

Original research article

# Meta-community selection favours reciprocal cooperation but depresses exploitation between competitors

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## ABSTRACT

The evolution of cooperation and mutualism has mainly been explored through individual- and group-level processes. However, community-level processes could also impose selection pressure on species interactions. By using a dome-shaped nonmonotonic interaction (DS interaction) with cooperation at low-density and competition at high-density, we studied how cooperation and exploitation are selected at the meta-community level. Our results showed that population densities of species and communities were both significantly associated with the number of DS interactions and the species interaction modes. The more cooperation a species received via DS interactions, the higher its density was. A community with more DS interactions, especially more reciprocal cooperation, showed a higher total population density. Both reciprocal cooperators and exploiters in a local community were more favoured than unidirectional cooperators within a closed community. When facing competition from a community without cooperators (with only competitors), both reciprocal cooperators and exploiters were favoured in a local community, but only reciprocal cooperators were more favoured when facing competition from another community with cooperators. Our results suggest that selection at the meta-community level could be an alternative mechanism for the evolution of cooperation and the depression of exploitation between competitors.

## 1. Introduction

The evolution of cooperation has been extensively studied (Axelrod and Hamilton, 1981). Several classic theories, such as kin-selection, group selection, social punishment and direct or indirect reciprocal rewards, have been proposed to explain the emergence of cooperation or altruism among selfish competitors or exploiters (Nowak, 2006). Starting from 90s in the last century, there have been an increasing number of works on the evolution of cooperation within a network framework (Nowak and May, 1992; Perc and Szolnoki, 2010; Rand et al., 2014; Santos and Pacheco, 2005; Szabó and Fáth, 2007), and made many important discoveries on how network structure can entangle with cooperation evolution largely due to an application of statistical physics (Perc et al., 2017; Santos and Pacheco, 2005; Szabó and Fáth, 2007). Recently, this field made more advances by investigating evolutionary games on multilayer networks (networks of networks) (Wang et al., 2015b).

Regarding the selection pressure on the evolution of cooperation, there is still no consensus on the level of selection. Many evolutionary biologists believed that natural selection acted primarily at the level of the individuals, while higher level selection has been controversial

since it was firstly suggested by Charles Darwin (Darwin, 1871; Smith, 1964). Early group-level selection theory argued that individual animals could take actions for good of the species (Burkhardt, 2005), which was mathematically proved unlikely to occur and supported by few empirical evidence (Smith, 1964). However, there is a rebuttal on the higher level selection in recent years, e.g., multilevel selection theory. This theory considered groups of individuals may have functional organizations that can act as selection “vehicles” (Nowak et al., 2010b; Wilson and Sober, 2010), e.g., groups of social insects or primates. Groups that cooperate better might survive and reproduce have an advantage than those that did not. Yet, it again raised a lot of debates (Abbot et al., 2011). Furthermore, natural selection pressures may not be limited to individuals or groups with a species, they may also affect the persistence or competitive ability of a species via intra- or interspecific interactions at the community-level (Goodnight, 1990; Goodnight, 2005). However, previous studies on evolution of cooperation usually focused on evolutionary scales, while recent works showed that ecological and evolutionary process could be entangled (Post and Palkovacs, 2009). The effects of ecological dynamics on evolution of cooperation were less well studied.

Unlike individual-level cooperation, mutualism or interspecific

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cooperation mainly involves two species interacting and benefiting each other. So far, the theoretical framework on the evolution of mutualism often requires repeated interactions between the same partners, rewards for cooperation and punishments for defection or exploitation (Axelrod and Hamilton, 1981; Nowak, 2006). Multi-level selection might also emerge on evolution of cooperation in evolving networks (Szolnoki and Perc, 2009a,b). From the perspective of community dynamics at ecological scales, linear cooperation and mutualism drive community instability due to infinite positive feedbacks in complex ecological networks (May, 2001) and thus are less favoured by natural selection at the community level. Recent studies indicate that cooperation between competitors (i.e., species cooperate at low density and compete at high density, also called dome-shaped nonmonotonic interaction or DS interaction) could facilitate species coexistence and persistence (Yan and Zhang, 2014; Zhang et al., 2015). An additional study indicates that DS interactions could promote biomass accumulation while maintaining the persistence of a community (Yan and Zhang, 2018). The biological meaning of a DS interaction is that cooperation between competitors occurs at low population densities, while competition occurs at high population densities (Zhang, 2003). It is reasonable to use DS interactions to investigate how cooperation and mutualism between competitors could be selected for at the community level.

Most natural communities are relatively connected, either physically or by species dispersal, and therefore form meta-communities at some spatial scales (Leibold et al., 2010; Levin and Horn, 2018). Thus, population and community dynamics are not only affected by local species interactions but are also impacted by species interactions from other linked communities through regular dispersal processes or occasional invasions. The dynamics of meta-communities could serve as a mechanism for the selection of species and interaction strategies at the community level (Johnson and Boerlijst, 2002; Miller and Travis, 1996; Szolnoki and Perc, 2009a,b; Wang et al., 2015a). Unlike previous studies on high-level selection that often examined the evolutionary fitness of groups of individuals within a species, the meta-community dynamics could affect the fitness of species at ecological scales, i.e., the density or dominance of species. Species may form distinct interaction types in their local communities, and when they confront new, but similar communities through dispersal, competition may occur, namely, competition between communities; the originally formed interactions of each local community will affect the consequences of community competition, thereby creating a selection force on species interactions. This meta-community framework could not only help to understand the effects of nonmonotonic interactions on community dynamics at a regional level but also provide a candidate framework for explaining the evolutionary mechanisms of cooperation and mutualism as driven by community-level selection at ecological scales, which is still poorly investigated.

This study aimed to integrate an ecological (meta-) community framework with the evolution of species interactions by studying the effects of DS interactions (i.e., with cooperation at low density) on population and meta-community dynamics. In this study, species population density, i.e., the persisting population density of a species within a local community, was defined as the fitness of a species within a local or a meta-community. The species population density represented the dominance of a species within a community, which was related to the fitness of populations associated with success of survival and reproduction. We chose the species population density as the fitness index within a community because it is a basic and important characteristic for species at the ecological scales and involved in both ecological and evolutionary processes. The community population density was defined as the sum of persisting population densities of all species within a community, which measured the dominance of the community within meta-communities. We defined a community with a higher total population density of all species had a higher fitness at the meta-community level. The local interaction structure was represented by 3-

species interaction *motifs*, which are small, functional and connected subgraphs in large interaction networks (Milo et al., 2002). Based on a 3-species community with linear competitions, we first replaced linear competition interactions with dome-shaped interactions and examined the effects of DS interactions on species- and community-level population densities. The community containing only linear interactions was designated the LC-community, and the community containing DS interactions was designated the DS-community for simplified description. Second, we investigated the meta-community dynamics by linking an LC-community and a DS-community via species dispersal. Finally, we linked various DS-communities together to study the selection of cooperation and exploitation at the meta-community level.

## 2. Methods

### 2.1. Dome-shaped interaction

To construct a 3-species LC-community, we used a linear competition model Eqs. (1.1) and (1.2). To construct a 3-species DS-community containing cooperation, the DS interaction was introduced by multiplying an extra term that shifted the interaction effect from positive to negative, with an increase in population density of the interaction partner, which resulted in cooperation at low density but competition at high density Eqs. (2.1) and (2.2).  $N_1$  and  $N_2$  are the population densities of species 1 and 2 respectively;  $r_1$  and  $r_2$  are the intrinsic growth rates;  $a_{12}$  and  $a_{21}$  are the competition coefficients;  $b$  and  $c$  are the threshold densities of the interaction shift ( $N < c/b$ , positive effect or cooperation,  $N > c/b$ , negative effect or competition,  $N = c/b$ , no effect or neutralism). Fig. 1 shows the phase plane analysis of the co-existing cases between two species with symmetrical linear competition and a DS interaction.

$$\frac{dN_1}{dt} = N_1(r_1 - N_1 - a_{12}N_2) \quad (1.1)$$

$$\frac{dN_2}{dt} = N_2(r_2 - N_2 - a_{21}N_1) \quad (1.2)$$

$$\frac{dN_1}{dt} = N_1[r_1 - N_1 - a_{12}N_2(b_{12}N_2 - c_{12})] \quad (2.1)$$

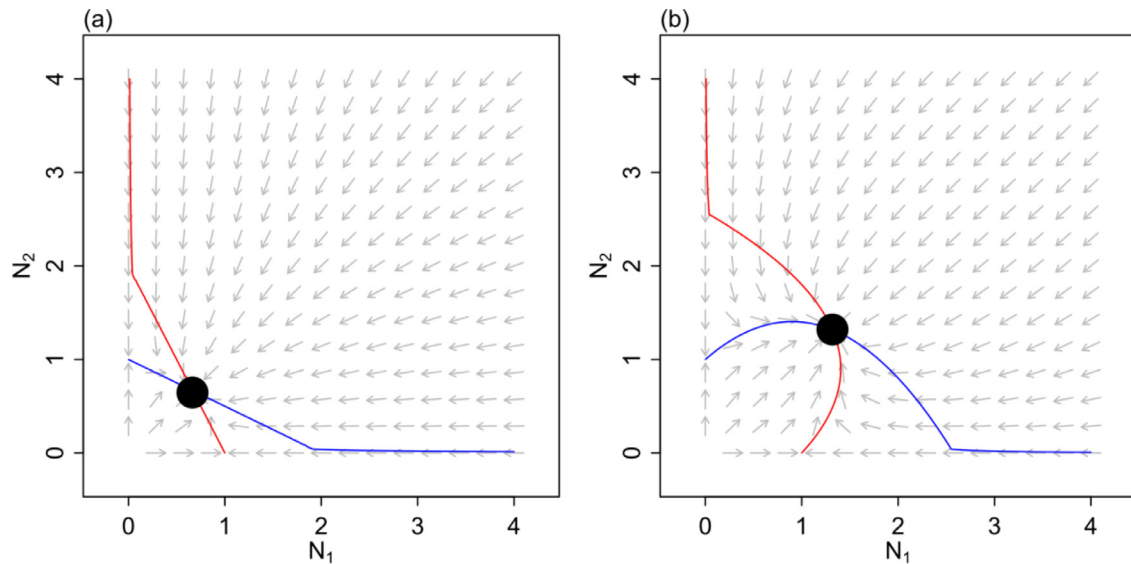
$$\frac{dN_2}{dt} = N_2[r_2 - N_2 - a_{21}N_1(b_{21}N_2 - c_{21})] \quad (2.2)$$

### 2.2. Construction of a 3-species community

We used a 3-species model to study the effects of DS interactions on species and community dynamics. First, we adopted a 3-species competition network, within which all three species showed linear symmetrical competition effects among themselves. Based on this LC-community (indicated by  $M_0$ , Fig. 2a), the dome-shaped interactions were then introduced, one by one, to the interaction between pairs of species (DS-communities, indicated by M1.1–M6.1, Fig. 2a) until all the interactions were replaced with DS interactions. There were some cases in which the same number of DS interactions were introduced, but the community structures were different (i.e., M2.1–2.4, M3.1–3.4, M4.1–4.4 in Fig. 2a). This replacement resulted in 15 types of DS-communities with different interaction structures.

### 2.3. The interaction mode of a species within a community

According to the interaction pattern a species had with its neighbouring species, its interaction mode was categorized into different types by considering the number of instances of reciprocal cooperation (RC), unidirectional exploitation (E) and unidirectional cooperation (C) present in the species. RC indicated that the species was involved in a reciprocal DS interaction (i.e., reciprocal cooperation at low density);



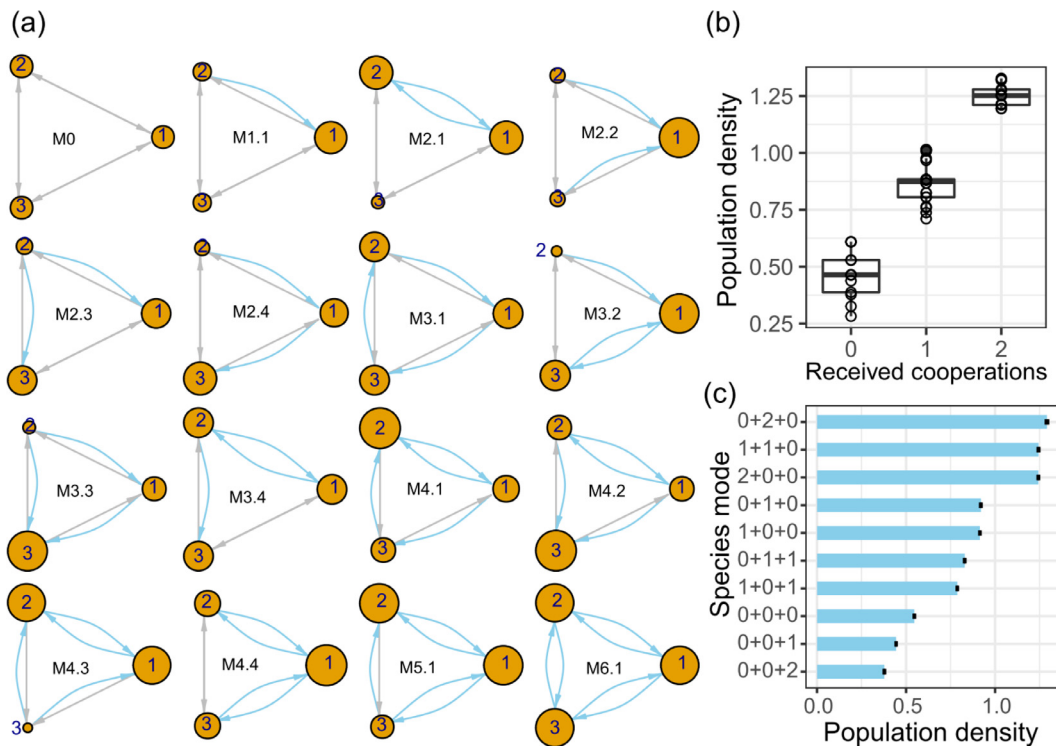
**Fig. 1.** The phase plane analyses of linear competition (a) and dome-shaped (DS, b) interaction models following Eqs. (1.1) and (1.2) and Eqs. (2.1) and (2.2), respectively. The results illustrated that the species with DS interactions have higher densities than those of linear competition.  $r_1 = r_2 = 1$ ,  $a_{12} = a_{21} = 0.5$ ,  $b_{12} = b_{21} = 1$ ,  $c_{12} = c_{21} = 1.8$ . The red lines indicate zero-growth isoclines for species 1 ( $N_1$ ), and the blue ones for species 2 ( $N_2$ ). For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.”

unidirectional exploitation (E) indicated that the species received a DS interaction from the other species; and unidirectional cooperation (C) indicated that the species contributed a DS interaction to the other species. One species can have multiple interactions simultaneously. For example, the interaction mode “RC + E + C” = “1 + 0 + 1” indicates that this species received one reciprocal cooperative interaction from

one species and no unidirectional cooperation from the other species, and contributed one unidirectional cooperative interaction.

2.4. Community and meta-community dynamics models

We adopted a set of differential equations to simulate population



**Fig. 2.** The relationships of simulated equilibrium densities with species interactions in 3-species local communities. (a) The equilibrium states of an LC-community (M0) and DS-communities (M1.1–6.1). The size of each circle is scaled to the equilibrium density. The grey straight arrows indicate linear negative effects. The blue curved arrows indicate dome-shaped effects containing cooperation at low density. (b) The relationship between species population density and the number of DS interactions a species received in a local community. (c) The relationship between species population density (mean  $\pm$  SE) and the interaction mode of a species (RC + E + C, i.e., reciprocal cooperation + unidirectional exploitation + unidirectional cooperation) in a local community. All pairwise comparisons are significantly different ( $P < 0.001$ ) except for the comparisons of “0 + 1 + 0” vs “1 + 0 + 0” and “1 + 1 + 0” vs “2 + 0 + 0.”

dynamics (Eq. (3)). In the model,  $N_i$  is the population density of species  $i$ ,  $r_i$  is the intrinsic growth rate,  $d_i$  is the self-density dependence coefficient (set to 1),  $a_{ij}$  represents the linear interaction effect of species  $j$  on species  $i$ , and  $a_{ik}$  represents the dome-shaped interaction effect of species  $k$  on species  $i$ . The coefficients  $b_{ik}$  and  $c_{ik}$  determine the threshold density, where the positive effect shifts to a negative effect.  $J$  and  $K$  represent the number of species showing linear and DS interaction effects, respectively.

$$\frac{dN_i}{dt} = N_i \left( r_i - d_i N_i - \sum_{j=1, j \neq i}^J a_{ij} N_j - \sum_{k=1, k \neq i}^K a_{ik} N_k (b_{ik} N_k - c_{ik}) \right) \quad (3)$$

The meta-community dynamics model (Eq. (4)) was modified from [Eq. \(3\)](#) by adding an extra dispersal component between two communities, where  $N_{ip}$  is the population density of species  $i$  in patch  $p$ . The subscript  $q$  indicates that the patch is connected to patch  $p$ . The dispersal process included immigration and emigration, both defined as a linear function of density.  $m_i$  is the dispersal coefficient, which assumed an identical dispersal ability for one species across patches.  $Q$  represents the number of patches connected to patch  $p$ .

$$\frac{dN_{ip}}{dt} = N_{ip} \left( r_i - d_i N_{ip} - \sum_{j=1, j \neq i}^J a_{ij} N_{jp} - \sum_{k=1, k \neq i}^K a_{ik} N_{kp} (b_{ik} N_{kp} - c_{ik}) \right) - m_i \left( N_{ip} - \sum_{q=1, q \neq p}^Q N_{iq} \right) \quad (4)$$

### 3. Simulation

#### 3.1. Simulation of local community dynamics

We first simulated the population dynamics of 1000 replicates for each type of community ( $M_0$ – $M_{6,1}$ ) to investigate the effects of DS interactions on the equilibrium density for each species and the total population density of each community (Fig. 2). In the study,  $r_i$  was set to be identical for all three species, which was randomly drawn from a uniform distribution [0.5, 1.5] for each simulation. The coefficient representing the negative competition effect of species  $j$  on species  $i$  was defined as  $a_{ij} = q_j \times q_j / (q_i + q_j)$ , where  $q$  was the competitive ability and was randomly drawn from a uniform distribution [0.01, 0.5]. Thus, a species with a high competitive ability imposed a relatively strong negative effect on its interacting partner. For this study, we let  $b = 1$  and randomly drew  $c$  from a uniform distribution [1, 2]. Initial population density of each species was randomly drawn from a uniform distribution [0, 5]. The simulation of population dynamics was integrated by the 4th order Runge–Kutta method for 20,000 time units (time step = 0.01) with the *deSolve* package in R version 3.4 (R Development Core Team, 2010; Soetaert et al., 2010).

#### 3.2. Simulation of meta-community dynamics

The meta-community dynamics were simulated by linking two communities that were assumed to be originally occupying two different patches (local community), through bi-directional dispersal of species (Fig. 3). We assumed linear competition interactions between species from two different local communities, but the species kept the same DS interactions with the partners from their original community, which assumed the integrity and preservation of the original community (i.e., a DS interaction between species was assumed to be conserved or heritable for these focal species). By using the simulated equilibrium densities of the respective original closed community as initial densities, we simulated the dynamics of meta-communities following Eq. (4).

Two scenarios were studied here, aiming to examine the

community-level selection of DS interactions (i.e., cooperation or exploitation). First, the LC-community was linked with various DS-communities to form different LC + DS meta-communities. This scenario was designed to test the selection of RC, E and C interaction modes when a DS-community faces competition with an LC-community. Second, we linked the DS-community with reciprocal cooperation interactions (i.e., M2.1 and M4.4) and those with either unidirectional cooperation or exploitation (i.e., M2.1 vs M2.2–2.4; M4.4 vs M4.1–4.3). The second scenario was designed to test the selection of RC, E and C modes when DS communities with same number of DS interactions competed with each other. Because linking two communities would lead to equilibrium states where the communities occupying the two patches (local community) were identical, we only showed the results for one community.

#### 3.3. Statistical analysis

Linear mixed models (LMM) were applied to test the difference in population density of a species (species population density) between different species modes. The species population density was set as the response variable, species interaction mode was set as the fixed factor, and the different communities nested within replicates were taken as the random factors. LMM was also applied for analysing the difference in total population density of a community (community population density) between communities, where the community population density was the response variable, community was the fixed factor, and replicate was the random factor. A post hoc test of the pairwise comparison was performed for the above models. All response variables were checked for approaching normal distributions. The R packages used included *lme4*, *lmerTest*, and *lsmeans* (R Development Core Team, 2010).

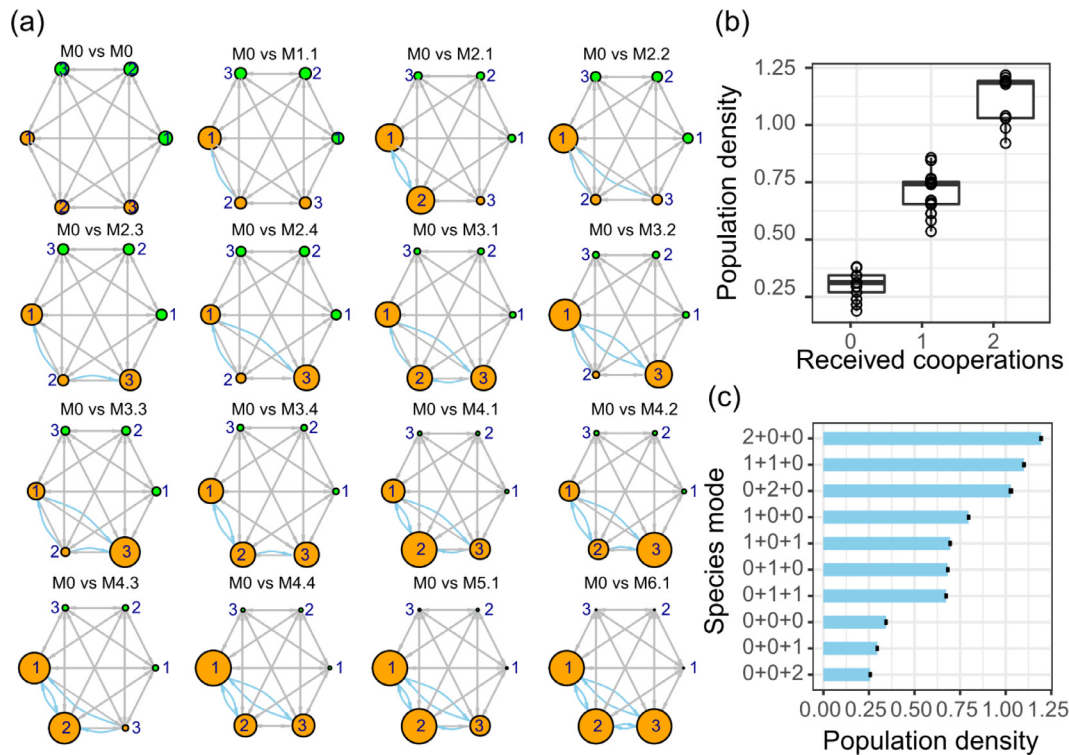
### 4. Results

#### 4.1. Local community dynamics

Introducing DS interaction into an LC-community substantially affected the species population density (Fig. 2a). The equilibrium density of a focal species depended on the number of DS interactions it received. The more DS interactions it received, the higher the population density it reached (Fig. 2b). The species interaction mode significantly affected the species population density in a local community ( $\chi^2 = 8.115 \times 10^4$ ,  $df = 9$ ,  $P < 0.001$ ; Fig. 2c, Fig. S1a). The species with more RC and E modes had a higher population density than those with a C mode. The species with “RC + E + C” modes of “0 + 2 + 0” had the highest population density, and those with a mode of “0 + 0 + 2” had the lowest density. The community population density generally increased with the number of DS interactions it contained; there were also significant differences between communities with same number of DS interactions ( $\chi^2 = 7.42 \times 10^4$ ,  $df = 15$ ,  $P < 0.001$ ; Fig. 4a).

#### 4.2. Meta-community dynamics linking LC and DS communities

When linking DS-communities with an LC-community, the species population density increased with the number of DS interactions it received, but the rank of the species population density of the species interaction mode was different from that for the local community dynamics ( $\chi^2 = 1.114 \times 10^5$ ,  $df = 9$ ,  $P < 0.001$ ; Fig. 3c, Fig. S1a). The species with an RC mode had a higher population density than those with E and/or C modes, while the unidirectional cooperators had lower densities. The species with the mode “2 + 0 + 0” had the highest population density, and the mode “0 + 0 + 2” had the lowest population density (Fig. 3c). More DS interactions led to a higher relative community population density of the DS-community (compared with the community population density of the LC-community; Fig. 4b).



**Fig. 3.** The relationships between simulated equilibrium densities and species interactions in different LC + DS meta-communities. (a) Meta-community dynamics were simulated by linking an LC-community with DS-communities. The green-filled circles indicate the species from the original LC-community, and the orange-filled circles indicate the species from the original DS-community. (b) The relationship between species population density and the number of DS interactions a species received in a meta-community. (c) The relationship between species population density (mean ± SE) and the interaction mode of a species (RC + E + C, i.e., reciprocal cooperation + unidirectional exploitation + unidirectional cooperation) in an LC + DS meta-community. All pairwise comparisons are significantly different ( $P < 0.001$ ) except for the comparison of “0 + 1 + 0” vs “0 + 1 + 1.”

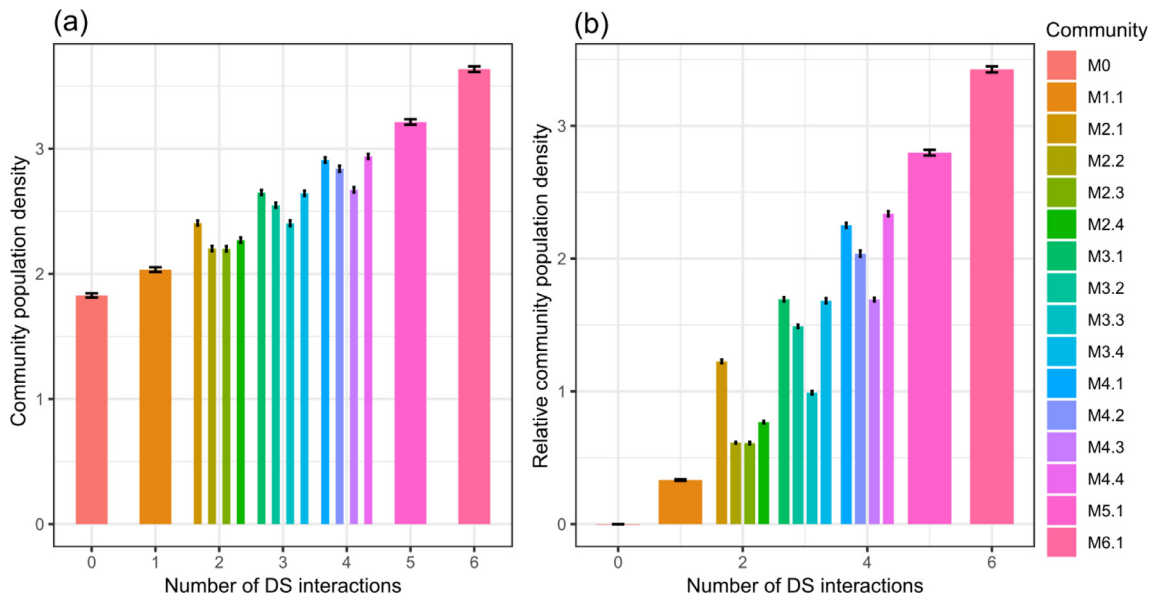
4.3. Meta-community dynamics by linking DS communities

When linking the communities with only RC modes (i.e., M2.1 and M4.4) and the communities with E and/or C modes, the density of the species with RC modes was always higher than those with E or/and C

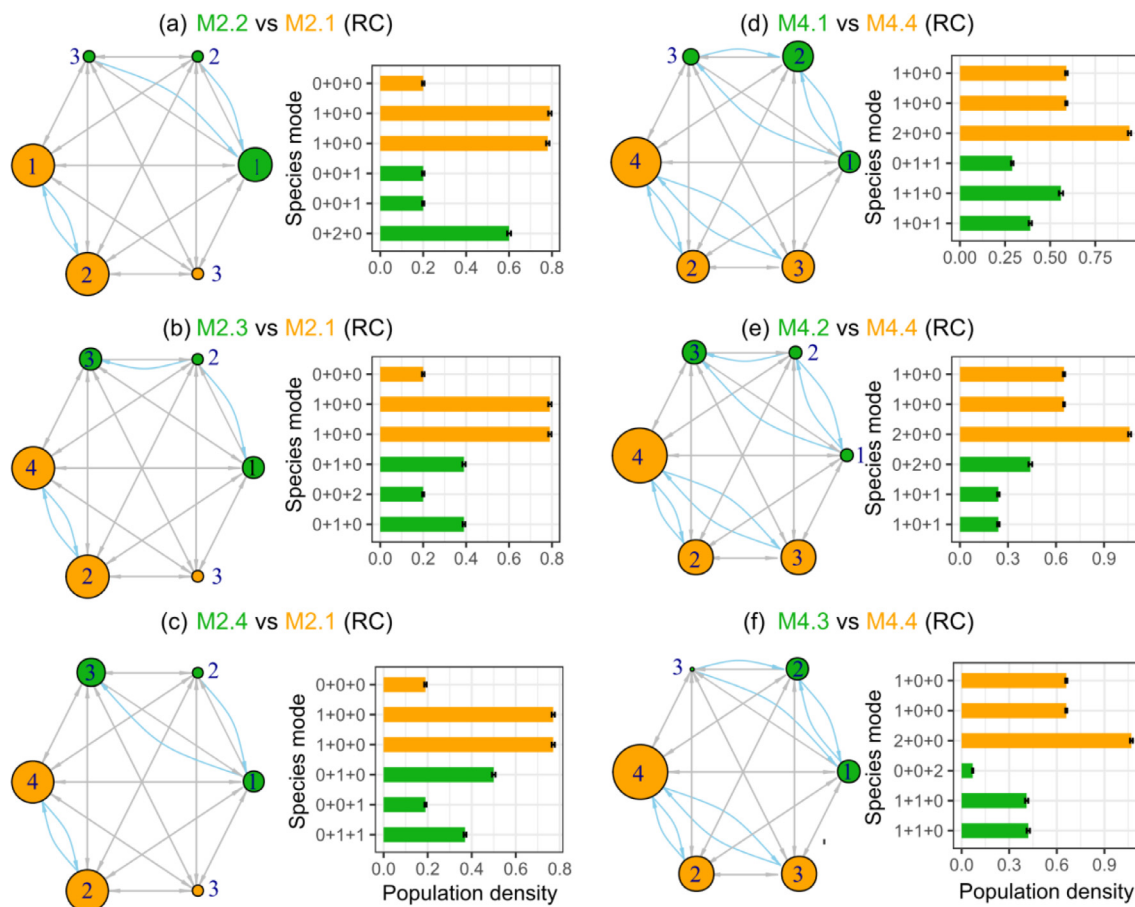
modes (Fig. 5).

5. Discussion

The evolutionary mechanism of cooperation has been extensively



**Fig. 4.** The relationships between number of DS-interactions and the community population density (mean ± SE) of each local community (a) or the relative community population density of the original DS communities in meta-communities (b). The meta-community was constructed by linking a DS community with an LC community. The relative community population density of the DS community = the community population density of the original DS community—that of the original LC community.



**Fig. 5.** The relationships between interaction structure and equilibrium density (mean  $\pm$  SE, based on 1000 replicates) of a species after linking the DS-communities with reciprocal cooperation only (RC) and with unidirectional exploitation (E) and/or unidirectional cooperation (C). The size of each circle is scaled to the equilibrium density. The orange circles indicate a species from a DS-community with only RC, while the green circles indicate a species from a DS-community with E and/or C. The grey straight arrows indicate the linear negative effects. The blue curved arrows indicate the dome-shaped effects containing cooperation at low density.

explored at the individual and group levels within an evolutionary game framework, but how ecological community-level processes shape the evolution of cooperation has been less well investigated in the literature. Our simulation results using DS interactions indicated that, within a local community, both reciprocal cooperation and unidirectional exploitation prevailed, but unidirectional cooperation was prohibited. Similar results were observed within a meta-community by allowing competition between an LC-community and a DS-community. However, within a meta-community, by allowing competition between the communities containing reciprocal cooperation and those with unidirectional exploitation or cooperation, reciprocal cooperation prevailed, but unidirectional exploitation was prohibited. The total population density of a community was positively associated with the number of DS interactions containing cooperation at low density. Our results suggested that reciprocal cooperation between competitors was favoured by natural selection at the meta-community level. Therefore, selection at the meta-community level may be an alternative evolutionary mechanism for the evolution of cooperation, not exploitation.

The game theory framework has been the main tool for studying the evolution of cooperation by analysing the costs and benefits of interactions between individuals. The repeated prisoner's dilemma, in which the same partners interact repeatedly, was proposed as a basic framework for studying cooperation between unrelated individuals (Axelrod and Hamilton, 1981; Trivers, 1971). Evolutionary theories about interspecific mutualism are largely inherited from the individual-level framework. Most of the relevant work involves the strategies of rewarding cooperation and punishing defection or the persistence of

previously successful behaviours (Traulsen and Nowak, 2006). Previous theories focused on fitness of individuals or groups of individuals, and usually assumed a behavioural response to the partner's behaviour for each iteration of a game, while at the community-level, the fitness of a species can be measured by population growth and density, which are long-term measurements affected by community or meta-community dynamics. Thus, individual-level selection favouring cooperation does not necessarily favour cooperation at the community level. For example, linear mutualism can lead to a destabilized community in which no species can persist (May, 2001). Actually, few species survive in an isolated environment, so species interactions in a local community have a large impact on the dominance or density of species (Callaway, 1995; Vázquez et al., 2007). Community-level selection has been suggested as an alternative selection force for species (Johnson and Seinen, 2002; Szolnoki and Perc, 2009b; Wilson, 1992). We have shown that the interaction mode of DS interactions had a significant impact on population density of a species. Within a local community, the species interaction mode largely determined the species' dominance within the community. Previous studies suggested that at low-density, mutualism between competitors (one type of DS interaction) can increase the equilibrium density of a species, indicating that DS interaction has an advantage over linear competition (Zhang, 2003). Similarly, in this study, the more positive feedbacks received through DS interactions were, the higher the population density of the focal species was. Within a local community, we found that unidirectional exploiters ("0 + 2 + 0") had a similar, or even a slightly higher, density than reciprocal cooperators ("2 + 0 + 0"), and unidirectional cooperators

("0 + 0 + 2") had the lowest density (Fig. 2). Thus, it seems that a local community should equally favour reciprocal cooperation and unidirectional exploitation but not unidirectional cooperation. Additionally, we found that there was some variation in density among species with the same interaction mode (Fig. S1), indicating that the population density of interacting partners also affects species dominance and density.

Through species dispersal, species interaction types that originated in different local communities (or patches) could act as a selective pressure on the species (Johnson and Boerlijst, 2002). Some previous studies showed that the spatial structure of communities affects the evolution of antagonistic interactions in model systems (Baalen and Sabelis, 1995; Haraguchi and Sasaki, 2000; Johnson and Boerlijst, 2002), but studies on mutualistic interactions are sparse (but see Yamamura et al., 2004). Our results from the analyses of meta-community dynamics showed that the population density of a species within a local community was affected by the invasion of interacting partners from other communities. Linking an LC-community with a DS-community led to a decrease in population density for all species, since each species faced more competition. However, the population density of the species that benefited from DS-interactions was still higher than that for the species from the LC-community, which suggests an advantage for DS interactions in community competition. Unlike in closed local communities, the reciprocal cooperators had a higher average population density than the exploiters, indicating that the reciprocal cooperators might have had some advantage over exploiters under the meta-community scenarios. We noted that the unidirectional exploiter (species 3 in M4.2) still had a similar density with the reciprocal cooperators in some cases. This question was further addressed by connecting communities with only low-density reciprocal cooperation (M2.1, M4.4) and communities with exploiters (M2.2–2.4, M4.1–M4.3). With the same number of DS interactions in the communities, the reciprocal cooperators (1 + 0 + 0 or 2 + 0 + 0) clearly had a higher density than the pure or partial exploiters. This is probably due to fact that the reciprocal cooperators (two species) in a local community imposed double-negative effects on the exploiters from the other local community. In a DS + DS meta-community, the exploiters were successfully prohibited, suggesting that DS-interactions are not only important in promoting cooperation between competitors but also essential in depressing exploitation.

For a long time, ecologists have focused on the relationship between total biomass or productivity and species richness across different communities, such as the positive or dome-shaped relationships (Gough et al., 1994; *Philosophical Transactions of the Royal Society of London B: Biological Sciences* et al., 1999), while its relationship with species interactions was not well studied, partly because the empirical evaluation of species interactions is often difficult (Wootton and Emmerson, 2005). However, it has been shown that, in plant communities, nurse plants provide facilitation effects for other plants and promote biomass accumulation during succession (Callaway, 2007; Cavieres and Badano, 2009). In this study, the introduction of DS interactions that allowed for low-density cooperation could significantly benefit the total population density of a community. From the results of local- and meta-community dynamics, the number of DS interactions in a community mainly determined the rank of total population density (Fig. 2). This was consistent with a previous study conducted using complex networks (Yan and Zhang, 2018). There was a variation in total population density for those communities having the same number of DS interactions, suggesting that the local interaction structure also affected the total population density of a community. At both the local- and meta-community levels, reciprocal cooperation was found to significantly increase community biomass accumulation. A special case was that of community M3.1; this community had indirect reciprocal cooperation and had a high total population density, because each species received a positive effect from DS interactions, suggesting that an indirect interaction mode also contributed to population density of a

species.

Unlike individual-based selection theory, multi-level selection theory states that selection acts on both individuals and groups, which can also favour cooperation (Wilson and Sober, 1994). Traulsen and Nowak (2006) found that during simulated competition between groups, groups of cooperators outweigh groups of defectors because individuals in cooperating groups reproduce more and split more often. Our model is different from group selection for cooperation in several aspects. First, our framework is not based on repeated games but on ecological meta-communities; and second, the fitness of a species did not depend on instant payoff but was based on the realized equilibrium population density which indicates the dominance of the species. Although a higher level of selection force was considered here, we stressed the roles of ecological meta-community dynamics in the natural selection of cooperation and exploitation.

In our attempt to incorporate ecological meta-community level process into evolution of cooperation, we noted our results were subject to several limitations that needed further investigation. First, in this study, our meta-community is only composed of two communities for simplification, while the spatial structure of meta-communities should be much more complicated in nature. The application of our results in complicated spatial communities remained to be tested, probably by integrating spatial networks and DS communities. Second, the meta-community process introduced two levels of community structure: one is the interaction structure within a local community, and the other is a combination of different interaction structures from different local communities. Although we focused on the level of species and above that, the setting of structured DS communities has a certain analogy with structured population that has been extensively studied for evolution of cooperation (Nowak et al., 2010a; Tarnita et al., 2009, 2011). How the merging of structured communities and populations impacts on evolution of cooperation still needs further investigation.

In conclusion, both the reciprocal cooperators and exploiters in a local community were more favoured than the unidirectional cooperators or those facing competition from other noncooperating communities, while the reciprocal cooperators in a local community were more favoured when facing competition from other cooperating communities. Our results suggest that selection at the meta-community level could be an alternative mechanism for the evolution of reciprocal cooperation and the depression of exploitation between competitors.

### Competing interests

We have no competing interests.

### Authors' contributions

Both authors contributed to study design, data analysis and writing. Both authors gave final approval for publication.

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### Supplementary materials

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