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Containment and volume orders of cooperation

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Abstract

Spatial structure can crucially affect the evolutionary dynamics of cooperation. In simple cases, based on pairwise interactions or similar strategies, the effect of spatial structure can be captured by a single relatedness or structure coefficient, with larger coefficients being more conducive to the evolution of cooperation. In more general situations, based on the interaction among multiple individuals with distinct strategies, the condition depends on several structure coefficients, and a simple comparison between different models is no longer straightforward. Here, we propose two ways of ordering population structures by their potential to promote the evolution of cooperation: the containment order and the volume order. We provide conditions for establishing comparability or incomparability in the containment order, give general results concerning the volume order, and illustrate our theory by comparing different models of spatial structure and evolutionary dynamics. Our framework allows to compare many previously studied models of population structure quantitatively. This comparison will be of great value for the unification and generalization of models for the evolution of cooperation in spatially structured populations.

Keywords. n-player games; structure coefficients; spatially structured populations; evolution of cooperation

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Introduction

The evolution of cooperation is a fascinating topic that has been studied from different perspectives and theoretical approaches (Axelrod, 1984; Sugden, 1986; Frank, 1998; Sober and Wilson, 1998; Rousset, 2004; Nowak, 2006). An issue that has led to considerable interest is the extent to which spatial structure allows cooperation to thrive (Hamilton, 1964; Taylor, 1992; Wilson et al., 1992; Ohtsuki and Nowak, 2006; Ohtsuki et al., 2006; Traulsen and Nowak, 2006; Grafen, 2007; Lehmann et al., 2007b,a; Szabó and Fáth, 2007; Taylor et al., 2007a,b; Ladret and Lessard, 2007; Grafen and Archetti, 2008; Tarnita et al., 2009; Nathanson et al., 2009; Ohtsuki, 2010; Lehmann and Rousset, 2010; Nowak et al., 2010; Wu et al., 2010b; Peña and Rochat, 2012; van Veelen and Nowak, 2012; Perc et al., 2013; Allen et al., 2013; Van Cleve and Lehmann, 2013; Débarre et al., 2014; Maciejewski et al., 2014; Van Cleve, 2015; Peña et al., 2015). Spatial structure can both enhance cooperation by inducing clustering or assortment (whereby cooperators tend to interact more often with other cooperators; Fletcher and Doebeli 2009; Bijma and Aanen 2010) and oppose cooperation by inducing increased local competition (whereby cooperators tend to compete more often with other cooperators; Platt and Bever 2009). In models assuming weak selection on either pairwise social interactions or phenotypically similar strategies, the balance between these two effects is captured by the "scaled relatedness coefficient" of inclusive fitness theory (Lehmann and Rousset, 2010; Van Cleve and Lehmann, 2013; Van Cleve, 2015; Peña et al., 2015) or the "structure coefficient" of evolutionary game theory (Tarnita et al., 2009; Nowak et al., 2010; Allen et al., 2013). With these coefficients, two different models of spatial structure and associated evolutionary dynamics can be unambiguously compared by ranking their coefficients: the greater the coefficient, the less stringent the conditions for cooperation to evolve. This way, different models of population structure can be ordered by their ability to promote the evolution of cooperation in a straightforward way.

Despite the theoretical importance of models with a single structure or relatedness coefficient, many examples of social evolution ranging from microbial cooperation (Griffin et al., 2004; Xavier and Foster, 2007; Gore et al., 2009; Li et al., 2015) to collective action in humans (Ostrom, 1990; Milinski et al., 2006; Hilbe et al., 2014; Pinheiro et al., 2014) might involve interactions between more than two individuals expressing distinct phenotypes. In these cases, the combined effects of spatial structure cannot be captured by a single value, as higher degrees of genetic association (e.g., "triplet relatedness"; Ohtsuki 2010) or structure coefficients are required to fully describe the condition under which cooperation is favored (Wu et al., 2013; Ohtsuki, 2014; Van Cleve, 2015). The need to account for several relatedness or structure coefficients has so far precluded a simple way of comparing population structures independent of the particular kind of game used to model cooperation.

Here, we propose a framework to order population structures by their ability to promote cooperation in the context of games between multiple players expressing phenotypically distinct strategies. Our framework allows to directly compare two population structures without referring to any concrete game. We will distinguish two cases. (i) In the simplest case, one population structure promotes cooperation in a class of games that is just a subset of the games in which cooperation is promoted for a second population structure (Fig. 1 left panel). In this case, the population structure that promotes cooperation in the larger set of games is a stronger promoter of cooperation. (ii) For some population structures, cooperation can be promoted in one game, but not in another (Fig. 1 right panel). In this case, we argue that the fraction of all games in which cooperation is promoted is a good measure to order population structures.

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Results

Games and polytopes

We consider a symmetric game between d players. Players adopt one of two pure strategies, A or B. A focal player's payoff depends on the player's own strategy and on the strategies of its $d-1$ co-players. If j co-players play A, an A-player obtains a_j, whereas a B-player obtains b_j. These interactions are represented by the payoff table

Opposing A-players	0	1	...	j	...	$d-1$
payoff to A	a_0	a_1	...	a_j	...	a_{d-1}
payoff to B	b_0	b_1	...	b_j	...	b_{d-1}

.

A game is determined by $2d$ real numbers and can thus be considered as a point in a $2d$-dimensional space.

We first need to say precisely what we mean by "favoring" cooperation. For our purposes, we say that cooperation is favored if a single cooperating mutant in a population of defectors has a higher probability of eventually reaching fixation than a single defecting mutant in a population of cooperators. This also means that cooperation is more abundant than defection in a mutation-selection process in the limit of low mutation (Tarnita et al., 2009). For weak selection, strategy A is favored over B if (Wu et al., 2013)

$$\sum_{j=0}^{d-1} \sigma_j \left(a_j - b_{d-1-j}\right) > 0, \tag{1}$$

where $\sigma_0, \ldots, \sigma_{d-1}$ are the d structure coefficients. If we assume an exponential mapping between payoff and fitness, we can generalize these conditions for certain population structures and go beyond the case of weak selection (Traulsen et al., 2008).

The structure coefficients are independent of a_j and b_j, but they depend on the type of spatial structure and update rule used to model the evolutionary dynamics. They are uniquely determined up to a constant factor. Setting one of these coefficients to one thus gives a single structure coefficient for two-player games (Tarnita et al., 2009). For $d > 2$, we use the vector $\boldsymbol{\sigma}$ to denote the structure coefficients and note that, if $\sigma_j \geq 0$ for all j, we can impose $\sum_{j=0}^{d-1} \sigma_j = 1$ without affecting the selection condition (1). For our purposes, this normalization turns out to be more useful than setting one coefficient to one. In Table 1, we provide examples of population structures and their corresponding structure coefficients.

In which sense can we say that a given population structure favors more cooperation than another population structure? To answer this question precisely, we first need to determine what we mean by "cooperation", as this could refer to different social behaviors, in particular if we move beyond two-player games (Kerr et al., 2004). We are interested in a particular subset of games that we call "cooperation games". In these games, players decide whether to cooperate (play A) or defect (play B), and payoffs are such that: (i) players prefer other group members to cooperate irrespective of their own strategy, and (ii) mutual cooperation is favored over mutual defection. In terms of our payoff parameters, these conditions imply

$$a_{j+1} \geq a_j \qquad \text{and} \qquad b_{j+1} \geq b_j \qquad \text{for } j = 0, 1, \ldots, d-2, \tag{2}$$

as well as

$$a_{d-1} > b_0. \tag{3}$$

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Conditions (2) and (3) are often used to characterize cooperative strategies in multiplayer social dilemmas (Uyenoyama and Feldman, 1980; Kerr et al., 2004; Hilbe et al., 2014), such as the provision of collective goods (Archetti and Scheuring, 2012; Peña et al., 2015). If we further restrict payoffs to values between 0 and 1,

$$0 \leq a_j \leq 1 \qquad \text{and} \qquad 0 \leq b_j \leq 1 \qquad \text{for } j = 0, 1, \ldots, d-1, \tag{4}$$

then the set of all cooperation games with d players is given by a (convex) polytope (Ziegler, 1995) in a $2d$-dimensional space, which we call $\mathcal{P}$ (see Methods).

A given population structure will favor the evolution of cooperation for some of these games only. More precisely, for a population structure $\mathcal{S}_i$ with structure coefficients $\boldsymbol{\sigma}_i$, the set of cooperation games for which $\mathcal{S}_i$ favors A over B is given by adding the selection condition (1) to the inequalities defining $\mathcal{P}$, i.e., (2), (3), and (4). The selection condition (1) defines a hyperplane and thus divides the space of all games into two: those for which cooperation is favored and those for which defection is favored. This shows that our problem essentially reduces to a geometric problem in $2d$ dimensions. We denote by $\mathcal{Q}_i$ the polytope containing the games for which cooperation is favored under population structure $\mathcal{S}_i$ (see Methods). This approach allows us to compare very different population structures that seem to have little in common at first sight.

Containment order

In the simplest case, the set of games $\mathcal{Q}_2$ for which cooperation is favored under population structure $\mathcal{S}_2$ is just a subset of the set $\mathcal{Q}_1$ for which cooperation is favored under population structure $\mathcal{S}_1$. If $\mathcal{Q}_2$ is fully contained in $\mathcal{Q}_1$, we say that population structure $\mathcal{S}_1$ is greater than population structure $\mathcal{S}_2$ in the containment order (Fishburn and Trotter, 1999), and we write $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$. The ordering $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$ implies that cooperation cannot be favored under $\mathcal{S}_2$ without also being favored under $\mathcal{S}_1$.

Establishing the containment order is equivalent to a polytope containment problem (Kaibel and Pfetsch, 2003), which can be solved numerically by linear programming (Eaves and Freund, 1982; Freund and Orlin, 1985). Here, we describe an alternative approach based on the theory of stochastic orders Shaked and Shanthikumar (2007). Assume that the structure coefficients σ_j are nonnegative and normalized, i.e., (i) $\sigma_j \geq 0$ for all $j = 0, \ldots, d-1$, and (ii) $\sum_j \sigma_j = 1$, so that they define a probability distribution over $j = 0, 1, \ldots, d-1$. Consider two population structures $\mathcal{S}_1$ and $\mathcal{S}_2$ with normalized structure coefficients $\boldsymbol{\sigma}_1$ and $\boldsymbol{\sigma}_2$, respectively. We show in Methods (see also Proposition 1 in Appendix B.1) that a sufficient condition leading to the containment order $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$ is that $\boldsymbol{\sigma}_1$ assigns higher probability to larger values of j than $\boldsymbol{\sigma}_2$ in the sense that the sequence $\boldsymbol{\sigma}_1$ cross the sequence $\boldsymbol{\sigma}_2$ exactly once from below (Fig. 2). This simple condition will allow us to establish the containment order for different classes of population structures.

It can happen that neither $\mathcal{Q}_1$ is entirely contained within $\mathcal{Q}_2$ nor $\mathcal{Q}_2$ is entirely contained within $\mathcal{Q}_1$. In these cases, $\mathcal{S}_1$ and $\mathcal{S}_2$ are incomparable in the containment order (i.e., neither $\mathcal{S}_1 \leq_{\text{con}} \mathcal{S}_2$ nor $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$) and we write $\mathcal{S}_1 \parallel_{\text{con}} \mathcal{S}_2$. We show in Methods (see also Proposition 2 in Appendix B.2) that a sufficient condition leading to such incomparability is that the sequences $\boldsymbol{\sigma}_1$ and $\boldsymbol{\sigma}_2$ cross twice (Fig. 2). In this case, there are both a subset of cooperation games favored under $\mathcal{S}_1$ but not under $\mathcal{S}_2$ and a subset of cooperation games favored under $\mathcal{S}_2$ but not under $\mathcal{S}_1$.

For the commonly discussed case of two-player games in structured populations (Tarnita et al., 2009; Nowak et al., 2010) the vector of structure coefficients $\boldsymbol{\sigma}$ consists of only two elements: σ_0 (usually set to one) and σ_1 (usually denoted by σ and referred to as "the" structure coefficient). Since two sequences of two elements each can only cross each other at most once, it follows that any two population structures

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can be ordered in the containment order if $d = 2$, i.e., the containment order is a total order for $d = 2$. Moreover, the containment order is given by a comparison of the structure coefficients σ, with larger σ leading to greater containment order. For $d \geq 3$, however, two vectors of structure coefficients $\boldsymbol{\sigma}$ can cross twice. In this case, their respective population structures cannot be compared in the containment order: for $d \geq 3$ and for the space of all possible population structures, the containment order is a partial order only (see Proposition 3 in Appendix B.3).

Volume order

In order to address this issue, we also propose the "volume order". Let $\mathcal{S}_1$ and $\mathcal{S}_2$ be two population structures characterized by structure coefficients $\boldsymbol{\sigma}_1$ and $\boldsymbol{\sigma}_2$ and hence by polytopes $\mathcal{Q}_1$ and $\mathcal{Q}_2$, respectively. We say that population structure $\mathcal{S}_1$ is greater than population structure $\mathcal{S}_2$ in the volume order, and write $\mathcal{S}_1 \geq_{\text{vol}} \mathcal{S}_2$, if

$$\frac{\text{Vol}\,(\mathcal{Q}_1)}{\text{Vol}\,(\mathcal{P})} \geq \frac{\text{Vol}\,(\mathcal{Q}_2)}{\text{Vol}\,(\mathcal{P})}, \tag{5}$$

where $\text{Vol}\,(\mathcal{X})$ is the volume of polytope $\mathcal{X}$. In other words, $\mathcal{S}_1 \geq_{\text{vol}} \mathcal{S}_2$ means that for a given d, cooperation is favored under $\mathcal{S}_1$ for a greater fraction of cooperation games than under $\mathcal{S}_2$. If two structures are ordered in the containment order, this implies that they are ordered in the volume order, but the converse is not true.

We can show (see Proposition 10 in Appendix B.4 for a proof) that the volume of all d-player cooperation games $\mathcal{P}$ is given by:

$$\text{Vol}\,(\mathcal{P}) = \frac{1}{(d!)^2} - \frac{1}{(2d)!}, \tag{6}$$

which decreases rapidly with the number of players d. For $d = 2$, this volume is equal to $5/24$. In this case, the four payoffs a_1, a_0, b_1, and b_0 can be ordered in $4! = 24$ possible ways, five of which satisfy inequalities (2) and (3), namely (i) $b_1 \geq a_1 \geq b_0 \geq a_0$ (prisoner's dilemma), (ii) $b_1 \geq a_1 \geq a_0 \geq b_0$ (snowdrift game), (iii) $a_1 \geq b_1 \geq b_0 \geq a_0$ (stag hunt), (iv) $a_1 \geq b_1 \geq a_0 \geq b_0$ (harmony game), and (v) $a_1 \geq a_0 \geq b_1 \geq b_0$ (prisoner's delight; Binmore 2004). For large d, the volume of cooperation games is approximately $1/(d!^2)$, which is the volume of games satisfying conditions (2) and (4). This means that condition (3) becomes less important when the number of players d is large.

For some population structures, the structure coefficients are symmetric, i.e., $\sigma_j = \sigma_{d-1-j}$ for all j. For these particular cases, the fraction of cooperation games for which cooperation is favoured becomes

$$\frac{\text{Vol}(\mathcal{Q})}{\text{Vol}(\mathcal{P})} = \frac{1}{2}\frac{\binom{2d}{d}}{\binom{2d}{d} - 1} \geq \frac{1}{2}, \tag{7}$$

where $\binom{2d}{d} = (2d)!/(d!)^2$ is the d-th central binomial coefficient (see Proposition 11 in Appendix B.4 for a proof). This fraction is equal to $3/5$ for $d = 2$, and reduces to $1/2$ in the limit of large d. Fig. 3 illustrates how (6) and (7) scale with the number of players d.

Examples

Let us now illustrate our approach with particular examples of population structures and associated evolutionary dynamics.

Consider first a well-mixed population of size $N \geq d$ updated with a death-birth (Moran) process. In the death-birth process, each time step one individual is chosen at random to die and another one is

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chosen proportional to its "fitness" to reproduce by making a copy of itself. We show that for any $d \geq 2$, well-mixed populations updated with a death-birth process are ordered in the containment order with respect to the total population size N, such that larger populations are more conducive to multiplayer cooperation (see Proposition 4 in Appendix B.4). Our result generalizes previous results for two-player games and phenotypically close strategies according to which smaller population sizes are less conducive to cooperation in the absence of mechanisms for strategy assortment (see, e.g., Tarnita et al. 2009 Eq. 22, or Van Cleve and Lehmann 2013 Eq. B.1). In the limit of large N and by Eq. (7), well-mixed populations updated with a death-birth process favor cooperation for exactly one half of all possible cooperation games.

Let us now consider the effect of introducing spatial structure while keeping the same update rule (death-birth process). One of the simplest spatial models is the cycle (Ellison, 1993). It has been shown that cycles updated with a birth-death process are better promoters of cooperation than well-mixed populations in the case of pairwise games (Ohtsuki and Nowak, 2006), phenotypically close strategies (Grafen, 2007; Lehmann et al., 2007a), and for several examples of multiplayer social dilemmas (such as linear public goods games, snowdrift games, and stag hunt games) for large population sizes (van Veelen and Nowak, 2012). Our theory allows us to extend this observation to all multiplayer cooperation games and arbitrary population sizes. Indeed, we show that for any given population size N, cycles are always greater than well-mixed populations in the containment order (see Proposition 6 in Appendix B.4). This implies that cycles are better promoters of cooperation than well-mixed populations for any cooperation game, any number of players d, and any population size N.

A second model of spatial structure for which structure coefficients are readily available is the group splitting model of Traulsen and Nowak (Traulsen and Nowak, 2006). In this model, a finite population of size N is subdivided into m groups, which can grow in size and split with probability q when reaching the maximum size n. In the limit of rare group splitting ($q \ll 1$), all groups are typically of the maximum size n and the structure coefficients can be calculated analytically for general d-player games (Kurokawa and Ihara, 2013), see Table 1. Consider well-mixed and group-splitting populations updated according to a death-birth process. If the number of groups is greater than two, the group splitting model is greater than any well-mixed population in the containment order (see Proposition 7 in Appendix B.4). Moreover, in the limit of $m \gg n$, the structure coefficients of the group splitting model become $\sigma_{d-1} = 1$ and $\sigma_j = 0$ for $j \neq d-1$. In this limit, the group splitting model is greater in the containment order than any other population structure. Hence, it is the population structure that favors cooperation most among all theoretically possible population structures.

The cycle and the group splitting model are better promoters of cooperation than well-mixed populations. But which one promotes cooperation under more cooperation games, the cycle or the group splitting model? It turns out that this depends on the parameters of the models. Consider cycles of size N and group splitting models with rare group splitting ($q \ll 1$) consisting of m groups of maximum size n, so that the total maximum population size is equal to $N = mn$. Let us also assume that the population size N is large. In this limit, the containment ordering depends on the number of groups m of the group splitting model, in the following way (see Proposition 8 in Appendix B.4). (i) If the number of groups is small ($m \leq (n + 4d - 6)/(2d - 3)$) the group splitting model is smaller than the cycle in the containment order. (ii) If the number of groups is intermediate ($(n + 4d - 6)/(2d - 3) < m < n + 2$) the group splitting model and the cycle are incomparable in the containment order. (iii) If the number of groups is large ($m \geq n + 2$) the group splitting model is greater than the cycle in the containment order.

For example, consider a cycle of size $N = 1000$ and a group splitting model with $m = 10$ groups of maximum size $n = 100$ (Fig. 4). In this case, the cycle is greater than the group splitting model in the containment order if $d \leq 7$, while the two population structures are incomparable in the containment order if $d \geq 8$. Concerning the volume order, exact computations and numerical simulations suggest that

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the cycle is greater than the group splitting model for $d \leq 12$, and smaller than the group splitting model otherwise.

Up until now we have investigated different models of spatial structure (the well-mixed population, the cycle, the group splitting model) with a single update rule (the Moran death-birth process). However, as we have discussed above, the structure coefficients depend both on spatial structure and on the update rule. What are the effects of changing the update rule while keeping the same spatial structure? As an example, consider the case of well-mixed populations with two different update rules: the death-birth process, where a random individual dies and its neighbors compete for the empty site, and the aspiration dynamics, where a random individual is likely to switch its strategy if the current payoff does not meet its aspiration level (Szabó and Tőke, 1998; Du et al., 2014). The two update rules can be ordered in the containment order only if $2^{d-1}(N-d) \leq d(N-1)$ (see Proposition 9 in Appendix B.4). In this case, aspiration dynamics is greater than the death-birth process, meaning that if cooperation is favored under the death-birth process it will also be favored under aspiration dynamics, but not vice versa. If $2^{d-1}(N-d) > d(N-1)$ the two structures are incomparable in the containment order. However, for any finite population size N, aspiration dynamics is greater in the volume order than the death-birth process. This means that, overall, cooperation is favored for more games under aspiration dynamics than under the death-birth process.

Discussion

Our approach to compare population structures sheds new light on existing results and debates on how to study and analyze the evolutionary dynamics of cooperation in spatially structured populations. We have shown how several existing results, obtained under the assumptions of pairwise interactions, phenotypically similar strategies, or particular classes of multiplayer social dilemmas, generalize to the case of general cooperation games that we have considered here. In particular, we found that the negative effects of small population sizes in finite well-mixed populations, and the positive effects of certain kinds of population structure such as the cycle and the group splitting model together with a death-birth process, are robust with respect to different model assumptions, such as the way of implementing the assumption of weak selection (Wild and Traulsen, 2007), and the particular choice of a game to model cooperation. More importantly, one can find two population structures such that there is a class of multiplayer games for which cooperation is favored under the first but not under the second, and a class of multiplayer games for which the opposite holds true (Fig. 1 right panel). Thus, arbitrarily choosing one or a few games from all possible cooperation games to compare the effects of population structure on the evolution of cooperation can be misleading, even if we focus on the comparison of fixation probabilities under weak selection. This is different from the case of either two-player games or phenotypically similar strategies, where a ranking of population structures is always possible in terms of a single real value, and where it is sufficient to focus on a single game without loss of generality (Tarnita et al., 2009; Lehmann and Rousset, 2010).

Our probabilistic interpretation of the (normalized) structure coefficients allows us to make a straightforward connection with the concept of assortment as developed for the case of linear public goods games (Fletcher and Doebeli, 2009; Bijma and Aanen, 2010). For our purposes, we need to generalize the concept of assortment to non-linear multiplayer games. To do so, let us rewrite the selection condition (1) as

$$\sum_{j=0}^{d-1} \sigma_j a_j > \sum_{j=0}^{d-1} \sigma_{d-1-j} b_j, \tag{8}$$

and reinterpret σ_j as the "effective" probability of interacting with j individuals of the own type (and

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$d-1-j$ of the other type). As given by (8), the selection condition states that A is favored over B if the expected payoff of an A-player is greater than that of a B-player when the "interaction environments" (Fletcher and Doebeli, 2009) are distributed according to $\boldsymbol{\sigma}$. For the linear public goods game, the selection condition (8) can be put in a form reminiscent of Hamilton's rule, with $(e_{\mathrm{A}} - e_{\mathrm{B}})/(n-1)$ playing the role of a measure of assortment (or relatedness), where $e_{\mathrm{A}} = \sum_j \sigma_j j$ (resp. $e_{\mathrm{B}} = \sum_j \sigma_{d-1-j} j$) is the mean number of cooperators among the $d-1$ interaction partners of a cooperator (resp. defector) (Bijma and Aanen, 2010). For more general cooperation games, the selection condition depends not only on the mean but also on higher moments of the distribution given by $\boldsymbol{\sigma}$. The stochastic order we have used for establishing the containment order is a way of measuring the association between strategies in this general case: there is more assortment the more the structure coefficients σ_j put weight on larger values of j. Hence, it can be said that population structures greater in the containment order are those characterized by greater "effective assortment" and thus more conducive to the evolution of cooperation. In the extreme case where $\sigma_{d-1} = 1$ (and $\sigma_j = 0$ for $j \neq d-1$), we have the case of a completely segregated population where As only interact with As and Bs only interact with Bs. In this case, the selection condition reduces to (3), and cooperation is always favored by definition.

We considered a very broad definition of cooperation and a particular measure of evolutionary success, and investigated subset containment relations and volumes of the resulting sets of linear inequalities. In this respect our approach is related to a classical study by Matessi and Jayakar (1976), who first defined an "altruism domain" from a set of linear inequalities involving "local fitness functions" and then investigated the problem of finding and measuring the relative volume of the "subset of the altruism domain in which A is more fit than B on average, that is, altruism can evolve". We note, however, that our definition of cooperation is different from the definition of altruism adopted by Matessi and Jayakar (i.e., the "multi-level interpretation" of altruism, in the sense of Kerr et al. 2004). In particular, we only focused on the group benefits, not the individual costs, associated to expressing the cooperative action A. Our measure of evolutionary success is also different, as we focused on the comparison of fixation probabilities in the limit of weak selection, whereas Matessi and Jayakar (1976) focused on the one-step change in frequency. Finally, Matessi and Jayakar (1976) limited themselves to "linear fitness functions" (equivalent to linear games in our setup) while we considered the whole space of cooperation games. The differences between our study and the one by Matessi and Jayakar pinpoints possible future work along these lines. For instance, alternative definitions of cooperation (Dawes, 1980; Kerr et al., 2004) and their associated space of "cooperation games" could be explored, possibly together with alternative measures of evolutionary success (Tarnita and Taylor, 2014). As long as it is possible to write all conditions as linear inequalities involving the payoffs of the game, our theory can be used and adapted to those cases. It would be interesting to see the extent to which comparisons of different population structures based on the containment and volume orders defined here are robust to changes on the way cooperation and evolutionary success are defined.

Our approach will help to organize the myriads of results on the promotion of cooperation in spatial structures, which are typically analyzed numerically by considering a small subset of games (Perc et al., 2013). The structure coefficients we propose to analyze change only with the spatial structure and with the update rule, but they allow to assess their consequences on evolutionary dynamics independently of the game at stake.

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Methods

Polytopes

A (convex) polyhedron can be defined as the intersection of finitely many closed halfspaces in $\mathbb{R}^n$, i.e., as the set of solutions to a system of m linear inequalities

$$\mathbf{T}\mathbf{x} \leq \mathbf{c}, \tag{9}$$

where $\mathbf{T}$ is a real $m \times n$ matrix, and $\mathbf{c}$ a real vector of size m (Ziegler, 1995). A (convex) polytope is a bounded polyhedron (Ziegler, 1995). When given by a system of linear inequalities such as (9), a polytope is said to be given in its $\mathcal{H}$-representation.

We represent a d-player game as a point in $\mathbb{R}^{2d}$ with coordinates

$$\mathbf{x} = (a_{d-1}, a_{d-2}, ..., a_0, b_{d-1}, b_{d-2}, ..., b_0)^{\mathrm{T}}, \tag{10}$$

and call $\mathcal{P}$ the polytope consisting of the set of all d-player cooperation games in the hypercube $[0,1]^{2d}$. Its $\mathcal{H}$-representation is implicitly given by the set of inequalities (2), (3), and (4). Furthermore, we call $\mathcal{Q}_i$ the polytope of cooperation games for which cooperation is favored under population structure $\mathcal{S}_i$. Its $\mathcal{H}$-representation is given by adding the inequalities given by (1) to the set of inequalities defining $\mathcal{P}$.

Structure coefficients

To order any two population structures we first need to calculate their structure coefficients $\boldsymbol{\sigma}$. In the limit of rare mutations, these can be calculated from the comparison of fixation probabilities, i.e., the condition $\rho_A > \rho_B$, where ρ_X denotes the fixation probability of a single mutant playing X (either A or B) in a population of resident types playing the opposite strategy (Tarnita et al., 2009). In general, this condition can be written in terms of selection coefficients (dependent on the payoffs of the game and the demographic parameters of the model) and expected coalescence times under neutrality (see, e.g., Van Cleve 2015 Eq. 24). This would allow, in principle, to make use of coalescent theory (Wakeley, 2008) to obtain analytical expressions for the structure coefficients. In practice, however, the expected coalescence times required for calculating the structure coefficients of general d-player games can be difficult to obtain (Ladret and Lessard, 2007; Van Cleve, 2015). In this case, and for simple population structures, the condition $\rho_A > \rho_B$ can be more easily calculated from first principles, and the structure coefficients extracted from the resulting expressions. This is the approach we followed here (see Appendix A). Alternatively, in cases such as small structured populations or well-mixed populations, the selection condition (1) and hence the structure coefficients can be explicitly calculated from the transition matrix of the evolutionary process (see McAvoy and Hauert 2015 Appendix C). Finally, we note that even in cases for which the structure coefficients are difficult to obtain by purely analytical means, they can estimated by numerical simulations, either indirectly (by estimating the expected times to coalescence) or directly (by computing fixation probabilities). In this last case, it is useful to focus on a special game for each σ_j (Wu et al., 2013).

Containment order

If the structure coefficients σ_j are (i) non-negative and (ii) sum up to one, they define a probability distribution over $j = 0, 1, \ldots, d-1$. In this case, the left-hand side of the selection condition (1) can be interpreted as the expected value $\mathrm{E}[f(J)]$, where $f(j) \equiv f_j = a_j - b_{d-1-j}$, and J is the random variable associated to the probability distribution $\boldsymbol{\sigma}$. Consider now two population structures $\mathcal{S}_1$ and $\mathcal{S}_2$ with

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structure coefficients $\boldsymbol{\sigma}_1$ and $\boldsymbol{\sigma}_2$, and associated random variables J_1 and J_2, respectively. With this notation, a sufficient condition leading to the containment order $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$ is that

$$\mathrm{E}\left[f(J_1)\right] \geq \mathrm{E}\left[f(J_2)\right] \tag{11}$$

for all cooperation games.

In order to evaluate this condition, we make use of the concept of (the usual) stochastic order (Shaked and Shanthikumar, 2007). A random variable J_1 is said to be greater than J_2 in the stochastic order, denoted by $J_1 \geq_{\text{st}} J_2$, if and only if $\mathrm{E}\left[\phi(J_1)\right] \geq \mathrm{E}\left[\phi(J_2)\right]$ for all increasing functions ϕ. Conveniently, and by (2), the sequence f_j is always increasing in j, allowing us to apply this idea directly (see Appendix B.1 for details). One advantage of expressing the containment order in terms of the stochastic order is that we can make use of results from the theory of stochastic orders (Shaked and Shanthikumar, 2007), hence transforming our original polytope containment problem into a problem of finding conditions under which random variables can be stochastically ordered. Some of these conditions follow from a simple inspection of the shape of the sequence of structure coefficients. For instance, a sufficient condition leading to the stochastic order $J_1 \geq_{\text{st}} J_2$ (and hence to the containment order $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$) is that the sequence $\boldsymbol{\sigma}_1 - \boldsymbol{\sigma}_2$ has exactly one sign change from $-$ to $+$ (Shaked and Shanthikumar, 2007). We can also show that if the sequence $\boldsymbol{\sigma}_1 - \boldsymbol{\sigma}_2$ has two sign changes, then $\mathcal{S}_1$ and $\mathcal{S}_2$ are incomparable in the containment order, i.e., neither $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$ nor $\mathcal{S}_1 \leq_{\text{con}} \mathcal{S}_2$ (see Appendix B.2). In this case, we can always find a subset of cooperation games for which the selection condition (1) holds true for $\mathcal{S}_1$ but not for $\mathcal{S}_2$, and another subset for which the opposite holds true.

Volume order

There are many exact methods for computing volumes of polytopes (Büeler et al., 2000), including triangulation methods (Cohen and Hickey, 1979) and signed decomposition methods (Lasserre, 1983; Lawrence, 1991). Computing the exact volume of a polytope is however known to be #P-hard (Dyer and Frieze, 1988), and a simple task only for low dimensions. We calculated exactly the volumes in Fig. 4 for $d \leq 6$ using the function "volume" of the class "Polyhedron" of the mathematics software Sage (version 6.5). For $d \geq 7$, we used a Monte Carlo method for approximating the volumes. For each value of d, we randomly generated 10^6 increasing sequences a_j and b_j, and retained only those which fulfilled (3). We then checked how many of these sequences verified the selection condition (1). The fraction of cooperation games was then approximated by the ratio between these two numbers.

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A Structure coefficients

For each population structure we consider, and in the limit of rare mutations, the structure coefficients can be calculated from the expression giving the comparison of fixation probabilities ρ_A and ρ_B under weak selection.

A.1 Moran process on a well-mixed population

The condition $\rho_A > \rho_B$ is given by (Gokhale and Traulsen 2010, Eq. S19)

$$\sum_{j=0}^{d-1} (Na_j - a_{d-1}) > \sum_{j=0}^{d-1} (Nb_j - b_0)\,,$$

which can be rewritten as

$$\sum_{j=0}^{d-2} N\,(a_j - b_{d-1-j}) + (N-d)\,(a_{d-1} - b_0) > 0.$$

Dividing both sides of the inequality by N and comparing with the selection condition (1), we obtain

$$\sigma_j = \begin{cases} 1 & \text{if } 0 \le j \le d-2 \\ \frac{N-d}{N} & \text{if } j = d-1 \end{cases}.$$

A.2 Aspiration dynamics on a well-mixed population

The condition $\rho_A > \rho_B$ is given by (Du et al. 2014, Eq. 3.3)

$$\sum_{j=0}^{d-1} \binom{d-1}{j} (a_j - b_j) > 0.$$

Due to the symmetry of binomial coefficients $\binom{d-1}{j} = \binom{d-1}{d-1-j}$, this can be rewritten as

$$\sum_{j=0}^{d-1} \binom{d-1}{j} (a_j - b_{d-1-j}) > 0.$$

Comparing this last expression with the selection condition (1), we obtain

$$\sigma_j = \binom{d-1}{j}.$$

A.3 Death-birth process on a cycle

Let us consider the model of population structure discussed by van Veelen and Nowak (2012). Each individual is placed on the node of a cycle. Every sequence of d players defines the participants in a d-player game. Individuals accumulate the payoffs from the d games they are involved in, each with d players. These payoffs are transformed to "fitness" via an exponential payoff-to-fitness mapping (Traulsen et al., 2008). Each time step, a randomly chosen individual is selected to die and its two neighbours compete for the vacant spot with a probability proportional to fitness.

If the population starts with a single mutant, mutants form a single connected cluster in the cycle at any time. The state of the population can hence be captured by the number of A-players in this cluster, i. Denote by $f_A^0(i)$ ($f_B^0(i)$) the payoff of an A-player (B-player) lying immediately at the boundary of a

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cluster of B-players (A-players), and by $f_A^1(i)$ ($f_B^1(i)$) the payoff of an A-player (B-player) right next to it (Fig. 5). Let $T_i^{\pm}$ be the probability that the number of A-players increases ($+$) or decreases ($-$) in one time step, when there are i A-players in the population. Hence $T_1^- = T_{N-1}^+ = \frac{1}{N}$ and

$$T_i^+ = \frac{2}{N}\frac{\exp(\omega f_A^0(i))}{\exp(\omega f_A^0(i)) + \exp(\omega f_B^1(i))}, \; 1 \le i \le N-2, \tag{12a}$$

$$T_i^- = \frac{2}{N}\frac{\exp(\omega f_B^0(i))}{\exp(\omega f_B^0(i)) + \exp(\omega f_A^1(i))}, \; 2 \le i \le N-1, \tag{12b}$$

where ω is a parameter measuring the strength of selection. Strategy A is favored if $\rho_A > \rho_B$, which is equivalent to (Nowak et al., 2004)

$$\prod_{i=1}^{N-1} \frac{T_i^+}{T_i^-} > 1. \tag{13}$$

For weak selection, (13) is equivalent to

$$\frac{\mathrm{d}}{\mathrm{d}\omega} \prod_{i=1}^{N-1} \frac{T_i^+}{T_i^-}\bigg|_{\omega=0} > 0. \tag{14}$$

Replacing (12) into (14), we get

$$\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}\omega} \prod_{i=1}^{N-1} \frac{T_i^+}{T_i^-}\bigg|_{\omega=0} &= \sum_{i=1}^{N-1} \frac{\mathrm{d}}{\mathrm{d}\omega}\frac{T_i^+}{T_i^-}\bigg|_{\omega=0} \\
&= \sum_{i=1}^{N-1} N\left(\frac{\mathrm{d}}{\mathrm{d}\omega}T_i^+ - \frac{\mathrm{d}}{\mathrm{d}\omega}T_i^-\right)\bigg|_{\omega=0} \\
&= \frac{1}{2}\sum_{i=1}^{N-1} f_A^0(i) + \frac{1}{2}\sum_{i=2}^{N-1} f_A^1(i) - \frac{1}{2}\sum_{i=1}^{N-1} f_B^0(i) - \frac{1}{2}\sum_{i=1}^{N-2} f_B^1(i).
\end{aligned} \tag{15}$$

The above expression is a linear combination of the payoff entries a_j and b_j. Further, by the selection condition (1), the coefficients of a_j are the same as those of b_{d-1-j}. Thus it is only necessary to calculate the coefficients of a_j, which only depend on the first two terms of (15). Using the expressions for $f_A^0(i)$ and $f_A^1(i)$ (see van Veelen and Nowak 2012, Appendix B) we finally obtain:

$$\sigma_j = \begin{cases} 1 & \text{if } j = 0 \\ \frac{2N}{N+1} & \text{if } 1 \le j \le d-3 \\ \frac{2N-1}{N+1} & \text{if } j = d-2 \\ \frac{3(N-d)}{N+1} & \text{if } j = d-1 \end{cases}. \tag{16}$$

It is noteworthy that the expression

$$(a_0 - b_0) + 2\sum_{i=1}^{d-2}(a_i - b_i) + 3(a_{d-1} - b_{d-1}) > 0,$$

obtained in van Veelen and Nowak (2012) is a sufficient condition for strategy A to be more abundant than strategy B. Our result (1) with structure coefficients given by (16) is the necessary and sufficient condition. In addition, we note that our result holds for general payoff-to-fitness mapping f, provided that $f'(0)$ is non-vanishing (Wu et al., 2010a).

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A.4 Moran process on a group splitting model

Consider the following multiplayer extension (Kurokawa and Ihara, 2013) of the group splitting model of Traulsen and Nowak (2006). The population is subdivided into m groups. Each population is allowed to grow to its maximum size n, then splits with probability q. Within populations, random groups of d individuals form and interact in a d-player game. When group splitting is rare ($q \ll 1$) and the mapping between payoffs and fitness is given by an exponential function, the ratio of fixation probabilities is given by (Kurokawa and Ihara 2013, Eq. 15):

$$\frac{\rho_A}{\rho_B} = \exp\left[\frac{m+n-2}{d} w \sum_{j=0}^{d-1} (C_j + \kappa B_j)\right], \tag{17}$$

where

$$C_j = a_j - b_j,$$
$$B_j = j\,(a_j - a_{j-1}) + (d-1-j)\,(b_{j+1} - b_j)\,,$$

are, respectively, the "direct" and "indirect" gains from switching from strategy A to strategy B (see Peña et al. 2015, Eqs. 6 and 7), and

$$\kappa = \frac{m-2}{m+n-2} \tag{18}$$

can be interpreted as the "scaled relatedness coefficient" of this model when the migration rate is zero (see Van Cleve and Lehmann 2013, Eq. B.4).

From (17), a necessary and sufficient condition for $\rho_A > \rho_B$ is that:

$$\sum_{j=0}^{d-1} (C_j + \kappa B_j) > 0, \tag{19}$$

which can be rearranged in terms of payoffs and structure coefficients in the form of (1),

$$\sum_{j=0}^{d-1} (C_j + \kappa B_j) = \sum_{j=0}^{d-1} a_j - \sum_{j=0}^{d-1} b_j + \kappa \left[d a_{d-1} - \sum_{j=0}^{d-1} a_j - d b_0 + \sum_{j=0}^{d-1} b_j \right],$$

so that condition (19) can be written as:

$$(1-\kappa) \sum_{j=0}^{d-2} (a_j - b_{d-1-j}) + (1 - \kappa + \kappa d)\,(a_{d-1} - b_0) > 0.$$

After dividing both sides of the inequality by $1-\kappa$, inserting the value of κ given in (18), and comparing with (1), we obtain

$$\sigma_j = \begin{cases} 1 & \text{if } 0 \le j \le d-2 \\ 1 + \frac{d(m-2)}{n} & \text{if } j = d-1 \end{cases}.$$

A.5 Normalized structure coefficients

For all population structures discussed in this section and listed in Table 1 of the main text, the structure coefficients are nonnegative. This is also true for many other population structures, at least for $d = 2$

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(Tarnita et al., 2009). In these cases, the structure coefficients can be normalized so that the containment order can be investigated using stochastic orders (Shaked and Shanthikumar, 2007). Henceforth, we refer to the normalized structure coefficients by $\boldsymbol{\sigma} = (\sigma_0, \ldots, \sigma_{d-1})$. Table 2 lists the normalized structure coefficients for the examples of population structures previously discussed.

B Containment order

B.1 A sufficient condition leading to the containment order

Consider two population structures $\mathcal{S}_1$ and $\mathcal{S}_2$ characterized by the (normalized) structure coefficients $\boldsymbol{\sigma}_1$ and $\boldsymbol{\sigma}_2$, and associated random variables J_1 and J_2, respectively. Let us also define the sequence of "gains from flipping":

$$f(j) \equiv f_j = a_j - b_{d-1-j}, \tag{20}$$

i.e., the gains in payoff experienced by a focal B-player interacting with j A-players (and $d-1-j$ B-players) after all players in the group, including the focal, flip their strategies (A-players become B-players and vice versa).

Because of condition (2), the gains from flipping are increasing. Hence, a sufficient condition for $\mathcal{S}_1$ to be greater than $\mathcal{S}_2$ in the containment order is that

$$\mathrm{E}\left[\phi(J_2)\right] \geq 0 \Rightarrow \mathrm{E}\left[\phi(J_1)\right] \geq 0, \text{ for all increasing functions } \phi : \mathbb{R} \to \mathbb{R}. \tag{21}$$

A sufficient condition for this is that

$$\mathrm{E}\left[\phi(J_1)\right] \geq \mathrm{E}\left[\phi(J_2)\right], \text{ for all increasing functions } \phi : \mathbb{R} \to \mathbb{R}, \tag{22}$$

which is fulfilled by definition if J_1 is greater than J_2 in the (usual) stochastic order, denoted by $J_1 \geq_{\mathrm{st}} J_2$ (Shaked and Shanthikumar (2007), p. 4).

There are many conditions leading to the stochastic ordering of two random variables (Shaked and Shanthikumar 2007, ch. 1). For instance, it is known that $J_1 \geq_{\mathrm{st}} J_2$ if and only if (Shaked and Shanthikumar 2007, p. 4)

$$\varsigma_{1,k} \leq \varsigma_{2,k} \text{ for all } k = 0, 1, \ldots, d-1, \tag{23}$$

where $\boldsymbol{\varsigma}$ is the distribution function corresponding to $\boldsymbol{\sigma}$, i.e.,

$$\varsigma_k = \Pr(J \leq k) = \sum_{j=0}^{k} \sigma_j, \text{ for } k = 0, 1, \ldots, d-1. \tag{24}$$

A simple sufficient condition leading to the set of inequalities given by (23) and hence to $J_1 \geq_{\mathrm{st}} J_2$ is that $S^-(\boldsymbol{\sigma}_1 - \boldsymbol{\sigma}_2) = 1$ (where $S^-(a)$ is the number of sign changes of the sequence a) and the sign sequence is $-, +$ (Shaked and Shanthikumar 2007, p. 10). That is, if the structure coefficients $\boldsymbol{\sigma}_1$ "put more weight" in larger values of j than the structure coefficients $\boldsymbol{\sigma}_2$, then $J_1 \geq_{\mathrm{st}} J_2$. We summarize this observation in the following proposition.

Proposition 1 (A sufficient condition leading to the containment order)**.** *Let $\mathcal{S}_1$ and $\mathcal{S}_2$ be two population structures with (normalized) structure coefficients $\boldsymbol{\sigma}_1$ and $\boldsymbol{\sigma}_2$, respectively. If $S^-(\boldsymbol{\sigma}_1 - \boldsymbol{\sigma}_2) = 1$ and the sign sequence is $-, +$, then $\mathcal{S}_1 \geq_{\mathrm{con}} \mathcal{S}_2$.*

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B.2 A sufficient condition leading to the incomparability in the containment order

Given two population structures $\mathcal{S}_1$ and $\mathcal{S}_2$, it could be that neither $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$ nor $\mathcal{S}_1 \leq_{\text{con}} \mathcal{S}_2$ holds true. We are also interested in establishing a simple sufficient condition leading to such incomparability in the containment order, that we denote by $\mathcal{S}_1 \parallel_{\text{con}} \mathcal{S}_2$. In order to derive this, suppose that the structure coefficients of $\mathcal{S}_1$ and $\mathcal{S}_2$ cross each other twice, i.e., that

$$S^-(\boldsymbol{\sigma}_1 - \boldsymbol{\sigma}_2) = 2. \tag{25}$$

Condition (25) implies that $S^-(\boldsymbol{\varsigma}_1 - \boldsymbol{\varsigma}_2) = 1$ (Whitt 1985, p. 621) and hence that (23) does not hold true. This in turn implies that J_1 and J_2 are incomparable in the stochastic order, i.e., $J_1 \parallel_{\text{st}} J_2$. Showing that (25) also implies $\mathcal{S}_1 \parallel_{\text{con}} \mathcal{S}_2$ however requires some additional arguments. Indeed, note that $J_1 \parallel_{\text{st}} J_2$ does not necessarily imply $\mathcal{S}_1 \parallel_{\text{con}} \mathcal{S}_2$: the stochastic order is a sufficient but not a necessary condition leading to the containment order (cf. (21) and (22)).

In order to prove that (25) leads to $\mathcal{S}_1 \parallel_{\text{con}} \mathcal{S}_2$, we make use of two other stochastic orders: the increasing convex order and the increasing concave order (Shaked and Shanthikumar 2007, p. 181). A random variable J_1 is said to be greater than J_2 in the increasing convex (resp. concave) order, denoted by $J_1 \geq_{\text{icx}} J_2$ (resp. $J_1 \geq_{\text{icv}} J_2$), if

$$\mathrm{E}\left[\phi(J_1)\right] \geq \mathrm{E}\left[\phi(J_2)\right], \text{ for all increasing convex (resp. concave) functions } \phi : \mathbb{R} \to \mathbb{R}. \tag{26}$$

A simple condition leading to these orders is given in the following lemma.

Lemma 1 (A sufficient condition leading to the increasing convex (resp. concave) order)**.** *Let X and Y be two random variables with density functions p and q respectively. If*

$$S^-(p - q) = 2 \quad \textit{with sign sequence } +, -, + \textit{ (resp. } -, +, -) \tag{27}$$

then $X \geq_{\text{icx}} Y$ (resp. $X \geq_{\text{icv}} Y$).

Proof. Denote by P and Q the distribution functions associated to X and Y, respectively. Condition (27) implies (Whitt 1985, p. 621)

$$S^-(P - Q) = 1 \quad \text{with sign sequence } +, - \text{ (resp. } -, +). \tag{28}$$

Since (28) implies the increasing convex (resp. concave) order (Shaked and Shanthikumar 2007, p. 194), this completes the proof. □

Let us now consider two population structures $\mathcal{S}_1$ and $\mathcal{S}_2$ whose structure coefficients satisfy (25). Without loss of generality, suppose that the sign pattern is $+, -, +$. By Lemma 1, it follows that $J_1 \geq_{\text{icx}} J_2$ and $J_2 \geq_{\text{icv}} J_1$. This suggests that there might be both (i) games with increasing and convex gains from flipping f_j for which $\mathcal{S}_1$ (but not $\mathcal{S}_2$) fulfills the selection condition (1), and (ii) games with increasing and concave gains from flipping f_j for which $\mathcal{S}_2$ (but not $\mathcal{S}_1$) fulfills the selection condition (1).

As an example of such games, consider a club goods game between cooperators (A) and defectors (B), where cooperators pay a cost c in order to provide an excludable collective good that only cooperators can use, while defectors refrain from contributing and hence from using the good (Peña et al., 2015). This

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game is characterized by the payoff sequences:

$$a_j = v_{j+1},$$
$$b_j = c,$$

where v_k gives the value of the collective good as a function of the total number of cooperators, $k = j+1$, and c is the payoff defectors obtain. We further assume that v_k is given by

$$v_k = v \sum_{\ell=0}^{k-1} u^\ell = v \frac{1-u^k}{1-u},$$

where $v > 0$ is some baseline value, and $u > 0$ is a synergy or discounting parameter. The gains from flipping of this game are then given by

$$f_j = v_{j+1} - c.$$

Let us first impose the condition:

$$\mathrm{E}\left[f(J_1)\right] > 0 > \mathrm{E}\left[f(J_2)\right] \tag{29}$$

so that $\mathcal{S}_1$ but not $\mathcal{S}_2$ satisfies the selection condition (1). Condition (29) is satisfied if

$$\frac{1}{\gamma_1} < \frac{v}{c} < \frac{1}{\gamma_2} \tag{30}$$

where

$$\gamma_i = \mathrm{E}\left[\frac{1-u^{J_i+1}}{1-u}\right], \text{ for } i = 1, 2.$$

Note that (30) is satisfied if $u > 1$, because in this case $(1-u^{j+1})/(1-u)$ is increasing and convex and $J_1 \geq_{\mathrm{icx}} J_2$.

Let us now impose the condition:

$$\mathrm{E}\left[f(J_2)\right] > 0 > \mathrm{E}\left[f(J_1)\right] \tag{31}$$

so that $\mathcal{S}_2$ but not $\mathcal{S}_1$ satisfies the selection condition (1). In this case, (31) is satisfied if

$$\frac{1}{\gamma_2} < \frac{v}{c} < \frac{1}{\gamma_1}, \tag{32}$$

which holds true if $0 < u < 1$, as in this case $(1-u^{j+1})/(1-u)$ is increasing and concave and $J_2 \geq_{\mathrm{icv}} J_1$.

We summarize the previous observations in the following proposition.

Proposition 2 (A sufficient condition leading to the incomparability in the containment order)**.** *Let $\mathcal{S}_1$ and $\mathcal{S}_2$ be two population structures with (normalized) structure coefficients $\boldsymbol{\sigma}_1$ and $\boldsymbol{\sigma}_2$, respectively. If $S^-(\boldsymbol{\sigma}_1 - \boldsymbol{\sigma}_2) = 2$ then $\mathcal{S}_1 \parallel_{\mathrm{con}} \mathcal{S}_2$, i.e., neither $\mathcal{S}_1 \geq_{\mathrm{con}} \mathcal{S}_2$ nor $\mathcal{S}_1 \leq_{\mathrm{con}} \mathcal{S}_2$ hold true. Moreover, if the sign sequence of $\boldsymbol{\sigma}_1 - \boldsymbol{\sigma}_2$ is $+, -, +$ (resp. $-, +, -$) it is possible to find cooperation games with convex (resp. concave) gains from flipping f_j such that the selection condition (1) is satisfied for $\mathcal{S}_1$ but not for $\mathcal{S}_2$ (resp. for $\mathcal{S}_2$ but not for $\mathcal{S}_1$) and cooperation games with concave (resp. convex) gains from flipping f_j such that the selection condition (1) is satisfied for $\mathcal{S}_2$ but not for $\mathcal{S}_1$ (resp. for $\mathcal{S}_1$ but not for $\mathcal{S}_2$).*

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B.3 The containment order is a total order for $d = 2$ but a partial order for $d \geq 3$

Propositions 1 and 2 allow us to prove the following result.

Proposition 3 (The containment order is total for $d = 2$ but partial for $d = 3$)**.** *Consider the set of all possible population structures $\{\mathcal{S}\}$ for a given group size d. $\{\mathcal{S}\}$ is totally ordered under $\leq_{\text{con}}$ for $d = 2$ but only partially ordered under $\leq_{\text{con}}$ for $d \geq 3$.*

Proof. For $d = 2$, the probability mass function given by the normalized structure coefficients $\boldsymbol{\sigma}$ consists of only two points. Consequently, $\boldsymbol{\sigma}_1 - \boldsymbol{\sigma}_2$ has either (i) no sign changes (i.e., $\boldsymbol{\sigma}_1 = \boldsymbol{\sigma}_2$), which implies $\mathcal{S}_1 =_{\text{con}} \mathcal{S}_2$; (ii) a sign change from $-$ to $+$, which implies $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$; or (iii) a sign change from $+$ to $-$, which implies $\mathcal{S}_1 \leq_{\text{con}} \mathcal{S}_2$. For $d \geq 3$, the probability mass function given by the normalized structure coefficients $\boldsymbol{\sigma}$ consists of $d \geq 3$ points. In this case, it is always possible to find $\mathcal{S}_1$ and $\mathcal{S}_2$ such that $\boldsymbol{\sigma}_1 - \boldsymbol{\sigma}_2$ has two sign changes. In this case, neither $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$ nor $\mathcal{S}_1 \leq_{\text{con}} \mathcal{S}_2$ hold true. □

B.4 Examples

In the following, we state several results concerning the containment order for the population structures listed in Table 2. We omit the proofs, as they are applications of Propositions 1 and 2 above.

Proposition 4 (Containment order for well-mixed populations with a Moran process)**.** *Denote by $\mathcal{S}_N^{\text{well-mixed}}$ a well-mixed population of size N with a Moran process as updating rule. Then $\mathcal{S}_N^{\text{well-mixed}} \leq_{\text{con}} \mathcal{S}_{N+1}^{\text{well-mixed}}$ for all $N \geq d$.*

Proposition 5 (Containment order for cycles with a Moran death-birth process)**.** *Denote by $\mathcal{S}_N^{\text{cycle}}$ a cycle of size N with death-birth updating. Then $\mathcal{S}_N^{\text{cycle}} \leq_{\text{con}} \mathcal{S}_{N+1}^{\text{cycle}}$ for all $N \geq d$.*

Proposition 6 (Containment order for cycles and well-mixed populations updated with a Moran death-birth process)**.** *Let $\mathcal{S}_N^{\text{cycle}}$ and $\mathcal{S}_N^{\text{well-mixed}}$ be respectively a cycle and a well-mixed population of size N, both updated with a Moran death-birth process. Then, for all d and all $N > d$, $\mathcal{S}_N^{\text{cycle}} \geq_{\text{con}} \mathcal{S}_N^{\text{well-mixed}}$.*

Proposition 7 (Containment order for group splitting models and well-mixed populations, both updated with a Moran death-birth process)**.** *Let $\mathcal{S}_{m,n}^{\text{group-splitting}}$ be a group splitting model with m groups of maximum size n and rare group splitting ($q \ll 1$), and $\mathcal{S}_N^{\text{well-mixed}}$ a well-mixed population of size N, both updated with a Moran death-birth process. We have that $\mathcal{S}_{1,N}^{\text{group-splitting}} =_{\text{con}} \mathcal{S}_N^{\text{well-mixed}}$, $\mathcal{S}_{2,n}^{\text{group-splitting}} =_{\text{con}} \mathcal{S}_\infty^{\text{well-mixed}}$ for any n, and $\mathcal{S}_{m,n}^{\text{group-splitting}} \geq_{\text{con}} \mathcal{S}_\infty^{\text{well-mixed}}$ for $m \geq 3$ and any n.*

Proposition 8 (Containment order for cycles and group splitting models, both updated with a Moran death-birth process)**.** *Let $\mathcal{S}_{m,n}^{\text{group-splitting}}$ be a group splitting model with m groups of maximum size n and rare group splitting ($q \ll 1$), and $\mathcal{S}^{\text{cycle}}$ be a cycle of size N, both updated with a Moran death-birth process. In the limit of large $N = mn$ we have:*

1. *If $m \leq \frac{n+4d-6}{2d-3}$ then $\mathcal{S}_{m,n}^{\text{group-splitting}} \leq_{\text{con}} \mathcal{S}_N^{\text{cycle}}$.*
2. *If $\frac{n+4d-6}{2d-3} < m < n+2$ then $\mathcal{S}_{m,n}^{\text{group-splitting}} \parallel_{\text{con}} \mathcal{S}_N^{\text{cycle}}$.*
3. *If $m \geq n+2$, then $\mathcal{S}_{m,n}^{\text{group-splitting}} \geq_{\text{con}} \mathcal{S}_N^{\text{cycle}}$.*

Proposition 9 (Aspiration dynamics vs. Moran process in well-mixed populations)**.** *Let $\mathcal{S}^{\text{aspiration}}$ and $\mathcal{S}_N^{\text{Moran}}$ be well-mixed populations of size $N \geq d$, updated with aspiration dynamics and a Moran process, respectively. We have:*

1. *If $2^{d-1}(N-d) \leq d(N-1)$ then $\mathcal{S}_N^{\text{Moran}} \leq_{\text{con}} \mathcal{S}^{\text{aspiration}}$.*
2. *If $2^{d-1}(N-d) > d(N-1)$ then $\mathcal{S}_N^{\text{Moran}} \parallel_{\text{con}} \mathcal{S}^{\text{aspiration}}$.*

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Volume order

In the following, we give a formula for the volume of cooperation games, as defined by inequalities (2)–(4). For this, we find convenient to define $\mathcal{I}$ as the polytope given by inequalities (2) and (4), and $\mathcal{J}$ as the polytope given by inequalities (2), (4), and $a_{d-1} \leq b_0$ (which is the opposite of (3)). The volumes of these two polytopes are easy to calculate exactly using probabilistic arguments. Indeed, we have the following two lemmas.

Lemma 2 (Volume of $\mathcal{I}$)**.** *We have that*

$$Vol(\mathcal{I}) = \frac{1}{(d!)^2}.$$

Proof. This problem is equivalent to calculating the probability that two sequences $(a_0, a_1, \ldots, a_{d-1})$ and $(b_0, b_1, \ldots, b_{d-1})$, with elements randomly and independently drawn from the interval $[0, 1]$, are such that $a_0 \leq a_1 \leq \ldots \leq a_{d-1}$ and $b_0 \leq b_1 \leq \ldots \leq b_{d-1}$. For each sequence, the probability of having a randomly ordered sequence of length d is $1/d!$, since $d!$ is the number of permutations of d distinct objects and only one of such permutations will be given in the specified order. Since the two sequences are independent, the total probability is given by $1/(d!)^2$. □

Lemma 3 (Volume of $\mathcal{J}$)**.** *We have that*

$$Vol(\mathcal{J}) = \frac{1}{(2d)!}.$$

Proof. This problem is equivalent to calculating the probability that the sequence $(a_0, \ldots, a_{d-1}, b_0, \ldots, b_{d-1})$ with elements randomly and independently drawn from the interval $[0, 1]$ is such that $a_0 \leq a_1 \leq \ldots \leq a_{d-1} \leq b_0 \leq b_1 \leq \ldots \leq b_{d-1}$. Following the same argument as in the proof of Lemma 2, this probability is equal to $1/(2d)!$. □

Making use of these two lemmas, we can find an expression for the volume of $\mathcal{P}$, the polytope of cooperation games. We state this result in the following proposition.

Proposition 10 (Volume of cooperation games)**.** *The volume of cooperation games is given by*

$$Vol(\mathcal{P}) = \frac{1}{(d!)^2} - \frac{1}{(2d)!}$$

Proof. Follows from Lemmas 2 and 3 upon noticing that $\mathcal{P} = \mathcal{I} - \mathcal{J}$. □

Some population structures, such as large well-mixed populations updated with a Moran process, and finite well-mixed populations updated with the aspiration dynamics, are such that their structure coefficients are symmetric, i.e., $\sigma_j = \sigma_{d-1-j}$ for all j. We are intereted in calculating the fraction of cooperation games for which such population structures favor strategy A. In order to calculate this result, we need the following lemma. The lemma may appear to be obvious for symmetry reasons, but the additional requirement that we are dealing with cooperation games (hence a subset of the hypercube of all possible games) adds a further complication.

Lemma 4. *Let $\mathcal{S}$ be a population structure with symmetric structure coefficients, i.e., $\sigma_j = \sigma_{d-1-j}$ for all j. Let also $\mathcal{I}_+$ be the subset of $\mathcal{I}$ for which A is favored over B. Then*

$$\frac{\mathrm{Vol}(\mathcal{I}_+)}{\mathrm{Vol}(\mathcal{I})} = \frac{1}{2}.$$

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Proof. Denote by $\mathcal{I}_-$ and $\mathcal{I}_0$ the subsets of $\mathcal{I}$ such that $\sum_{j=0}^{d-1}\sigma_j(a_j - b_{d-1-j}) < 0$ and $\sum_{j=0}^{d-1}\sigma_j(a_j - b_{d-1-j}) = 0$, respectively. Then we arrive at a partition of set $\mathcal{I}$, namely $\mathcal{I} = \mathcal{I}_+ \cup \mathcal{I}_0 \cup \mathcal{I}_-$. Since there must exist a j^* such that $\sigma_{j^*} \neq 0$, the solution space of $\sum_{j=0}^{d-1}\sigma_j(a_j - b_{d-1-j}) = 0$ is of lower dimension than $2d$, and hence $\mathrm{Vol}(\mathcal{I}_0) = 0$. Thus $\mathrm{Vol}(\mathcal{I}) = \mathrm{Vol}(\mathcal{I}_+) + \mathrm{Vol}(\mathcal{I}_-)$.

In the following, we prove that $\mathrm{Vol}(\mathcal{I}_+) = \mathrm{Vol}(\mathcal{I}_-)$. For this, we define the mapping

$$\psi((a_0, a_1, \cdots, a_{d-1}, b_0, b_1, \cdots, b_{d-1})) = (b_0, b_1, \cdots, b_{d-1}, a_0, a_1, \cdots, a_{d-1}). \tag{33}$$

For every $(a_0, a_1, \cdots, a_{d-1}, b_0, b_1, \cdots, b_{d-1}) \in \mathcal{I}_+$, $\sum_{j=0}^{d-1}\sigma_j(a_j - b_{d-1-j}) > 0$ holds, which implies that $\sum_{j=0}^{d-1}\sigma_j(b_{d-1-j} - a_j) < 0$ holds. Since $\sigma_j = \sigma_{d-1-j}$, we have $\sum_{j=0}^{d-1}\sigma_{d-1-j}(b_{d-1-j} - a_j) = \sum_{j=0}^{d-1}\sigma_j(b_j - a_{d-1-j}) < 0$. This implies that $\psi((a_0, a_1, \cdots, a_{d-1}, b_0, b_1, \cdots, b_{d-1})) \in \mathcal{I}_-$. Thus $\psi(\mathcal{I}_+) \subset \mathcal{I}_-$. Similarly, we have $\psi(\mathcal{I}_-) \subset \mathcal{I}_+$. Therefore $\psi(\mathcal{I}_+) = \mathcal{I}_-$. This leads to

$$\mathrm{Vol}(\mathcal{I}_-) = \left|\int_{\mathcal{I}_-} dx\right| = \left|\int_{\psi(\mathcal{I}_+)} dx\right|. \tag{34}$$

In addition, since ψ^2 is the identity mapping ($\psi^2 = I$), ψ is invertible and the inverse mapping is the mapping itself, i.e., $\psi^{-1} = \psi$. This leads to

$$\mathrm{Vol}(\mathcal{I}_-) = \left|\int_{\mathcal{I}_+} d\psi^{-1}(x)\right| = \left|\int_{\mathcal{I}_+} d\psi(x)\right| = \left|\int_{\mathcal{I}_+} \det(\psi)dx\right|. \tag{35}$$

Here $\det(\psi)$ is the determinant of the Jacobian matrix of the transformation ψ at x. Further, considering that ψ is a linear mapping, $\psi^2 = I$ implies $|\det(\psi)| = 1$. Thus (35) yields

$$\mathrm{Vol}(\mathcal{I}_-) = \left|\int_{\mathcal{I}_+} dx\right| = \mathrm{Vol}(\mathcal{I}_+). \tag{36}$$

Therefore $\mathrm{Vol}(\mathcal{I}) = \mathrm{Vol}(\mathcal{I}_+) + \mathrm{Vol}(\mathcal{I}_-) = 2\mathrm{Vol}(\mathcal{I}_+)$, or

$$\frac{\mathrm{Vol}(\mathcal{I}_+)}{\mathrm{Vol}(\mathcal{I})} = \frac{1}{2}.$$

□

With this lemma, we can prove the following proposition.

Proposition 11. *Let $\mathcal{S}$ be a population structure with positive symmetric structure coefficients, i.e., $\sigma_j = \sigma_{d-1-j}$ for all j, and $\mathcal{Q}$ the polytope asociated to all cooperation games for which A is favored over B under $\mathcal{S}$. Then*

$$\frac{\mathrm{Vol}(\mathcal{Q})}{\mathrm{Vol}(\mathcal{P})} = \frac{1}{2}\frac{\binom{2d}{d}}{\binom{2d}{d} - 1},$$

which is a decreasing function of d, and is equal to $1/2$ in the limit of large d.

Proof. It is easy to check that for every $(a_0, a_1, \cdots, a_{d-1}, b_0, b_1, \cdots, b_{d-1}) \in \mathcal{J}$, $\sum_{j=0}^{d-1-j}\sigma_j(a_j - b_{d-1-j}) \leq (a_{d-1} - b_0)\sum_{j=0}^{d-1-j}\sigma_j = (a_{d-1} - b_0) < 0$ holds true, which implies $\mathcal{J} \subset \mathcal{I}_-$. Since $\mathcal{J} \subset \mathcal{I}_-$ and $\mathcal{I} = \mathcal{I}_- \cup \mathcal{I}_0 \cup \mathcal{I}_+$, then $\mathcal{Q} = \mathcal{I}_+$. Moreover $\mathcal{P} = \mathcal{I} - \mathcal{J}$. Hence

$$\frac{\mathrm{Vol}(\mathcal{Q})}{\mathrm{Vol}(\mathcal{P})} = \frac{\mathrm{Vol}(\mathcal{I}_+)}{\mathrm{Vol}(\mathcal{I}) - \mathrm{Vol}(\mathcal{J})},$$

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and by Lemma 4

$$\frac{\mathrm{Vol}(\mathcal{Q})}{\mathrm{Vol}(\mathcal{P})} = \frac{1}{2}\frac{\mathrm{Vol}(\mathcal{I})}{\mathrm{Vol}(\mathcal{I}) - \mathrm{Vol}(\mathcal{J})}.$$

Using Lemmas 2 and 3, we finish the proof. □

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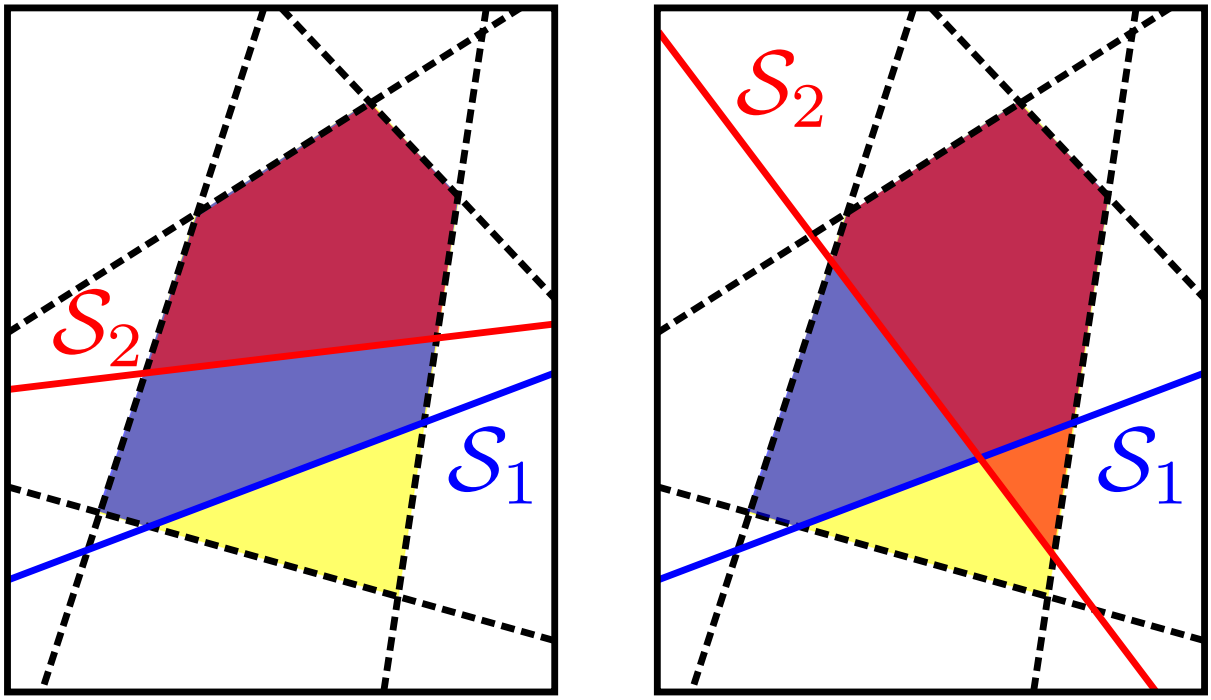

Figure 1: **Containment and volume orders of cooperation.** The set of d-player cooperation games is defined by a set of linear inequalities (*dashed lines*) defining a polytope in a $2d$-dimensional space. A given population structure (e.g., $\mathcal{S}_1$ or $\mathcal{S}_2$) is characterized by a selection condition defining a further linear inequality (*solid lines*). Here, we show a pictorial representation of the projection of such multidimensional objects to the plane, where polytopes are polygones. *Left:* The set of games for which cooperation is favored under $\mathcal{S}_2$ is contained in the set of the games for which cooperation is favored under $\mathcal{S}_1$. Hence, we say that $\mathcal{S}_1$ is greater than $\mathcal{S}_2$ in the containment order (denoted by $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$). *Right:* $\mathcal{S}_1$ and $\mathcal{S}_2$ cannot be ordered in the containment order (denoted by $\mathcal{S}_1 \parallel_{\text{con}} \mathcal{S}_2$) as there are both games for which $\mathcal{S}_1$ favors cooperation but not $\mathcal{S}_2$ (*purple polygon*), and games for which $\mathcal{S}_2$ favors cooperation but not $\mathcal{S}_1$ (*orange polygon*). In both the left and the right panels, $\mathcal{S}_1$ favors cooperation for more games than $\mathcal{S}_2$ does. Hence, we say that $\mathcal{S}_1$ is greater than $\mathcal{S}_2$ in the volume order (denoted by $\mathcal{S}_1 \geq_{\text{vol}} \mathcal{S}_2$).

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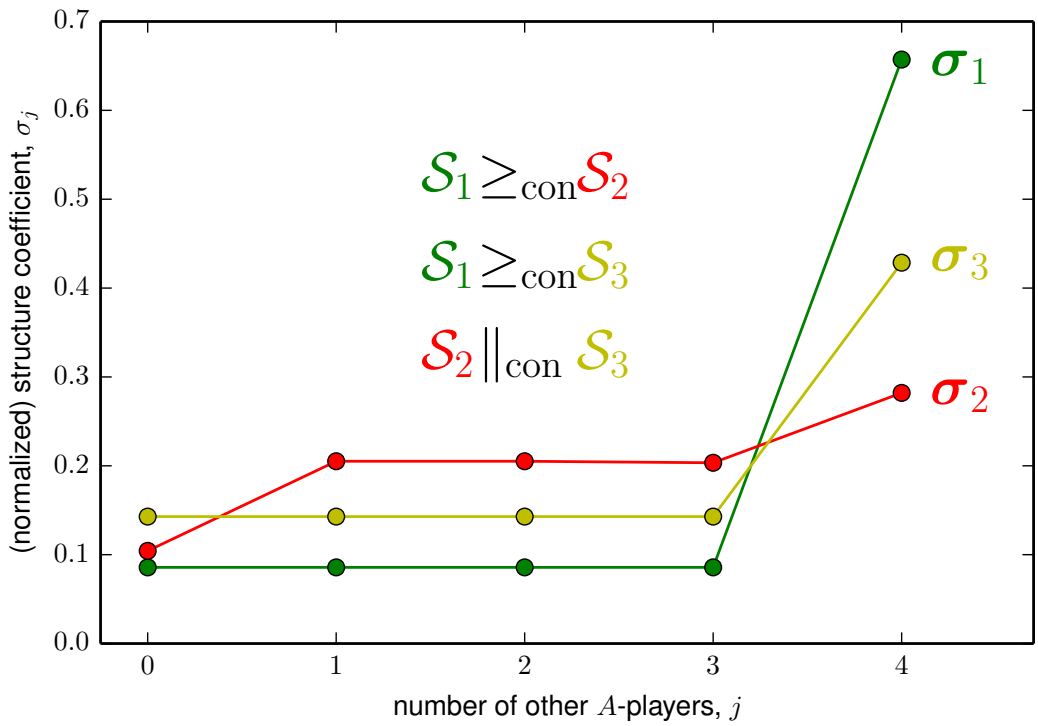

Figure 2: **Comparability in the containment order.** The structure coefficients $\boldsymbol{\sigma}_1$ and $\boldsymbol{\sigma}_2$ cross exactly once, implying that $\mathcal{S}_1$ and $\mathcal{S}_2$ are comparable in the containment order. Moreover, $\boldsymbol{\sigma}_1$ crosses $\boldsymbol{\sigma}_2$ from below; hence $\mathcal{S}_1$ is greater than $\mathcal{S}_2$ in the containment order ($\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_2$). Likewise, $\mathcal{S}_1 \geq_{\text{con}} \mathcal{S}_3$. Contrastingly, the structure coefficients $\boldsymbol{\sigma}_2$ and $\boldsymbol{\sigma}_3$ cross exactly twice, implying that $\mathcal{S}_2$ and $\mathcal{S}_3$ are incomparable in the containment order ($\mathcal{S}_2 \|_{\text{con}} \mathcal{S}_3$), i.e., neither $\mathcal{S}_2 \leq_{\text{con}} \mathcal{S}_3$ nor $\mathcal{S}_2 \geq_{\text{con}} \mathcal{S}_3$. For such cases, the volume order provides an alternative way to order these structures. Here, $\mathcal{S}_1$ is a group splitting model with $m = 10$ groups of maximum size $n = 6$ and rare probability of splitting ($q \ll 1$), $\mathcal{S}_2$ is a cycle of size $N = 60$, and $\mathcal{S}_3$ is a group splitting model with $m = 6$, $n = 10$, and $q \ll 1$.

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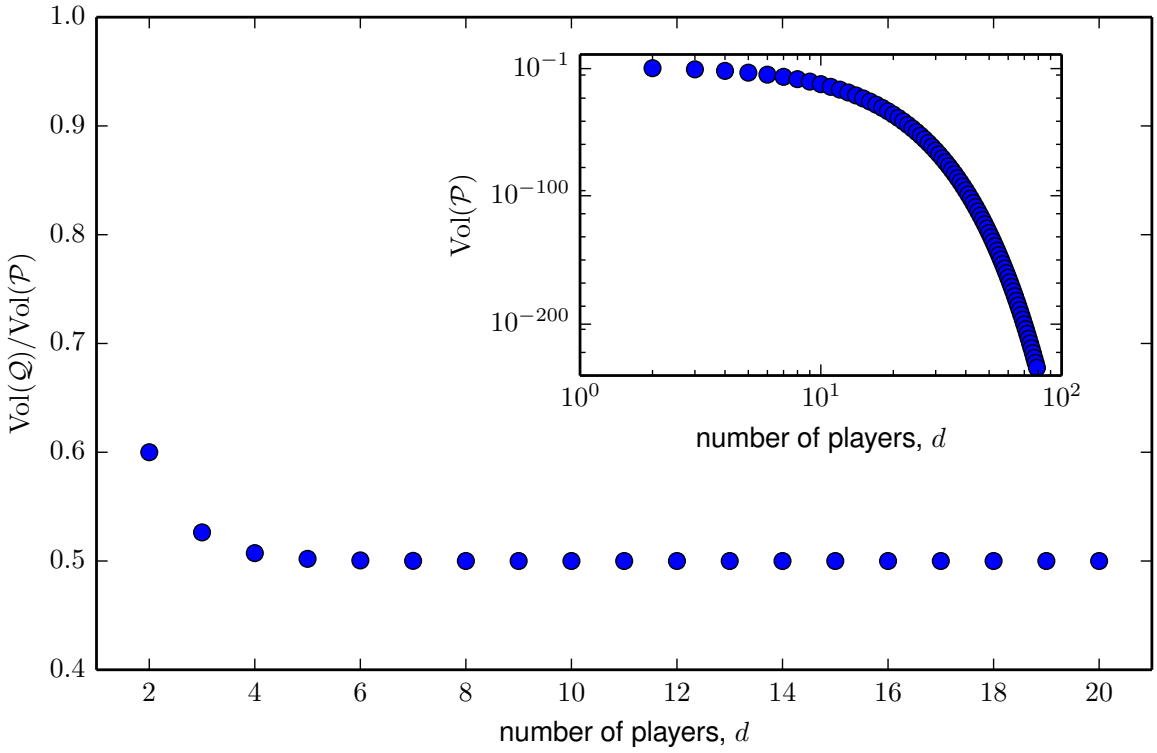

Figure 3: **Volumes of cooperation for population structures with symmetric structure coefficients.** Fraction of cooperation games for which cooperation is favored in population structures with symmetric structure coefficients (*main figure*) and volume of cooperation games (*inset figure*) as functions of the number of players d. As the number of players d increases, the probability that a population structure with symmetric structure coefficients promotes cooperation for a randomly chosen cooperation game quickly approaches $1/2$. At the same time, the probability that a randomly chosen game is a cooperation game quickly goes to zero, an effect that seems to be underappreciated in the literature emphasizing the importance of cooperation in evolution.

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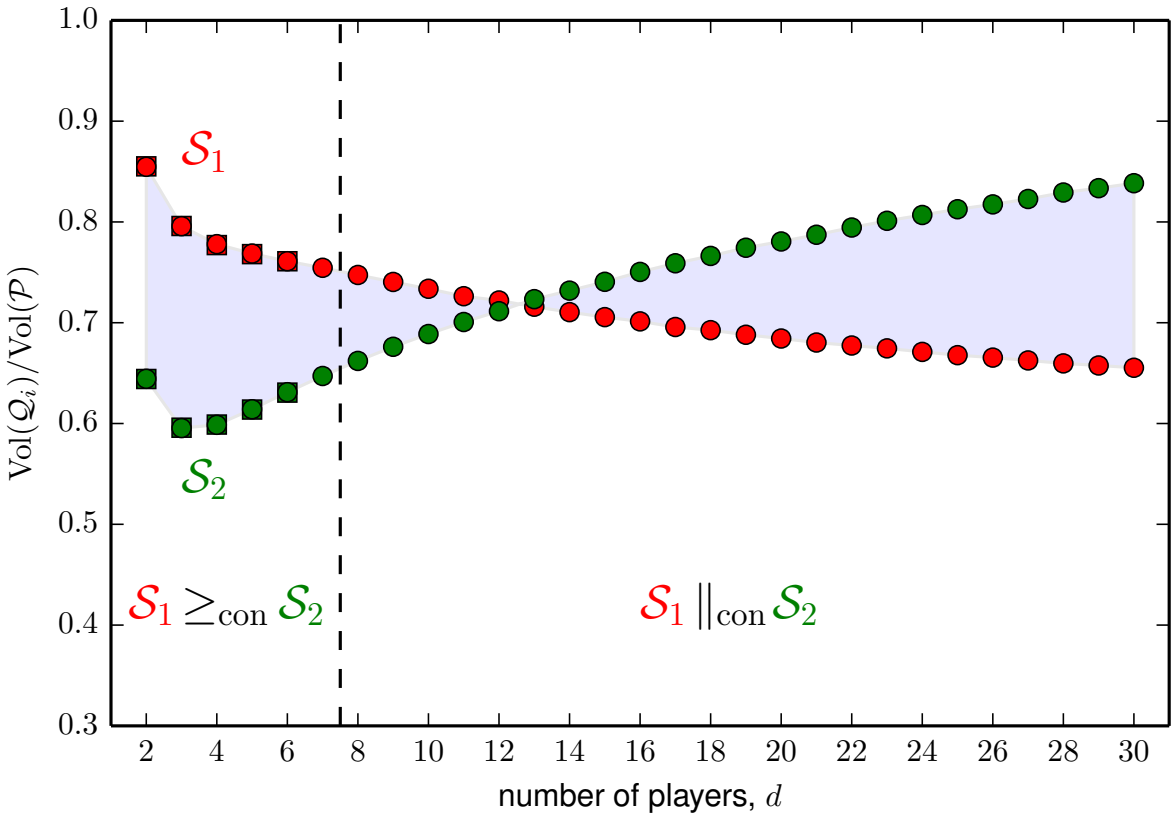

Figure 4: **Volumes of cooperation for two different population structures.** Normalized volumes of cooperation for a cycle of size $N = 1000$ ($\mathcal{S}_1$, *red symbols*) and a group splitting model with $m = 10$ groups of maximum size $n = 100$ ($\mathcal{S}_2$, *green symbols*). The volumes are calculated exactly for small values of d (*squares*) and approximately using a Monte Carlo method (*circles*). The cycle is greater than the group splitting model in the volume order for $d \leq 12$ and smaller in this sense for $d \geq 13$. It can also be shown that the cycle is greater than the group splitting model in the containment order for $d \leq 7$, but the two population structures are incomparable in the containment order for $d \geq 8$.

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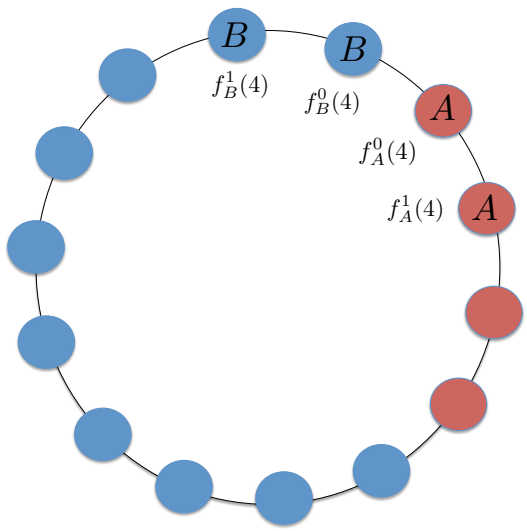

Figure 5: **Example of the death-birth process on a cycle.** The population is embedded on a cycle of size $N = 14$. There are $i = 4$ A-players. $f_A^0(i)$ (resp. $f_B^0(i)$) is the payoff of an A-player (resp. B-player) next to the boundary between A-players and B-players. $f_A^1(i)$ (resp. $f_B^1(i)$) is the payoff of an A-player (resp. B-player) second-to-next to the boundary between A-players and B-players.

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Table 1: **Structure coefficients for some population structures.**

Model	Structure coefficients	Refs.
Moran process (well-mixed population)	$\sigma_j = \begin{cases} 1 & \text{if } 0 \leq j \leq d-2 \\ \frac{N-d}{N} & \text{if } j = d-1 \end{cases}$	Kurokawa and Ihara (2009); Gokhale and Traulsen (2010)
Aspiration dynamics (well-mixed population)	$\sigma_j = \binom{d-1}{j}$	Du et al. (2014)
Death-birth process on a cycle ($d \geq 3$)	$\sigma_j = \begin{cases} 1 & \text{if } j = 0 \\ \frac{2N}{N+1} & \text{if } 1 \leq j \leq d-3 \\ \frac{2N-1}{N+1} & \text{if } j = d-2 \\ \frac{3(N-d)}{N+1} & \text{if } j = d-1 \end{cases}$	van Veelen and Nowak (2012)
Moran process on a group splitting model (rare group splitting)	$\sigma_j = \begin{cases} 1 & \text{if } 0 \leq j \leq d-2 \\ 1 + \frac{d(m-2)}{n} & \text{if } j = d-1 \end{cases}$	Traulsen and Nowak (2006); Kurokawa and Ihara (2013)

For our purposes, it will be useful to normalize the structure coefficients so that $\sum_j \sigma_j = 1$ (see Table 2). Parameters d and N refer to the number of players and population size, respectively. In the group splitting model, m is the number of groups and n is the group size.

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Table 2: **Normalized structure coefficients for some population structures.**

Model	Normalized structure coefficients
Moran process (well-mixed population)	$\sigma_j = \begin{cases} \frac{N}{d(N-1)} & \text{if } 0 \leq j \leq d-2 \\ \frac{N-d}{d(N-1)} & \text{if } j = d-1 \end{cases}$
Aspiration dynamics (well-mixed population)	$\sigma_j = \frac{\binom{d-1}{j}}{2^{d-1}}$
Death-birth process on a cycle ($d \geq 3$)	$\sigma_j = \begin{cases} \frac{N+1}{d(2N-3)} & \text{if } j = 0 \\ \frac{2N}{d(2N-3)} & \text{if } 1 \leq j \leq d-3 \\ \frac{2N-1}{d(2N-3)} & \text{if } j = d-2 \\ \frac{3(N-d)}{d(2N-3)} & \text{if } j = d-1 \end{cases}$
Moran process on a group splitting model	$\sigma_j = \begin{cases} \frac{n}{d(m+n-2)} & \text{if } 0 \leq j \leq d-2 \\ \frac{n+d(m-2)}{d(m+n-2)} & \text{if } j = d-1 \end{cases}$