The joint evolution of cooperation and competition

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ABSTRACT

In nature, cooperation among individuals is often accompanied by competition among the same individuals for the cooperatively produced rewards. In such a situation, the evolution of cooperative and competitive investments influences each other, but previous theoretical studies mostly focused on either cooperation or competition. Here we consider a generic situation in which individuals cooperatively produce rewards according to the continuous snowdrift game, and then rewards are divided among cooperating individuals according to a generalized tug-of-war game. Using adaptive dynamics and numerical simulations, we investigated the joint evolution of two continuous traits, the investment in cooperation and in competition, respectively. We found that competition for the division of rewards promotes evolutionary branching, and hence polymorphism in both the cooperative and the competitive traits. In polymorphic populations, cooperation levels are positively correlated with competition levels among strains, so that cooperators tend to benefit disproportionately from the benefits produced. We also found that the mean cooperation level within the population is promoted by the competition. Our results show that coevolution of cooperation and competition has qualitatively different outcomes compared to the evolution of only cooperation or only competition, and suggest that it is important to simultaneously consider multiple aspects of social interactions.

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1. Introduction

Cooperation is a ubiquitous social interaction, and many theoretical studies have investigated the conditions that are necessary for the evolution of cooperation (Hamilton et al. 1964a,b; Axelrod, 1984; Nowak, 2006; Ohtsuki et al., 2006; Fletcher and Doebeli, 2009). However, in nature social interactions are often multifaceted and involve various aspects of sociality. One important aspect of cooperation is the conflict over cooperatively produced rewards. Some empirical studies have reported that cooperative interactions are often accompanied by competition with group members for the division of the cooperative rewards. For example, microbes cooperatively produce decomposition products by sharing enzymes with neighbouring cells, but they compete with each other for absorbing the decomposition products (West et al., 2007). Animals often cooperate for hunting, but in the process of the division of hunted prey they often compete with each other (examples include sailfish (Herbert-Read et al., 2016), social spiders (Yip et al., 2017), Killer whales (Hoelzel, 1991) and primates (Kopp and Liebal, 2016). In group forming species, males often cooperatively guard a group of females from mating with males from

outside of the cooperative group, but they also compete within the group for mating with the females they guard (Rood, 1990; Davies, 1992). Simultaneous cooperation and competition also appear to be ubiquitous in human societies (Bouncken et al., 2015).

In these examples, social interactions contain aspects of both cooperation and competition within the cooperating group. On the one hand, the benefit from investing in competitive ability depends on the amount of public good produced from cooperative actions, and on the other hand, the benefit from an investment in cooperation depends on the competitive ability of a cooperating individual, i.e., on the share of the public good that the cooperating individual is able to secure for itself. This interdependence between cooperation and competition can be expected to generate dynamics for the joint evolution of these traits that are generally different from the evolution of either cooperation or competition in isolation. Some theoretical studies also suggested the joint evolution of multiple social traits can realize new evolutionary outcomes that are not predicted in the analysis with focusing only one social trait (Brown and Taylor, 2010; Mullon et al., 2016).

Nevertheless, cooperation and competition have been investigated separately in most previous theoretical studies. For example, the situation in which players cooperatively produce rewards that are shared equally has been considered by using various models, such as the snowdrift game (Maynard Smith, 1982), continuous snowdrift game (Doebeli et al., 2004) or public goods game

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(Kagel and Roth, 1995; Hauert et al., 2006). In these models, players either do or do not contribute (discrete strategies), or they contribute various amounts (continuous strategies) to the production of a public good. The public goods game also explicitly considers the division of cooperative rewards among group members. However, in these games it is typically assumed that the proportion of the division of cooperative rewards is equal, and the evolution of competitive interactions, i.e., an evolutionary departure from the assumption of equal shares, is not considered.

The process of the division of rewards has also been investigated using various models. For example, in the hawk-dove game (Maynard Smith and Price, 1973) aggressive behaviour can monopolize a reward, and division of rewards has e.g. been investigated when there is variation in fighting ability (Crowley, 2001; Dubois and Giraldeau, 2007) or in the response to an opponent's information (Mesterton-Gibbons, 1994). Optimal skew or transactional models (Vehrencamp, 1983) consider situations in which the division of the reward in the group can be controlled by one dominant individual, and the other subordinate individuals choose whether to join the group or not (Keller and Reeve, 1994; Reeve and Emlen, 2000). In the tug-of-war game (Reeve et al., al.1998) (sometimes called the "compromise model"), individuals can change the proportion of reward division by investment in competitive traits, and the optimization of investment in competition can be investigated (Hamilton, 2013). Finally, the war of attrition game considers a similar question (Bishop et al., 1978), with a focus on optimizing wait times for reaping rewards. While the above models have been used to address optimal behaviours or investment in competition for the division of a reward, the production of the reward has not been considered as an evolving quantity.

Few investigations have considered the co-occurrence of cooperation and competition. For example, Reeve and Hölldobler (2007) considered co-occurrence of between-group competition and within-group competition by using a tug-of-war game, in which the reward is first divided among groups, and then among group members. Because the investment in between-group competition can be considered as a kind of cooperation, this study partially addressed the problem of competitive cooperation, but it was limited in that the total amount of investment in competition was assumed to be fixed, and players could only optimize the ratio of between-group and within-group competition. Barker et al. (2012) investigated the optimization of investment in both cooperation and competition, but only the case where the costs of cooperation and competition are equal and linear in the amount of cooperation and competition. Yamauchi et al. (2018) considered a situation where cooperatively produced reward was divided among neighbours, but in their study the proportion of the obtained reward is determined by the amount of investment in cooperation, i.e., the investment in cooperation and investment in competition were not independently evolving traits. Overall, the joint evolutionary dynamics of investment in cooperation and investment in competition for the rewards produced by cooperation has not been investigated in sufficient detail and generality.

The aim of this study is to investigate the evolutionary dynamics in a model in which cooperative and competitive investments are separate and independent traits, with each trait being an important part of the selective environment determining evolution of the other trait. We consider a simple but general model in which individuals cooperatively produce a public good according to the continuous snowdrift game, and in which the public good is divided among cooperating individuals according to a tug-of-war game with continuously varying strategies. We investigated the joint evolution of investment in cooperation and investment in competition using adaptive dynamics and numerical simulations. The model shows a rich variety of evolutionary dynamics, in-

cluding evolutionary diversification in both traits, resulting in coexistence of different combinations of cooperation and competition. Overall, the results show that considering the joint evolution of cooperation and competition can be crucial for understanding social evolution.

2. Model

2.1. Continuous snowdrift game and tug-of-war game

In order to study the evolution of competitive cooperation, we combined the continuous snowdrift game (Doebeli et al., 2004) and the tug-of-war game (Reeve et al., 1998) in a single model for evolutionary dynamics.

In the continuous snowdrift game, two individuals cooperatively produce rewards based on their amount of investment in cooperation, which is a continuous trait hereafter called cooperation level or cooperative investment. The amount of produced reward is an increasing function of the sum of the investments of two individuals. In addition, each individual pays a cost, which is an increasing function of an individual's investment. In the resulting continuous game, it is known that evolutionary branching in the cooperation level can occur, i.e., even if the population is monomorphic initially, selection often causes diversification (Doebeli et al., 2004). In this case, cooperation levels become dimorphic, i.e., more cooperative and less cooperative individuals coexist within the evolving population. In the continuous snowdrift game, evolutionary branching occurs only when both the reward and the cost functions have concave shapes (Doebeli et al., 2004, see also Appendix A1).

In the tug-of-war game (Reeve et al., 1998), each individual has a continuous trait that determines the investment in competition, or the competition level. Two individuals compete with each other for a reward, and the proportion of the reward obtained depends on the relative amount of competitive investment of the two individuals. Each individual pays a cost that is an increasing function of the competitive investment. In contrast to the continuous snowdrift game, in this game evolutionary branching cannot occur regardless of the functional form of the benefit and cost functions (see Appendix A2).

2.2. Payoff function in competitive cooperation

To investigate competitive cooperation, we combine the continuous snowdrift game and the tug-of-war game by assuming that individuals cooperatively produce rewards following the continuous snowdrift game, and that these rewards are then competitively shared according to the tug-of-war game. Specifically, we assume that each individual has two of non-negative traits (x, y), where x is the cooperation level and y is the competition level. We assumed the cooperatively produced reward is a power function of the sum of the investments of two individuals. We also assumed that individuals with larger competitive investments get a larger share of the reward produced according to the ratio of exponential functions of the competitive investment (see Eq. (1) below). Each individual pays the costs of cooperation and competition as power functions of its own cooperation and competition level. Accordingly, when a focal individual (x', y') interacts with an (x, y)-individual, the payoff of the focal individual is

$$w(x', y' \mid x, y) = (x' + x)^p \frac{\exp(\varepsilon y')}{\exp(\varepsilon y') + \exp(\varepsilon y)} - \alpha x'^q - \beta y'^r \quad (1)$$

The parameter $\varepsilon \geq 0$ in Eq. (1) reflects the importance of competitive investments, with $\varepsilon = 0$ corresponding to the case where competitive investments are irrelevant. p, q and r are positive parameters determining the curvature of the functions describing

cooperative rewards, cooperative costs and competitive costs. The functional shapes become concave when p, q or r are less than 1, and convex when these parameters are larger than 1. α and β determine the relative magnitude of the costs of cooperation and competition, respectively ($0 < \alpha$ and $0 < \beta$). Note that we assume that the costs that an individual incurs are independent of the partner's investment levels. This assumption will be adequate when individuals cannot change cooperative investments in response to a partner's investments, e.g. because the competitive traits is not phenotypically plastic (e.g. body size).

If the investment in competition is fixed at the same level for all individuals in a population, Eq. (1) is mathematically the same as the one resulting from the continuous snowdrift game (Doebeli et al., 2004, see Appendix A1). Similarly, if the investment in cooperation is fixed at the same level for all individuals in a population, Eq. (1) is mathematically that same as the one resulting from the tug-of-war game (Reeve et al., 1998, see Appendix A2). Hereafter we call these cases "cooperation-only" and "competition-only" cases, respectively.

2.3. Joint evolution of cooperation and competition in monomorphic populations

First, we focus on the evolutionary dynamics in monomorphic populations. The payoff of a rare mutant (x', y') in a monomorphic resident population in which all individuals have traits (x, y) is given by Eq. (1). Using the framework of adaptive dynamics (for a detailed discussion of this theory, as well as the underlying assumptions, see e.g. Dieckmann and Law, 1996; Geritz et al., 1998; Doebeli, 2011), the selection gradients for the two traits x and y are

$$\frac{\partial w}{\partial x'}\bigg|_{\substack{x'=x \\ y'=y}} = 2^{p-2} p x^{p-1} - \alpha q x^{q-1} \tag{2a}$$

and

$$\frac{\partial w}{\partial y'}\bigg|_{\substack{x'=x \\ y'=y}} = 2^{p-2} \varepsilon x^{p} - \beta r y^{r-1} \tag{2b}$$

respectively. We assume that mutations occur separately and independently in the two traits x and y; then the adaptive dynamics of the two traits x and y is are proportional to the selection gradients for each trait. In this case, the curves defined in the (x, y)-plane by setting the selection gradients to 0 are the "nullclines" of the cooperation level and competition level, respectively (Fig. 1).

Eq. (2a) implies that the selection gradient for the cooperation level x is independent of the competition level y, i.e., competition has no influence on the evolution of cooperation in monomorphic populations. As a consequence, the evolutionary dynamics in monomorphic population can be investigated by first investigating evolutionary equilibrium states of the cooperation level, and then investigating the evolution of competition by studying Eq. (2b) under the assumption that the cooperation level is at an equilibrium.

The rate of evolutionary change in the cooperation level becomes 0 at the interior singular solution x^* obtained by setting Eq. (2a) to 0:

$$x^* = \left(\frac{2^{p-2} p}{\alpha q}\right)^{\frac{1}{q-p}} \tag{3}$$

Because p, q and α are positive, the singular solution (3) exists as long as $p \neq q$. When $p = q$, there is no interior singular solution, and the cooperation level either decrease to 0 (the lowest possible value by assumption) or increases without bound, depending on the parameters p and α (Appendix A3). However, in the biological context it seems to be unrealistic that the exponents of cooperative
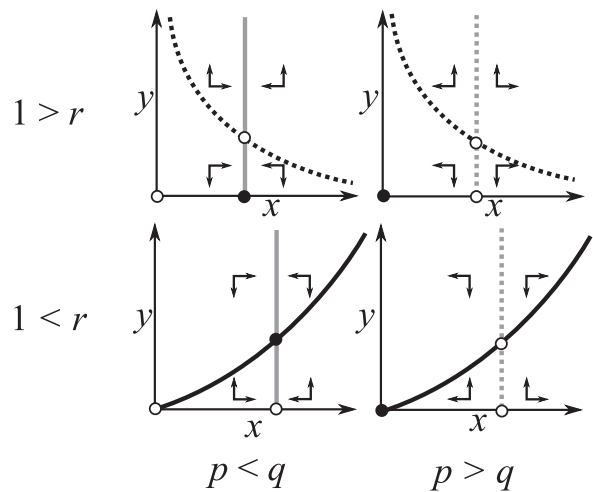
Fig. 1. The location of singular solutions and their convergence stability for representative sets of parameters. Solid and dotted curves show convergence stable and convergent unstable nullclines of the cooperation level x (grey) and competition level y (black), i.e., the set of points satisfying Eqs. (2a) and (2b) equal to zero. White and black circles are non-convergence stable and convergence stable singular solutions. There are three evolutionary equilibrium points regardless of parameter values, (0, 0), (x^*, 0) and (x^*, y^*), with $x^* > 0$ and $y^* > 0$. For any sets of parameters, exactly one of these is convergence stable.

benefit and cooperative cost functions (i.e., p and q) are exactly the same. Therefore, in the following analysis we assume $p \neq q$.

The singular solution x^* is convergent stable when

$$\frac{\partial}{\partial x}\left[\frac{\partial w}{\partial x'}\bigg|_{\substack{x'=x \\ y'=y}}\right]_{x=x^*} < 0 \tag{4}$$

It is easy to see (Appendix A3) that $p < q$ is the condition for inequality (4) to be satisfied, and hence for convergence stability of x^*. As a consequence, when $p < q$, the cooperation level always converges to the singular value x^* regardless of the evolutionary dynamics of the competition level y. When $p > q$, the cooperation level decreases to 0 over evolutionary time when the initial level is below the singular value x^*, and it increases without bound (unless a bound is imposed by assumption) if the initial level is larger than the singular value x^*. Hereafter, we represent this case as $x \to \infty$, or just simply ∞.

Next, we consider the evolution of competition assuming that the level of cooperation is x^*, i.e., assuming $p < q$. The selection gradient of the competition level becomes 0 at the singular solution y^* obtained by setting the selection gradient (2b) to 0:

$$y^* = \left(\frac{2^{p-2}\varepsilon\left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p}{q-p}}}{\beta r}\right)^{\frac{1}{r-1}} \tag{5}$$

Because ε, r and β are positive, y^* always exist as long as $r \neq 1$. Again, there is no singular solution of competition level at $r = 1$, but the realized evolutionary outcomes are easily categorized (Appendix A3). In the following analysis, we focus on the case $r \neq 1$.

y^* is convergence stable when

$$\frac{\partial}{\partial y}\left[\frac{\partial w}{\partial y'}\right]_{\substack{x=x^* \\ y=y^*}} < 0 \tag{6}$$

and it is easy to see (Appendix A3) that $r > 1$ is the condition for this inequality to be satisfied. It follows that (x^*, y^*) with x^* given by (3) and y^* given by (5) is a globally convergent stable solution when $p < q$ and $r > 1$. When $p < q$ and $r < 1$, y^* is not convergent

stable, and depending on the initial state the competition level goes 0 (when the initial trait value of y is $< y^*$) or keep increasing (when the initial trait value of y is $> y^*$), i.e., the strategy of the population converges to $(x^*, 0)$ or (x^*, ∞).

When $p > q$ the cooperation level decreases to 0 or diverges to infinity. In the former case, the selection gradient for the competition level becomes negative for all y for small enough x (see Eq. (2b)), therefore such systems evolve to $x = 0$ and $y = 0$. In the latter case, y also diverges to infinity (see Eq. (2b)), i.e., $x \to \infty$ and $y \to \infty$. Overall, monomorphic population thus evolve to the following states (assuming that the initial trait values are not 0, x^* or y^*, respectively):

(x^*, y^*) when $p < q$ and $1 < r$,
$(x^*, 0)$ or (x^*, ∞) when $p < q$ and $1 > r$, and
$(0, 0)$ or (∞, ∞) when $p > q$

(Fig. 1).

In particular, except for cases in which one or both traits diverge to infinity, the evolutionary dynamics converges to one of the states (x^*, y^*), $(x^*, 0)$ or $(0, 0)$. Despite being convergent stable, these states may or may not be evolutionarily stable (Geritz et al., 1998). Evolutionary stability is determined by the Hessian matrix of second derivatives of the invasion fitness function, Eq. (1), evaluated at the convergent stable state (see Appendix A3). If this Hessian matrix is negative definite, the convergence stable state is also evolutionarily stable, and hence represents an endpoint of the evolutionary dynamics. Conversely, if the Hessian has one or two positive eigenvalues, the population can undergo evolutionary diversification and become polymorphic. Considering first the interior equilibrium (x^*, y^*), whose convergence stability requires $p < q$ and $1 < r$, the additional condition for the Hessian not to be negative definite, and hence the conditions for evolutionary branching is

$$1 < r \text{ and } 2q - 1 - \frac{\varepsilon p}{2(r-1)} \left(\frac{2^{p-2} \varepsilon \left(\frac{2^{p-2} p}{\alpha q} \right)^{\frac{p}{q-p}}}{\beta r} \right)^{\frac{1}{r-1}} < p < q \quad (7)$$

(see Appendix A3).

If (7) is satisfied, the direction of evolutionary branching is given by the eigenvector of the maximal eigenvalue of the Hessian, which has non-zero values for both x and y elements (Appendix A3). Thus, branching occurs in both the cooperation level and the competition level. We note that (7) is a necessary condition for the occurrence of evolutionary branching in the cooperation-only model (Appendix A3). Thus, while the singular solution for the cooperative trait and its convergence stability under competitive cooperation are mathematically identical to the cooperation-only model (Appendix A1), the condition for evolutionary stability of the singular point in competitive cooperation is more severe than that in the cooperation-only model. Consequently, evolutionary branching occurs for a wider range of parameters with competitive cooperation.

At the boundary equilibrium $(x^*, 0)$, the selection gradient in the y-direction is negative and evolutionary branching cannot occur in the y-direction (negative y-values are not possible by assumption). Therefore, evolutionary stability only needs to be checked in the x-direction: $(x^*, 0)$ is evolutionarily stable if the fitness of a rare mutant $(x, 0)$ has a local maximum at $x = x^*$. It follows (see Appendix A2) that the conditions for $(x^*, 0)$ to be convergence stable and evolutionarily unstable are

$$r < 1 \text{ and } p < q < 1 \quad (8)$$

If (8) is satisfied, evolutionary branching occurs in the level of cooperation. It can be shown that after branching, the selection

gradient for the competition level is always negative in both coexisting strains resulting from evolutionary branching (Appendix A4). As a consequence, the level of competition will remain at 0 in the coexisting strains, and the evolutionary dynamics of cooperation after branching becomes mathematically equivalent to that occurring in the continuous snowdrift game without competition (Doebeli et al., 2004). Finally, when the evolutionary dynamics converges to $(0, 0)$, both selection gradients in x and y continue to be negative and evolutionary branching is not possible.

2.4. Numerical simulation of evolutionary dynamics after evolutionary branching

After evolutionary branching, the evolving population becomes polymorphic and contains multiple strains each with a different set of cooperation and competition levels. The evolutionary dynamics can become rather complicated, and we have therefore used numerical simulations for further investigations of these dynamics. Specifically, we implemented simulations of the deterministic dynamics of 2-dimensional trait distributions with mutations. In these simulations, we discretize phenotype space by first choosing an upper boundary b for both phenotypes, and then dividing the permissible phenotype space into n^2 squares with side length $d = b/n$ for some integer n. For any given population, let $f_t(i, j)$ be the frequency, at time t, of individuals in the population that have a strategy in a square "bin" of phenotype space whose lower left corner has coordinate $(i*d, j*d)$, where i and j run from 0 to $n - 1$. We assume that the dynamics of $f_t(i, j)$ is determined by the mean per capita fitness in the corresponding bin of phenotype space:

$$W_t(i, j) = \sum_k \sum_l f_t(k, l) \; w(id_x, jd_y | kd_x, ld_y) \quad (9)$$

where w is the payoff function (1). Then $f_t(i, j)W_t(i, j)$ is the total number of offspring of the individuals in the corresponding bin of phenotype space.

We incorporate mutation by assuming that with probability γ, offspring have a phenotype belonging to one of the phenotype bins that are adjacent to the parent bin. Thus, the frequency of the (i, j)-bin in the next generation is:

$$\begin{aligned} g_t(i, j) &= (1 - \gamma)f_t(i, j)W_t(i, j) \\ &+ \frac{\gamma}{4}f_t(i+1, j)W_t(i+1, j) + \frac{\gamma}{4}f_t(i-1, j)W_t(i-1, j) \\ &+ \frac{\gamma}{4}f_t(i, j+1)W_t(i, j+1) + \frac{\gamma}{4}f_t(i, j-1)W_t(i, j-1) \end{aligned}$$
(10)

The first term on the r.h.s. of Eq. (10) is the number of offspring of individuals in the (i, j)-bin without mutation, and the other terms represent offspring with mutations of individuals from neighbouring bins. (The above expression is adjusted accordingly for phenotypes on the boundary of trait space, i.e., when i or j have values 0 or $n - 1$.) We can then simulate the replicator-mutator equation (Hadeler, 1981; Bomze and Burger, 1995) for the discretized trait distribution $f_t(i, j)$ by iterating the following equation for small enough time steps δ:

$$f_{t+1}(i, j) = f_t(i, j) + \delta \left[g_t(i, j) - f_t(i, j)\bar{W}_t \right] \quad (11)$$

where $\bar{W}_t$ is the mean fitness in the population, i.e.,

$$\begin{aligned} \bar{W}_t &= \sum_i \sum_j g_t(i, j) \\ &= \sum_i \sum_j f_t(i, j) \; W_t(i, j) \end{aligned} \quad (12)$$

By iterating (11), we essentially solve a partial differential equation describing the dynamics of the frequency distribution of

an evolving population. For purposes of comparison, we used an analogous procedure to simulate the evolutionary dynamics in the cooperation-only model.

3. Results

3.1. Evolutionary outcomes

We used numerical simulations of the dynamics of frequency distributions to investigate scenarios of evolutionary diversification, i.e., scenarios in which the analytical results predicted evolutionary branching. Fig. 2 shows typical examples of the results of the numerical simulations. In Fig. 2a, evolutionary diversification results in two coexisting strains, one with high cooperative and competitive investments, and the other with low investments in both cooperation and competition. In Fig. 2b, multiple evolutionary branching occurs, and a polymorphism with more than two coexisting strains emerges from the evolutionary dynamics. Fig. 2c shows another salient case, in which the evolving population undergoes repeated bouts of diversification followed by extinction of one of the emerging phenotypic branches. As a consequence, the mean levels of cooperation and competition fluctuate over evolutionary time.

From our extensive simulations, we found that the curvature of the cooperative reward and cost functions have a strong influence on evolutionary outcomes (Figs. 3 and 4). When both reward and
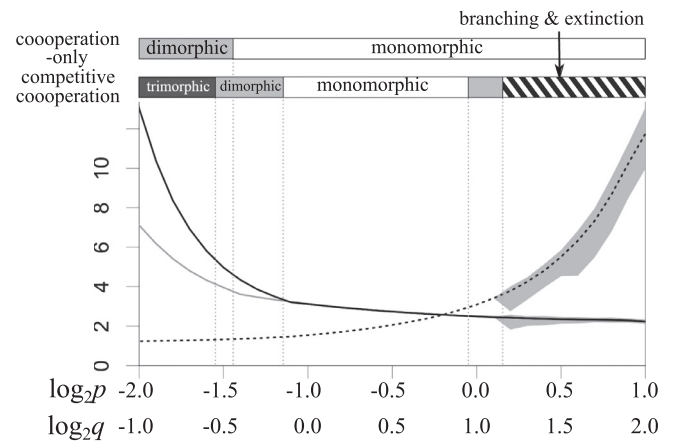

Fig. 3. Comparison between the cooperation-only model and the full model with competitive cooperation with changing curvatures of the cooperative reward function and the cooperative cost function. The bars at the top indicate the number of strains in the corresponding cooperation-only models (upper bar) and in the full model with competitive cooperation (lower bar), and the lower panel shows the mean cooperation level in cooperation-only models (solid grey line) and the mean cooperation level (solid black line) and the mean competition level (dotted black line) in competitive cooperation models. Grey shaded regions are parameters leading to fluctuations in cooperation and competition levels due to repeated branching and extinction (as shown in Fig. 2c). The other parameters were $\varepsilon = 1.0$, $r = 2.0$, $\alpha = 0.1$, $\beta = 0.2$.
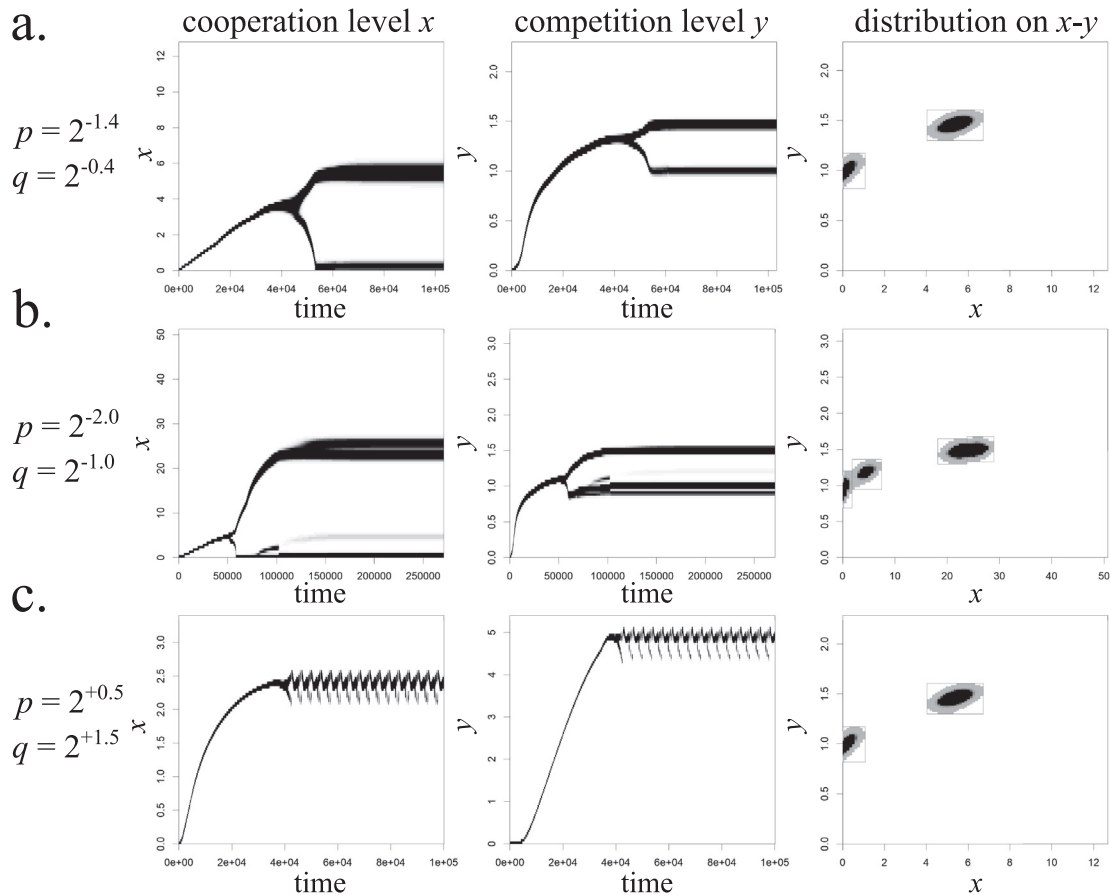
Fig. 2. Evolutionary dynamics of the cooperation level (left panels) and the competition level (centre panels); the right panels show the distributions of strategies at the end of the simulations, representing an evolutionary stable state (darker areas represent higher frequencies). The top row (a) shows an example of evolutionary branching leading of coexistence of two strains. The middle row (b) shows an example with secondary branching, leading to the coexistence of four strains. The bottom row (c) shows an evolutionary pattern of repeated branching and extinction. Other parameters are $\varepsilon = 1$, $r = 2$, $\alpha = 0.1$, $\beta = 0.2$, $k = 1$.
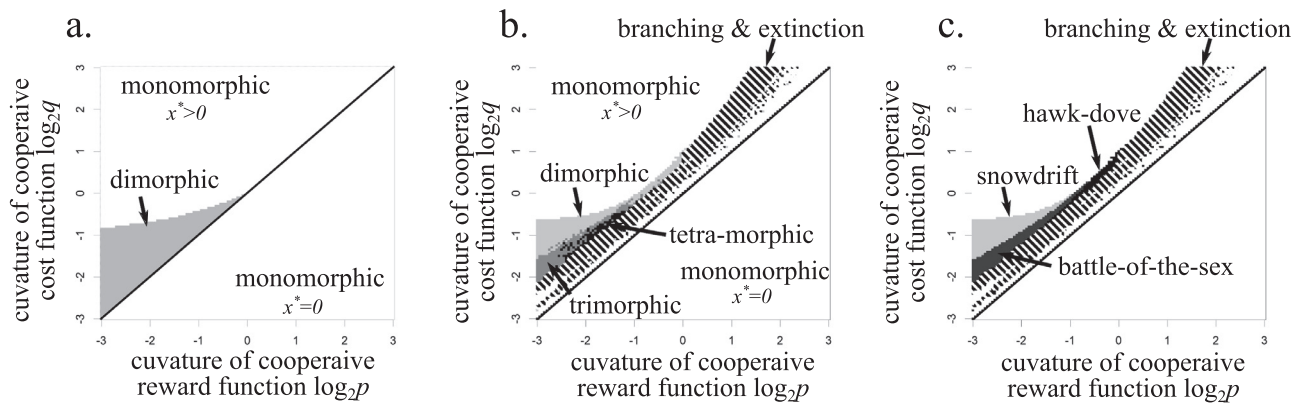
Fig. 4. Evolutionary outcomes depending on the curvature of the cooperative reward function (p: horizontal axis) and the curvature of the cooperative cost function (q: vertical axis). Panels (a) and (b) show the number of strains in the corresponding cooperation-only model and in the full model for competitive cooperation, respectively, at the evolutionary stable state (white: no branching, light grey: dimorphic, dark grey: trimorphic, black: tetra-morphic). In the hatched region, repeated evolutionary branching and extinction occurs. Panel (c) shows the category of social interaction emerging in polymorphic populations as determined by the rows of pairwise payoff matrices (see main text for explanation): light-grey: snowdrift game, dark grey: battle-of-the-sexes game, black: hawk-dove game. For panels (b) and (c), we ran simulations for 14,641 parameter combinations; in 134 the simulations were extremely slow and finished before the evolutionary dynamics reached a stable state. For those parameter combinations, we substituted the majority result for neighbouring parameter combinations for drawing the figures. The other parameters ware $\varepsilon = 1.0$, $r = 2.0$, $\alpha = 0.1$, $\beta = 0.2$.
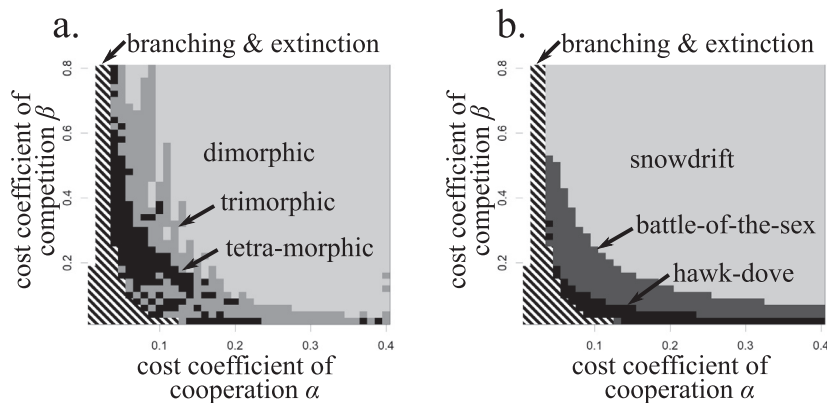
Fig. 5. (a) The number of strains at the evolutionarily stable state and (b) the category of social interaction for different magnitude of the cost of cooperation (α: horizontal axis) and competition (β: vertical axis). In panel (a), white: no branching, light grey: dimorphic, dark grey: trimorphic, black: tetra-morphic, hatched: repeated evolutionary branching and extinction. In panel (b), light-grey: snowdrift game, dark grey: battle-of-the-sexes game, black: hawk-dove game. For panel (a) and (b), we ran simulations for 1600 parameter combinations. In 9 cases the simulations terminated before the evolutionary dynamics reached a stable. For those parameter combinations, we substituted the majority result for neighbouring parameter combinations for drawing the figures. The other parameters ware $\varepsilon = 1.0$, $p = 0.25$, $q = 0.5$, $r = 2.0$.

cost functions are concave ($\log_2 p < 0$ and $\log_2 q < 0$) multiple evolutionary branching into trimorphic or tetramorphic populations can occur (grey or dark region in Fig. 4b). We note that the parameter region where evolutionary branching occurs (non-white regions) is wider in competitive cooperation (Fig. 4b) than that in the corresponding cooperation-only cases (Fig. 4a), as predicted by our analytical arguments. Also, trimorphic or tetramorphic populations did not emerge (dark grey and black regions) in simulations of cooperation-only scenarios (Fig. 4a). When the reward function is concave and the cost function is convex ($\log_2 p < 0 < \log_2 q$), branching rarely occurs and the population stays monomorphic. When both reward and cost functions are convex ($0 < \log_2 p$ and $0 < \log_2 q$), the dynamics tend to show repeated branching and extinction. Occurrence of the repeated branching-extinction scenarios is also promoted when the curvatures of the reward and cost functions are similar ($p \cong q$ in Fig. 4b).

The magnitude of the cost of cooperation and competition, described by the parameters α and β, also affects the evolutionary outcomes (Fig. 5a). For example, the number of coexisting strains increases when either α or β is small (dark grey and black regions in Fig. 5a), but very small costs lead to repeated branching and extinction (hatched region in Fig. 5a). The parameter regions where repeated branching and extinction occurs becomes wider

when the influence of investments in competition ε is large (not shown on Figures).

Overall, the numerical simulations revealed two interesting and robust patterns in the evolutionary dynamics after branching. First, in polymorphic populations, the mean cooperation level is always positively correlated with the mean competition level. Thus, more cooperative strains tend to be more competitive (right panels of Fig. 2a and b). Second, in polymorphic populations, the average level of cooperation evolving in competitive cooperation models is always higher than in polymorphic cooperation-only populations (grey and black solid lines in Fig. 3). Thus, the presence of competition for rewards generated by cooperation tends to increase the average cooperation level in polymorphic populations.

3.2. Categorization of social interactions in polymorphic populations

Since coexisting strains both cooperate and compete with each other, it is interesting to investigate the nature of the social interactions occurring in polymorphic populations. In such populations, a payoff matrix can be defined by calculating the mean payoff from interactions in each pair of coexisting strains. When focusing on any pair of strains, we call the strain with the higher level of cooperation the "cooperator", and the other one the "cheater", and

we denote by R the payoff for a cooperator playing another cooperator, and by S the payoff for a cooperator playing a cheater. The payoff for a cheater playing another cooperator and for a cheater playing another cheater are denoted by T and P, respectively. We note that because of the positive correlation between cooperation and competition, in any given pair cooperators always have a higher competition level than the cheater in that pair.

We categorize the relationship of each pair of strains based on the relative magnitude of the elements of the respective payoff matrix. Comparing elements within columns reveals whether or not the strains in a given pair can coexist. Recall that there may be more than two strains coexisting in polymorphic populations, so that coexistence of pairs of strains is not automatically guaranteed. In the matrix element notation introduced above, coexistence requires $T > R$ and $S > P$, in which case the corresponding 2-player game has a stable interior equilibrium.

The relative magnitude of the row elements indicates the preferred type of interaction partner for a given strain. For example, if $R > S$ then cooperators get a higher payoff when playing against another co-operator than when playing against a cheater. If in addition we have $T > P$, both strains in a coexisting pair prefer to play the cooperator, a situation which we refer to as a "snowdrift game". In contrast, when $R < S$ and $T < P$, both strains get a higher payoff when playing the cheater strain. Because the cheater strain (i.e., the strain with lower cooperation) is always the weaker competitor in the pair, we refer to this situation as a "hawk-dove game", because both strains in the pair prefer to play against the weaker competitor, reminiscent of the classic hawk-dove game. The other two possible cases occur when each strain gets a higher payoff when playing against the other strain, or when each strain gets a higher payoff when playing against itself. In accordance with classical terminology (Farrell, 1987) we call the former case a "battle-of-the-sexes game" and the latter a "coordination game".

By applying the above classification scheme to many pairs of strains from polymorphic evolved populations, we found that the majority of the resulting payoff matrices had column structured that allowed coexistence. In other words, the great majority of pairs of strains were able to coexist, even if they came from polymorphic populations with more than two coexisting strains. In particular, this implies that rock-paper-scissors coexistence was rare in polymorphic populations. However, the row structure of the resulting payoff matrices showed different types of social interactions depending on the parameter values. When the concaveness of the benefit function is large, the row elements most often reflected a snowdrift game (light grey region in Fig. 4c), but when the concavity becomes less pronounced, the social relationship shifts to a battle-of-the-sexes or a hawk-dove game (dark grey and black regions in Fig. 4c). Similarly, when the costs of both cooperation and competition are large enough, the row structures reflect a snowdrift game, but if either cost becomes small enough, the social interaction tends to shift to a battle-of-the-sexes or a hawk-dove game (Fig. 5b).

Interestingly, the type of game seems to change with the number of strains in the population: in the parameter regions where population are dimorphic, the social relationship tends to be a snowdrift game (light grey regions in Fig. 4b (or 5a) mostly overlap with light grey regions in Fig. 4c (or 5b)), but battle-of-the-sexes or hawk-dove games tend to occur when polymorphic population contain more than two distinct phenotypic strains (dark grey and black regions in Fig. 4b (or 5a) mostly overlap with dark grey and black regions in Fig. 4c (or 5b)).

4. Discussion

Although in nature cooperative interactions often occur in the context of competition for cooperatively produced rewards, most often cooperation and competition have been studied separately using different theoretical frameworks. Consequently, how cooperation and competition influence each other's evolution is a largely open question. In this study, we combined cooperation and competition as continuous traits in a model based on evolutionary game theory, and we showed that evolution of competitive cooperation can be qualitatively different from the evolutionary dynamics seen in cooperation-only or competition-only models. Therefore, considering the joint evolution of cooperation and competition may be important for understanding social interactions.

One of the findings that is qualitatively different from cooperation-only or competition-only scenarios is the fact that evolutionary branching is promoted in competitive cooperation in the sense that it occurs for a wider range of parameters than in the corresponding single-trait models. This result has two aspects. First, competition promotes evolutionary branching in the cooperative trait compared to cooperation-only models, and the number of strains coexisting after evolutionary diversification tends to be larger. Second, evolutionary branching in the cooperative trait generates branching in the competitive trait, whereas evolutionary branching does not occur at all in the corresponding competition-only models (i.e., competition on its own cannot drive evolutionary branching in these models). It is known that evolutionary branching can occur more easily when the dimension of trait space is higher (Doebeli and Ispolatov, 2010; Débarre et al. 2014; Svardal et al., 2014). By considering competitive cooperation, we increased the dimension of trait space form the corresponding single-trait models. This increase in dimension allows for conditions under which mutants that vary in both traits from the current resident can invade an evolutionarily unstable resident, whereas mutants that vary in only one trait dimension from the resident cannot. Consequently, the co-occurrence of cooperation and competition relaxes the conditions for evolutionary branching. This result can be also explained from the viewpoint of social niche construction theory (Power et al. 2011; Akçay and Cleve, 2012; Ryan et al., 2016; Saltz et al., 2016): the existence of competition constructed a new "social niche" for cooperation, which causes the promotion of the evolutionary branching in cooperative traits. Note that in our model the social niche construction is bidirectional between cooperation and competition, i.e., we can also interpret the promotion of the evolutionary branching in competitive traits as due to a social niche constructed by the evolution of the cooperation.

Another robust result of our analysis is that in polymorphic populations, more cooperative strains are always more competitive than less cooperative strains. In other words, the levels of cooperation and competition are positively correlated among coexisting strains. This can be explained by variation in the importance of competition depending on the level of cooperation. Because more cooperative individuals produce more shared rewards, the expected benefit from an additional investment in competition increases with the cooperation level. In other words, contribution to the public good increases the incentive for investment in competition.

Although few empirical studies have directly investigated the relationship between levels of cooperation and competition, some studies have reported data supporting the prediction of a correlation between cooperative and competitive effort among individuals. For example, social hover wasps cooperatively defend their nest against attacks from other nests, and it has been shown that higher-rank individuals within the nest defend more frequently than lower-rank ones (Cronin and Field, 2007). Because higher rank is associated with higher reproductive success, the rank can be regarded as the competition level. Thus, the correlation between frequency of defence and rank is viewed as a correlation between the levels of cooperation and competition

within the nest. A similar scenario has been reported in blue monkeys, who cooperatively defend their territory for resources, and where higher-ranked individuals, who enjoy preferential access to food, exhibit the defensive behaviour more often than lower-rank ones (Cords, 2007). These examples seem to support our results, but the behaviours of social animals are generally influenced by various factors. For example, the difference of defensive behaviour depending on the social rank might also be explained by the "silver spoon" effect, see Monaghan (2008). Additional empirical studies focusing on both cooperative and competitive traits would be required for teasing apart such alternative explanations.

A third robust result of our analysis is that the existence of the competition increases the average cooperation level within polymorphic populations. This is a somewhat counterintuitive outcome, because within-group competition is often thought to be a factor that prevents the maintenance of cooperation (Aureli et al., 2002; Barker et al., 2012). The fact that competition promotes cooperation in our models can be explained as follows. In the absence of the competition, the division of shared rewards is equal. Therefore, free-riders can exploit cooperators, thus preventing the maintenance of high average levels of cooperation. With competitive cooperation, however, good competitors can directly increase their payoff by additional investments in cooperation, because being a good competitor ensures a more than proportional return from an investment in cooperation. Thus, unequal division of rewards promotes cooperation.

A final robust result of our analysis is that with competitive cooperation, evolutionary branching is often followed by extinction of some of the coexisting strains, which in turn is followed again by evolutionary diversification. In such scenarios, the level of diversity fluctuates over evolutional time. Such repeated branching and extinction tend to occur when the investment in competition has a relatively large influence on payoffs (i.e., the competition parameter ε is large), and the costs of cooperation and/or competition are small. In such scenarios, small differences in the level of competition have a large effect, leading to an "arms race"-like (Abrams, 1986) escalation of the competition level that can lead to extinction. Our results suggest that factors that make it difficult to attain high levels of competition promote the maintenance of stable polymorphisms.

The form of the function determining how rewards are divided could also be a factor causing an arms race-like escalation. We assumed that the ratio of the exponential functions of the competitive investment determines the reward division, where the difference between two individuals' competitive investments determines the division ratio. In such a case, additional investment in competition always generates the same degree of advantage in reward division, regardless of the mean level of competition, and so the escalation of competition level can easily occur. Another functional form for the division of rewards is the ratio of power functions of the competitive investment (Cant, 2012). In this form, the advantage from the additional investment in competition becomes smaller when the competition level is higher, which might prevent escalation of the competition level, and hence the occurrence of repeated branching and extinction. We note that these two functional forms can be obtained from each other through a transformation of variables, although such a transformation would also change the form of the competitive cost function (Appendix B). This means that the difference between the two forms of the division of reward is mathematically equivalent to a difference between competitive cost functions. Therefore, when we consider all possible cost functions, the set of all evolutionarily outcomes are the same for either functional form of the division of rewards.

The problem of cheating is ubiquitous in the context of cooperation. With competitive cooperation, there is a twist to this problem: cooperators can "exploit" cheaters by enforcing unequal division of public goods through superior competitive ability. Interestingly, the interaction with competitive cooperators can still be beneficial for cheaters. For example, in polymorphic populations in which the social interaction are described by the battle-of-the-sexes game, more cooperative (and hence more competitive) individuals exploit less cooperative individuals by unequal division of rewards, but even the less cooperative individuals get larger payoffs by playing with more cooperative individuals (i.e., by playing the exploitative strategy) than from playing themselves, because in such a scenario, a smaller share of a larger reward is better than larger share of a smaller reward. In other words, for each strain the interaction with the other strains is beneficial. Scenarios in which cooperators effectively exploit cheaters are not possible in models with cooperation-only, and hence a characteristic feature of competitive cooperation. Interestingly, when polymorphisms result in social interactions of the battle-of-the-sexes type, the polymorphic populations often contain more than two coexisting phenotypic strains (Figs. 4 and 5), resulting in social hierarchies with multiple ranks. Numerous empirical studies have reported the existence of social hierarchies in a range of different organism (Majolo et al., 2012; Bush et al., 2016; Devost et al., 2016), and competitive cooperation could be one of the mechanisms causing the evolution of such social structures.

Competitive cooperation can occur when the cooperatively produced public good is divisible, but not all cooperation leads to the production of such public goods. For example, when cooperation involves alarm calls or group vigilance, the reward of cooperation is information about imminent predator attack, which is not divisible. Similarly, voluntary vaccination in human society is a kind of cooperation for preventing the outbreak of disease (Boone, 2014). In this cooperation the reward is the reduction of the probability of outbreak, which is not divisible. In general, evolutionary outcomes may depend on whether cooperatively produced public goods are divisible or not. In particular, cooperative polymorphisms might be more common when the public good produced allows for unequal division.

Social interactions are often multifaceted and comprise various processes. The simultaneous consideration of the evolution of multiple aspects of social interactions increases the dimension of trait space in which evolution unfolds. This can generate novel evolutionary outcomes that are not predicted when the focus is on a single social trait (Brown and Taylor, 2010; Mullon et al., 2016). Some previous studies also indicated the importance of considering multiple social components (Brown and Taylor, 2010; Rueffler et al., 2012; Mullon et al., 2016; Kuijper and Johnstone, 2017), but overall, it seems that knowledge about the influence of the joint evolution of various social traits is still insufficient. Our study revealed that the joint evolution of two major social components, cooperation and competition, can generate novel evolutionary outcomes and predictions.

Acknowledgements

Appendix A. Evolutionary dynamics in monomorphic population

A1. Evolution of cooperation in the cooperation-only model

Here we consider the case that the competition level y is fixed, i.e., the cooperation-only model. Then the payoff function Eq. (1) becomes

$$w(x', x) = \frac{1}{2}(x' + x)^p - \alpha x'^q - \hat{D} \tag{A1}$$

where $\hat{D}$ is a constant. Using the framework of adaptive dynamics (Dieckmann and Law, 1996; Geritz et al., 1998; Doebeli, 2011), the selection gradient for the cooperation level x is

$$\frac{\partial w}{\partial x'}\bigg|_{x'=x} = 2^{p-2}px^{p-1} - \alpha qx^{q-1} \tag{A2}$$

The interior singular solution $x^* > 0$ at which the right hand side of (A2) becomes 0 is

$$x^* = \left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{1}{q-p}} \tag{A3}$$

Because p, q and α are positive, there is always one positive singular solution as long as $p \neq q$. When $p = q$, there is no interior singular solution; then the selection gradient for x given by Eq. (A2) becomes

$$px^{p-1}\left(2^{p-2} - \alpha\right) \tag{A4}$$

In this case, the sign of the selection gradient is the sign of $2^{p-2} - \alpha$ regardless of the cooperation level x. When $2^{p-2} < \alpha$, the selection gradient is always negative, and the cooperation level decrease to 0 (we always assume $x \geq 0$). Otherwise, the selection gradient is always positive, and the cooperation level keeps increasing. When $2^{p-2} = \alpha$, selection is neutral at any x.

The interior singular solution x^* is convergent stable (CS) when

$$\frac{\partial}{\partial x}\left[\frac{\partial w}{\partial x'}\bigg|_{x'=x}\right]_{x=x^*} < 0 \tag{A5}$$

Evaluating this condition yields

$$p(p-1)(2x^*)^{p-2} < \alpha q(q-1)x^{*q-2} \tag{A6}$$

and substituting Eq. (A3) for x^*, the condition that x^* is CS becomes

$$p < q \tag{A7}$$

Consequently, when $p < q$, the cooperation level converge to x^* regardless of the initial trait value. On the other hand, when $p > q$, the dynamics of the cooperation level depends on the initial state: if evolution starts at $x < x^*$, the trait value x decreases to 0, otherwise the trait keeps to increasing to ever higher levels, i.e., $x \to \infty$.

After convergence to the singular solution x^*, the condition for evolutionary stability (ES) is

$$\frac{\partial^2 w}{\partial x'^2}\bigg|_{x'=x=x^*} < 0 \tag{A8}$$

Evaluating this expression yields

$$\frac{1}{2}p(p-1)(2x^*)^{p-2} < \alpha q(q-1)x^{*q-2} \tag{A9}$$

and substituting Eq. (A3) for x^* gives the condition that x^* is ES as

$$p < 2q - 1 \tag{A10}$$

Evolutionary branching occurs when the singular solution is CS but not ES, i.e., when

$$2q - 1 < p < q \tag{A11}$$

It is clear that $2q - 1 < q$ is satisfied only when $q < 1$. Thus, evolutionary branching can only occur when $p < 1$ and $q < 1$, i.e., when both the benefit and the cost functions are concave. Because evolutionary branching occurs only when both mutants with larger and smaller trait value than the singular solution can invade into the resident population, evolutionary branching does not occur when $x = 0$ and $x \to \infty$.

A2. Evolution of competition in the competition-only model

Next, we consider the case where the cooperation level x is fixed, i.e., the competition-only model. The payoff function is

$$w(y'|y) = \hat{B}\frac{\exp(\varepsilon y')}{\exp(\varepsilon y') + \exp(\varepsilon y)} - \hat{C} - \beta y'^r \tag{A12}$$

where $\hat{B}$ and $\hat{C}$ are constants. Again, by following the adaptive dynamics theory, the selection gradient of the competition level y is

$$\frac{\partial w}{\partial y'}\bigg|_{y'=y} = \frac{\varepsilon\hat{B}}{4} - \beta ry^{r-1} \tag{A13}$$

The interior singular solution y^* is obtained by setting the right hand side of (A0) to 0:

$$y^* = \left(\frac{\varepsilon\hat{B}}{4\beta r}\right)^{\frac{1}{r-1}} \tag{A14}$$

Because β, r and γ are positive, there is always one positive singular solution as long as $r \neq 1$. When $r = 1$, the selection gradient $\varepsilon\hat{B}/4 - \beta$ becomes a constant and there is no interior singular solution. Then, the competition level decrease to 0 if $\varepsilon\hat{B}/4 < \beta$, or increase without bound if $\varepsilon\hat{B}/4 > \beta$ (selection is neutral when $\varepsilon\hat{B}/4 = \beta$).

Evaluating the expressions (A5) and (A8) with replacing x' and x by y' and y yields the conditions for convergence stable and for evolutionary stable at the interior singular solution y^*, respectively. Both of them become same expression:

$$-\beta r(r-1)y^{*r-2} < 0 \tag{A15}$$

Because β, r and y^* are positive, (A15) becomes

$$1 < r \tag{A16}$$

Because the convergence stable singular points are always evolutionarily stable, evolutionary branching (which requires CS and not ES) cannot occur in this model.

A3. Coevolution of cooperation and competition

In the monomorphic population, the selection gradient of cooperation level in full model Eq. (2a) is equal formula with that in cooperation-only model Eq. (A2). This means that the equilibrium cooperation level x^* and its convergent stability is same with the cooperation-only model, i.e., when $p \neq q$ the interior singular solution x^* shown in Eq. (3) exists and it is convergent stable when $p < q$ (see (A5), (A6) and (A7) for the derivation). When $p = q$, the sign of which is determined by $2^{p-2} - \alpha$ (see Eq. (A4)), i.e., cooperation level decrease to 0 when $2^{p-2} < \alpha$, otherwise the cooperation level keeps increasing without bound (selection is neutral at any x When $2^{p-2} = \alpha$).

When the level of cooperation x is x^*, the singular solution y^* derived as Eq. (5) is convergent stable when

$$-\beta r(r-1)y^{*r-2} < 0 \tag{A17}$$

which is yielded by evaluating Eq. (6). Because β, r and y^* are positive, this condition is satisfied when $r > 1$. When $r \neq 1$, the population converge to some certain state as we described in the main text. When $r = 1$, the selection gradient for competition level Eq. (2b) becomes

$$2^{p-2}\varepsilon\left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p}{q-p}} - \beta \tag{A18}$$

Eq. (A18) is constant. Therefore, the competition level decrease to 0 when Eq. (A18) is negative, otherwise the competition level keeps increasing without bound (i.e., $y \to \infty$). When Eq. (A18) is

equal to zero, selection is neutral at any y. When $x = 0$ and $x = \infty$, the population finally reach to $(0, 0)$ and (∞, ∞), respectively (see the main text).

Overall, monomorphic population reach to the following state:

(x^*, y^*) when $p < q$ and $r > 1$
$(x^*, 0)$ or (x^*, ∞) when $p < q$ and $r < 1$
$(x^*, 0)$ when $p < q$ and $r = 1$ and $2^{p-2}\varepsilon \left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p}{q-p}} < \beta$
(x^*, ∞) when $p < q$ and $r = 1$ and $2^{p-2}\varepsilon \left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p}{q-p}} > \beta$
$(x^*, \forall y)$ when $p < q$ and $r = 1$ and $2^{p-2}\varepsilon \left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p}{q-p}} = \beta$
$(0, 0)$ or (∞, ∞) when $p > q$
$(0, 0)$ when $p = q$ and $2^{p-2} < \alpha$
(∞, ∞) when $p = q$ and $2^{p-2} > \alpha$
$(\forall x, \forall y)$ when $p = q$ and $2^{p-2} = \alpha$

where $\forall x$ or $\forall y$ means selection is neutral at any x or y. By ignoring the cases $r = 1$ or $p = q$, the state becomes into three cases in the main text (Fig. 1).

After the resident reach to the singular point (x^*, y^*), (x^*, y^*) is evolutionarily stable if all eigenvalues of the Hessian matrix H are negative at the singular point, where

$$
H = \begin{pmatrix} \left.\frac{\partial^2 W}{\partial x'^2}\right|_{\substack{x=x'=x^* \\ y=y'=y^*}} & \left.\frac{\partial^2 W}{\partial x' \partial y'}\right|_{\substack{x=x'=x^* \\ y=y'=y^*}} \\ \left.\frac{\partial^2 W}{\partial x' \partial y'}\right|_{\substack{x=x'=x^* \\ y=y'=y^*}} & \left.\frac{\partial^2 W}{\partial y'^2}\right|_{\substack{x=x'=x^* \\ y=y'=y^*}} \end{pmatrix}
$$

$$
= \begin{pmatrix} 2^{p-3}p\left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p-2}{q-p}}\{p-1-2(q-1)\} & 2^{p-3}\varepsilon p\left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p-1}{q-p}} \\ 2^{p-3}\varepsilon p\left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p-1}{q-p}} & -\beta r(r-1)\left(\frac{2^{p-2}\varepsilon\left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p}{q-p}}}{\beta r}\right)^{\frac{r-2}{r-1}} \end{pmatrix}
$$
(A19)

According to the Routh–Hurwitz stability criterion, all eigenvalues of a two dimensional matrix M is negative when $\det(M) > 0$ and $\text{tr}(M) < 0$, where det and tr mean the determinant and the trace, respectively. The former and the latter conditions of the Hessian matrix H are

$$
2q - 1 - p > \frac{\varepsilon p}{2(r-1)}\left(\frac{2^{p-2}\varepsilon\left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p}{q-p}}}{\beta r}\right)^{\frac{1}{r-1}}
$$
(A20a)

and

$$
2q - 1 - p > -\frac{2\varepsilon(r-1)}{p}\left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{2}{q-p}}\left(\frac{2^{p-2}\varepsilon\left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p}{q-p}}}{\beta r}\right)^{\frac{-1}{r-1}}
$$
(A20b)

Because now we focus on the convergent stable solution at (x^*, y^*), $p < q$ and $r > 1$. Then, the right-hand sides of (A20a) and (A20b) are always positive and negative, respectively; i.e., (A20a) is a sufficient condition for (A20b). Consequently, Eq. (A20a) is the additional condition for a CS singular solution is evolutionarily stable. We conclude from the convergence stability of (x^*, y^*) (i.e., $p < q$ and $r > 1$) and Eq. (A20a) that evolutionary branching occurs

at (x^*, y^*) when

$$
1 < r \text{ and } 2q - 1 - \frac{\varepsilon p}{2(r-1)}\left(\frac{2^{p-2}\varepsilon\left(\frac{2^{p-2}p}{\alpha q}\right)^{\frac{p}{q-p}}}{\beta r}\right)^{\frac{1}{r-1}} < p < q
$$
(A21)

When the third term of the left-hand side in the second condition of (A21) is zero, this condition becomes equal to the condition for the evolutionary branching in the cooperation-only model (A11). Although this term depends on the parameter p, it is always positive as long as the first condition of (A21) is satisfied. This implies that the condition for evolutionary branching in the competitive cooperation model is less restrictive than that in the cooperation-only model, hence evolutionary branching can occur for a larger region of parameter space when cooperation and competition coevolve.

Evolutionary branching occurs in the direction of the eigenvector of the largest eigenvalue of the Hessian matrix H, i.e., the vector $\mathbf{x}$ satisfying

$$
H\mathbf{x} = \lambda \mathbf{x}
$$
(A22)

where λ is the maximum eigenvalue of H. Because both nondiagonal elements of H are non-zero, both coordinates of the eigenvector of the maximal eigenvalue are non-zero. This means that evolutionary branching occurs in both the cooperation and the competition level.

The singular point $(x^*, 0)$ is evolutionarily stable if

$$
\frac{1}{2}p(p-1)(2x^*)^{p-2} - \alpha q(q-1)x^{*q-2} < 0
$$
(A23)

By solving this,

$$
p < 2q - 1
$$
(A24)

This condition is the same as the condition for evolutionary stability of the singular solution in cooperation-only model (see Eq. (A10)).

A4. Evolutionary dynamics after evolutionary branching when r < 1

After a monomorphic population converges to the singular point $(x^*, 0)$ (i.e., $p < q$ and $r < 1$), evolutionary branching in the cooperation level occurs if $p < 2q - 1$. Even after the branching, investment in competition is never selected, i.e., the competition level y will remain at 0 for all individuals within polymorphic populations. To see this, consider a population containing m coexisting strains with different cooperation levels $x_1, x_2 \ldots x_m$ but whose competition levels are δ (i.e., $y_1 = y_2 = \ldots = y_m = \delta$), which is

a lowest evolutionarily reachable competition level. Assuming the fractions of these strains within the population are $f_1, f_2 \ldots f_m$ (i.e., $f_1 + f_2 + \ldots + f_m = 1$), the fitness of a rare mutant (x', y') appearing in such a population is

$$W(x', y' | x_{1\ldots m}, f_{1\ldots m})$$
$$= \left\{ \sum_{i=1}^{m} (x' + x_i)^p \right\} \frac{\exp(\varepsilon y')}{\exp(\varepsilon y') + \exp(\varepsilon \delta)} - \alpha x'^q - \beta y'^r \quad (A25)$$

and hence the selection gradient for the competitive trait of kth strain is

$$\left. \frac{\partial W}{\partial y'} \right|_{\substack{x' = x_k \\ y' = \delta}} = \frac{\varepsilon}{4} \sum_{i=1}^{m} (x_k + x_i)^p - \beta r \delta^{r-1} \quad (A26)$$

Because now we assume $y \geq 0$, $\delta = 0$. When we take the limit of δ to 0, the second term of the right-hand side of Eq. (A26) becomes extremely large because $r < 1$. It follows that the selection gradient for the competition level is always negative around $y = 0$, hence the competition level cannot evolve away from 0 when $r < 1$.

Appendix B. Functional form of the division of rewards

In our model, we assumed that the division of rewards is determined by the ratio of exponential functions of the competitive investment. However, we can also consider other functional forms for reward division. One general form is the ratio of power functions of the competitive investment (Cant, 2012). When the division of reward is determined by this functional form, the fitness function (1) in the main text becomes

$$w(x', y' | x, y) = (x' + x)^p \frac{y'^d}{y'^d + y^d} - \alpha x'^q - \beta y'^r \quad (B1)$$

where d is a coefficient determining the effect of the competitive investments the reward division.

Defining a new variable Y by

$$Y = \frac{d}{\varepsilon} \log(y)$$

and noting that $\exp(\varepsilon Y) = y^d$, the fitness function (B1) can be rewritten as

$$w(x', Y' | x, Y) = (x' + x)^p \frac{\exp(\varepsilon Y')}{\exp(\varepsilon Y') + \exp(\varepsilon Y)}$$
$$- \alpha x'^q - \beta \exp\left(\frac{\varepsilon r}{d} Y'\right) \quad (B2)$$

This is equal to the fitness function of our model Eq. (1), except for the functional form of the cost of competitive investments, which becomes an exponential function. It follows that the set of all possible evolutionary outcomes is the same for the different functional forms of the division of rewards, up to a transformation of the function determining the costs of competitive investments.

References

Abrams, P.A., 1986. Adaptive responses of predators to prey and prey to predators: the failure of the arms-race analogy. Evolution 40, 1229–1247. https://doi.org/10.1111/j.1558-5646.1986.tb05747.x.

Akçay, E., Cleve, J.V., 2012. Behavioral responses in structured populations pave the way to group optimality. Am. Nat. 179, 257–269. https://doi.org/10.1086/663691.

Aureli, F., Cords, M., van Schaik, C.P., 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. Anim. Behav. 64, 325–343. https://doi.org/10.1006/anbe.2002.3071.

Axelrod, R.M., 1984. The Evolution of Cooperation. Basic Books.

Barker, J.L., Barclay, P., Reeve, H.K., 2012. Within-group competition reduces cooperation and payoffs in human groups. Behav. Ecol. 23, 735–741. https://doi.org/10.1093/beheco/ars020.

Bishop, D.T., Cannings, C., Maynard Smith, J., 1978. The war of attrition with random rewards. J. Theor. Biol. 74, 377–388. https://doi.org/10.1016/0022-5193(78)90220-5.

Bomze, I.M., Burger, R., 1995. Stability by mutation in evolutionary games. Games Econ. Behav. 11, 146–172. https://doi.org/10.1006/game.1995.1047.

Boone, A.R., 2014. The Vaccine Dilemma: Epidemiological Game Theory of Vaccination in Set Structured Populations.

Bouncken, R.B., Gast, J., Kraus, S., Bogers, M., 2015. Coopetition: a systematic review, synthesis, and future research directions. Rev. Manag. Sci. 9, 577–601. https://doi.org/10.1007/s11846-015-0168-6.

Brown, S.P., Taylor, P.D., 2010. Joint evolution of multiple social traits: a kin selection analysis. Proc. R. Soc. Lond. B 277, 415–422. https://doi.org/10.1098/rspb.2009.1480.

Bush, J.M., Quinn, M.M., Balreira, E.C., Johnson, M.A., 2016. How do lizards determine dominance? Applying ranking algorithms to animal social behaviour. Anim. Behav. 118, 65–74. https://doi.org/10.1016/j.anbehav.2016.04.026.

Cant, M.A., 2012. Suppression of social conflict and evolutionary transitions to cooperation. Am. Nat. 179, 293–301. https://doi.org/10.1086/663679.

Cords, M., 2007. Variable participation in the defense of communal feeding territories by blue monkeys in the Kakamega Forest, Kenya. Behaviour 144, 1537–1550. https://doi.org/10.1163/156853907782512100.

Cronin, A.L., Field, J., 2007. Rank and colony defense against conspecifics in a facultatively eusocial hover wasp. Behav. Ecol. 18, 331–336. https://doi.org/10.1093/beheco/arl091.

Crowley, P.H., 2001. Dangerous games and the emergence of social structure: evolving memory-based strategies for the generalized hawk-dove game. Behav. Ecol. 12, 753–760. https://doi.org/10.1093/beheco/12.6.753.

Davies, N.B., 1992. Dunnock behaviour and social evolution. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford, New York.

Débarre, F., Nuismer, S.L., Doebeli, M., 2014. Multidimensional (Co)Evolutionary stability. Am. Nat. 184, 158–171. https://doi.org/10.1086/677137.

Devost, I., Jones, T.B., Cauchoix, M., Montreuil-Spencer, C., Morand-Ferron, J., 2016. Personality does not predict social dominance in wild groups of black-capped chickadees. Anim. Behav. 122, 67–76. https://doi.org/10.1016/j.anbehav.2016.10.001.

Dieckmann, U., Law, R., 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. J. Math. Biol. 34, 579–612. https://doi.org/10.1007/BF02409751.

Doebeli, M., 2011. Adaptive Diversification. Princeton University Press, Princeton, N.J.

Doebeli, M., Hauert, C., Killingback, T., 2004. The evolutionary origin of cooperators and defectors. Science 306, 859–862. https://doi.org/10.1126/science.1101456.

Doebeli, M., Ispolatov, I., 2010. Complexity and diversity. Science 328, 494–497. https://doi.org/10.1126/science.1187468.

Dubois, F., Giraldeau, L.-A., 2007. Food sharing among retaliators: sequential arrivals and information asymmetries. Behav. Ecol. Sociobiol. 62, 263–271.

Farrell, J., 1987. Cheap talk, coordination, and entry. RAND J. Econ. 18, 34–39. https://doi.org/10.2307/2555533.

Fletcher, J.A., Doebeli, M., 2009. A simple and general explanation for the evolution of altruism. Proc. R. Soc. Lond. B 276, 13–19. https://doi.org/10.1098/rspb.2008.0829.

Geritz, S.A.H., Kisdi, E., Meszena, G., Metz, J.A.J., 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evol. Ecol. 12, 35–57.

Hadeler, K.P., 1981. Stable polymorphisms in a selection model with mutation. SIAM J. Appl. Math. 41, 1–7. https://doi.org/10.1137/0141001.

Hamilton, I.M., 2013. The effects of behavioral plasticity and leadership on the predictions of optimal skew models. Behav. Ecol. 24, 444–456. https://doi.org/10.1093/beheco/ars182.

Hamilton, W.D., 1964a. The genetical evolution of social behaviour. J. Theor. Biol. 7, 1–52. https://doi.org/10.1016/0022-5193(64)90038-4.

Hamilton, W.D., 1964b. The genetical evolution of social behaviour. II. J. Theor. Biol. 7, 17–52. https://doi.org/10.1016/0022-5193(64)90039-6.

Hauert, C., Holmes, M., Doebeli, M., 2006. Evolutionary games and population dynamics: maintenance of cooperation in public goods games. Proc. R. Soc. B 273, 2565–2571. https://doi.org/10.1098/rspb.2006.3600.

Herbert-Read, J.E., Romanczuk, P., Krause, S., Strömbom, D., Couillaud, P., Domenici, P., Kurvers, R.H.J.M., Marras, S., Steffensen, J.F., Wilson, A.D.M., Krause, J., 2016. Proto-cooperation: group hunting sailfish improve hunting success by alternating attacks on grouping prey. Proc. R. Soc. B 283, 20161671. https://doi.org/10.1098/rspb.2016.1671.

Hoelzel, A.R., 1991. Killer whale predation on marine mammals at Punta Norte, Argentina; food sharing, provisioning and foraging strategy. Behav. Ecol. Sociobiol. 29, 197–204.

Kagel, J.H., Roth, A.E. (Eds.), 1995. The Handbook of Experimental Economics. Princeton University Press, Princeton, NJ.

Keller, L., Reeve, H.K., 1994. Partitioning of reproduction in animal societies. Trends Ecol. Evol. 9, 98–102. https://doi.org/10.1016/0169-5347(94)90204-6.

Kopp, K.S., Liebal, K., 2016. Here you are!–Selective and active food sharing within and between groups in captive Sumatran orangutans (Pongo abelii). Behav. Ecol. Sociobiol.; Heidelb. 70, 1219–1233. http://dx.doi.org/10.1007/s00265-016-2130-2.

Kuijper, B., Johnstone, R.A., 2017. How sex-biased dispersal affects sexual conflict over care. Am. Nat. 189, 501–514. https://doi.org/10.1086/691330.

Majolo, B., Lehmann, J., Vizioli, A., de, B., Schino, G., 2012. Fitness-related benefits of dominance in primates. Am. J. Phys. Anthropol. 147, 652–660. https://doi.org/10.1002/ajpa.22031.

Maynard Smith, J., 1982. Evolution and the Theory of Games. Cambridge University Press.

Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. Nature 246, 15–18. https://doi.org/10.1038/246015a0.

Mesterton-Gibbons, M., 1994. The Hawk—Dove game revisited: effects of continuous variation in resource-holding potential on the frequency of escalation. Evol. Ecol. 8, 230–247. https://doi.org/10.1007/BF01238275.

Monaghan, P., 2008. Early growth conditions, phenotypic development and environmental change. Philos. Trans. 363, 1635–1645.

Mullon, C., Keller, L., Lehmann, L., 2016. Evolutionary stability of jointly evolving traits in subdivided populations. Am. Nat. 188, 175–195. https://doi.org/10.1086/686900.

Nowak, M.A., 2006. Five rules for the evolution of cooperation. Science 314, 1560–1563. https://doi.org/10.1126/science.1133755.

Ohtsuki, H., Hauert, C., Lieberman, E., Nowak, M.A., 2006. A simple rule for the evolution of cooperation on graphs and social networks. Nature 441, 502–505. https://doi.org/10.1038/nature04605.

Powers, S.T., Penn, A.S., Watson, R.A., 2011. The concurrent evolution of cooperation and the population structures that support it. Evolution 65, 1527–1543. https://doi.org/10.1111/j.1558-5646.2011.01250.x.

Reeve, H.K., Emlen, S.T., 2000. Reproductive skew and group size: an N-person staying incentive model. Behav. Ecol. 11, 640–647. https://doi.org/10.1093/beheco/11.6.640.

Reeve, H.K., Emlen, S.T., Keller, L., 1998. Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? Behav. Ecol. 9, 267–278. https://doi.org/10.1093/beheco/9.3.267.

Reeve, H.K., Hölldobler, B., 2007. The emergence of a superorganism through intergroup competition. PNAS 104, 9736–9740. https://doi.org/10.1073/pnas.0703466104.

Rood, J.P., 1990. Group size, survival, reproduction, and routes to breeding in dwarf mongooses. Anim. Behav. 39, 566–572. https://doi.org/10.1016/S0003-3472(05)80423-3.

Rueffler, C., Hermisson, J., Wagner, G.P., 2012. Evolution of functional specialization and division of labor. PNAS 109, E326–E335. https://doi.org/10.1073/pnas.1110521109.

Ryan, P.A., Powers, S.T., Watson, R.A., 2016. Social niche construction and evolutionary transitions in individuality. Biol. Philos. 31, 59–79. https://doi.org/10.1007/s10539-015-9505-z.

Saltz, J.B., Geiger, A.P., Anderson, R., Johnson, B., Marren, R., 2016. What, if anything, is a social niche? Evol. Ecol. Lond. 30, 349–364. http://dx.doi.org/10.1007/s10682-015-9792-5.

Svardal, H., Rueffler, C., Doebeli, M., 2014. Organismal complexity and the potential for evolutionary diversification: complexity and evolutionary diversification. Evolution 68, 3248–3259. https://doi.org/10.1111/evo.12492.

Vehrencamp, S.L., 1983. A model for the evolution of despotic versus egalitarian societies. Anim. Behav. 31, 667–682. https://doi.org/10.1016/S0003-3472(83)80222-X.

West, S.A., Diggle, S.P., Buckling, A., Gardner, A., Griffin, A.S., 2007. The social lives of microbes. Annu. Rev. Ecol. Evol. Syst. 38, 53–77. https://doi.org/10.1146/annurev.ecolsys.38.091206.095740.

Yamauchi, A., van Baalen, M., Sabelis, M.W., 2018. Spatial patterns generated by simultaneous cooperation and exploitation favour the evolution of altruism. J. Theor. Biol. 441, 58–67. https://doi.org/10.1016/j.jtbi.2017.12.027.

Yip, E.C., Levy, T., Lubin, Y., 2017. Bad neighbors: hunger and dominance drive spacing and position in an orb-weaving spider colony. Behav. Ecol. Sociobiol. 71, 128. https://doi.org/10.1007/s00265-017-2357-6.