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Impacts of consumer–resource interaction transitions on persistence and long-term interaction outcomes of random ecological networks

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Despite the prevalence of context-dependent interaction transitions in ecological systems, their impacts on persistence and interaction diversity have scarcely been explored in complex ecological networks. By using multispecies bi-directional and unidirectional consumer–resource models, representing a continuum of interaction transitions (sign change of interaction outcomes), we investigated the effects of structural interaction transitions on persistence (the fraction of remaining species) and long-term interaction outcomes in random ecological networks. We found that high interaction strength of exploiting resources generally decreased persistence, and high strength of providing resources increased persistence when the strength of exploiting resources was low in more complex networks; also, the networks with high persistence had a high proportion of mutualistic interactions relative to antagonistic interactions present initially and over the long term. The shifting of interaction strengths shaped the long-term interaction compositions. Meanwhile, population dynamics, especially species extinction, affected the difference between initial and long-term interactions. Based on classical consumer–resource theory, these results establish a transitional continuum of interaction outcomes in ecological networks and imply a theoretical association among interaction transition, community persistence and interaction diversity.

Keywords: consumer–resource model, ecological network, interaction transition, persistence

Introduction

According to the positive (+), negative (−) and neutral (0) effects of species on one another, ecologists have long classified species interactions into six forms in natural communities, i.e. competition, amensalism, predation, mutualism, commensalism and neutralism. However, an increasing amount of empirical evidence shows that interactions can be context-dependent on biotic and abiotic factors, and interaction transitions, i.e. the sign change of interaction outcomes, appear to be prevalent in nature (Thompson 1988, Holland and DeAngelis 2009, Chamberlain et al. 2014). For example, pollinator-mediated interactions among plants may vary from facilitation

to competition as density changes from low to high due to the tradeoff between attracting pollinators and risking interspecific pollen transfer (Campbell and Motten 1985, Steven et al. 2003). A mutualism–commensalism transition was found in ant–aphid and ant–plant systems (Breton and Addicott 1992). In forests, some rodents have been reported to facilitate plants through seed dispersal at low density but show negative effects on plants by excessive predation at high density (Li and Zhang 2007). Numerous studies have also been conducted on the varying frequency of facilitative and competitive interactions in plant communities across abiotic stress gradients (Maestre et al. 2009).

In natural ecosystems, species are usually involved in multiple interactions with other species, forming so-called ecological interaction networks. Since the theoretical work by May (1972), the diversity–stability debate has been an ongoing topic in ecology (McCann 2000). This debate has boosted a growing body of work exploring the structure of ecological networks and their relationships with ecosystem stability (Bastolla et al. 2009, Thébault and Fontaine 2010, Allesina and Tang 2012, Allesina et al. 2015, Bunin 2017). Earlier studies have often limited the type of interaction networks, such as food webs and mutualistic networks. Although many studies have incorporated various density-dependent functional responses to adjust interaction strength in ecological networks (Nunney 1980, Abrams and Allison 1982, Kondoh 2003, Kawatsu and Kondoh 2018), the type of interaction was usually fixed or only shifted between non-neutral and neutral effects. The assumption of fixed interaction types may have overlooked the context-dependent mechanisms underlying interaction transitions (Thompson 1988) and hindered us from a full understanding of ecosystem stability (Zhang et al. 2015). Recent studies have used theoretical or empirical ecological networks to show that variety or a combination of interaction types could have a remarkable impact on the stability of community dynamics (Melián et al. 2009, Allesina and Tang 2012, Kéfi et al. 2012, 2015, 2016, Mougi and Kondoh 2012, Suweis et al. 2014, García-Callejas et al. 2018, Gracia-Lázaro et al. 2018). However, the hybrid networks (with more than one type of interaction) were usually constructed by empirically or theoretically organizing different types of interactions in previous studies, while little is known about the effects of interaction variety caused by context-dependent interaction transitions. Interestingly, recent work has shown that the dome-shaped, density-dependent interaction transitions significantly increased the persistence of ecological networks (Yan and Zhang 2014, 2018a), suggesting a need for further exploration of the relationship between community dynamics and various interaction transitions.

Density-dependency is an important resource of context-dependent interaction transition. Only a few early theoretical explorations exist for this kind of interaction transition in simple systems. For example, some studies introduced a set of functions (with different names), i.e. alpha function, non-monotonic function or bi-directional consumer–resource

model, that can change the sign of the interaction according to the species density (Hernandez 1998, Hernandez and Barradas 2003, Zhang 2003, Neuhauser and Fargione 2004, Holland and DeAngelis 2009, Wang and DeAngelis 2012). In spite of the different forms of interaction transitions and the respective assumptions, these models all showed that multiple equilibrium states could be achieved and thus could affect the population dynamics. Beyond the multiple equilibrium states caused by the non-monotonic interaction transitions, Zhang (2003) found the dome-shaped density-dependent transition reflected by a parabolic function could promote stability of two interacting competitors and their carrying capacity. Nonetheless, a large knowledge gap still exists concerning interaction transitions and stability in complex ecological networks.

MacArthur's consumer–resource model and its various derivations have long been applied in specified biological interactions (MacArthur 1970) and large interaction networks (Advani et al. 2018). In this study, by using the bi-directional consumer–resource (BCR) model proposed by Holland and DeAngelis (2009), we hope to further investigate how the consumer–resource (CR) interaction transition affects network persistence (a measure of stability) and long-term outcomes of species interactions in ecological networks. The interaction transition was generally believed to change the interaction signs (+, − or 0) between two species (Zhang et al. 2015). In previous studies, the interaction transition was investigated in the context of density-dependency for a given model structure (Hernandez 1998, Zhang 2003). In the BCR models, one species is assumed to play the dual role of a consumer and a resource, and the interaction transition involved both species density and interaction strength parameters (Holland and DeAngelis 2009), whereas in this study, we focused on the latter, i.e. the structural interaction transition through varying relative strengths of exploiting and providing resources. By introducing BCR models into ecological networks, we examined the following three questions. 1) How is the network persistence affected by interaction transitions between exploiting and providing resources in networks with different species number and connectance? 2) How does the initial composition of interactions affect network persistence, and what is the relationship between the long-term composition of interactions and network persistence? 3) How do the structural and density-dependent interaction transitions shape the long-term interaction composition of ecological networks?

Methods

Bi-directional consumer–resource model

The model, proposed by Holland and DeAngelis (2009), assumed one species can exhibit both positive and negative effects on another species, thus being a resource exploiter and provider simultaneously. Possibly, the presence of a

third-party species could affect the interaction transition, but the empirical mechanism underlying this effect was still unclear (Frederickson 2017). Therefore, we assumed, for simplicity, that the interaction between any pair of species was not directly altered by another species. The interaction outcome depends on the functional outcome altered by interaction strength and population density. We extended this model to a multi-species version (Eq. 1), in which any pair of species can show a bi-directional consumer–resource interaction.

$$\frac{dN_i}{dt} = N_i \left(r_i + \sum_{j=1, j \neq i}^{J} \frac{\alpha_{ij} N_j}{b_j + N_j} - \sum_{j=1, j \neq i}^{J} \frac{\beta_{ij} N_j}{e_i + N_i} - d_i N_i \right) \quad (1)$$

The N_i is the population density of the species i, r_i is the intrinsic increase rate, α_{ij} is the per capita interspecific strength of species j benefiting species i by providing resource (species j as the resource), β_{ij} is the per capita interspecific strength of species j consuming (or in some cases just imposing costs on) species i (species j as the consumer), b and e are the respective half-saturation constants (which were both set as 0.5 for simplification), and d is the negative density-dependent strength.

For a given set of parameters in this model, the net positive or negative effect of species j on i depended on the density of both species. This is different from previous models (Hernandez 1998, Hernandez and Barradas 2003, Zhang 2003) in which the net effect only depended on the population density of species j. For this model, when α was much greater than β, the interaction tended to approach mutualism; when α was much smaller than β, it tended to approach competition; and when α and β were similar, it tended to be generalized predation (or a consumer–resource relationship).

Construction of bi-directional consumer–resource (BCR) ecological networks

For compatibility with May's work (1972) and limited available empirical networks with diversified interactions, we randomly constructed ecological networks to form a gradient of complexity and a null model for future exploration. The species number was set as $S = 20$, 40 and 80. The connectance was set as $C = 0.1$, 0.2, 0.4 and 0.8. Briefly, when the S and C were set, we calculated the number of paired links ($S \times C$) and then constructed an interaction matrix by randomly assigning these paired links (value = 1) to the cells. Each species was checked if it was connected to at least another species; if not, this process was repeated until a connected matrix was achieved. Based on Eq. 1, two interaction matrices were constructed to represent the strengths of providing and exploiting resources, i.e. the α and β matrix (Supplementary material Appendix 1 Fig. A1a). The values of α and β were both randomly drawn from half-normal distributions, with the means set to 0 and the standard deviations (SD) ranging from 0.1 to 2.0, with a gradient of 0.1. The varying gradients of the SD values led to different strengths of the α and β matrices, resulting in different initial compositions of interactions

(Supplementary material Appendix 1 Fig. A2). The half-normal distribution of interaction coefficients correspond to right-skewed distributions of interaction magnitudes that are commonly discovered in empirical works (Wootton 1997, McCann et al. 1998). The networks were referred to as BCR networks. One hundred replicate networks (varied in realized connections and values of interaction strengths) were generated for each combination of parameter sets, which resulted in 480 000 simulated networks.

Additional analyses were conducted for unidirectional consumer–resource models, in which one of the paired species only played a resource or consumer role. By using a matrix presentation of interaction strengths, we set the values of the lower triangle of the α-matrix as 0 to represent unidirectional consumer–resource interaction networks without mutualism (UCR-CP networks, Supplementary material Appendix 1 and 2 Fig. A1b) and set the values of the lower triangle of the β-matrix as 0 to represent unidirectional consumer–resource interaction networks without competition (UCR-PM networks, Supplementary material Appendix 1 Fig. A1c).

Simulation of community dynamics

To investigate the long-term persistence of the above ecological networks, we numerically solved Eq. 1 by using the lsoda algorithm for 10 000 time units, implemented by the deSolve package in R software (<www.r-project.org>, Soetaert et al. 2010). During the simulation, the population density was set to 0 if it was inferior to 1×10^{-6}. The r and d were randomly sampled from uniform distributions ranging from −1.5 to 1.5 and from 0.5 to 1.5, respectively. The initial population densities for the species were randomly sampled from a uniform distribution ranging from 0.1 to 10.

Network persistence

We analysed the change of network persistence and interaction outcomes at various levels of species number, connectance and strengths of providing and exploiting resources. Two measures of persistence were introduced: net and stable persistence. Following previous studies (Brose et al. 2006, Saavedra et al. 2011), the net persistence of each ecological network was calculated as the fraction of species remaining (population density $> 1 \times 10^{-6}$) at the end of the simulation. We considered a network as having achieved equilibrium when the variances of the population densities over the last 100 time steps were all lower than 1×10^{-6}. Because, in most cases, the network had some species going extinct, the local stability of a network with extinct species is not of interest to this study. We introduced the stable persistence measure considering the local stability of equilibriums, calculated by multiplying net persistence and local stability (stable = 1; unstable = 0). The local stability of each network was evaluated using a Jacobian matrix and numerically solved equilibria, implemented by the jacobian.full function in R package rootsolve (Soetaert 2016). Thus, a network might have a

non-zero net persistence, but if it was locally unstable, the stable persistence is 0.

Interaction outcomes

For the dual roles each species plays in this model, the interaction outcome depended on the interaction strengths (α_{ij} and β_{ij}) and population densities. For each pair of species, we identified the interactions by summing this part of $\left(\alpha_{ij} N_j / \left(b_j + N_j\right)\right) - \left(\beta_{ij} N_j / \left(e_i + N_i\right)\right)$ with the population density: if its value $\leq -1 \times 10^{-6}$, the effect of N_j on N_i was assigned as negative ($-$); if its value $\geq 1 \times 10^{-6}$, the effect of N_j on N_i was assigned as positive ($+$); for other cases, the effect of N_j on N_i was assigned as neutral (0). The species with zero density were excluded from this analysis. In this way, the interaction between each pair of species was defined as competition ($--$), amensalism (-0), predation ($+-$), mutualism ($++$), commensalism ($+0$) and neutralism (00). Two descriptions on interaction outcomes were introduced in this study: the initial proportion (I_i, i = interaction type) of each interaction was calculated using the initial population density and the long-term proportion (L_i) of each interaction was calculated using the final population density at the end of each simulation. During our simulation, we found that the instances of amensalism (-0), commensalism ($+0$) and neutralism (00) were very few due to the low probability of an exact combination of densities and parameter values that showed a neutral effect, so we only focused on the presentation of results on competition ($--$), predation ($+-$) and mutualism ($++$) (Supplementary material Appendix 1 Fig. A3). As the variation (SE) within the replicates for each parameter set was relatively small, the results of persistence and proportions of interaction outcomes were shown as average values in results section.

Density-dependent changes of interaction outcomes

Although the relative strengths of providing and exploiting resources largely determined the initial interactions, the transition from initial to long-term interaction was also affected by population dynamics. Once a network was constructed, the initial interactions of each type could be lost due to species extinction ($m_{i,\text{ex}}$ = the number of lost interactions due to species extinction, i = competition, predation or mutualism) and density-dependent sign change ($m_{i,\text{sign}}$ = the number of lost interactions due to density-dependent sign change), eventually forming the long-term interactions at the equilibrium states. We thus calculated which proportions were lost (from intial interactions) due to species extinction ($P_{i,\text{ex}} = m_{i,\text{ex}} / (m_{i,\text{ex}} + m_{i,\text{sign}})$) and density-dependent sign change ($P_{i,\text{sign}} = m_{i,\text{sign}} / (m_{i,\text{ex}} + m_{i,\text{sign}})$) for competition, predation and mutualism, respectively. Preliminary analyses showed that most interactions were lost due to species extinction. Because its difference between long-term and initial proportion for each interaction type was mainly related to the disproportionate loss of interaction types, not the absolute number, we

also calculated each interaction type's respective proportion out of all lost interactions due to species extinction ($E_i = m_{i,\text{ex}} /$ sum of m_{ex} of all three interaction types) and analysed its relationship with the difference between long-term and initial proportions ($D_i = L_i - I_i$).

Results

Because UCR-CP and UCR-PM networks were derived from BCR networks, we focused on presenting the results of the BCR networks. Generally, increases of species number and connectance decreased the net and stable persistence of the BCR networks. Both persistence measures decreased with the strengths of exploiting resources (β) at different levels of species number and connectance (Fig. 1, 2), while the strengths of providing resources (α) benefited both persistence measures at lower levels of β strengths in more complex networks (with high species number and connectance). The stable persistence was generally lower than net persistence, and in some networks with median levels of complexity (e.g. S = 40, 80 and C = 0.2), a slight decline was observed in the stable persistence with the increase of α strengths when β strengths were high (Fig. 2).

The networks with more initial mutualistic interactions and fewer antagonistic interactions (predation and competition) had higher net and stable persistence, and the networks with higher persistence contained a higher proportion of long-term mutualistic interactions (Fig. 3, Supplementary material Appendix 1 Fig. A4–A7). Additional analyses on UCR-CP and UCR-PM networks showed similar results, but the effects of the α strengths were very weak and even negative on stable persistence in the UCR-CP networks (Supplementary material Appendix 3).

The α and β strengths were interactively associated with the initial and long-term outcomes of different interactions in the BCR networks. Generally, the intial and long-term proportions of competition both decreased sharply with the α strengths but increased with the β strengths; the proportions of the initial predation interaction were highest when both strengths were similar, whereas the long-term ones decreased with α strengths but increased with the β strengths; the proportions of mutualism followed an opposite pattern of competition (Fig. 4, Supplementary material Appendix 1 Fig. A8). Additional analyses on unidirectional CR networks showed similar results on the long-term proportions of competition and mutualism but had some variation in the long-term proportions of predations with BCR networks; a higher proportion of predation was found when α strengths were higher than β strengths in the UCR-CP networks; a higher proportion of predation was found when α was lower in the UCR-PM networks (Supplementary material Appendix 2–3).

For all interaction types, species extinction caused the largest proportion of interactions lost in the most cases, whereas only few interactions were lost due to sign-changes
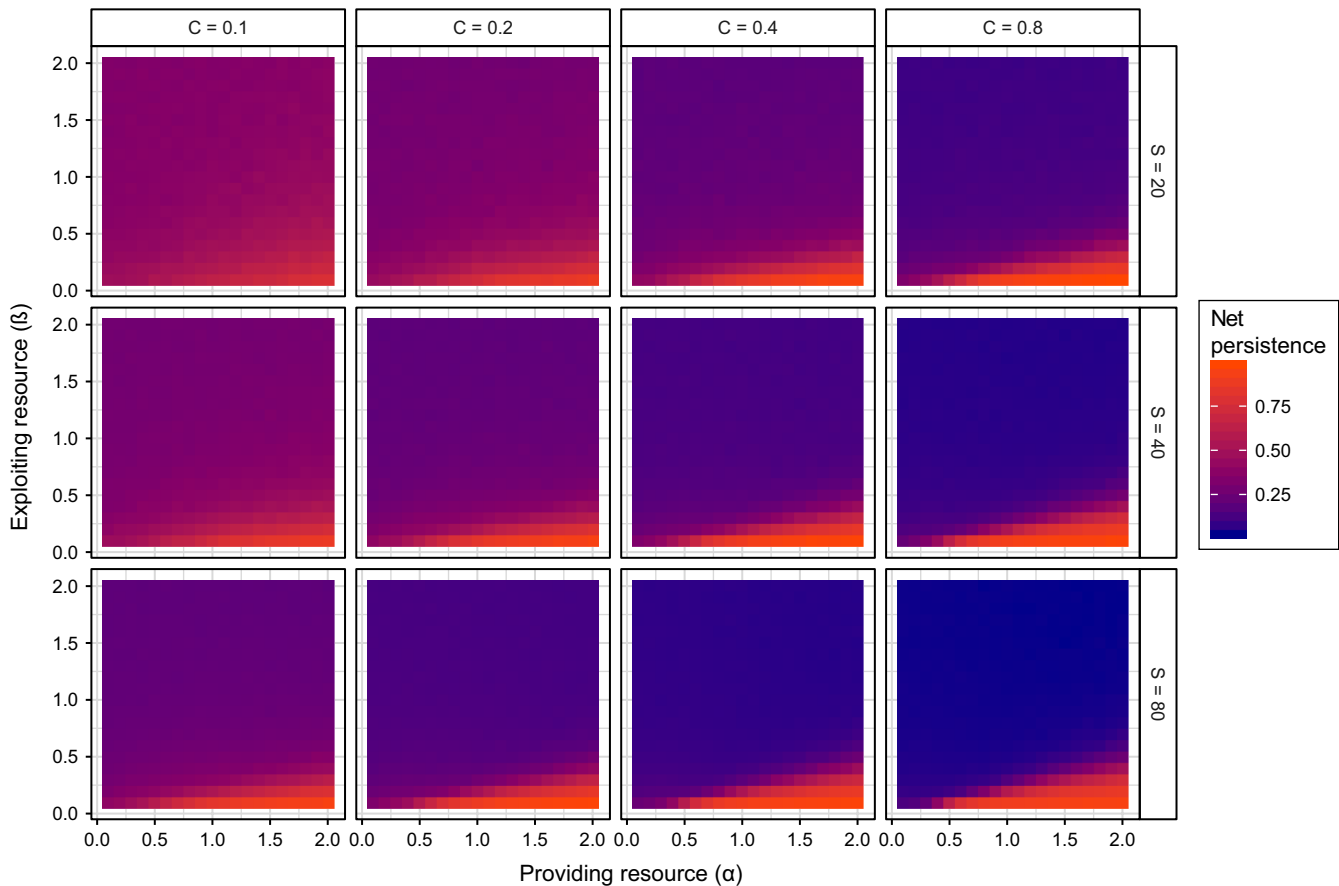
Figure 1. The effects of strengths of providing (α) and exploiting (β) resources on the net persistence of bi-directional consumer–resource (BCR) networks with different levels of species number (S) and connectance (C).

(Fig. 5a, Supplementary material Appendix 1 Fig. A9). The higher the proportion of one interaction type lost due to species extinction was, the more negatively it contributed to the long-term state compared to its initial state (i.e. lower increase or higher decrease, Fig. 5b, Supplementary material Appendix 1 Fig. A10).

Discussion

Although context-dependent interaction transitions have been commonly documented in the ecological literature (Chamberlain et al. 2014), the relationship among interaction transition, interaction diversity and persistence has been largely unknown in ecological networks. By simulating consumer–resource interaction transitions in random networks (Holland and DeAngelis 2009), we found that net and stable persistence decreased with the strength of exploiting resources but increased with the strength of providing resources in ecological networks with high-level species number and connectance. A higher initial proportion of mutualistic interactions relative to antagonistic interactions resulted in higher net and stable persistence. Meanwhile, a higher proportion of long-term mutualistic interactions were observed in the

networks with both types of persistence. Finally, the strengths of providing and exploiting resources, as well as population dynamics, interactively affected the long-term outcomes of different interactions. These results highlighted that community-level structural interaction transitions among competition, predation and mutualism might alter long-term dynamics and interaction diversity.

May (1972) demonstrated that the network complexity destabilized random ecological networks, where the complexity is measured as the species number, connectance and magnitude of interaction strength. Later studies confirmed this rule in other types of simulated ecological networks (Allesina and Tang 2012). Low-magnitude interaction strength or density-dependent satiation of strong interaction strength have been shown as able to benefit community stability (Nunney 1980, Kawatsu and Kondoh 2018). For a long time, the weak interaction hypothesis was believed to be one important mechanism for maintaining ecosystem stability (McCann et al. 1998). In this study, the stability of persisting species was incorporated by the stable persistence measure. Weak strength of exploiting resources contributed positively to the net and stable persistence. In more complex networks, the α strengths contributed positively to both types of persistence only when the β strengths were low; in less complex
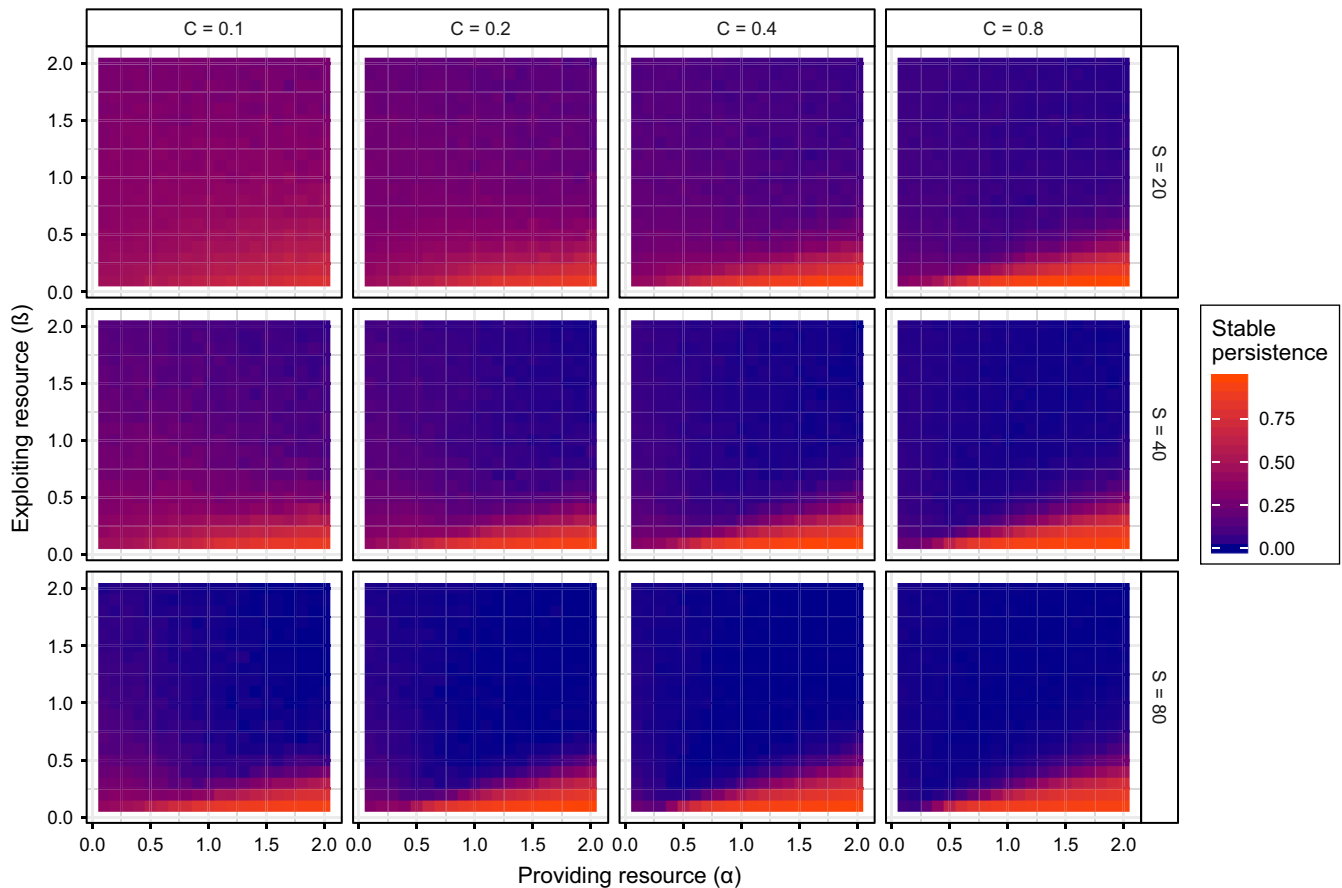
Figure 2. The effects of strengths of providing (α) and exploiting (β) resources on the stable persistence of bi-directional consumer–resource (BCR) networks with different levels of species number (S) and connectance (C).

networks (e.g. S = 40 or 80 and C = 0.2), the stable persistence decreased slightly with the α strengths. Our results seemed to be consistent with the weak interaction hypothesis in the sense of the diluting effect of weak β strengths and combining weak β strengths with strong α strengths (McCann et al. 1998). Nonetheless, since an interaction transition was involved, the net and stable persistence should be explained not only by altered interaction strength but also by the involvement of the sign changes in the interaction outcomes.

Real ecological communities are often composed of various interaction types (Melián et al. 2009, Pocock et al. 2012, Kéfi et al. 2015). Recent studies suggested that non-randomly structured interaction compositions have a substantial impact on community dynamics (Mougi and Kondoh 2012, Kéfi et al. 2016, García-Callejas et al. 2018, Gracia-Lázaro et al. 2018, Miele et al. 2018). Gross (2008) found that positive interactions among competitors can produce species-rich model communities. Under some combinations of interactions types, an increase in mutualistic interactions might promote persistence, local stability and spatial stability (Melián et al. 2009, Mougi and Kondoh 2012, Lurgi et al. 2016, García-Callejas et al. 2018). Mutualism has been shown as possibly supporting species diversity when competition is weak in mutualistic systems (Pascual-García

and Bastolla 2017, Gracia-Lázaro et al. 2018). Miele et al. (2018) applied a consumer–resource model and found that competition for space had a negative effect on diversity, biomass and production of niche-based food webs, while facilitation for recruitment had a positive effect. Similarly, our work has shared the same purpose of exploring the effects of interaction types on community dynamics. We found, consistent with these recent findings, a positive contribution of mutualism to both net and stable persistence at low-levels of antagonistic interactions and negative contribution of competition in random networks. Despite the similar consequence of changing interaction variety, the basic difference between previous studies and our work is the way of introducing interaction variety. Previous studies often directly introduced the variety of interaction types either by specifically theoretical assumptions or empirical network structure, whereas the interaction variety in this study was caused by simulating structural interaction transition between pairwise species, which enabled us to show a continuum of interaction composition. Altering the strength of providing and exploiting resources of one species can shift pairwise antagonistic interactions to mutualism (Supplementary material Appendix 1 Fig. A2), which contributed positively to the persistence of complex ecological networks
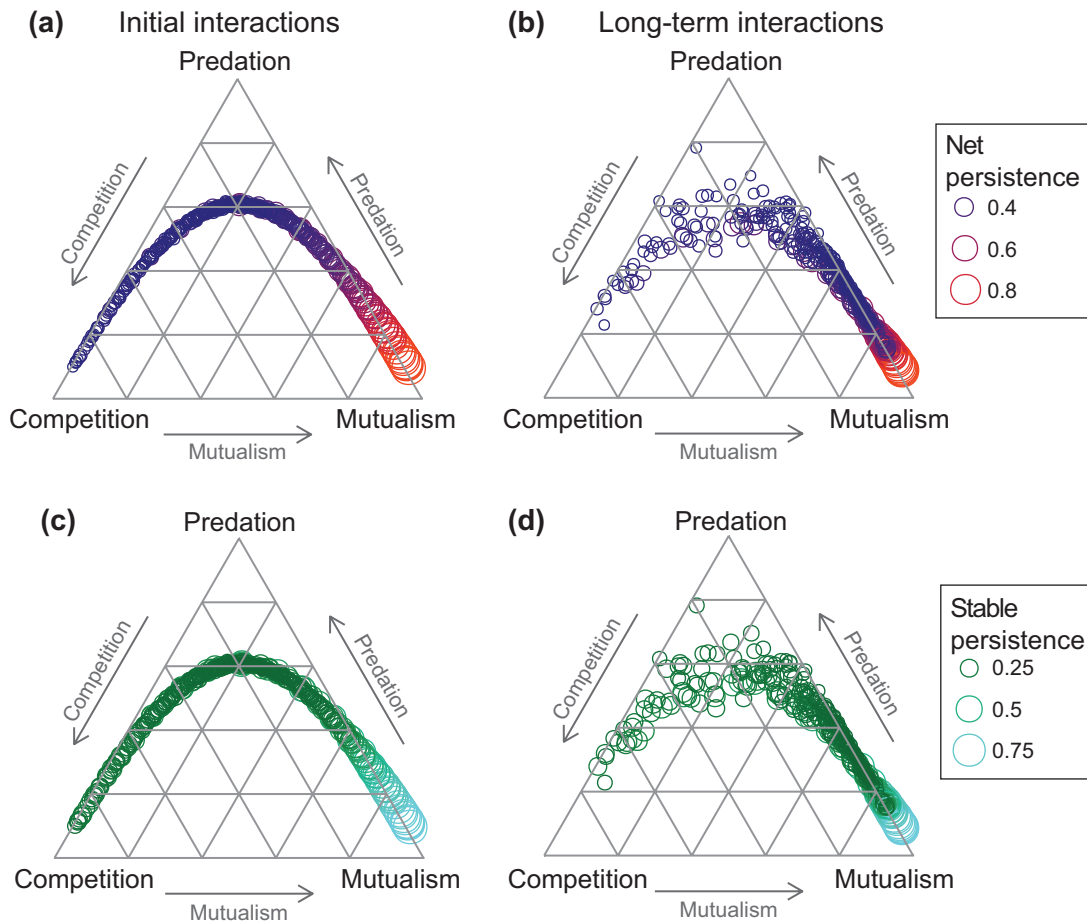
Figure 3. The relationships of initial (a, c) and long-term (b, d) compositions of interactions with the net and stable persistence of bi-directional consumer–resource (BCR) networks. Species number = 40; connectance = 0.2. Each circle in a ternary plot indicates the average composition of three types of interactions; the closer the circle is to one interaction, the higher the proportion in a network.

(Supplementary material Appendix 1 Fig. A4–A7). Therefore, what we have simulated is the context-dependent sign change of pairwise interaction outcomes, which might be one driving force for community dynamics.

The persistence (i.e. net persistence in this study) and local stability of ecological networks were both frequently used as stability measures in previous studies (Thébault and Fontaine 2010, Mougi and Kondoh 2012). We used stable persistence to consider both the fraction of persisting species and their local stability. Our results showed that stable persistence was usually lower than net persistence, and the relationships between interaction strength and two persistence measures were slightly different. Although a thorough analytic analysis is difficult for local stability of BCR networks due to high nonlinearity, we might have some clues from phase plane analysis of a two-species symmetrical BCR model. Actually, Holland and DeAngelis (2009) have explicitly analysed the properties of the two-species model, here we just redid the analyses along the parameter gradients for our simulation. As shown from Supplementary material Appendix 1 Fig. A11, when the strength of providing resources ($\alpha_{ij} = \alpha_{ji}$) was much greater than that of exploiting resources ($\beta_{ij} = \beta_{ji}$),

the zero-growth isoclines intersected at a stable feasible equilibrium, approaching a saturated mutualistic interaction; when α was much smaller than β, no stable coexisting equilibrium point could be achieved, approaching a strong competitive interaction. For some cases, the zero-growth isoclines were similar to non-monotonic interactions as demonstrated in previous studies (Hernandez 1998, Zhang 2003). Particularly, some were similar to an ellipse shape (Yan and Zhang 2018b), resulting in more complicated intersections between these zero-growth isoclines. Looking at the diagonal plots where $\alpha = \beta$ in Supplementary material Appendix 1 Fig. A9, the magnitude of the strength is crucial, and the status of the equilibrium points shifted from stable to unstable as the magnitude of the strength increased. However, our results might not be fully justified from two-species cases. Multi-species systems have distinct properties that can tangle the well-established dynamics of simple systems, thereby exhibiting completely different behaviours (Tikhonov and Monasson 2017). As seen in our results, the change of persistence along gradients of α and β was different at different levels of species number and connectance. Further exploration is thus needed in future studies.
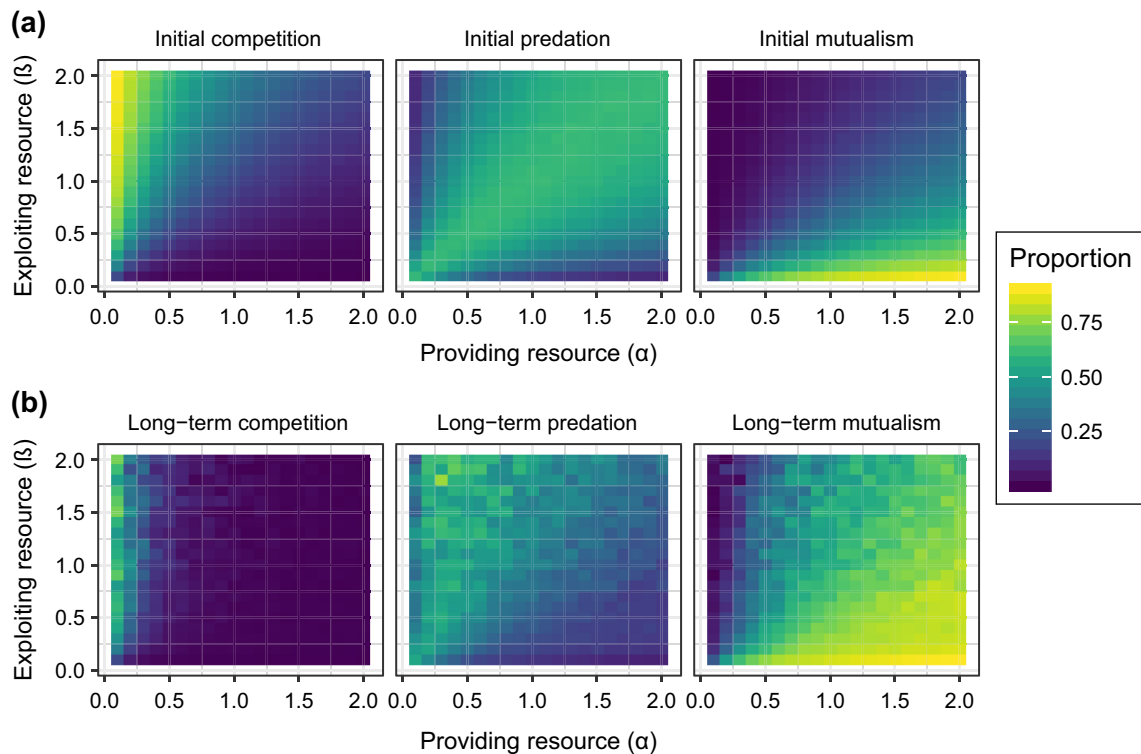
Figure 4. The effects of strengths of providing (α) and exploiting (β) resources on the initial (a) and long-term (b) proportions of interactions of competition, predation and mutualism in bi-directional consumer–resource (BCR) networks. Species number = 40; connectance = 0.2.

From previous theoretical and empirical studies, the outcomes of species interactions may depend on both the interaction structure and population density (Abrams 1987, Holland and DeAngelis 2009). Thereby, one can speculate that, in a multispecies system, the long-term outcomes of species interactions depend on the interaction structure, dynamic stability and density distribution. The ongoing diversity–stability debate stimulated numerous studies on ecological networks, but most of them focused on the performance of species and populations, asking questions about local stability, response to disturbance, temporal variation, etc. (McCann 2000). To our knowledge, few works studied the composition of species interactions due to interaction transitions. Our results show that the change of relative strengths of providing and exploiting resources largely shaped long-term interaction composition. An increasing tendency to provide but not to exploit resources caused a community with more antagonistic interactions and less mutualistic interactions to shift to one with less antagonistic interactions and more mutualistic interactions. However, we also found a density-dependent interaction change, including lost interactions due to species extinction and density-dependent sign change, which caused a difference between initial and long-term compositions. This suggested population dynamics were also involved in forming the long-term interactions, to which the disproportionate loss, mainly due to species extinction, made the most significant contribution. This is reasonable since persistence is quite low in many cases. The higher the proportion out of

all lost interactions due to species extinction was, the lower the increase or higher the decrease in the long-term proportion compared with its initial proportion. Meanwhile, species extinction (indicated by persistence) was also affected by interaction strengths. These results implied both structural interaction transitions and population dynamics are entangled in shaping the long-term interaction composition, which merits further exploration in future studies.

The interaction transitions between one pair of species could occur when both species play consumer and resource or only one of them plays consumer or resource (Holland and DeAngelis 2009). Although simulations of bi-directional and unidirectional networks showed similar results in most cases, some variations occurred due to the structural differences among the BCR, UCR-CP and UCR-PM networks. First, compared with bi-directional CR networks, unidirectional CR networks lacked either a mutualistic or competitive interaction. The overall net and stable persistence of the UCR-PM networks was higher than that of the BCR and UCR-CP networks, which again confirmed the positive contribution of mutualism (Supplementary material Appendix 1 Fig. A12, A13). Second, the effects of the relative strengths of providing and exploiting resources were slightly different. Compared with the BCR and UCR-PM networks, the UCR-CP networks represented mixed antagonistic networks; thus, the effects of the strength of providing resources (α) on persistence were much weaker than those of exploiting resources (β), and the composition of predation and competition
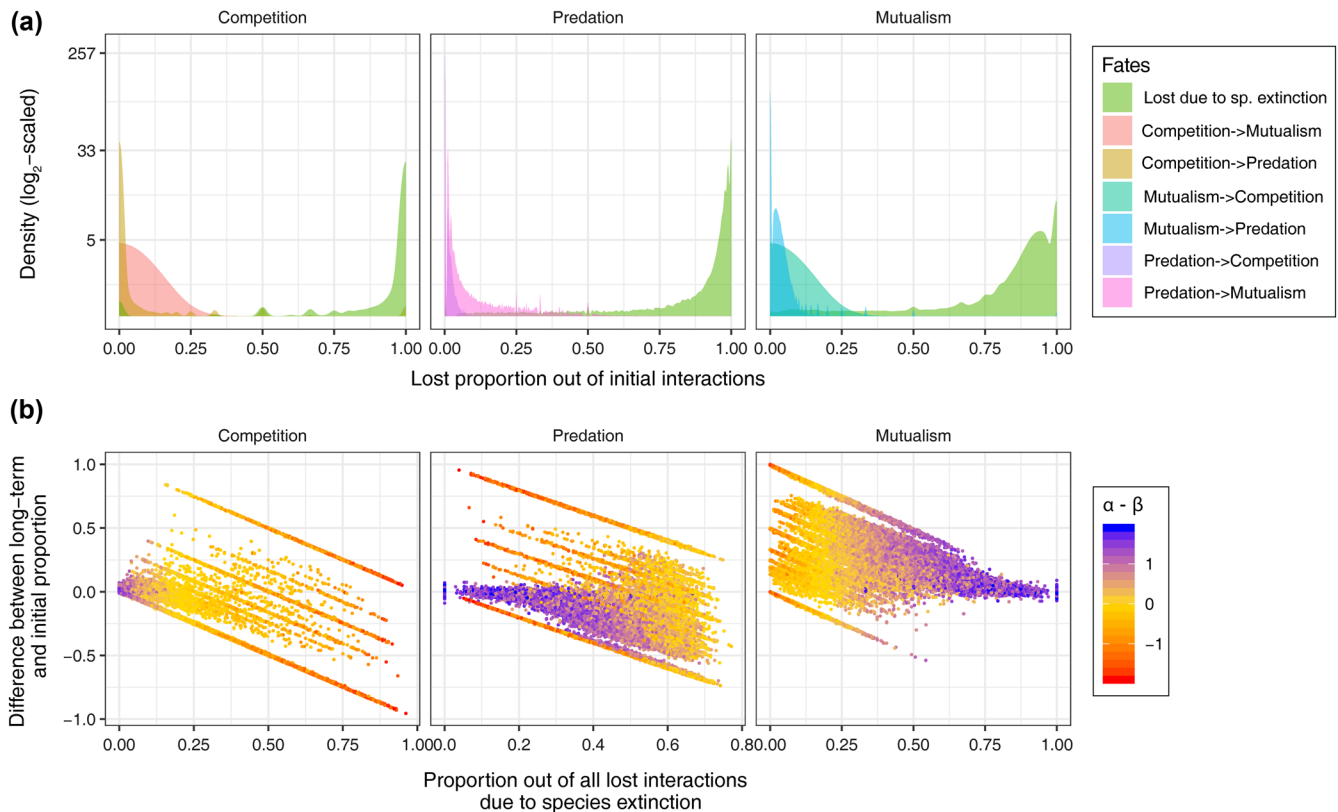
Figure 5. The distributions of lost proportions out of initial interactions (a, P_i) and the relationship between the proportion of lost proportion due to species extinction (E_i) and the long-term-initial difference (long-term proportion minus initial proportion, D_i) (b). Species number = 40; connectance = 0.2.

showed little impact on the persistence. Third, due to the differential design of the BCR, UCR-CP and UCR-PM networks, the effects of providing and exploiting strengths on long-term interaction compositions were different. These differences probably came from the differential overall distribution of the two types of strength, because UCR-CP and UCR-PM both had a large proportion of 0 values that pushed down the respective average strengths of providing or exploiting resources.

As a first attempt to incorporate BCR interaction into ecological networks, we should point out several limitations of this work. First, simulated random networks could not capture the non-random structure of empirical ecological networks, so the implication of our results for real communities remains to be tested. Currently, the empirical networks with both mixed interactions and interaction transitions are rarely available. Accumulating empirical examples of hybrid networks and context-dependent interaction transitions will be a challenge for testing our simulation results. Second, our results might be applicable only for the parameters tested in this study. Recent theoretical works showed that only a subspace of critical parameters (such as intrinsic growth rate) led to feasible equilibriums, namely, structural stability (Song et al. 2018). The BCR networks were also subject to this limitation, and it is worthy for further exploration

in future studies. Third, for nonlinear systems such as BCR networks, multiple equilibria and non-steady dynamics (like cycles and chaos) made evaluation of local stability rather complicated. Although we discarded occasional cyclic and chaotic dynamics data in our analyses, and ran replicates to consider multi-equilibria, further efforts should be made on these properties of BCR networks.

In conclusion, this work has extended the previous exploration on interaction transitions in simple theoretical systems and revealed significant relationships among interaction transitions, persistence and interaction diversity. With the changing strengths of exploiting and providing resources, the interaction outcomes shifted among competition, predation and mutualism, which consequently altered network persistence in random ecological networks, implying the sign changes of interaction outcomes might have a substantial impact on structure and stability of ecological networks. We thus urge more efforts to quantify interaction transitions and their consequences in natural ecosystems.

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