondoh, 2012 and Fig. 2B in Suweis et al., 2013). Note that the complexity–stability relationship in the communities with a single interaction type can be positive depending on choice of parameter values (f_i and parameter variation, for example; see Suweis et al., 2013 and Fig. B6). We have confirmed that with our parameter settings the communities with a single type interaction do not show a strong positive complexity–stability relationship, which allows us to isolate the effect of mixing of different interaction types on the complexity effects on stability.
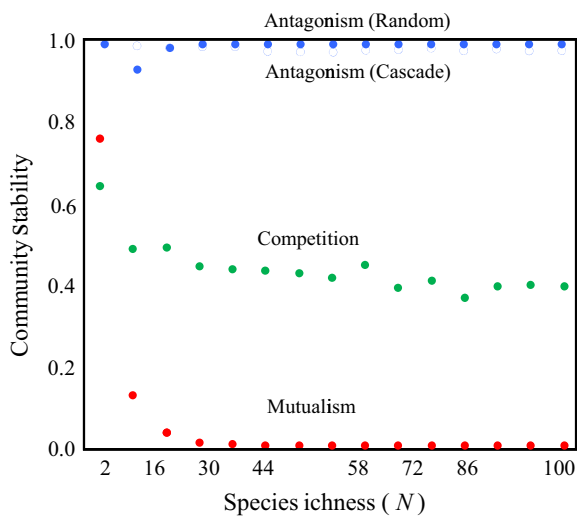

Fig. 1. Species richness–stability relationships in communities with single interaction types. We assumed a type I functional response. Circles with different colors indicate different communities with different types of interaction. We assumed $P=0.7$.

The stability of hybrid communities with two interaction types of interactions responded similarly to changes in the mixing ratio of different interaction types. A community dominated by a single type of interaction was unstable; the highest stability was observed at the intermediate mixing ratio level, regardless of the two interaction types (Fig. 2, Figs. B2–B6). However, a competitive and mutualistic hybrid community showed less stability than other mixtures (mathematical analysis shown in Appendix A). The unimodal pattern was less resolved, and observed under restricted parameter choices (Figs. B2–B5). Interaction-type mixing affected the relationship between complexity and stability. Positive relationships were consistently observed in hybrid communities of moderate interaction type mixing (see Fig. 2, Figs. B2–B6, Appendix A), irrespective of the choices in network structure (random or cascade), and functional response (Type I or II).

The addition of a third interaction type had a marked impact on community stability (Fig. 3, Figs. B7–B10). Stable two-interaction-type hybrid communities, such as antagonistic–mutualistic ($p_C=0$) and antagonistic–competitive ($p_M=0$) (Fig. 3, see also Fig. 2) were highly destabilised by the addition of even a small amount of a third interaction type. Similarly, the hybrid competitive and mutualistic interaction community ($p_A=0$ in Fig. 3, see also Fig. 2), which we found relatively unstable, was strongly stabilised by adding a small proportion of antagonistic interaction. The three types of interactions naturally coexist, and the model indicated the highest stability was attained at a moderate mixing of the three interaction types (Fig. 3, Figs. B7–B10).

The moderate mixing of different interaction types resulted in a positive complexity–stability relationship in both two- and three-interaction-type hybrid communities. However, the pattern was qualitatively different depending on the number of interaction types and the network structure. In two-interaction-type hybrid communities, the parameter region for stable coexistence became broader as complexity (high species richness, more connected pairs) increased in random networks, while in cascade networks, as complexity increased, the parameter region narrowed. In contrast, in three-interaction-type hybrid communities, as complexity increased, the stable region narrowed in random networks
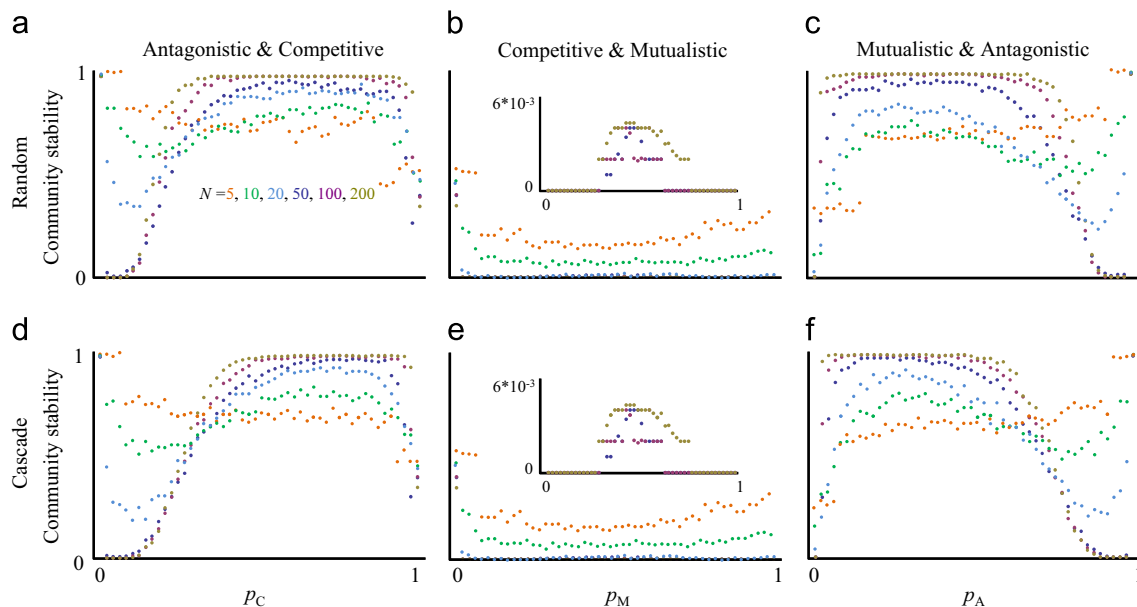

Fig. 2. Hybrid community stability with two interaction types. ((a)–(f)) Exhibit different network structures, and hybrid community types. We assumed a type I functional response. Colours indicate different values of N. We assumed $P=0.7$. ((a) and (d)) Hybrid community stability with antagonistic and competitive interactions in relationship to the proportion of competitive links (p_C). ((b) and (e)) Hybrid community stability with competitive and mutualistic interactions in relationship to the proportion of mutualistic links (p_M). ((c) and (f)) Hybrid community stability with mutualistic and antagonistic interactions in relationship to the proportion of antagonistic links (p_A).
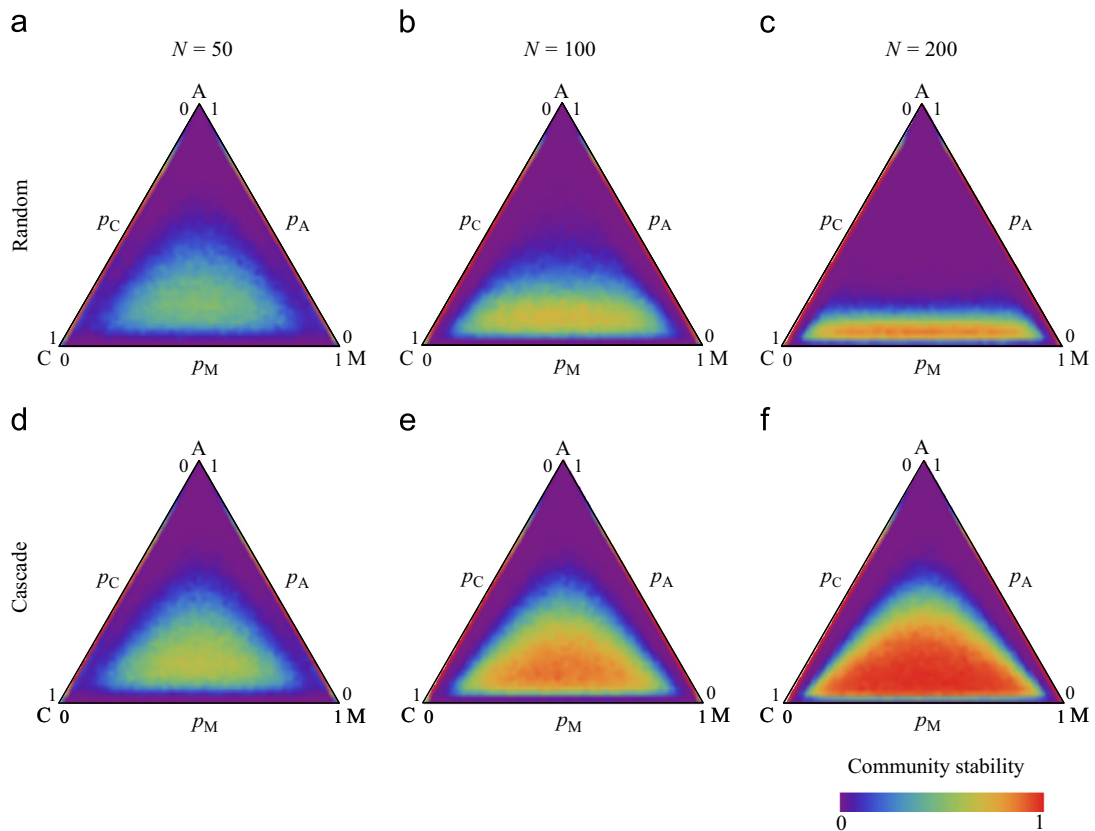
Fig. 3. Hybrid community stability with three types of interaction. ((a)–(f)) Exhibit different network structures, and species number *N*. We assumed a type I functional response. The symbols, A, C, and M, shown in the corners of each triangle indicate communities with a single interaction type; antagonistic, competitive, and mutualistic interactions, respectively. The three triangle sides correspond to hybrid communities with two interaction types. Contours indicate community stability.

(see Appendix A for an analytical analysis), while it widened in cascade networks.

4. Discussion

The primary effects of interaction-types and composition on community dynamics were elucidated by two key theoretical findings. First, we detected considerable variance in stability between communities with different interaction-type compositions. Among individual communities, antagonistic and competitive exhibited increased stability relative to mutualistic communities; among hybrid communities, antagonism–mutualism were least stable, congruent with former studies (Yoshino et al., 2007; Allesina and Tang, 2012), which clearly established that interaction-type was the critical determinant in community dynamics. Second, a moderate mixing of different interaction types consistently stabilised any choice of two from the three interaction types i.e. antagonism, mutualism, and competition, and also for a three-interaction-type mixing. A skewed composition was likely to destabilise. Indeed, a two-interaction-type hybrid community was highly destabilised by adding a small proportion of a third interaction type. These results provide general support for the stabilising effect of moderate interaction-type mixing based only on the analysis of a mutualism–antagonism community model (Mougi and Kondoh, 2012) compared to other combinations and interaction-type richness.

Mougi and Kondoh (2012) reported that the coexistence of antagonism and mutualism reversed the classically negative complexity–stability relationship into a positive association. Here, by analysing a wider range of hybrid community models, we showed that the emergence of positive complexity–stability relationships is not specific to an antagonism–mutualism hybrid community,

but is a general feature observed in other kinds of hybrid communities. Since May's seminal paper was published (May, 1972), the factors maintaining complex communities have long been debated (Pimm, 1984; McCann, 2000; Montoya et al., 2006; Ives and Carpenter, 2007). Our results add a novel hypothesis to the list of mechanisms hypothesised to maintain natural communities (Rozdilsky and Stone, 2001; Kondoh, 2003; Okuyama and Holland, 2008).

Our study provides new research directions in community ecology. We enhanced our understanding of community ecology, where interspecific interactions, and their network structures have a major effect on population and community dynamics. This community ecology paradigm has been supported by numerous empirical and theoretical studies (Neutel et al., 2002; Bascompte et al., 2006; Otto et al., 2007). However, communities comprised of one interaction type have been independently evaluated (Fontaine et al., 2011). Our study indicated this research approach might result in misleading predictions. In communities modelled with a single interaction type, the complexity level was not likely to stabilise the system. Hence, complex communities in natural systems might be incorrectly evaluated as unstable. However, if different interaction types are mixed within a community, a stable complex system should be predicted, because incorporating all major interaction types resulted in more complex communities, and enhanced community stability. Future studies that assess interaction type diversity might increase development of interaction networks.

Our model indicated community network structure can play a key role in maintaining complex communities. An important advance in food-web ecology shows real food webs exhibit a non-random structure (De Ruiter et al., 1995; Krause et al., 2003; Kondoh, 2008; Kondoh et al., 2010). A number of 'recipes' to

reproduce realistic food webs (Cohen et al., 1990; Solow and Beet, 1998; Williams and Martinez, 2000; Cattin et al., 2004; Stouffer et al., 2005; Brose et al., 2006) agree that species can be arranged in a hierarchical manner, according to the roles assigned to predator–prey interacting pairs. The present study revealed a hierarchical food web pattern played an essential role in creating a positive complexity–stability relationship in the three-interaction-type hybrid community. This relationship was observed in a broader interaction-type mixture range in a hierarchically structured (cascade) network relative to random networks. The stabilising effects of interaction type mixing exhibited similar results. The stabilising effect of interaction-type diversity was dependent on network complexity. Interaction type diversity did not stabilise a simple community; species maintenance in nature can be understood as an interplay between interaction-type mixing and hierarchical food-web structure.

In the present model we assume that the average interaction strength decreases with increasing species richness or connection probability due to allocation of interaction effort (constant effort allocation; Suweis et al., 2013). As mentioned in the earlier paper (Mougi and Kondoh, 2012; Suweis et al., 2013), this is not only ecologically feasible, but also a key assumption for the positive complexity–stability relationship to arise in a hybrid community. However, the positive complexity–stability relationship is not explained solely by the assumption of constant effort allocation (see Suweis et al., 2013 for such an interpretation). Indeed, increasing complexity stabilizes community dynamics, while a positive complexity–stability relationship is not a general pattern in communities with a single interaction type with the present model setting (Fig. 1), clearly suggesting that mixing different types of interaction is essential for the positive complexity–stability relationship to emerge.

The present study poses an interesting question regarding how simple ecological communities emerged, and developed into more complex, present day communities throughout the evolutionary time scale (Thompson, 1994; Levin, 1998). Our theoretical model indicates that species and interaction diversity simultaneously affect community stability. Consequently, an evolutionary pattern in species and interaction diversity in the biosphere should be preserved, as unstable ecosystems might be too fragile to persist (Pimm, 1991). For example, as predicted by our model, interaction diversity reverses the negative species richness effect on community stability into a positive effect. In such a case, species diversification, which is destabilising in the absence of interaction diversity, is unlikely to occur prior to evolutionary diversification of species interactions. Interaction type diversification should set the stage for species diversification. Complex community evolution is an interesting topic from a complexity–stability viewpoint.

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2014.06.030.

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